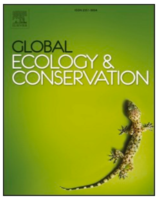
Global Ecology and Conservation 33 (2022) e01967

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco



Review Paper

Making hollow trees: Inoculating living trees with wood-decay fungi for the conservation of threatened taxa - A guide for conservationists

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ARTICLE INFO

Keywords:
Artificial inoculation
Veteranisation
Tree cavity
Heart-rot
Fungi conservation

ABSTRACT

Decaying wood and cavities in living trees are fundamental determinants of forest biodiversity. However, a long history of forestry and land-use change has created a fragmented network ofwoodland with a depleted stock of veteran trees that support these microhabitats. Decomposition isa slow process and it may take heart-rot fungi hundreds of years to establish before hollowing evenbegins. A major challenge to forest restoration, therefore, is how these habitats can be restored orreplicated. One approach is to inoculate trees with heart-rot fungi as a direct intervention toaccelerate tree hollowing. We identify two types of conservation inoculation that could be beneficialin forest conservation: (1) *Veteranising inoculations* designed to benefit cavity and decay dependantfauna; and (2) *Translocation inoculations*, to reintroduce locally extinct, dispersal-limited heart-rotfungi.

Tree inoculations have a hundred-year pedigree but successes have been mixed and there are nolong-term published studies. Reflecting on previous heart-rot inoculations we discuss elements ofthe inoculation protocol to aid design of conservation inoculations. Conservation inoculations havethe potential to be a useful tool in forest restoration and we hope to stimulate wider uptake as adirect method for conservation.

1. Introduction

In forests and wood pasture, much of the biota is dependent on the myriad of microhabitats created by large, old trees (Lindenmayer, 2017; Lindenmayer and Laurance, 2017; Müller et al., 2014; Read, 2000) and the continuity and diversity of dead wood resources both in space and time (Lachat et al., 2013). The global loss of populations of large old trees is of serious concern with implications for the species and ecological processes they support (Lindenmayer et al., 2014, 2012). Conservation interventions for these habitats aim to accelerate ecological processes and mimic the features of mature trees and woodland (Bauhus et al., 2009; Sebek et al., 2013; Smith, 2018). The restoration and creation of forests and wood pasture habitat pose a unique challenge because of the long time that it takes for trees to age, and for these microhabitats to develop and accumulate.

Saproxylic fungi, i.e. fungi dependent on deadwood, are a significant component of the forest biota and underpin the functioning of forest systems as drivers of decomposition and nutrient cycling, modifying woody debris chemistry allowing other species to use the substrate, forming structural cavities in trees, and are a primary food resource for some taxa (e.g. saproxylic and mycotrophic species)

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https://doi.org/10.1016/j.gecco.2021.e01967
Received 7 July 2021; Received in revised form 5 December 2021; Accepted 12 December 2021

(Boddy and Heilmann-Clausen, 2008). Many of the conservation actions used for creating old-forest features seek to mimic these functions, such as: deliberately damaging living trees (termed veteranisation) (Bengtsson et al., 2012); creating or retaining standing dead trunks (often referred to as snags or kelo trees) (Lewis, 1998); and supplementing forests with dead wood to increase the volume of the resource (Elo et al., 2019). All of these conservation interventions increase or maintain forest diversity and community resilience, however, they are all dependent on the stochastic arrival of naturally colonising saproxylic fungi, and take time. Further, while some saproxylic invertebrates and vertebrates do not have very specific requirements for the type of decaying wood they occupy, others are extremely specific for a particular tree species, or wood decayed by particular species of fungi, or of particular types of decay (e.g. white rot or brown rot), or even of specific sequences of fungi (Box 1, Table 1). To provide habitat more rapidly for rare invertebrates and for roosts, nests and dens of vertebrates, boxes (aerial or at ground level) sometimes filled with wood mould, or holes cut in tree trunks, are often used to simulate natural cavities (Jansson et al., 2009, Box 2). These again suffer from lack of appropriate fungal inhabitants, decay time and longevity.

The problem of stochastic establishment of wood-decay fungi, and slow natural development of decay cavities, can be circumvented by artificial inoculation with an appropriate known fungus. Successful inoculation of threatened wood decay fungi into felled or fallen wood is relatively easy, and is engendering considerable interest as a conservation tool (Nordén et al., 2020). Inoculation of fungi into living trees has also been practiced as a conservation tool but is less straightforward. Nonetheless, there are two scenarios in which inoculation may be appropriate for conservation of standing tree-inhabiting organisms: (1) for producing decay and cavity formation in trees at an earlier stage than would naturally occur, which can be termed 'veteranisation inoculations'; and (2) for the conservation of specific rare or threatened heart-rot fungi, sometimes called 'translocation inoculations'. The methods used in both types of conservation inoculation are broadly similar, however they have unique considerations relevant to the conservation objectives of each. Within the context of nature conservation, we review previous work on artificial inoculation of living trees with heart-rot fungi. Success has been mixed, and so we then provide a methodological commentary and discussion to draw out key elements that practitioners must consider when designing a conservation inoculation programme, including tree and fungus species selection, inoculum specification, field protocol and monitoring (Section 2; Fig. 1 and 2; Supplementary Appendix A). To aid inoculation design we have compiled a table summarising protocols used in previous inoculation studies and include it in Supplementary Appendix B. Review method is included in Supplementary Appendix C. We have limited the scope of the review to wood decay basidiomycetes and avoid reference to ascomycete inoculations for biocontrol of wood decay fungi and, with a few specific exceptions, inoculations of pathogenic wood decay basidiomycetes.

1.1. *A brief history of tree inoculation*

Inoculating trees with wood-decay basidiomycetes is not a new concept, however, while methods have been broadly similar, their rationale has changed (Supplementary Appendix B). Hartig (1874) and Moller (1904) both successfully inoculated young pine (*Pinus sylvestris*) trees with pine wood colonised by *Porodaedalea pini* (*P. pini; syn. Trametes pini*) over 100 years ago. Early studies like these focussed on understanding tree ageing and forest pathology in the context of timber production. Continuing into the 20th century, inoculation studies tended to be focussed on determining rates of decay in valuable timber species of both angiosperms and conifers (e.

Box 1
Designing conservation inoculations for wildlife.

Artificial inoculations can be designed to help to produce habitat for saproxylic or cavity-using species and communities. The majority of conservation inoculations for wildlife habitat have been aimed at the primary cavity excavators - woodpeckers and sapsuckers (Picidae) (Bednarz et al., 2013; Bull and Partridge, 1986; Conner et al., 1983; Filip et al., 2011; Parks et al., 1996). However, it has been suggested that accelerating cavity development with fungi could also benefit arboreal rodents, marsupials, bats, non-excavating birds and saproxylic invertebrates (Borowski and Piętka, 2014; Carey and Sanderson, 1981; Gibbons and Lindenmayer, 2002; Kunz and Lumsden, 2003). It is conceivable that inoculating trees with fungi could be used as a conservation measure for any vertebrate or invertebrate species where the abundance or density of tree cavities or decaying wood is limiting population growth.

An effective veteranizing inoculation strategy for producing habitat for wildlife should reflect the ecology and behaviour of the target fauna. Specifically, it should aim to replicate the characteristics of the cavities or decaying wood that they use. This might include associations with specific tree or fungus species, decay type, tree height or diameter of the tree, as well as preference for spatial aspects such as height, orientation and position within the landscape (Bunnell, 2013; Table 1) for examples of such associations).

Some of the most important characteristics of tree cavities for secondary cavity users (e.g. volume, entrance width, depth of wood mould) are the result of the decay development, and cannot easily be planned for in inoculation design. Woodpeckers can accelerate the formation of cavities with a large number of non-excavating birds and mammals dependant on them for the nest, roost or den sites (Remm and Lõhmus, 2011). Creating heart-rot conditions favourable for woodpeckers could increase the rate at which cavities develop for secondary users. Depending on the beneficiary, other conservation interventions (e.g. artificial cavities, Box 2) could be used in parallel to support secondary cavity-users in the short-term.

Table 1
Characteristics of cavities selected by different cavity using fauna. Veteranizing inoculation design should account for the habitat preferences of the target taxa.

Cavity/tree characteristic	Cavity-using fauna	Example reference
Fungi species	Excavating cavity-nesting birds	Bull and Partridge (1986); Conner et al. (1976); Jackson and Jackson (2004)
	Bats	Parsons et al. (2003)
	Invertebrates	Nikitsky and Schigel (2004)
Rot type (white/brown	Invertebrates	Alexander (2002); Andersson (1999); Nikitsky and Schigel (2004); Yee et al. (2006)
Tree species	Excavating cavity-nesting birds	Martin et al. (2004)
	Non-excavating cavity nesting birds	Martin et al. (2004)
	Bats	Boonman (2000); Kalcounis and Brigham (1998)
	Invertebrates	Jonsell et al. (1998)
Tree DBH	Excavating cavity-nesting birds	Conner et al. (1983)
	Non-excavating cavity nesting birds	Bonaparte and Cockle (2017); Martin et al. (2004)
	Arboreal mammals	Lutermann et al. (2010); Penton et al. (2020);Smith and Lindenmayer (1988)
	Invertebrates	Ranius (2002)
Tree height	Excavating cavity-nesting birds	Bull and Peterson (1986)
	Non-excavating cavity nesting birds	Bonaparte and Cockle (2017)
	Bats	Sedgeley and O'Donnell (1999)
	Arboreal mammals	Smith and Lindenmayer (1988)
Cavity Orientation	Excavating cavity-nesting birds	Conner (1975); Landler et al. (2014)
Cavity Height	Excavating cavity-nesting birds	Conner et al. (1983)
	Non-excavating cavity nesting birds	de la Parra-Martínez et al. (2015);Nilsson (1984)
	Arboreal mammals	Smith and Lindenmayer (1988)
	Invertebrates	Martin (1989); Ranius (2002)
Dependence on primary cavity excavator (e.g. woodpecker/sapsucker)	Non-excavating cavity nesting birds	Daily et al. (1993); Martin et al. (2004); Saab et al. (2004)
	Bats	Boonman (2000)
Position of tree in the landscape	Excavating cavity-nesting birds	Bull and Partridge (1986)
	Non-excavating cavity nesting birds	Bonaparte and Cockle (2017)
	Invertebrates	Sverdrup-Thygeson et al. (2010)
Distance to forest edge	Non-excavating cavity nesting birds	(Aitken et al., 2002; Remm et al., 2006)
	Bats	Boonman (2000)
	Arboreal mammals	Smith and Lindenmayer (1988)

g. Hirt, 1949; Hirt and Eliason, 1938; Silverborg, 1959; Silverborg and Larsen, 1967; Toole, 1964, 1956). The rationale for studies in the latter half of the 20th century expanded to include understanding tree physiology and defence against microorganisms (Boddy and Rayner, 1984; Shigo, 1977; Shigo and Sharon, 1968; Whitney and Denyer, 1969), the variability in heart-rot prevalence between forest stands (Davidson and Etheridge, 1963), anomalies between natural infection and inoculation (Whitney and Denyer, 1970), fungal interactions in vivo (Basham, 1975) and testing inoculation protocols (Toole, 1967, 1966). Commercial cultivation of economically valuable fungi (Lee et al., 2008; Park et al., 2010) and studies of pathology of trees (Burcham et al., 2015; Deflorio et al., 2009, 2008b) and fungi (Vainio et al., 2017), and testing non-destructive methods of monitoring decay (Bieker et al., 2010; Deflorio et al., 2008a) have also taken an artificial inoculation approach in recent years.

A shift towards inoculating trees for conservation began in the 1970s where decay was initiated in trees to benefit cavity nesting mammals (Carey and Sanderson, 1981) and birds (Bull and Partridge, 1986; Conner et al., 1983). The creation of such 'wildlife trees' with varying inoculation methods were tested and refined with positive results over 5–10 year monitoring periods (Bednarz et al., 2013; Brandeis et al., 2002; Filip et al., 2011, 2004; Manning, 2003; Parks et al., 1996) and sometimes used to mitigate impacts from forestry (e.g. Manning and Manley, 2014). More recently inoculations have also been trialled to create habitat for the conservation of saproxylic invertebrates (Borowski and Piętka, 2014;) and reintroduction of rare fungi (Abrego et al., 2016; Boddy et al., 2004; Piętka and Grzywacz, 2005, 2006) using similar methods. The increasing interest in conservation inoculations has led to the development of ethical principles to guide best practice for inoculation of red-listed fungi (Nordén et al., 2020, Section 1.3).

Box 2
Creating old tree microhabitat: alternatives to veteranising inoculations.

Artificial inoculation is not the only method used for conserving the cavity-inhabiting community. Supplementary cavities (i.e. artificial boxes or carved hollows) work well and veteranizing young trees to simulate features of large old trees are increasingly used.

Supplementary cavities

Artificial boxes and carved hollows typically provide habitat for cavity fauna in the mid-late stages of a cavity's development, with a hollow accessible to small mammals and birds or a quantity of wood mould suitable for beetle larvae. The structure of boxes and carved hollows can seem ideal for their intended taxa, but they are not always functionally equivalent, and do not benefit some species (Griffiths et al., 2017; Lindenmayer et al., 2009). Carved hollows have a longer life span than boxes and remain usually better insulated than boxes (Griffiths et al., 2018; Rueegger, 2017) but both lack the structural complexity that supports a diverse cavity community(Siitonen, 2012). Boxes neglect species that require the early stages of heartwood decomposition or a specific habitat niche within the cavity, e.g. beetles inhabiting cavity walls (Siitonen, 2012; Stokland, 2012). Wood mould is important for saproxylic invertebrates, and can be mimicked by filling supplementary cavities with organic matter (Hilszczański et al., 2014; Jansson et al., 2009). Microclimates within such wood-mould boxes are closer to those found in natural cavities (Hilszczański et al., 2014) but the organic matter rapidly decomposes (15-30% loss of volume over 3 years) so needs frequent topping up (Jansson et al., 2009). Carved hollows are likely to facilitate heart-rot over time (similar to veteranisation, below), though no long-term studies have yet been reported.

Tree veteranisation

Tree veteranisation is the deliberate damaging or wounding of young trees to accelerate the development of microhabitats typical of large, old trees (veterans) (Bengtsson, 2019; Bengtsson et al., 2015; Boddy, 2021). The techniques used for wounding vary: burning, girdling, bark stripping, removing large branches or cutting holes into the trunk are being trialled in oak. Unlike snag creation, veteranisation does not aim to kill the tree (Bull and Partridge, 1986).

Veteranisation is dependent on the random establishment and colonisation of non-functional wood by wood-decay fungi either latently present in the sapwood or arriving as spores at the wound site. Few studies have investigated the long-term value of veteranisation (Bengtsson et al., 2012), but it can be seen as analogous to pollarding where exposed pruning wounds allow fungal propagules to colonise the heartwood. Pollarded trees can be richer in cavity habitat than unmanaged trees of a comparable size (Nordén et al., 2018; Sebek et al., 2013). It is assumed that veteranisation methods will lead to accelerated heart-rot and cavity formation in a similar way. In both pollard and veteranized trees, the identity of the decay agent, their functional qualities (e.g. white vs brown rot) and the succession of the cavity community is expected to be largely random, though there are no long-term studies which have demonstrated this. In contrast, artificially inoculating trees uses a specific species with the intention of eliciting a specific desired outcome. In this way, the decay agent can be selected for its functional traits or for its ecological or trophic relationship with other taxa (see Box 1).

Like natural cavity formation, decay initiated by either veteranisation or artificial inoculation is slow. Inoculation is, therefore, a long-term conservation action which should be complementary to other alternative methods that mimic or instigate their formation.

1.2. Veteranising inoculations – increasing the frequency of cavities and decaying wood

Decayed wood in living trees and the cavities or hollows formed are keystone microhabitats since they support a disproportionately large number of species (Hardenbol et al., 2019). Worldwide, over 1800 bird species are cavity-nesters with more than half of these thought to be obligate-cavity users (van der Hoek et al., 2017). For cavity-using terrestrial mammals, the number is estimated at several hundred - 1000 (Siitonen and Jonsson, 2012). In the UK alone over 1800 species of invertebrates are dependent on decaying wood at some point in their life cycle (Alexander, 2002). In Sweden, 11% of the red-listed saproxylic taxa are obligate tree hollow specialists associated with cavities in pedunculate oak (*Quercus robur*) (Jonsell et al., 1998).

The combination of the primary colonising heart-rot fungi with a succession of other wood-decay fungi, plus saproxylic fauna, leads to the formation of hollows and cavities in the living tree. As decay proceeds, cavities expand and their structure becomes more complex, with an associated increase in richness of the community (Siitonen, 2012). Trees, such as oak (*Quercus* spp.), beech (*Fagus sylvatica*), *Eucalyptus regnans* and lime (*Tilia* spp.), can live for well over 500 years old, with cavities persistently occupied and enlarged over centuries.

Dramatic changes in land use and management over the past 300 years has, however, led to a significant decline in the number of large old trees that would have heart-rot (Lindenmayer et al., 2012). In Europe, a move away from traditional silvicultural practices of pollarding and coppicing towards plantation forestry and whole tree extraction has led to a much younger demographic of trees compared to traditionally managed or primeval forest (Savill, 2015). Oaks (*Q. robur/petraea*) in Europe and *Eucalyptus regnans* in Australia, for example, rarely form cavities before 200 y and 180 y respectively (Gibbons et al., 2000; Ranius et al., 2009), long after they would typically be felled in modern forestry. The loss of veteran trees poses an obvious problem for woodland biodiversity in the contemporary forest landscape with its paucity of cavities. A more insidious problem is the failure to replace them as the current stock

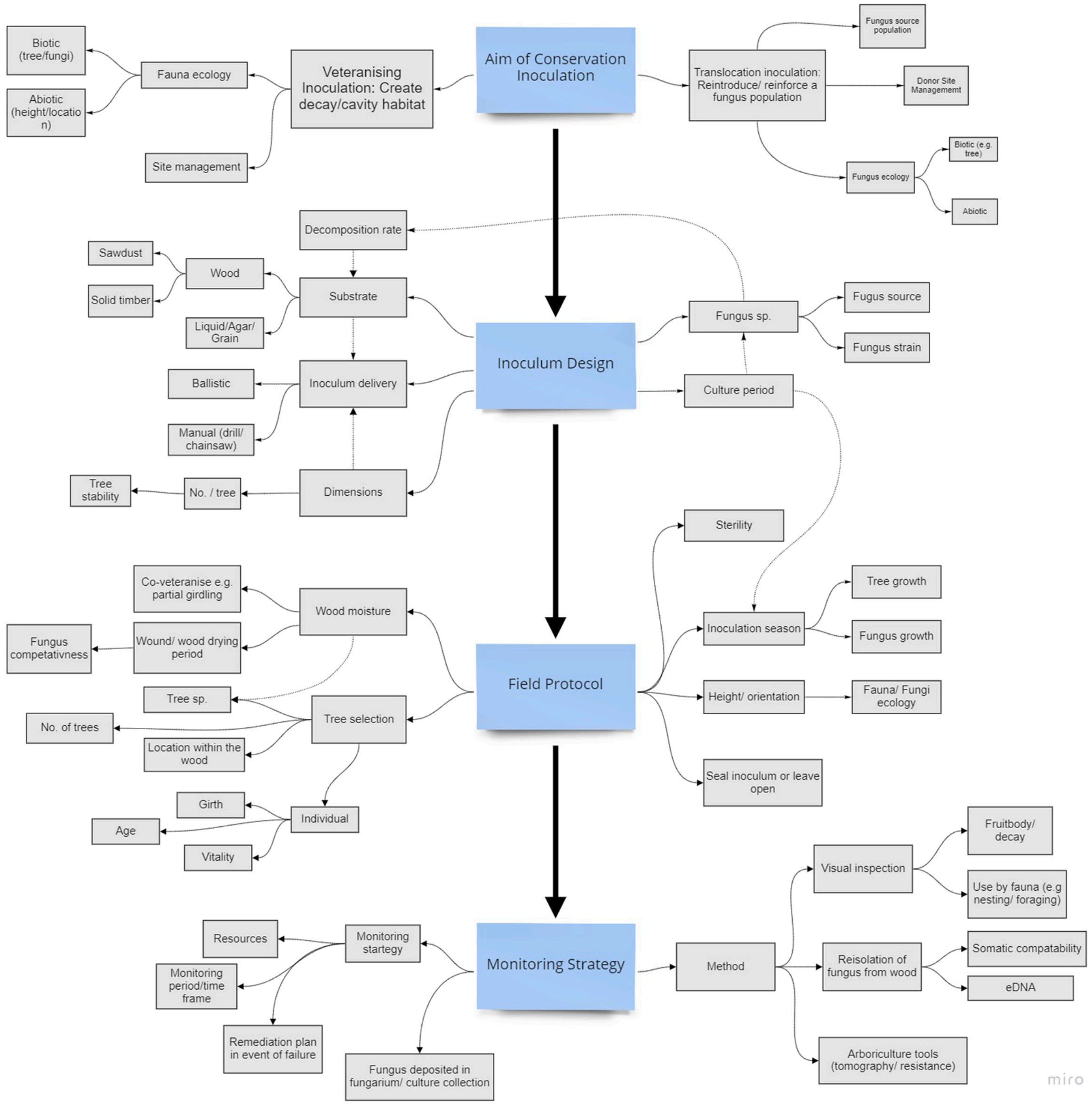

Fig. 1. Conservation inoculation conceptual framework illustrating the 4 stages of designing a conservation inoculation: Aim of the Conservation inoculation; Inoculum design; Field protocol; and Monitoring strategy (blue boxes) with thick arrows representing transition to the following stage. Considerations and design options (grey boxes) are linked to the relevant stage of the design by thin grey lines. Dashed lines indicate relationships or dependencies between design considerations and options.

of cavity-bearing trees gradually die. This is inevitably followed by declines in the hollow-associated fauna (Manning et al., 2013; Ranius et al., 2008). Decomposition of heartwood in living trees is a slow process and consequently the development of cavities is slow. In an old-growth subtropical montane forest in China, the mean horizontal expansion of tree cavities was estimated as 2 mm y^{-1}. At this rate a cavity large enough to support a honey-bee nest may take as long as 50–100 y to develop (Zheng et al., 2016). Artificially inoculating living trees before heart-rot fungi would typically begin to colonise them has the potential to considerably increase the number and density of tree cavities for the benefit of saproxylic and cavity-using species.

1.3. *Translocation Inoculations – conserving rare or threatened heart-rot fungi*

Artificially inoculating living trees with threatened or vulnerable heart-rot fungi could be a valuable tool for their long-term conservation. Fungi have been neglected in conservation science despite being subject to the same threats as plants and animals and no less deserving of conservation action (Griffith, 2012; Heilmann-Clausen et al., 2015; May et al., 2019). Recognition of the need to conserve fungi combined with better data has led to increased efforts of national red-listing and published IUCN statuses (Ainsworth

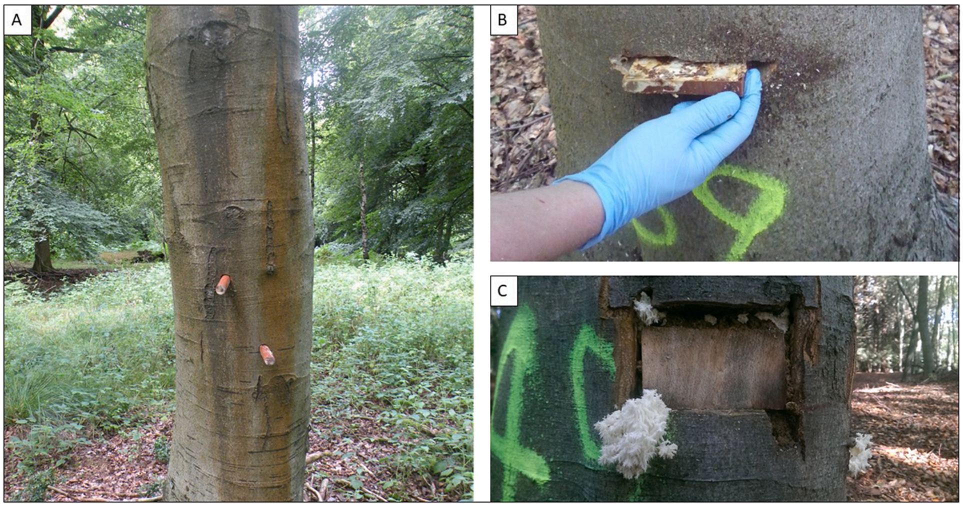

Fig. 2. (A) A translocation inoculation of the heart-rot fungus *Hericium erinaceus* into a woodland in southern England where it is locally extinct. Wood dowels, 2.5 cm × 12 cm, were colonised for 6 months before inoculating into the trunk of a beech (*Fagus sylvatica*). Each dowel was colonised with the same individual allowing mycelium to coalesce within the tree and create a greater decay column. Dowels were left flush with the bark but not sealed.(B) A veteranising inoculation in beech using the common white-rot species *Ganoderma adspersum* The wide inoculum allows maximum contact with the xylem vessels. The wound was made with a chainsaw and the inoculum held in place with compacted sawdust. (C) An approach designed to meet veteranising and translocation outcomes using the rare species *Hericium coralloides*. A 10 cm × 10 cm x 7 cm beech wood block was colonised for 3 months in the laboratory. A large cavity was cut into the tree to for the inoculum; its large size should allow the fungus to expand extensively into the tree tangentially and radially, as well as longitudinally. Gaps around the wood blocks were filled with pre-colonised sawdust/ swarf. Monitoring surveys recorded fruit bodies within 1 y. The sawdust inoculum holding the main wood block in place had been partially excavated by invertebrates.

et al., 2018; Mueller, 2017).

Some guilds of wood-decay fungi are particularly vulnerable to the management and fragmentation of forests (Abrego et al., 2017). A significant proportion of the European red-listed wood-decay fungi are dependent on environments with large-volume dead wood and late decay stages (Bässler et al., 2012; Heilmann-Clausen and Christensen, 2005; Lindblad, 1998; Pouska et al., 2010; Simmel et al., 2017). Heart-rot species are especially vulnerable due to their dependence on older living trees (Heilmann-Clausen and Christensen, 2005, 2004) and tight association with old-growth forest (Heilmann-Clausen and Boddy, 2008). Moreover, rare species are often dispersal limited and suffer from genetic inbreeding (Edman et al., 2004a, 2004b; Stenlid and Gustafsson, 2001).

Conservation translocations (i.e. species reintroductions and / or population reinforcement) are widely used for rare and dispersal-limited taxa (Seddon, 2010). Translocating a species from one site to another can assist colonisation of suitable habitat where management is appropriate, but connectivity to an existing population is poor. Artificial inoculation is a viable conservation method for wood-decay fungi but has only recently been considered (Abrego et al., 2016; Boddy et al., 2004; Nordén et al., 2020; Piętka and Grzywacz, 2005).

As with conservation translocation of plants and animals, the reintroduction/reinforcement of populations of wood-decay fungi must be carried out following IUCN guidelines (IUCN/SSC, 2013). In addition, Nordén et al. (2020) describe ten best practice principles specifically for the conservation translocations of fungi. These principles detail the need for both practical and ethical considerations when planning a conservation translocation for fungi. It is essential that any artificial inoculation of trees for conservation of fungi must undergo rigorous risk assessment, including consideration of effects on the existing fungal communities in the area, and the long-term management of the site to ensure the underlying reasons for the species decline (e.g. recruitment into older age classes) have ceased.

Designing conservation programmes for rare or red-listed fungi can be limited by knowledge of their ecology (Molina et al., 2011). Knowledge of the taxonomic status, dispersal strategies, tree species preference, relationships with other taxa and genetic variability are essential to the design of the translocation inoculation. Such knowledge is available for some species, for example, the rare oak polypore (*Buglosoporus quercinus*) (Boddy et al., 2004; Crockatt, 2008; Crockatt et al., 2010) and orange polypore (*Hapilopilus croceus*) (Greaves, 2017; Sunhede, 1997). Both species are strongly associated with veteran oaks and large volume logs. Changes in land use and forest management have accelerated the loss of large old oaks leaving many populations fragmented and susceptible to local extinction (Crockatt et al., 2010; Sunhede, 1997), leaving these species vulnerable with decreasing populations. As a result, both are listed as Vulnerable by The Global Fungal Red List Inititaive (2020a, 2020b). They could, thus, benefit from translocation inoculations either within or between sites to aid the recovery of their population. Other obvious candidates in Europe are the bearded tooth (*Hericium erinaceum*) and coral tooth (*H. coralloides*) (Boddy et al., 2011, 2004; Boddy and Wald, 2002; Crockatt, 2008. Fig. 1A and C) both of which are locally rare and red listed in several countries.

Many heart-rot fungi are only successful competitors in heartwood since they are adapted to the stressful conditions present there

(Boddy et al., 2017). However, some fungi that colonise the heartwood of standing trees sometimes persist in the wood when it falls and continue to produce fruit bodies for a further 5–15 y or more (Hepting and Roth, 1950), so translocation inoculations of these species into felled wood may provide an alternative or adjunct to living tree inoculation. In the absence of competitors, it is relatively easy for fungi to establish from inocula into felled wood since it is better aerated. There are in excess of 18 examples of inoculations of red-listed and other non-commercial species into fallen and felled wood (Abrego et al., 2016; Boddy et al., 2004; Grace and Mudge, 2015; Nordén et al., 2020; Piętka and Grzywacz, 2005, 2006, Supplementary Appendix B). The favourable conditions in logs can lead to earlier and more sustained fruiting than living-tree inoculations. This has the benefit of basidiospores dispersing into the woodland and colonising surrounding trees much sooner (Box 3, Supplementary Appendix A Table S3). The heart-rot species bearded tooth and bears' head tooth (*H. americium*) fruited prolifically in inoculated logs with peak production after 3–4 y (Grace and Mudge, 2015). The fungi may be short-lived in logs, being quickly replaced by more competitive species especially if in contact with the forest floor. However, one benefit of log-based translocation inoculations is that they can be supplemented with logs brought in from outside of the translocation site to raise the propagule pressure.

2. Designing conservation inoculation for living trees

2.1. Species selection

Choosing an appropriate fungus species for inoculation is fundamental to the design of a conservation inoculation programme. The relationship between fungus and tree (and other taxa, Box 1), and the influence of taxa and even individual strain/clone traits will influence choice. Inoculations are a long-term strategy and thought must be given to the future viability of tree and fungus. Horizon scanning should be undertaken as part of the selection process to identify any potential future threats that might jeopardise the long-term conservation goals of an inoculation (Sutherland and Woodroof, 2009). This might include emergent pests and diseases, impacts of climate change, current and future land-use, land ownership and government policy. Specific threats to heart-rot fungi are less well documented than for trees where the impacts from climate change and invasive pests and diseases tend to be better understood. Ash species (*Fraxinus* spp.), for example, face an uncertain future in Europe and North America from the threat of the Asian ash-dieback *Hymenoscyphus fraxineus*, and emerald ash-borer beetle *Agrilus planipennis* (Enderle et al., 2019; Valenta et al., 2017). Conservation inoculations of such tree species might best be avoided if the long-term gains from the intervention are not likely to be realised. A more insidious issue might be the decoupling of the association between fungus and tree species. The jelly-ear fungus *Auricularia auricula-judae* for example has undergone a host-shift at least partially in response to climate change. Where it was only known from elder *Sambucus nigra* in southern UK until the late 1970's (Gange et al., 2011), it now associates with a much wider range of broadleaved trees while significantly reducing its association with elder. The reasons for this are unclear and unfortunately for horizon scanning conservation inoculations, near impossible to predict.

2.1.1. Which species of fungus?

Translocation inoculation is a direct conservation intervention to preserve a threatened species and so the inoculation is designed

Box 3

Translocation inoculation and the colonisation of new resources.

A major concern for translocation inoculations is how the introduced species will disperse through the receptor site. As a reintroduction, the long-term survival of a fungus depends on the second generation colonising new resources. For most heart-rot basidiomycetes, dispersal is via wind-spread basidiospores, though animal vectors, e.g. woodpeckers (Picidae) (Elliott et al., 2019; Jusino et al., 2016), and invertebrates (Birkemoe et al., 2018; Boddy and Jones, 2008) sometimes have a role. Mechanisms that trigger spore germination vary between species (Fries, 1984), and the percentage successful germination is also variable, sometimes being very low (<1 % on artificial agar media) in some rare species, e.g. *Hericium erinaceus* and *Hericum coralloides* (Boddy et al., 2011; Crockatt, 2008) and *Buglossoporus quercinus* (Crockatt et al., 2010). Timing of production of spore-bearing fruit bodies (basidiocarps) varies depending on the ecological strategies of the fungi and on physiological factors influenced by the nutrient and climatic environment (Moore et al., 2008). Many heart rot fungi are K-selected and fruit relatively late in their lives, compared with primary colonisers of sapwood, and require large volumes of wood to support their large fruit bodies which, in the case of perennial fruit bodies, continue to produce spores for many months or even several years (Rayner and Boddy, 1988). By contrast, some species, with smaller long-lived or fleshy ephemeral fruit bodies, fruit earlier in their lives. For example, common *Pleurotus* species and rare *Hericium* species (Boddy et al., 2011).

Although fruit bodies have sometimes been reported following tree inoculations (Supplementary Appendix A Table S3, Figure 2C) this is uncommon due to the limited duration of the studies (Supplementary Appendix B). This contrasts with log inoculation where the resource endures in the environment for less time than standing trees, so the fungi tend to fruit more rapidly (Abrego et al., 2016; Grace and Mudge, 2015). Abrego et al. (2016) inoculated seven rare wood decay species into spruce (*Picea abies* logs), four of which produced fruit bodies within 6 y. Fruit bodies of two of these, *Antrodiella citrinella* and *Fomitopsis rosea*, were found on uninoculated logs within 100 m of the inoculated logs, suggesting that they had spread from the originally inoculated logs.

around the species itself. The choice of fungus is, therefore, based on its conservation/threat status and the decision to inoculate may come from a species action plan to support its declining population, and selection criteria have been reviewed by Nordén et al. (2020). Veteranising inoculations on the other hand aim to initiate a specific decay response primarily for other taxa and so the choice of fungi should be based primarily on the ecology of the beneficiary organisms (see Box 1). Choosing an appropriate fungus and strain for veteranising inoculation will be influenced by its ecological, life-history and functional traits, for example, its association with a tree species (see Section 2.1.3), interaction with other forest biota (Box 1; Table 1), geographic location and home range of the fungus, rate of heartwood decomposition and decay strategy (Nordén et al., 2020). To date, artificial inoculation studies in living trees have used over 50 species of saprotrophic basidiomycetes (Supplementary Appendix B). Basidiomycetes known to cause heart-rot in living trees are the most obvious candidates for both veteranising and translocation inoculations since they possess the enzymatic machinery and stress tolerance to decompose heartwood. Inoculation of heartwood-inhabiting ascomycetes are of course possible (Basham, 1975; Deflorio et al., 2009, 2008b; Shigo, 1977) but are functionally less important for heartwood decomposition of living trees (with some notable exceptions e.g. *Kretzschmaria deusta*, though it is unlikely ever to be desirable to inoculate with this species because it causes a decay hazard).

One of the most important factors in fungus selection for veteranising inoculations is the rate at which it can colonise the tree and decompose the heartwood. The faster decomposition occurs, the quicker the resource is available for other taxa to utilise. Fungal growth rates differ between species and depending on the tree species into which they are inoculated. Conner et al. (1983) inoculated trees to establish heart-rot suitable for woodpecker nest excavation. Under the same conditions, *Sarcodontia pachyodon* extended at twice the rate of *Laetiporus sulphureus* when inoculated into the red oaks *Q. falcata* and *Q. nigra* (annual vertical extension 28.6 cm y^{-1} and 14.8 cm y^{-1} for each fungus respectively). It was concluded that since both species were isolated from woodpecker cavities, *S. pachydon* was the most appropriate species to use for conservation inoculations since trees could be used by pileated woodpecker (*Drycopus pileatus*) after 6 y but only after 12 y with L. *sulphureus*. The rate at which an inoculated species colonises a tree is generally determined by destructive sampling (Supplementary Appendix B), but for most species this information is not available. In such cases the best approach may be to use several species which are considered to be functionally important for cavity development.

A final consideration in fungus selection is the need to know exactly which species you are inoculating (Nordén et al., 2020). Fungal taxonomy is a shifting baseline and there is a high incidence of cryptic species. Even common wood-decay species sometimes comprise two or more genetically distinct but morphologically similar species (Banik and Burdsall, 2000; Hallenberg et al., 2013). The identity of any species should be confirmed prior to inoculation, and samples deposited in a local fungarium or culture collection in case future examination is needed.

2.1.2. Which fungal strain?

A central principle of conservation inoculation is to ensure that the intervention does not interfere with the natural genetic variation within the population (Nordén et al., 2020). It is, therefore, essential that strains are sourced from as close as possible to the receptor site, and should be of known provenance, which often excludes commercially available strains. Inbreeding and genetic swamping should be prevented by ensuring that more than one local strain is used. This requires collaboration between stakeholders, including academics, conservationists, inoculum producers and commercial cultivators, culture collections and amateur mycologists.

There can be substantial intraspecific variation in fungal traits (Dawson et al., 2019) and this is reflected in artificial inoculation studies. Different strains of *Inonotus obliquus* inoculated into *Betula platyphylla* had an almost 3-fold difference in vertical extension rate (Lee et al., 2008). It may not be possible to account fully for this in an inoculation programme but needs to be considered since this variation may affect its overall success. Faster growing strains would allow more rapid colonisation of trees and decomposition. However differences in extension rate may be the result of trade-offs with other traits (Maynard et al., 2019). If rapid extension is at the expense of traits such as competitiveness, environmental tolerance, resource efficiency etc., long-term survival may be limited.

Some of the intraspecific variation in traits within wood decay fungi may be due to local or host adaption and can impact on the outcome of inoculations. Strains of *Stereum sanguinolentum* isolated from white spruce (*Picea glauca*) grew three times slower than a strain from balsam fir (*Abies balsamea*) when inoculated into living balsam fir, perhaps representing host-adaption of the balsam fir strain to the characteristics of balsam heartwood (Whitney and Denyer, 1970). However, other differences between extension rates of different strains of *Porodaedalea pini* and *S. sanguinolentum* were less easily explained. Since knowledge of strain variability may not be readily available, it is sensible to inoculate multiple strains into the tree species/genus from which it was isolated.

2.1.3. Which tree?

Any tree with central tissue which is non-functional in water conduction could be inoculated. At least 34 gymnosperms and angiosperms tree species have been artificially inoculated with wood-decay basidiomycetes (Supplementary Appendix B). Choice of tree species will depend on the target beneficiary and the type of conservation inoculation. Specific association of tree species with a heart-rot fungus will govern selection in both translocation and veteranising inoculations. Availability or abundance of trees, wildlife association (Box 1) and decomposition rate will also affect choice for veteranising inoculations.

Although some heart-rot species are generalists, many are specialists adapted to the physical and chemical properties of the heartwood of specific tree taxa (Krah et al., 2018; Rayner and Boddy, 1988). *Fistulina hepatica*, for example, is found exclusively on oak (and occasionally *Castanaea*) with its high content of tannins and other polyphenols and low pH, despite it being able to grow on other wood species in laboratory conditions and in the absence of competitors (Cartwright and Findlay, 1936; Hillis, 2012). Similarly, *Inonotus obliquus* is found predominantly on birch (*Betula* spp.), but has been successfully inoculated, (albeit without replicates) into aspen (*Populus tremuloides*), sugar maple (*Acer saccharum*) and American beech (*Fagus grandifolia*) (Hirt, 1949). Inoculating specialist heart-rot fungi into tree species other than those with which it is commonly associated, however, makes little ecological sense.

Oak trees are a prime target for veteranising because of the large invertebrate biodiversity that they harbour (Jonsell et al., 1998; Mitchell et al., 2019), and for translocation inoculations because of the rare and threatened taxa they support (Boddy et al., 2004; Mitchell et al., 2019). In Europe, the oaks *Quercus robur/Q. petraea* have a tannin content as high as 5% (Mosedale et al., 1996), which presents a challenge as it reduces the colonisation rate of inoculated fungi (Deflorio et al., 2008b). In three North American oak species, inoculated with *Crustodontia chrysocreas*, *Perenniporia compacta*, L. *sulphureus* and *Inonotus andersonii*, the decay column was smallest in the *Q. alba* with the highest tannin content and longest in *Q. coccinea* with the lowest tannin content (Berry, 1976; Rowe W.J., 1979). It is, however, notable that veteranising oaks without inoculation show very little advancement in the development of the heart-rot community after 6 y (Menkis et al., 2020) so despite the low colonisation rates attributed to tree exudates, inoculation may still be the more efficient option.

With generalist species of fungi, colonisation and decomposition rates can vary considerably between tree species. Balsam fir and black spruce are both commonly decayed by *S. sanguinolentum* and *P. pini*. For *S. sanguinolentum*, the mean volume of the decay columns in black spruce were 40% smaller than those in balsam fir 22 months after inoculation. *P. pini* decay columns were three times larger in black spruce than in balsam fir (Whitney and Denyer, 1970). Similarly in angiosperms, *Phellinus rimosus* inoculated into aspen extended at 58 cm y^{-1} compared to 27 cm y^{-1} in American beech and 3.6 cm y^{-1} in sugar maple (Silverborg, 1959). Little is known about decomposition of heartwood for the majority of fungi-tree combinations. However, following a large inoculation trial, Filip et al. (2011) were able to recommend successful fungi-conifer pairs for veteranising inoculations in the US Pacific Northwest.

Within a tree species there can be considerable variation in decay resistance (Guilley et al., 2004; Yu et al., 2003). The cross-sectional area of decay from *Heterobasidium parviporum* differed significantly between four Norway spruce (*Picea abies*) clones into which it was inoculated (Vainio et al., 2017). This is an important consideration for plantation forestry where vegetative propagation of clones is widely practised (Wu, 2019). Intraspecific genetic differences or environmental effects on tree growth rates can also affect the success of inoculation. In Norway spruce inoculated with *S. sanguinolentum*, the frequency of establishment was significantly higher in dominant trees (i.e. those with a greater crown relative to the average crown size) than subdominant trees with a smaller relative crown (El-Atta, 1984). It also grew faster when inoculated into faster-growing individuals of balsam fir (Whitney and Denyer, 1970). This effect has been seen in other conifers (Edman et al., 2006; Yu et al., 2003) but whether there are similar relationships in angiosperms is unclear. Identifying faster growing trees for inoculations may not be straightforward for semi-natural forests, but it is possible for plantations where planting dates are known.

Tree age is also an important consideration. Both translocation and veteranising inoculations should target younger trees before naturally initiated decay begins, as there will be no competition for other decay fungi, and any naturally established decay is important habitat. Trees need to be sufficiently old for heartwood to have developed for the fungi to colonise.

2.2. *Inoculum culture and field protocol*

Methods for artificial inoculation all involve the application of a pure culture of a wood-decay fungus to a wound made in a tree. There has, however, been significant variation in the inoculation protocol with only a few direct experimental comparisons (e.g. Filip et al., 2004; Manning, 2003; Toole, 1967, 1966). Despite this, conservation inoculation needs to address adequately the many different factors in the inoculum specification and field protocol that might influence both its ease of use as a conservation tool and the likelihood of successfully meeting its objectives (Fig. 1). Such factors include: choice of inoculum substrate, dimensions of the inoculum, the culture period, timing of the field inoculation, sealing or leaving open the inoculum wounds, wood moisture in the living tree, the orientation and height of the inoculum and whether to deliver the inoculum manually or with ballistics using an inoculum loaded gun. These aspects are discussed in Supplementary Appendix A and a summary table of methods previously used in other inoculation studies is given in Supplementary Appendix B.

2.3. *Monitoring inoculations*

Any conservation intervention must be assessed to understand how successful the action has been and whether remediation should be triggered to prevent failure (Legg and Nagy, 2006). Monitoring strategies (Hellawell, 1991) must, therefore, be part of all conservation inoculations (Nordén et al., 2020), particularly given the variability of successful establishment and the lack of long-term studies. The majority of most studies have reported findings less than 10 years after inoculation (Supplementary Appendix B), but much longer timeframes are necessary, though this will vary depending on the aim of the inoculation.

As an absolute minimum, inoculations should be monitored for visible signs that the fungi have established in the trees. This includes visible mycelium in the wound and around the inoculum, sporocarps of the fungus emerging from the tree, or cankers close to the inoculation wound. Indirect signs are also a good indicator of establishment and include woodpecker excavations or wood-boring beetle exit holes (Brandeis et al., 2002). However, confirming successful establishment of inoculated fungi requires reisolation (Bednarz et al., 2013; Huss et al., 2002) or molecular detection (Abrego et al., 2016; Gonthier et al., 2015) from a sample chip or a core of wood taken from the vicinity of the inoculum. Direct extraction of DNA is quick and simple, and can reveal the presence of species other than that inoculated. However, obtaining a living culture has the advantage that it can be paired against the original strain to confirm that it is the same genetic individual that was inoculated. Destructive sampling (i.e. felling the trees and reisolating the fungi) of a small number of inoculated trees will give the best indication of extent of decay and limits of colonisation through the tree, and is important for research though counterproductive if inoculations were solely for conservation. Non-invasive arboriculture tools, such as sonic tomography combined with resistograph measurements can aid inoculation monitoring (Bieker et al., 2010; Deflorio et al., 2008a; Rinn et al., 1996) and have the added advantage of being more accessible than isolation and DNA extraction to conservation practitioners.

3. Accessibility and barriers to inoculation

3.1. Knowledge and skills

There are likely to be barriers to conservation inoculations that prevent many practitioners from using them as a conservation tool. We recognise that the vast majority of conservationists do not have the knowledge and skills in mycology and fungus cultivation needed for widespread uptake. Suitable cultures may be difficult to acquire from fungaria, and bespoke cultures of local strains even more difficult to obtain. In the academic sphere, fungal research continues to lag behind flora and fauna despite their critical roles in ecosystem function (Hawksworth, 2006). However there are many knowledgeable field mycologists who are not professional mycologists and there is a flourishing community of home cultivators. Conservation inoculations must be seen as an exciting opportunity for partnership working between land-managers, arborists, ecologists and foresters with customary conservation skills integrated with those of mycologists, cultivators and fungaria. However, there is a spectrum of engagement between academia and boots-on-the-ground conservation. Even accessing this review may be out of reach for many. It is critically important therefore that mycologists reach out to conservationists and vice versa if conservation inoculations are to meet their potential impact. Veteranising inoculations alone demonstrate the critical role of fungi in forest conservation, and we urge mycologists to seize this opportunity to raise the profile of fungi in practical conservation and promote conservation inoculations with practitioners.

3.2. Cost

Cost of conservation inoculations are inherently low and does not require a high-tech laboratory. In a large-scale programme in Canada, Manning (2003) estimated the cost of a veteranising inoculation at 10–13 m in height at roughly CA$40/tree (US$24) largely due to day rates of tree-climbing arborists which was marginally more than using a rifle inoculation ($21/tree). In a UK veteranising inoculation to establish a butt-rot (i.e. tree climbing not required) in 60 trees with two inoculum/tree cost roughly £ 1.60/tree (US $2.25) with field assistance from volunteers (Wainhouse, unpublished). The cost was estimated to increase to £ 8.50 (US$11.80) if cultivator and arborist services were required. We do, however, recognise that any cost could be a barrier on tight conservation budgets.

4. Conclusion

The loss of old, hollowing trees and the failure to replace them pose a threat to the organisms dependent on them. A multitude of policy actions and innovative conservation interventions are urgently needed. We have outlined two clear roles for conservation inoculations. Firstly, veteranising inoculations can be used to accelerate decay onset and cavity formation in living trees to create habitat for other species. The selection of a specific fungus to elicit a specific response through species association or rate of colonisation is a potentially powerful tool for creating this micro-habitat. There is a long research pedigree demonstrating that fungi can be inoculated successfully into living trees. However, uptake has been limited, and variability in successful reisolation of the inoculated fungus emphasises the need for prudent and considered inoculation design. The second role of inoculation - translocation inoculation - is to reintroduce or reinforce populations of rare heart-rot fungi in a fragmented treescape.

We recognise there are barriers to conservation inoculations, such as a lack of mycological expertise, so we strongly encourage conservationists, land managers, foresters and mycologists to work in partnership to design exciting and robust inoculation projects that draw on the technical knowledge of each. We stress that conservation inoculation is a relatively cheap intervention and cost should not be an insurmountable issue. Decomposition processes are slow, so restoring the dead wood habitat in living trees needs immediate action and long-term planning. Fungal inoculation into trees is a potentially powerful conservation tool to help deadwood and cavity organisms survive into the future, and we strongly advocate its wider use.

Author contributions

Written and compiled by the authors.

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.

Acknowledgements

The thanks the funders of the PhD studentship (MW) Buglife (Back from the Brink) Heritage Lottery Fund Partnership, Ancients of the Future), Cardiff University School of Biosciences, City of London Corporation, and The Crown Estate. Many thanks to reviewers for their extremely helpful comments.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2021.e01967.

References

Abrego, N., Norberg, A., Ovaskainen, O., 2017. Measuring and predicting the influence of traits on the assembly processes of wood-inhabiting fungi. J. Ecol. 105, 1070–1081. https://doi.org/10.1111/1365-2745.12722.

Abrego, N., Oivanen, P., Viner, I., Nordén, J., Penttilä, R., Dahlberg, A., Heilmann-Clausen, J., Somervuo, P., Ovaskainen, O., Schigel, D., 2016. Reintroduction of threatened fungal species via inoculation. Biol. Conserv. 203, 120–124. https://doi.org/10.1016/j.biocon.2016.09.014.

Ainsworth, A.M., Canteiro, C., Dahlberg, A., Douglas, B., Furci, G., Mueller, G.M., Scheidegger, C., Senn-Irlet, B., Wilkins, T., Williams, E., 2018. Conservation of fungi. State of the World's Fungi. Report. Royal Botanic Gardens, Kew.

Aitken, K.E.H., Wiebe, K.L., Martin, K., 2002. Nest-site reuse patterns for a cavity-nesting bird community in interior British Columbia. Auk 119, 391–402. https://doi.org/10.1093/auk/119.2.391.

Alexander, K.N.A., 2002. The invertebrates of living and decaying timber in Britain & Ireland, English Nature Research Reports.

Andersson, H., 1999. Red-listed or rare invertebrates associated with hollow, rotting or sapping trees or polypores in the town of Lund. Entomol. Tidskr. 120, 169–183.

Banik, M.T., Burdsall Jr., H.H., 2000. Incompatibility groups among North American populations of *Laetiporus sulphureus* sensu lato. Mycologica 92, 649–655.

Basham, J.T., 1975. Heart rot of Jack Pine in Ontario. IV. Heartwood-inhabiting fungi, their entry and interactions within living trees. Can. J. For. Res 5, 706–721.

Bässler, C., Müller, J., Svoboda, M., Lepšová, A., Hahn, C., Holzer, H., Pouska, V., 2012. Diversity of wood-decaying fungi under different disturbance regimes-A case study from spruce mountain forests. Biodivers. Conserv. 21, 33–49. https://doi.org/10.1007/s10531-011-0159-0.

Bauhus, J., Puettmann, K., Messier, C., 2009. Silviculture for old-growth attributes. For. Ecol. Manag. 258, 525–537. https://doi.org/10.1016/j.foreco.2009.01.053.

Bednarz, J.C., Huss, M.J., Benson, T.J., Varland, D.E., 2013. The efficacy of fungal inoculation of live trees to create wood decay and wildlife-use trees in managed forests of western Washington, USA. For. Ecol. Manag. 307, 186–195. https://doi.org/10.1016/j.foreco.2013.06.041.

Bengtsson, V., 2019. Veteranisation: using tools to speed up habitat production in trees. Woodwise 12–14.

Bengtsson, V., Hedin, J., Niklasson, M., 2012. Veteranisation of oak – managing trees to speed up habitat production, in: Trees beyond the Wood Conference Proceedings. pp. 1–11.

Bengtsson, V., Niklasson, M., Hedin, J., 2015. Tree veteranisation – using tools instead of time. Conserv. L. Manag. 14–17.

Berry, F.H., 1976. Decay in oak inoculated with four heart rot fungi. Proc. Am. Phytopathol. Soc. 3, 215–216.

Bieker, D., Kehr, R., Weber, G., Rust, S., 2010. Non-destructive monitoring of early stages of white rot by *Trametes versicolor* in *Fraxinus excelsior*. Ann. For. Sci. 67, 210. https://doi.org/10.1051/forest/2009103.

Birkemoe, T., Jacobsen, R.M., Sverdrup-Thygeson, A., Biedermann, P.H.W., 2018. Insect-fungus interactions in dead wood systems. In: Ulyshen, M.D. (Ed.), Saproxylic Insects. Springer, Cham, pp. 377–427.

Boddy, L., 2021. Fungi and Trees: their complex relationships. Arboricultural Association, Stroud, UK.

Boddy, L., Crockatt, M.E., Ainsworth, A.M., 2011. Ecology of *Hericium cirrhatum*, *H. coralloides* and *H. erinaceus* in the UK. Fungal Ecol. 4, 163–173. https://doi.org/10.1016/j.funeco.2010.10.001.

Boddy, L., Heilmann-Clausen, J., 2008. Basidiomycete community development in temperate angiosperm wood. In: Boddy, L., Frankland, J.C., van West, P. (Eds.), British Mycological Society Symposia Series. Academic Press, pp. 211–237.

Boddy, L., Hiscox, J., Gilmartin, E.C., Johnston, S.R., Heilmann-Clausen, J., 2017. Wood decay communities in angiosperm wood. In: Dighton, J., White, J.F. (Eds.), The Fungal Community: Its Organization and Role in the Ecosystem, pp. 169–190. https://doi.org/10.1201/9781315119496-13.

Boddy, L., Jones, T.H., 2008. Interactions between basidiomycota and invertebrates. In: Boddy, L., Frankland, J., van West, P. (Eds.), Ecology of Saprotrophic Basidiomycetes. Elsevier, pp. 155–179.

Boddy, L., Rayner, A.D.M., 1984. Internal spread of fungi inoculated into attached oak branches. N. Phytol. 98, 155–164. https://doi.org/10.1111/j.1469-8137.1984.tb06105.x.

Boddy, L., Wald, P., 2002. *Creolophus* (=*Hericium*) *cirrhatus*, *Hericium erinaceus* and *H. coralloides* in England. English Nat. Res. Reports.

Boddy, L., Wald, P., Parfitt, D., Rogers, H.J., 2004. Preliminary ecological investigation of four wood-inhabiting fungi of conservation concern - oak polypore *Piptoporus quercinus* (=*Buglossoporus pulvinus*) and the tooth fungi *Hericium/Creolophus* spp. Engl. Nat. Res. Rep. https://doi.org/10.1016/j.futures.2008.07.021.

Bonaparte, E.B., Cockle, K.L., 2017. Nest niche overlap among the endangered Vinaceous-breasted Parrot (Amazona vinacea) and sympatric cavity-using birds, mammals, and social insects in the subtropical Atlantic Forest, Argentina. Condor Ornithol. Appl. 119, 58–72.

Boonman, M., 2000. Roost selection by noctules (Nyctalus noctula) and Daubenton's bats (Myotis daubentonii). J. Zool. 251, 385–389. https://doi.org/10.1017/S0952836900007123.

Borowski, J., Piętka, J., 2014. Możliwości odtwarzania mikrośrodowisk bezkręgowców saproksylicznych. Stud. i Mater. CEPL w Rogowie 41, 232–239.

Brandeis, T.J., Newton, M., Filip, G., Cole, E.C., 2002. Cavity-Nester habitat development in artificially made Douglas-Fir Snags. J. Wildl. Manag. 66, 625–633.

Bull, E., Peterson, S., 1986. Resource partitioning among woodpeckers in northeastern Oregon. Search.

Bull, E.L., Partridge, A.D., 1986. Methods of killing trees for use by cavity nesters. Wildl. Soc. Bull. 14, 142–146. https://doi.org/10.2307/3782061.

Bunnell, F.L., 2013. Sustaining cavity-using species: patterns of cavity use and implications to forest management. ISRN For. 2013, 1–33. https://doi.org/10.1155/2013/457698.

Burcham, D.C., Wong, J.Y., Ali, M.I.M., Abarrientos, N.V., Fong, Y.K., Schwarze, F.W.M.R., 2015. Characterization of host-fungus interactions among wood decay fungi associated with *Khaya senegalensis* (Desr.) A. Juss (Meliaceae) in Singapore. For. Pathol. 45, 492–504. https://doi.org/10.1111/efp.12199.

Carey, A.B., Sanderson, H.R., 1981. Routing to accelerate tree-cavity formation. Wildl. Soc. Bull. 9, 14–21.

Cartwright, K., Findlay, W., 1936. The Principal Heart Rots of English Oak. Forest products Research. His Majesty's Stationary Office, London.

Conner, R.N., 1975. Orientation of entrances to woodpecker nest cavities. Auk 92, 371–374.

Conner, R.N., Dickson, J.G., Williamson, J.H., 1983. Potential woodpecker nest trees through artificial inoculation of heart rots. Snag habitat Manag. proc. Symp. Flagstaff, 1983 68–72.

Conner, R.N., Orson, K., Miller, Jr, Adkisson, C.S., 1976. Woodpecker dependence on trees infected by fungal heart rots. Wilson Bull. 88, 575–581.

Crockatt, M., 2008. Ecology of the rare oak polypore Piptoporus auercinus and the tooth fungi Hericium cirrhatum. H. coralloides. and H. erinaceus in the UK. University of Cardiff.

Crockatt, M.E., Campbell, A., Allum, L., Ainsworth, A.M., Boddy, L., 2010. The rare oak polypore Piptoporus quercinus: population structure, spore germination and growth. Fungal Ecol. 3, 94–106. https://doi.org/10.1016/j.funeco.2009.09.001.

Daily, G.C., Ehrlich, P.R., Haddad, N.M., 1993. Double keystone bird in a keystone species complex. Proc. Natl. Acad. Sci. USA 90, 592–594. https://doi.org/10.1073/pnas.90.2.592.

Davidson, A.G., Etheridge, D.E., 1963. Infection of Balsam Fir, *Abies balsamea* (L.) Mill. by *Stereum sanguinolentum* (ALB.and SCHW. EX FR.) FR. Can. J. Bot. 41, 759–765. https://doi.org/10.1139/b63-063.

Dawson, S.K., Boddy, L., Halbwachs, H., Bässler, C., Andrew, C., Crowther, T.W., Heilmann-Clausen, J., Nordén, J., Ovaskainen, O., Jönsson, M., 2019. Handbook for the measurement of macrofungal functional traits: a start with basidiomycete wood fungi. Funct. Ecol. 33, 372–387. https://doi.org/10.1111/1365-2435.13239.

de la Parra-Martínez, S.M., Renton, K., Salinas-Melgoza, A., Muñoz-Lacy, L.G., 2015. Tree-cavity availability and selection by a large-bodied secondary cavity-nester: the Military Macaw. J. Ornithol. 156, 489–498. https://doi.org/10.1007/s10336-014-1150-9.

Deflorio, G., Fink, S., Schwarze, F.W.M.R., 2008a. Detection of incipient decay in tree stems with sonic tomography after wounding and fungal inoculation. Wood Sci. Technol. 42, 117–132. https://doi.org/10.1007/s00226-007-0159-0.

Deflorio, G., Franz, E., Fink, S., Schwarze, F.W.M.R., 2009. Host responses in the xylem of trees after inoculation with six wood-decay fungi differing in invasiveness. Botany 87, 26–35. https://doi.org/10.1139/B08-129.

Deflorio, G., Johnson, C., Fink, S., Schwarze, F.W.M.R., 2008b. Decay development in living sapwood of coniferous and deciduous trees inoculated with six wood decay fungi. . Ecol. Manag. 255, 2373–2383. https://doi.org/10.1016/j.foreco.2007.12.040.

Edman, M., Gustafsson, M., Stenlid, J., Ericson, L., 2004a. Abundance and viability of fungal spores along a forestry gradient - Responses to habitat loss and isolation? Oikos 104, 35–42. https://doi.org/10.1111/j.0030-1299.2004.12454.x.

Edman, M., Gustafsson, M., Stenlid, J., Jonsson, B.G., Ericson, L., 2004b. Spore deposition of wood-decaying fungi: Importance of landscape composition. Ecography 27, 103–111. https://doi.org/10.1111/j.0906-7590.2004.03671.x.

Edman, M., Möller, R., Ericson, L., 2006. Effects of enhanced tree growth rate on the decay capacities of three saprotrophic wood-fungi. For. Ecol. Manag. 232, 12–18. https://doi.org/10.1016/j.foreco.2006.05.001.

El-Atta, H.A., 1984. Fungal colonisation of extraction wounds in conifers. University of Edinburgh.

Elliott, T.F., Jusino, M.A., Trappe, J.M., Lepp, H., Ballard, G.A., Bruhl, J.J., Vernes, K., 2019. A global review of the ecological significance of symbiotic associations between birds and fungi. Fungal Divers. 98, 161–194. https://doi.org/10.1007/s13225-019-00436-3.

Elo, M., Halme, P., Toivanen, T., Kotiaho, J.S., 2019. Species richness of polypores can be increased by supplementing dead wood resource into a boreal forest landscape. J. Appl. Ecol. 56, 1267–1277. https://doi.org/10.1111/1365-2664.13364.

Enderle, R., Stenlid, J., Vasaitis, R., 2019. An overview of ash (*Fraxinus* spp.) and the ash dieback disease in Europe. CAB Rev. Perspect. Agric. Vet. Sci. Nutr. Nat. Resour. 14. https://doi.org/10.1079/PAVSNNR201914025.

Filip, G., Chadwick, K., Zambino, P., Omdal, D., Ramsey-kroll, A., Schmitt, C., Saavedra, A., Rall, W., Parks, C., 2011. Seven- to 14-Year Effects of Artificially Inoculating Living Conifers to Promote Stem Decay and Subsequent Wildlife Use in Oregon and Washington Forests.

Filip, G., Parks, C.G., Fred, A.Baker, Stephen, E.Daniels, 2004. Technical note-artificial inoculation of decay fungi into douglas-fir with rifle or shotgun to produce wildlife trees in Western Oregon. West. J. Appl. 19, 211–215.

Fries, N., 1984. Spore germination in the higher basidiomycetes. Proc. Plant Sci. 93, 205–222. https://doi.org/10.1007/BF03053077.

Gange, A.C., Gange, E.G., Mohammad, A.B., Boddy, L., 2011. Host shifts in fungi caused by climate change? Fungal Ecol. 4, 184–190. https://doi.org/10.1016/j.funeco.2010.09.004.

Gibbons, P., Lindenmayer, D., 2002. Tree Hollows and Wildlife Conservation in Australia. CSIRO publishing. https://doi.org/10.1071/9780643090033.

Gibbons, P., Lindenmayer, D.B., Barry, S.C., Tanton, M.T., 2000. Hollow formation in eucalypts from temperate forests in Southeastern Australia. Pac. Conserv. Biol. 6, 218–228. https://doi.org/10.1071/PC000217.

Gonthier, P., Guglielmo, F., Sillo, F., Giordano, L., Garbelotto, M., 2015. A molecular diagnostic assay for the detection and identification of wood decay fungi of conifers. For. Pathol. 45, 89–101. https://doi.org/10.1111/efp.12132.

Grace, J., Mudge, K.W., 2015. Production of Hericium sp. (Lion's Mane) mushrooms on totem logs in a forest farming system. Agrofor. Syst. 89, 549–556. https://doi.org/10.1007/s10457-015-9790-1.

Greaves, D.R., 2017. Population biology and ecology in the rare and endangered *Hapalopilus croceus*. Biology Education Centre, Uppsala University, and SLU: Department of Forest Mycology and Plant Pathology, Almas allé 5, 756 51, Uppsala, Sweden.

Griffith, G.W., 2012. Do we need a global strategy for microbial conservation? Trends Ecol. Evol. 27, 1–2. https://doi.org/10.1016/j.tree.2011.10.002.

Griffiths, S.R., Bender, R., Godinho, L.N., Lentini, P.E., Lumsden, L.F., Robert, K.A., 2017. Bat boxes are not a silver bullet conservation tool. Mamm. Rev. 47, 261–265. https://doi.org/10.1111/mam.12097.

Griffiths, S.R., Lentini, P.E., Semmens, K., Watson, S.J., Lumsden, L.F., Robert, K.A., 2018. Chainsaw-carved cavities better mimic the thermal properties of natural tree hollows than nest boxes and log hollows. Forests 9, 1–27. https://doi.org/10.3390/f9050235.

Guilley, E., Charpentier, J.P., Ayadi, N., Snakkers, G., Nepveu, G., Charrier, B., 2004. Decay resistance against *Coriolus versicolor* in Sessile oak [*Quercus petraea* Liebl.: analysis of the between-tree variability and correlations with extractives, tree growth and other basic wood properties. Wood Sci. Technol. 38, 539–554. https://doi.org/10.1007/s00226-004-0250-8.

Hallenberg, N., Nilsson, R.H., Robledo, G., 2013. Species complexes in *Hericium* (Russulales, Agaricomycota) and a new species - *Hericium rajchenbergii* - from southern South America. Mycol. Prog. 12, 413–420. https://doi.org/10.1007/s11557-012-0848-4.

Hardenbol, A.A., Pakkala, T., Kouki, J., 2019. Persistence of a keystone microhabitat in boreal forests: Cavities of Eurasian Three-toed Woodpeckers (*Picoides tridactylus*). For. Ecol. Manag. 450, 117530 https://doi.org/10.1016/j.foreco.2019.117530.

Hartig, R., 1874. Wichtige Krankheiten der Waldbäume. Julius Springer, Berlin.

Hawksworth, D.L., 2006. Mycology and mycologists. Proc. 8th Int. Mycol. Congr. 65–72.

Heilmann-Clausen, J., Barron, E.S., Boddy, L., Dahlberg, A., Griffith, G.W., Nordén, J., Ovaskainen, O., Perini, C., Senn-Irlet, B., Halme, P., 2015. A fungal perspective on conservation biology. Conserv. Biol. 29. https://doi.org/10.1111/cobi.12388.

Heilmann-Clausen, J., Boddy, L., 2008. Distribution patterns of wood-decay basidiomycetes at the landscape to global scale. In: Br. Mycol. Soc. Symp. Ser., 28, pp. 263–275. https://doi.org/10.1016/S0275-0287(08)80016-1. Chapter 14.

Heilmann-Clausen, J., Christensen, M., 2005. Wood-inhabiting macrofungi in Danish beech-forests - Conflicting diversity patterns and their implications in a conservation perspective. Biol. Conserv. 122, 633–642. https://doi.org/10.1016/j.biocon.2004.10.001.

Heilmann-Clausen, J., Christensen, M., 2004. Does size matter? On the importance of various dead wood fractions for fungal diversity in Danish beech forests. For. Ecol. Manag. 201, 105–117. https://doi.org/10.1016/j.foreco.2004.07.010.

Hellawell, J.M., 1991. Development of a rationale for monitoring. In: Goldsmith, B. (Ed.), Monitoring for Conservation and Ecology. Conservation Biology. Springer, Dordrecht.

Hepting, G.H., Roth, E.R., 1950. The fruiting of heart-rot fungi on felled trees. J. For. 48, 332–333.

Hillis, W., 2012. Heartwood and tree exudates (Vol. 4). Springer Science & Business Media.

Hilszczański, J., Jaworski, T., Plewa, R., Jansson, N., 2014. Surrogate tree cavities: boxes with artificial substrate can serve as temporary habitat for *Osmoderma barnabita* (Motsch.) (Coleoptera, Cetoniinae). J. Insect Conserv. 18, 855–861. https://doi.org/10.1007/s10841-014-9692-y.

Hirt, R.R., 1949. Decay in northern hardwoods by *Fomes igniarius, Poria obliqua*, and *Polyporus glomeratus*. Phytopathology 39, 475–480.

Hirt, R.R., Eliason, E.J., 1938. The development of decay in living trees inoculated with *Fomes pinicola*. J. For. 36, 705–709.

Huss, M., Bednarz, J.C., Juliano, D.M., Varland, D.E., 2002. The Efficacy of Inoculating Fungi into Conifer Trees to Promote Cavity Excavation by Woodpeckers in Managed Forests in Western Washington. USDA Forest Service Gen. Tech.

IUCN/SSC, 2013. Guidelines for Reintroductions and Other Conservation Translocations IUCN. Version 1.0. Gland, Switzerland.

Jackson, J.A., Jackson, B.J.S., 2004. Ecological relationships between fungi and woodpecker cavity sites. Condor 106, 37–49. https://doi.org/10.1093/condor/106.1.37.

Jansson, N., Ranius, T., Larsson, A., Milberg, P., 2009. Boxes mimicking tree hollows can help conservation of saproxylic beetles. Biodivers. Conserv. 18, 3891–3908. https://doi.org/10.1007/s10531-009-9687-2.

Jonsell, M., Weslien, J., Ehnström, B., 1998. Substrate requirements of red-listed saproxylic invertebrates in Sweden. Biodivers. Conserv. 7, 749–764. https://doi.org/10.1023/A:1008888319031.

Jusino, M.A., Lindner, D.L., Banik, M.T., Rose, K.R., Walters, J.R., 2016. Experimental evidence of a symbiosis between red-cockaded woodpeckers and fungi. Proc. R. Soc. B Biol. Sci. 283. https://doi.org/10.1098/rspb.2016.0106.

Kalcounis, M.C., Brigham, M., 1998. Secondary use of aspen cavities by tree-roosting big brown bats. J. Wildl. Manag. 62, 603–611.

Krah, F.S., Bässler, C., Heibl, C., Soghigian, J., Schaefer, H., Hibbett, D.S., 2018. Evolutionary dynamics of host specialization in wood-decay fungi. BMC Evol. Biol. 18, 1–13. https://doi.org/10.1186/s12862-018-1229-7.

Kunz, T.H., Lumsden, L.F., 2003. Ecology of cavity and foliage roosting bats. Bat Ecology, pp. 3–87.

Lachat, T., Bouget, C., Bütler, R., Müller, J., 2013. Deadwood: quantitative and qualitative requirements for the conservation of saproxylic biodiversity. In: Kraus, D., Krumm, F. (Eds.), Integrative Approaches as an Opportunity for the Conservation of Forest Biodiversity. European Forest Institute, pp. 92–103. https://doi.org/10.1080/00207233.2014.889472.

Landler, L., Jusino, M.A., Skelton, J., Walters, J.R., 2014. Global trends in woodpecker cavity entrance orientation: latitudinal and continental effects suggest regional climate influence. Acta Ornithol. 49, 257–266. https://doi.org/10.3161/173484714X687145.

Lee, B.-H., Ka, K.-H., Park, H., Lee, H.-M., Bak, W.-C., Ryu, S.-R., 2008. Artificial inoculation of *Inonotus obliquus* on B*etula platyphylla* var. Japonica. Korean J. Mycol. 36, 144–147. https://doi.org/10.4489/kjm.2008.36.2.144.

Legg, C.J., Nagy, L., 2006. Why most conservation monitoring is, but need not be, a waste of time. J. Environ. Manag. 78, 194–199. https://doi.org/10.1016/j.jenvman.2005.04.016.

Lewis, J.C., 1998. Creating snags and wildlife trees in commercial forest landscapes. West. J. Appl. 13, 97–101. https://doi.org/10.1093/wjaf/13.3.97.

Lindblad, I., 1998. Wood-inhabiting fungi on fallen logs of Norway spruce: Relations to forest management and substrate quality. Nord. J. Bot. 18, 243–255. https://doi.org/10.1111/j.1756-1051.1998.tb01877.x.

Lindenmayer, D.B., 2017. Conserving large old trees as small natural features. Biol. Conserv. 211, 51–59. https://doi.org/10.1016/j.biocon.2016.11.012.

Lindenmayer, D.B., Laurance, W.F., 2017. The ecology, distribution, conservation and management of large old trees. Biol. Rev. 92, 1434–1458. https://doi.org/10.1111/brv.12290.

Lindenmayer, D.B., Laurance, W.F., Franklin, J.F., 2012. Ecology: global decline in large old trees. Science 338, 1305–1306. https://doi.org/10.1126/science.1231070.

Lindenmayer, D.B., Laurance, W.F., Franklin, J.F., Likens, G.E., Banks, S.C., Blanchard, W., Gibbons, P., Ikin, K., Blair, D., Mcburney, L., Manning, A.D., Stein, J.A.R., 2014. New policies for old trees: averting a global crisis in a keystone ecological structure. Conserv. Lett. 7, 61–69. https://doi.org/10.1111/conl.12013.

Lindenmayer, D.B., Welsh, A., Donnelly, C., Crane, M., Michael, D., Macgregor, C., McBurney, L., Montague-Drake, R., Gibbons, P., 2009. Are nest boxes a viable alternative source of cavities for hollow-dependent animals? Long-term monitoring of nest box occupancy, pest use and attrition. Biol. Conserv. 142, 33–42. https://doi.org/10.1016/j.biocon.2008.09.026.

Lutermann, H., Verburgt, L., Rendigs, A., 2010. Resting and nesting in a small mammal: sleeping sites as a limiting resource for female grey mouse lemurs. Anim. Behav. 79, 1211–1219. https://doi.org/10.1016/j.anbehav.2010.02.017.

Manning, A.D., Gibbons, P., Fischer, J., Oliver, D.L., Lindenmayer, D.B., 2013. Hollow futures? Tree decline, lag effects and hollow-dependent species. Anim. Conserv. 16, 395–403. https://doi.org/10.1111/acv.12006.

Manning, E.T., Manley, I.A., 2014. Results of Fungal Inoculation Treatments as a Habitat Enhancement Tool in the East Kootenay Region of British Columbia: 2007–2013.Prov. B.C., Victoria, B.C. Exten. Note 112., ⟨www.for.gov.bc.ca/hfd/pubs/Docs/En/En112.htm⟩.

Manning, T., 2003. Fungal Inoculation of Trees as a Habitat Enhancement Tool in Second-Growth Forests TFL 37 and TFL 44 Operational Trial 2002 (Year 1) Progress Report.

Martin, K., Aitken, K.E.H., Wiebe, K.L., 2004. Nest sites and nest webs for cavity-nesting communities in interior British Columbia, Canada: nest characteristics and niche partitioning. Condor 106, 5–19. https://doi.org/10.1650/7482.

Martin, O., 1989. Smældere (Coleoptera, Elateridae) fra gammel løvskov i Danmark. Entomol. Medd. 57, 1–2.

May, T.W., Cooper, J.A., Dahlberg, A., Furci, G., Minter, D.W., Mueller, G.M., Pouliot, A., Yang, Z., 2019. Recognition of the discipline of conservation mycology. Conserv. Biol. 33, 733–736. https://doi.org/10.1111/cobi.13228.

Maynard, D.S., Bradford, M.A., Covey, K.R., Lindner, D., Glaeser, J., Talbert, D.A., Tinker, P.J., Walker, D.M., Crowther, T.W., 2019. Consistent trade-offs in fungal trait expression across broad spatial scales. Nat. Microbiol. 4, 846–853. https://doi.org/10.1038/s41564-019-0361-5.

Menkis, A., Redr, D., Bengtsson, V., Hedin, J., Niklasson, M., Nordén, B., Dahlberg, A., 2020. Endophytes dominate fungal communities in six-year-old veteranisation wounds in living oak trunks. Fungal Ecol., 101020 https://doi.org/10.1016/j.funeco.2020.101020.

Mitchell, R.J., Bellamy, P.E., Ellis, C.J., Hewison, R.L., Hodgetts, N.G., Iason, G.R., Littlewood, N.A., Newey, S., Stockan, J.A., Taylor, A.F.S., 2019. OakEcol: a database of Oak-associated biodiversity within the UK. Data Brief 25, 104120. https://doi.org/10.1016/j.dib.2019.104120.

Molina, R., Horton, T.R., Trappe, J.M., Marcot, B.G., 2011. Addressing uncertainty: how to conserve and manage rare or little-known fungi. Fungal Ecol. 4, 134–146. https://doi.org/10.1016/j.funeco.2010.06.003.

Möller, A., 1904. Über die Notwendigkeit und Möglichkeit wirksamer Bekämpfung des Kiefernbaumschwammes, *Trametes pini* (Thore) Fries. Zeits. Forst-u. Jagdw. 36: 11, 677–715.

Moore, D., Gange, A.C., Gange, E.G., Boddy, L., 2008. Fruit bodies: their production and development in relation to environment. In: Boddy, L., Frankland, J., van West, P. (Eds.), Ecology of Saprotrophic Basidiomycetes, pp. 79–103. https://doi.org/10.1016/S0275-0287(08)80007-0.

Mosedale, J.R., Charrier, B., Crouch, N., Janin, G., Savill, P.S., 1996. Variation in the composition and content of ellagitannins in the heartwood of European oaks (*Quercus robur* and *Q petraea*). A comparison of two French forests and variation with heartwood age. Ann. des Sci. 53, 1005–1018. https://doi.org/10.1051/forest:19960508.

Mueller, G.M., 2017. Progress in conserving fungi. BGjournal 14, 30–33.

Müller, J., Jarzabek-Müller, A., Bussler, H., Gossner, M.M., 2014. Hollow beech trees identified as keystone structures for saproxylic beetles by analyses of functional and phylogenetic diversity. Anim. Conserv. 17, 154–162. https://doi.org/10.1111/acv.12075.

Nikitsky, N.B., Schigel, D.S., 2004. Beetles in polypores of the Moscow region: checklist and ecological notes. Entomol. Fenn. 15, 6–22. https://doi.org/10.33338/ef.84202.

Nilsson, S.G., 1984. The evolution of nest-site selection among hole-nesting birds: the importance of nest predation and competition. Ornis Scand. 15, 167–175. https://doi.org/10.2307/3675958.

Nordén, B., Jordal, J.B., Evju, M., 2018. Can large unmanaged trees replace ancient pollarded trees as habitats for lichenized fungi, non-lichenized fungi and bryophytes? Biodivers. Conserv. 27, 1095–1114. https://doi.org/10.1007/s10531-017-1482-x.

Nordén, J., Abrego, N., Boddy, L., Bässler, C., Dahlberg, A., Halme, P., Hällfors, M., Maurice, S., Menkis, A., Miettinen, O., Mäkipää, R., Ovaskainen, O., Penttilä, R., Saine, S., Snäll, T., Junninen, K., 2020. Ten principles for conservation translocations of threatened wood-inhabiting fungi. Fungal Ecol. 44, 100919 https://doi.org/10.1016/j.funeco.2020.100919.

Park, H., Ka, K.-H., Lee, B.-H., Ryu, S.-R., 2010. Fruit-body Production of *Inonotus obliquus* on Living *Betula platyphylla* var. Japonica. Korean J. Mycol. 38, 83–84. https://doi.org/10.4489/kjm.2010.38.1.083.

Parks, C.G., Bull, E.L., Filip, G., 1996. Using artificially inoculated decay fungi to create wildlife habitat. In: Bradford, P., Manning, T., L'Anson, B. (Eds.), Wildlife Tree/Stand-Level Biodi- Versity Workshop Proceeding. British Columbi Environment, Victoria, BC, pp. 87–89.

Parsons, S., Lewis, K.J., Psyllakis, J.M., 2003. Relationships between roosting habitat of bats and decay of aspen in the sub-boreal forests of British Columbia. . Ecol. Manag. 177, 559–570. https://doi.org/10.1016/S0378-1127(02)00448-6.

Penton, C.E., Woolley, L.A., Radford, I.J., Murphy, B.P., 2020. Overlapping den tree selection by three declining arboreal mammal species in an Australian tropical savanna. J. Mammal. 101, 1165–1176. https://doi.org/10.1093/jmammal/gyaa074.

Piętka, J., Grzywacz, A., 2005. *In situ* inoculation of larch with the threatened wood-decay fungus *Fomitopsis officinalis* (basidiomycota) - Experimental studies. Pol. Bot. J. 50, 225–231.

Piętka, J., Grzywacz, A., 2006. Attempts at active protection of *Inonotus obliquus* by inoculating birches with its mycelium. Acta Mycol. 41, 305–312. https://doi.org/10.5586/am.2006.031.

Pouska, V., Svoboda, M., Lepšová, A., 2010. The diversity of wood-decaying fungi in relation to changing site conditions in an old-growth mountain spruce forest, Central Europe. Eur. J. . Res. 129, 219–231. https://doi.org/10.1007/s10342-009-0324-0.

Ranius, T., 2002. Influence of stand size and quality of tree hollows on saproxylic beetles in Sweden. Biol. Conserv. 103, 85–91. https://doi.org/10.1016/S0006-3207(01)00124-0.

Ranius, T., Eliasson, P., Johansson, P., 2008. Large-scale occurrence patterns of red-listed lichens and fungi on old oaks are influenced both by current and historical habitat density. Biodivers. Conserv. 17, 2371–2381. https://doi.org/10.1007/s10531-008-9387-3.

Ranius, T., Niklasson, M., Berg, N., 2009. Development of tree hollows in pedunculate oak (*Quercus robur*). For. Ecol. Manag. 257, 303–310. https://doi.org/10.1016/j.foreco.2008.09.007.

Rayner, A.D.M., Boddy, L., 1988. Fungal Decomposition of Wood. Its Biology and Ecology. John Wiley and Sons Ltd.

Read, H., 2000. Veteran Trees: A Guide to Good Management.

Remm, J., Lõhmus, A., 2011. Tree cavities in forests - The broad distribution pattern of a keystone structure for biodiversity. For. Ecol. Manag. 262, 579–585. https://doi.org/10.1016/j.foreco.2011.04.028.

Remm, J., Lõhmus, A., Remm, K., 2006. Tree cavities in riverine forests: what determines their occurrence and use by hole-nesting passerines? For. Ecol. Manag. 221, 267–277. https://doi.org/10.1016/j.foreco.2005.10.015.

Rinn, F., Schweingruber, F.H., Schär, E., 1996. Resistorgraph and X-ray density charts of wood comparative evaluation of drill resistance profiles and X-ray density charts of different wood species. Holzforschung 50, 303–311. https://doi.org/10.1515/hfsg.1996.50.4.303.

Rowe W.J., C.A H., 1979. Extrctives in eastern hardwoods: A review. Gen. Tech. Rep. FPL 18. USDA For. Serv. For. Prod. Lab. 17.

Rueegger, N., 2017. Artificial tree hollow creation for cavity-using wildlife – Trialling an alternative method to that of nest boxes. For. Ecol. Manag. 405, 404–412. https://doi.org/10.1016/j.foreco.2017.09.062.

Saab, V.A., Dudley, J., Thompson, W.L., 2004. Factors influencing occupancy of nest cavities in recently burned forests. Condor 106, 20–36. https://doi.org/10.1650/7485.

Savill, P., 2015. High forest management and the rise of even-aged stands. In: Kirby, K., Watkins, C. (Eds.), Europe's Changing Woods and Forests. CABI.

Sebek, P., Altman, J., Platek, M., Cizek, L., 2013. Is active management the key to the conservation of saproxylic biodiversity? Pollarding promotes the formation of tree hollows. PLoS One 8, 1–6. https://doi.org/10.1371/journal.pone.0060456.

Seddon, P.J., 2010. From reintroduction to assisted colonization: moving along the conservation translocation spectrum. Restor. Ecol. 18, 796–802. https://doi.org/10.1111/j.1526-100X.2010.00724.x.

Sedgeley, J.A., O'Donnell, C.F.J., 1999. Roost selection by the long-tailed bat, *Chalinolobus tuberculatus* , in temperate New Zealand rainforest and its implications for the conservation of bats in managed forests. Biol. Conserv. 88, 261–276. https://doi.org/10.1016/S0006-3207(98)00069-X.

Shigo, A.L., 1977. *Phialophora melinii*: inoculations in Wounded Red Maple. Phytopathology 67, 1333–1337. https://doi.org/10.1094/phyto-67-1333.

Shigo, A.L., Sharon, E.R., 1968. Discoloration and decay in hardwoods following inoculation with hymenomycetes. Phytopathology 58, 1493–1498.

Siitonen, J., 2012. Microhabitats. Biodiversity in Dead Wood, pp. 150–182. https://doi.org/10.1017/CBO9781139025843.008.

Siitonen, J., Jonsson, B.G., 2012. Other associations with dead woody material. In: Stockland, J.N., Siitonen, J., Jonsson, B.G. (Eds.), Biodiversity in Deadwood. Cambridge University Press, Cambridge, pp. 58–81.

Silverborg, S.B., 1959. Rate of Decay in Northern Hardwoods following artificial inoculation with some common heartrot fungi. For. Sci. 5, 223–228.

Silverborg, S.B., Larsen, M.J., 1967. Rate of Decay in Pinus strobus Following Artificial Inoculation with Fomes Pini. PLANT Dis. Report. 51, 829–831.

Simmel, J., Bässler, C., Poschlod, P., 2017. Ellenberg indicator values for macromycetes – a methodological approach and first applications. Fungal Ecol. 27, 202–212. https://doi.org/10.1016/j.funeco.2016.09.004.

Smith, A.P., Lindenmayer, D., 1988. Tree hollow requirements of leadbeater's possum and other possums and gliders in timber production ash forests of the victorian central highlands. Wildl. Res. 15, 347–362. https://doi.org/10.1071/WR9880347.

Smith, P.L., 2018. Copying ancient woodlands: a positive perspective. Biodivers. Conserv. 27, 1041–1053. https://doi.org/10.1007/s10531-017-1494-6.

Stenlid, J., Gustafsson, M., 2001. Are rare wood decay fungi threatened by inability to spread? Ecol. Bull. 85–91. https://doi.org/10.2307/20113266.

Stokland, J.N., 2012. Host-tree associations. In: Stokland, J.N., Siitonen, J., Jonsson, B.G. (Eds.), Biodiversity in Dead Wood. Cambridge University Press, Cambridge, pp. 82–110.

Sunhede, S., 1997. Vedsvampar på ek-Saffransticka. Ekbladet 12, 19–23.

Sutherland, W.J., Woodroof, H.J., 2009. The need for environmental horizon scanning. Trends Ecol. Evol. 24, 523–527. https://doi.org/10.1016/j.tree.2009.04.008.

Sverdrup-Thygeson, A., Skarpaas, O., Ødegaard, F., 2010. Hollow oaks and beetle conservation: the significance of the surroundings. Biodivers. Conserv. 19, 837–852. https://doi.org/10.1007/s10531-009-9739-7.

The Global Fungal Red List Inititaive, 2020a. The Global Fungal Red List: Piptoporus quercinus [WWW Document]. URL ⟨http://iucn.ekoo.se/iucn/species_view/100829/⟩ (accessed 6.4.20).

The Global Fungal Red List Inititaive, 2020b. The Global Fungal Red List: Hapalopilus croceus [WWW Document]. URL ⟨http://iucn.ekoo.se/iucn/species_view/445931⟩ (accessed 6.4.20).

Toole, R.E., 1967. Rates of Wood Decay Behind Open and Closed Wounds. PLANT Dis. Report. 51, 600.

Toole, R.E., 1966. Comparison of Two Methods for Inoculating Nuttall Oaks with Pleurotus Ostreatus. PLANT Dis. Report. 50, 552–553.

Toole, R.E., 1964. Progress of Oak Heart Rot Varies with Height in Tree. PLANT Dis. Report. 48, 585.

Toole, R.E., 1956. Heartrot in Bottomland Red Oaks Two Years After Inoculation. PLANT Dis. Report. 40, 823–825.

Vainio, E.J., Jurvansuu, J., Hyder, R., Kashif, M., Piri, T., Tuomivirta, T., Poimala, A., Xu, P., Mäkelä, S., Nitisa, D., Hantula, J., 2017. Heterobasidion partitivirus 13 mediates severe growth debilitation and major alterations in the gene expression of a fungal forest pathogen. J. Virol. 92, 1–15. https://doi.org/10.1128/jvi.01744-17.

Valenta, V., Moser, D., Kapeller, S., Essl, F., 2017. A new forest pest in Europe: a review of Emerald ash borer (*Agrilus planipennis*) invasion. J. Appl. Entomol. 141, 507–526. https://doi.org/10.1111/jen.12369.

van der Hoek, Y., Gaona, G.V., Martin, K., 2017. The diversity, distribution and conservation status of the tree-cavity-nesting birds of the world. Divers. Distrib. 23, 1120–1131. https://doi.org/10.1111/ddi.12601.

Whitney, R.D., Denyer, W.B.G., 1970. Inoculations with Stereum sanguinolentum and Fomes pini in Black Spruce and Balsam Fir. For. Sci. 16, 160–164.

Whitney, R.D., Denyer, W.B.G., 1969. Resin as a barrier to infection of white spruce by heartrotting fungi. For. Sci. 15, 266–267.

Wu, H.X., 2019. Benefits and risks of using clones in forestry–a review. Scand. J. For. Res. 34, 352–359. https://doi.org/10.1080/02827581.2018.1487579.

Yee, M., Grove, S.J., Richardson, A.M.M., Mohammed, C.L., 2006. Brown rot in inner heartwood: why large logs support characteristic saproxylic beetle assemblages of conservation concern. Insect Biodiversity and Dead Wood, pp. 42–56.

Yu, Q., Yang, D.-Q., Zhang, S.Y., Beaulieu, J., Duchesne, I., 2003. Genetic variation in decay resistance and its correlation to wood density and growth in white spruce. Can. J. For. Res. 33, 2177–2183.

Zheng, Z., Zhang, S., Baskin, C., Baskin, J., Schaefer, D., Yang, X., Yang, L., 2016. Hollows in living trees develop slowly but considerably influence the estimate of forest biomass. Funct. Ecol. 30, 830–838. https://doi.org/10.1111/1365-2435.12566.