

# Global Ecology and Conservation

## 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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## 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 of woodland with a depleted stock of veteran trees that support these microhabitats. Decomposition is a slow process and it may take heart-rot fungi hundreds of years to establish before hollowing even begins. A major challenge to forest restoration, therefore, is how these habitats can be restored or replicated. One approach is to inoculate trees with heart-rot fungi as a direct intervention to accelerate tree hollowing. We identify two types of conservation inoculation that could be beneficial in forest conservation: (1) *Veteranising inoculations* designed to benefit cavity and decay dependant fauna; and (2) *Translocation inoculations*, to reintroduce locally extinct, dispersal-limited heart-rot fungi.

Tree inoculations have a hundred-year pedigree but successes have been mixed and there are no long-term published studies. Reflecting on previous heart-rot inoculations we discuss elements of the inoculation protocol to aid design of conservation inoculations. Conservation inoculations have the potential to be a useful tool in forest restoration and we hope to stimulate wider uptake as a direct 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.

Saproxyllic 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. saproxyllic and mycotrophic species)

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(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 Piętko, 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 Lohmus, 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 Bats Invertebrates	Bull and Partridge (1986); Conner et al. (1976); Jackson and Jackson (2004) Parsons et al. (2003) Nikitsky and Schigel (2004) Alexander (2002); Andersson (1999); Nikitsky and Schigel (2004); Yee et al. (2006)
Rot type (white/brown)	Invertebrates	
Tree species	Excavating cavity-nesting birds Non-excavating cavity nesting birds Bats Invertebrates	Martin et al. (2004) Martin et al. (2004) Boonman (2000); Kalcounis and Brigham (1998) Jonsell et al. (1998)
Tree DBH	Excavating cavity-nesting birds Non-excavating cavity nesting birds	Conner et al. (1983) Bonaparte and Cockle (2017); Martin et al. (2004) Lutermann et al. (2010); Penton et al. (2020); Smith and Lindenmayer (1988) Ranius (2002)
Tree height	Arboreal mammals Invertebrates Excavating cavity-nesting birds Non-excavating cavity nesting birds Bats Arboreal mammals	
Cavity Orientation	Excavating cavity-nesting birds	Bull and Peterson (1986) Bonaparte and Cockle (2017) Sedgeley and O'Donnell (1999) Smith and Lindenmayer (1988)
Cavity Height	Excavating cavity-nesting birds Non-excavating cavity nesting birds Arboreal mammals Invertebrates	Conner et al. (1983) de la Parra-Martínez et al. (2015); Nilsson (1984) Smith and Lindenmayer (1988) Martin (1989); Ranius (2002)
Dependence on primary cavity excavator (e.g. woodpecker/sapsucker)	Non-excavating cavity nesting birds Bats	Daily et al. (1993); Martin et al. (2004); Saab et al. (2004) Boonman (2000)
Position of tree in the landscape	Excavating cavity-nesting birds Non-excavating cavity nesting birds Invertebrates	Bull and Partridge (1986) Bonaparte and Cockle (2017) Sverdrup-Thygeson et al. (2010)
Distance to forest edge	Non-excavating cavity nesting birds Bats Arboreal mammals	(Aitken et al., 2002; Remm et al., 2006) Boonman (2000) 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 Piętko, 2014;) and reintroduction of rare fungi (Abrego et al., 2016; Boddy et al., 2004; Piętko 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; Ruegger, 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).

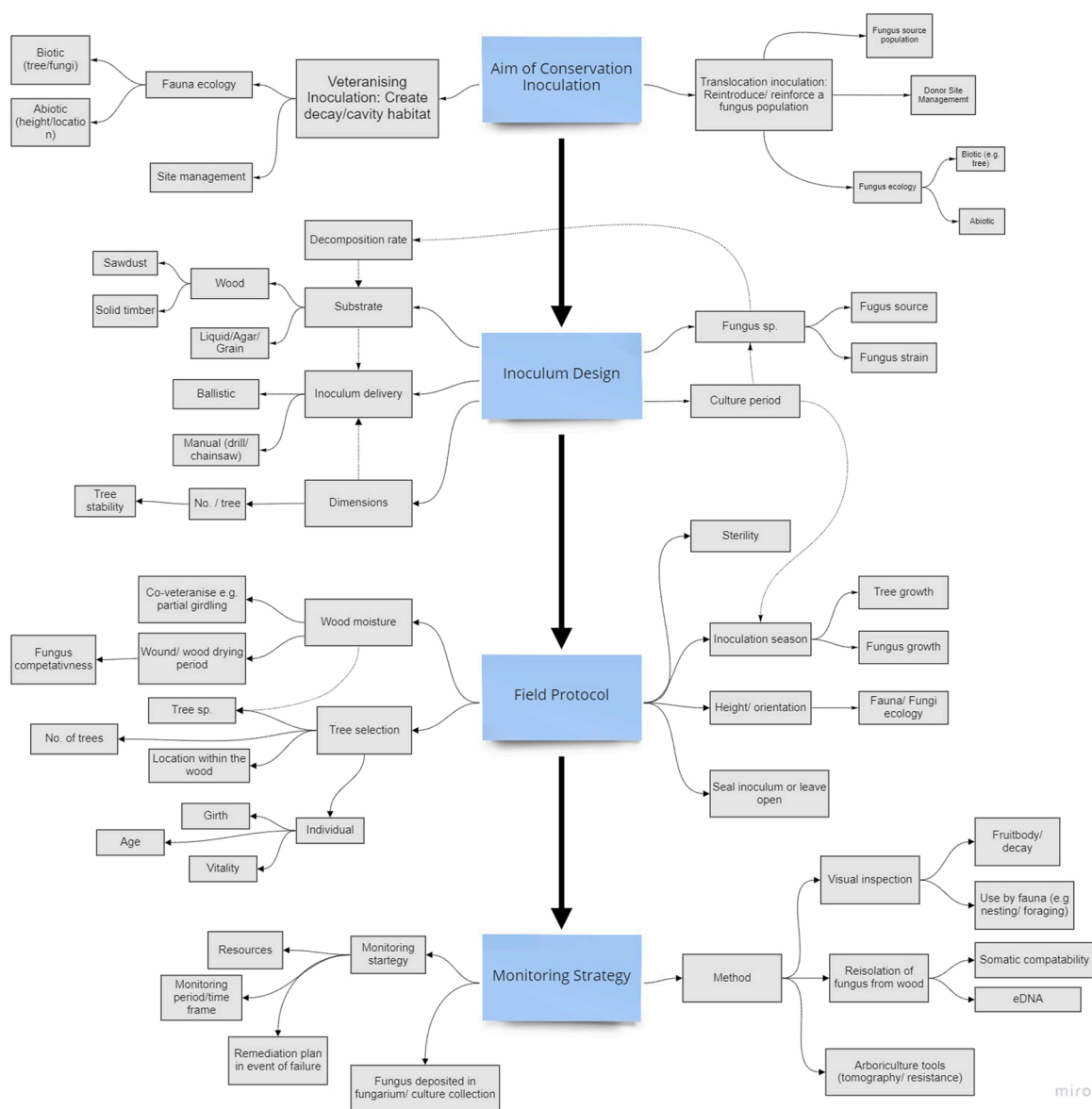
Like natural cavity formation, decay initiated by either veteranisation or artificial inoculation is slow. Inoculation is, therefore, a long-term conservation action which should be complementary to other alternative methods that mimic or instigate their formation.

**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  $2 \text{ mm y}^{-1}$ . 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 × 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; Piętko 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 (*Buglossoporus 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 Initiative (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; Piętko 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. americanum*) 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 (Birkmoe 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 *Hericum* 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, *Antrodia 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 pachydon* 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<sup>-1</sup> and 14.8 cm y<sup>-1</sup> 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 *Castanea*) 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<sup>-1</sup> compared to 27 cm y<sup>-1</sup> in American beech and 3.6 cm y<sup>-1</sup> 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 (Norden 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.

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## 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](https://doi.org/10.1016/j.gecco.2021.e01967).

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