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Ten principles for conservation translocations of threatened wood-inhabiting fungi

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Abstract

Unlike for many other organism groups, conservation translocations of fungi are still rare. Encouraged by recent successful translocations, there is a growing interest in applying this conservation tool to threatened wood-inhabiting fungi. When combined with other conservation or restoration measures, translocation can be an effective measure for preventing further population decline in the short term, and species extinctions in the long term. Translocations can be appropriate for rare and specialist fungal species that occur as small local populations in isolated patches across fragmented landscapes, where there is a low likelihood of successful dispersal between distant host trees that have special qualities and are situated in suitable conditions. As species translocations are a controversial topic, the pros and cons of translocation as a conservation tool for threatened fungi need careful consideration. We highlight the uncertainties and risks that are connected to fungal translocations, and propose ten principles adhering to the precautionary principle.

Keywords

Cryptic species; dispersal limitation; extinction; forest fragmentation; genetic variation; habitat loss; population viability; reintroduction; species interactions; species restoration

Introduction

Conservation translocation, *i.e.* the intentional human-mediated movement of species from one place to another with a primary objective of conservation benefits (IUCN/SSC 2013), has been widely applied as a conservation tool for decades (Seddon *et al.* 2007; Seddon *et al.* 2014). There have been both successes (Hooson & Jamieson 2003; Kuussaari *et al.* 2015) and failures. The latter include failed establishment of the translocated individuals (Frazer 1992; Armstrong *et al.* 2007), and unintended translocations, due to unclear taxonomy or species misidentification of the translocated individuals (Parker *et al.* 2012). Conservation translocations have mostly involved vertebrates (Frazer 1992; Hooson & Jamieson 2003; Perez *et al.* 2012; Tosi *et al.* 2015), but also invertebrates such as butterflies (Kuussaari *et al.* 2015), and vascular plants (Godefroid *et al.* 2011; Weisenberger *et al.* 2014). Among fungi, lichens have been translocated for conservation purposes (Lidén *et al.* 2004; Smith 2014), foliar endophytic fungi have been transplanted in endangered plants to improve their disease resistance (Zahn & Amend 2017), and mycorrhizal fungi have been inoculated in soils to restore grassland ecosystems (Koziol & Bever 2017). Inoculating wood-inhabiting fungi in relatively young living trees, to initiate decay typically establishing in older trees and thereby increase the biodiversity value through tree veteranisation, has been suggested (Read 2000).

Translocations of fungi for purposes other than conservation are also taking place, with some of them at a large scale. The wood-inhabiting fungus *Phlebiopsis gigantea* is commonly applied as a spore suspension on cut stumps, for biocontrol of the tree pathogen *Heterobasidion* spp. in European and North American production forests (Pirttilä & Frank 2018). In Fennoscandia, the commercial biocontrol agent Rotstop® (Verdera Oy, Espoo, Finland), which is based on two strains of *P. gigantea*, is widely used (applied on 47 000 ha of forest land yearly) and known to influence the early colonizer community structure in treated stumps (Vasiliauskas *et al.* 2005; Samils *et al.* 2009). A Canadian strain of the wood-decay basidiomycete *Chondrostereum purpureum* has been developed into a biological herbicide Chontrol® (MycoLogic Inc., Victoria, Canada) to control stump sprouting and regrowth of deciduous tree stumps (Bailey 2010). Another example of extensive use of a single fungal strain is the Indian strain of *Piriformospora indica*, a plant-root colonizing basidiomycete that enhances the growth of several crop plant species, and is used in many field and greenhouse experiments in Asia and Europe (e.g. Serfling *et al.* 2007). Furthermore, several wood-inhabiting fungi – including species that are nationally red-listed (threatened or near-threatened) in some countries, such as *Grifola frondosa* and *Hericium erinaceu*s – are grown commercially for food and medical use, and mycelium or spore inocula are sold for home cultivation (Mayuzumi & Mizuno 1997). These can be of domestic origin, but are often of foreign origin, and detailed information about the strain being used is often unavailable. Many of these species are cultivated outdoors, which has the potential for unintentional introduction of non-native strains into the natural environment.

Translocation of native species of fungi to their original habitats to preserve the species and their populations is still rare, but of increasing interest as a part of the conservation toolbox for threatened fungi. Many wood-inhabiting fungi have declined world-wide, which is well-documented in Europe (Dahlberg *et al.* 2010). In Finland, Sweden and Norway, where fungi have been included in the official national Red List assessments since 1986, 1990 and 1997, respectively, populations of many wood-inhabiting species have declined or gone extinct in some part (region) of the country due to the extensive loss and fragmentation of dead-wood rich forests (Kotiranta *et al.* 2010; ArtDatabanken 2015; Henriksen & Hilmo 2015; Kotiranta *et al.* 2019). For instance, in Norway, half of the assessed polypore species are red-listed (Henriksen & Hilmo 2015), mainly due to intensive forest management. These species can have viable populations (Gilpin & Soulé 1986) only in landscapes with a well-connected network of forests with a continuous supply of dead wood of species-specific quality. Improved management practices and interventions aiming at increasing dead wood in forests seem to increase the overall richness of wood-inhabiting fungi, but have no significant positive impact on most rare species at least in the short term (Peltoniemi *et al.* 2013; Komonen *et al.* 2014; Pasanen *et al.* 2014). Red-listed wood-inhabiting fungal species are seldom found in forests with less than 20-50 m^3 ha^{-1} of dead wood (Penttilä *et al.* 2004; Hottola *et al.* 2009; Junninen & Komonen 2011; Nordén *et al.* 2018), and stand age has an independent positive effect on the occurrence of red-listed wood-inhabiting fungi (Nordén *et al.* 2018). Sufficient amounts of suitable dead wood habitats and high forest age are challenging to produce through management practices or dead-wood creation. Suitable dead wood habitat needs to be available within the distance of effective dispersal of the species (i.e. close enough to their present occurrences) which may be only a kilometer or less (Norros *et al.* 2012; Peay *et al.* 2012; Norros *et al.* 2015). Isolation of local populations and increasing risk of local extinction is of great concern in today's highly fragmented forest landscapes, where species have difficulties in reaching isolated forest patches with sufficient continuum of dead wood (Abrego *et al.* 2017a; Mair *et al.* 2018; Nordén *et al.* 2018). This is especially true for ecologically specialized species which tend to be rare and for which resources, typically large logs that may take decades to decompose, are rare in space and time (Nordén *et al.* 2013).

In this commentary, we focus on reintroduction and reinforcement, which are the two types of conservation translocation currently applied or considered for wood-inhabiting fungi. Reintroduction is the intentional movement and release of an organism within its indigenous range from which it has disappeared, whereas reinforcement is the intentional movement and release of an organism into an existing population of conspecifics (IUCN/SSC 2013). We, henceforth, use the common term *conservation translocation* to discuss these two measures. We realize that the term itself also entails more proactive measures, such as assisted colonization and ecological replacement (IUCN/SSC 2013), but these are not included in our discussion. Red-listed wood-inhabiting fungal species have been translocated in Finland, Germany, Norway, Poland, Slovenia, Sweden and the UK (Table 1) with a conservation purpose (Pietka & Grzywacz 2005; Pietka & Grzywacz 2006) or in connection with ecological studies (Abrego *et al.* 2016b). The translocations that have already been monitored for several years have proven to be successful: all of the inoculated species were able to establish in the dead wood or living trees and in some cases even fruit during the monitoring period which ranges 3-20 years so far (Pietka & Grzywacz 2005; Abrego *et al.* 2016b; Dahlberg et al. unpublished data), except for one study (Pietka & Grzywacz 2006) where the species did not establish. The success of these pilot studies has raised an increasing interest, among conservation biologists and environmental authorities, in translocating wood-inhabiting fungal species for conservation purposes.

As the translocation practice is relatively new and has risks involved, it has also raised concerns among mycologists and conservationists. In this commentary, we identify and discuss benefits and concerns related to reintroduction and reinforcement of wood-inhabiting fungi from the standpoint of preventing extinctions of threatened species in the long term. We further suggest principles that should be applied for fungal translocation projects to ensure their ecological soundness. We discuss mainly scientific and technical issues. Our ethical standpoint is that we are morally obliged, as well as bound by international and national agreements, to strive to protect native species that are declining because of human actions. We consider this more important than preserving authenticity, in cases where authenticity means impoverished species communities reflecting human-manipulated landscape history, which has led to new standards of how wilderness is defined (Dudley 2011). In our opinion, translocation is a part of the conservation toolbox, a means of taking back particular native species to their natural habitats that the species cannot any longer reach because of dispersal limitation that is caused by human transformation of the forest landscapes.

Reintroduction and reinforcement of rare species may reduce the risk of extinction

The benefit of reintroducing threatened fungal species to suitable habitats within their historical range may be that of turning extinction debt into a species credit (Hanski 2000): in landscapes that have experienced large-scale intensive forestry, even the sites that currently hold much dead wood, e.g. due to restoration actions, wind-falls or insect outbreaks, may remain beyond reach for a large number of threatened species without translocation actions, due to dispersal limitation (Kouki *et al.* 2012; Elo *et al.* 2019). In more detail, the benefits of translocation may include a higher number of occupied patches, larger population sizes, increased connectivity of unoccupied patches, and lower risk of regional or national extinction. For species that have extremely reduced population sizes, current populations consisting of only a small number of individuals in isolated forest fragments, with low chance for (re)colonisations of (old or) new localities for years or decades, reintroductions are likely to be the only way to rescue the species from extinction at the regional, national and eventually even global scales. Reinforcing a still existing but small local population may strengthen it and, therefore, reduce the risk of local extinction, while simultaneously adding to the reduced genetic diversity in that patch. In many cases it may, nevertheless, be better to increase the number of occupied patches through reintroducing the species to localities where it is known or assumed to have existed before, which will increase the dispersal frequency and gene flow at the landscape scale. Fungal conservation translocation can be relatively inexpensive, as compared with the cost of buying forest land for protection. Forest protection and other conservation measures that simultaneously help many species, are, however, always the primary conservation measures; in the long term, a sufficient area of well-connected high-quality forest reserves is the only solution for conservation of forest species. Translocation of individual species may be included as auxiliaries, when the future habitat availability in the area has been ensured.

Challenges related to fungal translocations

Many of the concerns and risks related to fungal translocations derive from gaps in knowledge about the taxonomy, population genetic structure and ecology or ecological impacts on other species, and are shared with other organism groups (IUCN/SSC 2013). In addition, there are also issues that are specific to fungi. Compared to many other species groups, the source populations of fungi to be translocated are not jeopardized, as typically a piece of one fruit body or mycelium or a mere spore print is enough for preparing countless inocula, and thus we do not consider the potential weakening of the source population to be a major challenge. The six challenges listed below describe the points of discussion that seem to cause most concern when considering reintroducing or reinforcing wood-inhabiting fungi. For each of them, we also describe a mitigation measure.

Challenge 1: are we certain about what species we are translocating?

The first challenge is incomplete taxonomic knowledge. As with other organism groups there are often issues of unclear taxonomy, cryptic species and misidentifications of translocated individuals. DNA methods have recently revealed hitherto unknown new species of wood-inhabiting fungi, even in well-studied genera (Korhonen *et al.* 2018; Miettinen & Niemelä 2018; Miettinen *et al.* 2018). Furthermore, the standard DNA marker for identifying fungi (nrDNA internal transcribed spacer; ITS) is not always sufficiently variable to delimit closely related species in basidiomycetes, or the differences are so minor (1-2 base pairs) that they may have been interpreted as intraspecific variation (Spirin *et al.* 2015; Spirin *et al.* 2017; Korhonen *et al.* 2018). Consequently, ITS-based species concepts may have to be revised in the future, which introduces risks in any decisions based on current knowledge.

Mitigation: It is pivotal to select for translocation only species that are well known in terms of taxonomy, ecology and conservation status, to avoid unnecessary interventions for species with a different identity or population status than assumed. Current DNA methods make it possible to reduce the risk connected to the first challenge through verifying the identity of the translocated species as well as the local species at the translocation site. We, however, advocate the use of multi-locus DNA markers to delimit species.

Challenge 2: how will the translocated species affect the resident community?

The second challenge is the incomplete knowledge of species interactions in the hyperdiverse fungal communities in dead wood (Rajala *et al.* 2015). We do not know how the reintroduced or reinforced species will affect the current communities through competition or other kinds of (positive or negative) interactions. Both the negative and the positive effects may extend to other organisms, for instance, specialized rare insects hosted by red-listed wood-inhabiting fungi (Komonen *et al.* 2000).

As a potential *risk*, a translocated species could, directly or indirectly, cause the disappearance of an even more threatened but poorly known species already inhabiting the wood (for example an inconspicuous ascomycete or heterobasidiomycete species that are difficult to detect) (Spirin *et al*. 2016). Furthermore, if the translocated species establishes a new population, it could prevent colonization by other threatened species that arrive into the forest patch where translocation has taken place; however, other threatened species have evolved to co-exist in the same landscape, forest patch or even in the same log, otherwise they would have become extinct a long time ago. Translocated fungal individuals may also affect the resident community indirectly through the mycoviruses that they may carry. Mycoviruses are poorly known for their diversity, host specificity, distribution and effects on host fungi. Often they seem to have no apparent effect on the host fungus, but may in some cases cause reduced mycelial growth, sporulation or competitive ability (Rana 2019).

Potential *positive effects* of translocations on the resident communities and the ecosystem include facilitation of natural colonisation of other threatened species. There are known cases where a threatened fungal species depends on another red-listed fungal species (e.g. *Piloporia sajanensis*, on *Trichaptum laricinum*) (Niemelä *et al.* 1995). Threatened fungal or insect species may use dead wood modified by the translocated fungus, or directly the fruit bodies of the translocated species. Fungal fruit bodies are known to host rich communities of fungicolous insects and fungi, and some of the species are specialists in one host species (Jonsell & Nordlander 2004, Koskinen et al. 2019, Maurice et al. in prep.). In addition to the importance to other species, some threatened fungal species may have specific ecologically valuable functions (e.g. tree hollow creation). The main functions of threatened fungal species are often well known, whereas the associated communities of fungicolous insects and fungi typically remain deficiently known.

Mitigation: To alleviate the potential of direct negative effects on other species, translocation should target only a small proportion of logs of certain quality in an area, especially where there is a high diversity of species of wood-inhabiting fungi. Alternatively, translocation could be targeted to artificially created dead wood, which also adds the amount of dead wood substrate. Only a part of the suitable forest patches in a landscape should be targeted to make the risk of driving other threatened species to local extinction, as a direct effect of the translocation, negligible. Using strains that originate from strong local populations should reduce the risk of the strain carrying harmful mycoviruses, but it is possible that a mycovirus that is harmless to the translocated species could be harmful to other species in the translocation site. However, since mycoviruses are spread via hyphal fusion, interspecific spread is unlikely.

To extend the benefits of translocation from the translocated species to other species and ecosystem properties or functions, priority should be given to keystone species that host other rare species and/or have important functions in the forest ecosystem.

Challenge 3: how will we affect the genetic variation in the translocated species?

The third challenge is the potential impact of translocations to intraspecific genetic diversity. The impact can be either positive, through increasing genetic diversity where it has been lost, or negative, through breaking up natural patterns of genetic variation across the species range and thus, for example, hampering local adaptation. Maintaining genetic diversity is an essential aspect of conservation (Razgour *et al.* 2019) and thus information on genetic population structure is important when planning which species to translocate and from where, for reinforcing the existing genotypic and phenotypic diversity (Forsman 2014). Current knowledge on intraspecific fungal genetic diversity is, however, scarce.

Among the few red-listed species that have been studied, most show reduced genetic variation in fragmented landscapes, e.g. *Buglossoporus quercinus* on standing *Quercus* heartwood (Crockatt *et al.* 2010), *Datronia caperata* in mangrove (Parrent *et al.* 2004), and *Phlebia centrifuga* (Franzén *et al.* 2007) and *Phellopilus nigrolimitatus* (Sønstebø et al. unpublished data) on *Picea* logs. Thus, it is likely that many threatened fungi in isolated forest patches suffer from reduced genetic variation, potentially making them less able to adapt, for example, to climate change. However, for most threatened species we lack information about the level of intraspecific genetic variation. At best, translocations can recover genetic diversity, and thus the viability of the local populations. At worst, translocations can lead to the mixing of natural patterns of genetic variation by replacing local strains by strains used as the inocula, thus losing potentially valuable local adaptations. Introduced genetic material may have a large impact especially on rare species, which should be considered if there are local adaptations that should be safeguarded.

Mitigation: To avoid concerns that may arise from breakup of natural genetic variation, selected strains for inoculation should originate as close as possible to the translocation site. They should further originate from strong source populations that presumably have maintained their genetic variation. Both of these recommendations may, however, be difficult to fulfil as the main aim of a conservation translocation is to elevate the population size of a species that have few individuals in the focal region. Several strains should be used, rather than a single strain, to contribute to the genetic and phenotypic diversity and to increase the chances of translocating an individual that has high fitness in the environment of the translocation site.

Challenge 4: where to translocate depends on the drivers of decline

The fourth challenge is that often the relative roles of different drivers of population decline or distribution change are unclear. For instance, translocation to a forest seemingly suitable for the species may fail if the primary cause of the disappearance or decline of the species was changed climatic conditions rather than loss and fragmentation of natural forests (Mair *et al.* 2018). Careful consideration of the threat factors and the use of pilot experiments is necessary for cost-efficient translocations and for avoiding unnecessary interventions that do not result in successful translocations. Increased understanding of the environmental requirements and threats are needed especially before considering translocation in the form of assisted migration beyond the current or historical distribution, to presumed favourable climatic conditions.

Mitigation: To reduce the problem of poor knowledge of the causes of decline or rarity of the species, the species selected for translocation should be well-studied in terms of their ecology, trends in population size and distribution, and the relative roles of different threat factors. Poor knowledge about the historical distribution in some countries may make it difficult to assess the causes of decline and therefore translocation. Long-term data on the distribution at a larger spatial scale (e.g. Europe; Andrew *et al.* 2017) may help expert evaluation of the threats in such cases.

Challenge 5: will the fungal indicator species concept be disrupted?

The fifth challenge concerns the common use of particular fungal species as biodiversity indicator species (Halme *et al.* 2017) in Northern Europe. Certain species, associated with natural forests, are considered indicators of conservation value of forests (Nitare & Hallingbäck 2010; Niemelä 2016), and their presence has been shown to correlate with landscape-level habitat connectivity (Nordén *et al.* 2018). Their presence has also been proposed to correlate with the diversity of other wood-inhabiting species (Haugseth *et al.* 1996; Nitare & Hallingbäck 2010). In forest patches where indicator species have been reintroduced, this correlation no longer exists. In other words, reintroduced species no longer have indicator value in those locations that, in a strict sense, have lost their authenticity along with translocations. Assuming that the translocated species are able to spread to the landscape neighboring the translocation site, the species will indicate suitability of local habitat but not connectivity or continuity. From a conservation biology or restoration ecology viewpoint, however, in such cases improved conservation status of threatened species may be considered of more value than loss of authenticity.

Mitigation: Information about translocations should be made available through appropriate public databases, to make it possible to distinguish between natural and translocated local populations, which should be well feasible as long as translocation is conducted at a small scale only. If an indicator species is known to be present in a forest area due to translocation, then its presence can be disregarded in assessments based on indicator species. In practical conservation work successful translocation areas are probably already priority landscapes, in which case the loss of indicator value has little practical significance. In the future, the availability of improved sequencing methods may make it possible to routinely identify the translocated strains so that their origin (natural vs. translocated) can be identified. However, this requires sequencing a large number of individuals for a large number of markers which, at the moment, is relatively costly and data analysis is computationally challenging. To enable molecular characterization of the translocated strains at a later point in time, living cultures should be maintained, or alternatively frozen tissue or high-quality DNA extractions should be stored.

Challenge 6: evaluating success of translocation and impact

The sixth challenge concerns the need to systematically evaluate the success and impact of translocations. Monitoring of the translocation sites is necessary to evaluate the translocation success and the possible negative or positive effects on other species, particularly threatened species. Interesting questions that monitoring may help answer include the dependence of translocation success on log characteristics, resident fungal community, site characteristics and climate. In many cases, it will be possible to evaluate the direct and indirect impacts of a translocation only after several decades, in particular the success of spreading to neighboring sites and impacts on the resident communities. The time delay from translocation to its full impacts is expected to be especially long for communities with slow natural dynamics, such as those inhabiting decorticated and dry kelo pines (Niemelä *et al.* 2002) in late stage of decomposition. Unfortunately, time frames spanning several decades are far beyond the duration of most conservation or research projects.

Mitigation: The arrangements for both short- and long-term monitoring should be included in translocation projects at the planning stage. In the short term, sampling of wood from the inoculated logs, followed by culturing or direct DNA extraction and sequencing, can give an initial indication of whether the inoculated fungus was able to grow out of the inoculum dowel into the surrounding wood. In the long term, the emergence of fruit bodies should be monitored both in the translocation site and in the surrounding areas. Environmental sequencing, if combined with genetic characterization of the translocated strains, could also be used in monitoring of the focal and nearby sites. Monitoring should be designed to separate the effects of translocation and other effects on the resident community, including the same effect that drove the translocated species to low regional frequency, warranting a translocation. To ensure resources for long-term monitoring, translocation projects could be made in the context of government, university or institutionally funded programmes, or in collaboration with NGOs or conservation bodies who may empower citizen science for monitoring of wood-inhabiting fungi.

There are other challenges in addition to the six mentioned above. These include challenges related to defining the species natural range, availability of economic resources, public and forest owner opinions, and legal restrictions. As an example, in Finland some threatened species (e.g. *Skeletocutis jelicii* and *Perenniporia tenuis*) have a legal status that poses restrictions for forest use around their occurrences. If such species establish from translocated populations outside the intended area, restrictions caused by their occurrence may be considered negligent, and the owner of the translocation site may have to compensate for possible economic losses to other landowners. If fungal translocations become a widely used conservation tool, the legislation and other regulations should be adjusted to prevent the emergence of unnecessary conflicts between different stakeholders. It is also essential that ethical aspects of translocations are openly communicated and evaluated by people with different ethical standpoints (Nagle 1998; Joseph *et al.* 2009). Especially, the risks to other species should be acknowledged and evaluated, but also considered in the context of the primary threats to threatened species. The major threat is the loss of large amounts of wood due to forestry operations, which has a strong negative and spatially extensive effect on all threatened forest fungi. This threat is much greater than the potential negative effects of carefully designed conservation translocation can plausibly have on communities of wood-inhabiting fungi. Nevertheless, conservation translocation could potentially have a negative effect on other threatened species at the local scale, which must be considered.

Conclusions

For responsible conservation translocations that follow the principles listed below, the possible risks of translocations are likely to be outweighed by the possible benefits. Such benefits may include increased number of occupied patches and consequently increased gene flow and viability of the populations of the threatened species, and therefore lower risk of extinction. The necessity of translocation and the target species should, however, be carefully evaluated (Fig. 1) before any actions are taken, to avoid unnecessary interventions. We suggest ten principles - adhering to the precautionary principle - for conservation translocations of threatened wood-inhabiting fungal species. These follow the guidelines proposed by Pérez et al. (2012), but have been modified for relevance to wood-inhabiting fungi. We consider problematic all translocations where the conditions listed below are not met.

Ten principles for conservation translocations of threatened wood-inhabiting fungi

1. Species that are selected for translocation are well known in terms of taxonomy and ecology, as well as in terms of current distribution and population size, and their temporal trends. Flagship species should not be favored over less charismatic but equally well-known species.
2. Species that are prioritized for translocation are threatened species that are not easily aided through other means of conservation, such as small set-aside areas or retention trees in forestry, and that seem unlikely to colonise suitable unoccupied habitats by natural dispersal, therefore being threatened by regional extinction. Among the most threatened species, priority is given to keystone species that host other threatened or rare species (insects, fungi) or that have important ecosystem functions, such as creation of tree hollows.
3. The strains for translocations should be attained from several source populations to capture the genetic diversity within the species, and at the same time from the closest possible locations to the target areas to reduce the risk of breaking natural patterns of genetic variation and, in particular, of losing local adaptations.
4. Species identity has been confirmed for candidate strains before use. The strains should be stored in a public culture collection for future genetic characterization (e.g. whole-genome sequencing to allow identification of individuals and their degree of relatedness with offspring). As a back-up, high-quality DNA extractions of the strains should also be archived.
5. Species should be translocated only to forest patches that they do not currently inhabit but which are located within their natural range, and where there is reason to assume that the

species can establish a viable population. A suitable area could be a nature reserve, where the continuity of dead wood has been disrupted prior to current protection and where future continuity of dead wood formation is aimed at. Reinforcement of already occupied sites can be justified if it prevents a local extinction in the long term or if the population viability is likely to be compromised due to lack of genetic variation, in the case of species that are rare both at the landscape and the local scale, for instance because of high level of ecological specialization, or dependence on other, in many cases rare, wood-inhabiting fungal species (Abrego *et al.* 2017b).

6. Potential sites should be surveyed prior to translocation to establish suitability of the site (see point 5), and to form a baseline for monitoring community composition following translocation. The survey should be either a repeated fruit body survey focusing on all fungi, not only some morphogroups, or a combination of fruit body survey and an environmental DNA survey (Runnel *et al.* 2015; Abrego *et al.* 2016a). Sites with especially long survey history should, however, be left without translocations to allow for monitoring of the natural dynamics of unmanipulated species assemblages. This kind of sites can ideally serve as control sites to which changes in community composition in similar translocation sites can be compared.
7. To minimize the direct impact on other species, such as the risk of losing other threatened species through competitive exclusion, translocation should be done on artificially created new dead wood or only in a small proportion of dead wood in a forest patch, and in a small proportion of forest patches suitable for the species within a forest landscape. These proportions should balance the risk of losing other threatened species through competitive exclusion, against the risk of failing to establish a viable population of the translocated threatened species.
8. The identity of the translocated species, the origin of the strains, and translocation sites need to be systematically documented, and the information made publicly available.
9. Translocation should not be used as a substitute, but rather an ancillary, for other conservation measures such as establishing new conservation areas and opting for more biodiversity-oriented forestry practices. It makes little sense to translocate species that have gone extinct from a

landscape, if the threat factors that caused the extinction remain. A good network of high-quality conservation areas is the only sustainable long-term solution to ensure habitat for all threatened forest species.

10. Research (Fig. 2) and careful monitoring of translocation patches should be performed to: (1) evaluate the translocation success; (2) understand what circumstances offer the highest likelihood for colonization success; and (3) determine the consequences of the translocation on the local communities. Species inventories should be conducted before (see point 6) the translocation and after with an interval of e.g. 2-10 years, depending on the rate of system dynamics. This will enable the detection of potential changes in local communities that the translocations may cause. We recommend that the inoculated logs should be surveyed using both fruit bodies and high-throughput sequencing of wood samples (Ovaskainen *et al.* 2013), and the rest of the forest patch surveyed using at least one of the methods to a sufficient extent (Runnel *et al.* 2015; Abrego *et al.* 2016a). This monitoring should ideally continue for several decades, as the effects of translocation on communities may be apparent only after a long time lag, although funding difficulties may preclude long-term monitoring.

Any reintroductions performed as a part of a research project aiming to fill current knowledge gaps, should obviously also address the above conditions for conservation translocations. An ecological study may, however, need also to include common species (condition 2) and occupied patches (as controls) as well as patches that lie within the historical but outside the current distribution (condition 5). This may be necessary for a better understanding of the relative roles of habitat loss and fragmentation versus climate change as drivers of population decline and distribution changes, the effects of the resident community on translocation success, and the effects of the translocation on the resident community. Such studies should use particular precaution, conducting them at a small scale, and ensuring that the strains used are not spread to locations far from their origin.

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References

Abrego, N., Christensen, M., Bässler, C., Ainsworth, A. & Heilmann-Clausen, J. (2017a). Understanding the distribution of wood-inhabiting fungi in European beech reserves from species-specific habitat models. *Fungal Ecology*, 27, 168-174.

Abrego, N., Dunson, D., Halme, P., Salcedo, I. & Ovaskainen, O. (2017b). Wood-inhabiting fungi with tight associations with other species have declined as a response to forest management. *Oikos*, 126, 269-275.

Abrego, N., Halme, P., Purhonen, J. & Ovaskainen, O. (2016a). Fruit body based inventories in wood-inhabiting fungi: Should we replicate in space or time? *Fungal Ecology*, 20, 225-232.

Abrego, N., Oivanen, P., Viner, I., Nordén, J., Penttilä, R., Dahlberg, A. *et al.* (2016b). Reintroduction of threatened fungal species via inoculation. *Biological Conservation*, 203, 120-124.

Andrew, C., Heegaard, E., Kirk, P., Bässler, C., Heilmann-Clausen, J., Krisai-Greilhuber, I. *et al.* (2017). Big data integration: Pan-European fungal species observations' assembly for addressing contemporary questions in ecology and global change biology. *Fungal Biology Reviews*, 31, 88-98.

Armstrong, D.P., Castro, I. & Griffiths, R. (2007). Using adaptive management to determine requirements of re-introduced populations: the case of the New Zealand hihi. *Journal of Applied Ecology*, 44, 953-962.

ArtDatabanken (2015). *The 2015 Swedish Red List*. ArtDatabanken SLU, Uppsala.

Bailey, K.L. (2010). Canadian innovations in microbial biopesticides. *Canadian Journal of Plant Pathology*, 32.

Boddy, L., Wald, P.M., 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). In: *English Nature Research Report*. English Nature Peterborough.

Crockatt, M.E., Campbell, A., Allum, L., Ainsworth, A.M. & Boddy, L. (2010). The rare oak polypore P*iptoporus quercinus*: Population structure, spore germination and growth. *Fungal Ecology*, 3, 94-106.

Dahlberg, A., Genney, D.R. & Heilmann-Clausen, J. (2010). Developing a comprehensive strategy for fungal conservation in Europe: current status and future needs. *Fungal Ecology*, 3, 50-64.

Dudley, N. (2011). Authenticity in Nature: Making Choices about the Naturalness of Ecosystems. Routledge, UK. 256 pages.

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. 56, 1267-1277.

Forsman, A. (2014). Effects of genotypic and phenotypic variation on establishment are important for conservation, invasion, and infection biology. 111, 302-307.

Franzén, I., Vasaitis, R., Penttilä, R. & Stenlid, J. (2007). Population genetics of the wood-decay fungus *Phlebia centrifuga* P. Karst. in fragmented and continuous habitats. *Molecular Ecology*, 16, 3326-3333.

Frazer, N.B. (1992). Sea-turtle conservation and halfway technology. *Conservation Biology*, 6, 179-184.

Gilpin, M.E. & Soulé, M.E. (1986). Minimum viable populations: Processes of species extinction. In: *Conservation biology: The science of scarcity and diversity.* (ed. Soulé, ME). Sunderland Mass: Sinauer Associates, pp. 13-34.

Godefroid, S., Piazza, C., Rossi, G., Buord, S., Stevens, A.D., Aguraiuja, R. *et al.* (2011). How successful are plant species reintroductions? *Biological Conservation*, 144, 672-682.

Halme, P., Holec, J. & Heilmann-Clausen, J. (2017). The history and future of fungi as biodiversity surrogates in forests. *Fungal Ecology*, 27, 193-201.

Hanski, I. (2000). Extinction debt and species credit in boreal forests: modelling the consequences of different approaches to biodiversity conservation. *Annales Zoologici Fennici*, 37, 271-280.

Haugseth, T., Alfredsen, G. & Lie, M.H. (1996). *Nøkkelbiotoper og artsmangfold i skog*. Naturvernforbundet i Oslo og Akershus, Oslo.

Henriksen, S. & Hilmo, O. (2015). The Norwegian Red List of species. Artsdatabanken Trondheim.

Hooson, S. & Jamieson, I.G. (2003). The distribution and current status of New Zealand Saddleback Philesturnus carunculatus. *Bird Conservation International*, 13, 79-95.

Hottola, J., Ovaskainen, O. & Hanski, I. (2009). A unified measure of the number, volume and diversity of dead trees and the response of fungal communities. *Journal of Ecology*, 97, 1320-1328.

IUCN/SSC (2013). Guidelines for Reintroductions and Other Conservation Translocations. Version 1.0. IUCN Species Survival Commission. Gland, Switzerland.

Jonsell, M. & Nordlander, G. (2004). Host selection patterns in insects breeding in bracket fungi. *Ecological Entomology* 29: 697-705

Joseph, L.N., Maloney, R.F. & Possingham, H.P. (2009). Optimal Allocation of Resources among Threatened Species: a Project Prioritization Protocol. *Conservation Biology*, 23, 328-338.

Junninen, K. & Komonen, A. (2011). Conservation ecology of boreal polypores: A review. *Biological Conservation*, 144, 11-20.

Komonen, A., Halme, P., Jäntti, M., Koskela, T., Kotiaho, J.S. & Toivanen, T. (2014). Created substrates do not fully mimic natural substrates in restoration: the occurrence of polypores on spruce logs. *Silva Fennica*, 48.

Komonen, A., Penttilä, R., Lindgren, M. & Hanski, I. (2000). Forest fragmentation truncates a food chain based on an old-growth forest bracket fungus. *Oikos*, 90, 119-126.

Korhonen, A., Seelan, J.S.S. & Miettinen, O. (2018). Cryptic species diversity in polypores: the *Skeletocutis nivea* species complex. *Mycokeys*, 45-82.

Koskinen, J., Roslin, T., Nyman, T., Abrego, N., Mitchell, C. & Vesterinen, E.J. (2019). Finding flies in the mushroom soup: Host specificity of fungus-associated communities revisited with a novel molecular method. *Molecular Ecology* 28: 190-202.

Kotiranta, H., Junninen, K., Halme, P., Kytövuori, I., von Bonsdorff, T., Niskanen, T. *et al.* (2019). Aphyllophoroid fungi. In: *The 2019 Red List of Finnish Species.* (eds. Hyvärinen, E, Juslén, A, Kemppainen, E, Uddström, A & Liukko, U-M). Ministry of the Environment and Finnish Environment Institute Helsinki, pp. 234-247.

Kotiranta, H., Junninen, K., Saarenoksa, R., Kinnunen, J. & Kytövuori, I. (2010). Aphyllophorales & Heterobasidiomycetes. In: *The 2010 Red List of Finnish species.* (eds. Rassi, P, Hyvärinen, E, Juslén, A & Mannerkoski, I). Ministry of Environment and Finnish Environment Institute Helsinki, pp. 249-263.

Kouki, J., Hyvärinen, E., Lappalainen, H., Martikainen, P. & Similä, M. (2012). Landscape context affects the success of habitat restoration: large-scale colonization patterns of saproxylic and fire-associated species in boreal forests. *Diversity and Distributions*, 18, 348-355.

Koziol, L. & Bever, J.D. (2017). The missing link in grassland restoration: arbuscular mycorrhizal fungi inoculation increases plant diversity and accelerates succession. *Journal of Applied Ecology*, 54, 1301-1309.

Kuussaari, M., Heikkinen, R.K., Heliölä, J., Luoto, M., Mayer, M., Rytteri, S. *et al.* (2015). Successful translocation of the threatened Clouded Apollo butterfly (*Parnassius mnemosyne*) and metapopulation establishment in southern Finland. *Biological Conservation*, 190, 51-59.

Lidén, M., Pettersson, M., Bergsten, U. & Lundmark, T. (2004). Artificial dispersal of endangered epiphytic lichens: a tool for conservation in boreal forest landscapes. *Biological Conservation*, 118, 431-442.

Mair, L., Jönsson, M., Räty, M., Bärring, L., Strandberg, G., Lämås, T. *et al.* (2018). Land use changes could modify future negative effects of climate change on old-growth forest indicator species. *Diversity and Distributions*, 24, 1416-1425.

Mayuzumi, Y. & Mizuno, T. (1997). III. Cultivation methods of maitake (*Grifola frondosa*). *Food Reviews International*, 13, 357-364.

Miettinen, O. & Niemelä, T. (2018). Two new temperate polypore species of *Skeletocutis* (Polyporales, Basidiomycota). *Annales Botanici Fennici*, 55, 195-206.

Miettinen, O., Vlasák, J., Rivoire, B. & Spirin, V. (2018). *Postia caesia* complex (Polyporales, Basidiomycota) in temperate Northern Hemisphere. *Fungal Systematics and Evolution*, 1, 101-129.

Nagle, J.C. (1998). Playing Noah. *Minnesota Law Review*, 82, 1171-1260.

Niemelä, T. (2016). Polypores of Finland. *Norrlinia*, 31, 1-432.

Niemelä, T., Renvall, P. & Penttilä, R. (1995). Interactions of fungi at late stages of wood decomposition. *Annales Botanici Fennici*, 32, 141-152.

Niemelä, T., Wallenius, T. & Kotiranta, H. (2002). The kelo tree, a vanishing substrate of specified wood-inhabiting fungi. *Polish Botanical Journal*, 47, 91–101.

Nitare, J. & Hallingbäck, T. (2010). *Signalarter: indikatorer på skyddsvärd skog: flora över kryptogamer*. Skogsstyrelsens förlag, Jönköping.

Nordén, J., Penttilä, R., Siitonen, J., Tomppo, E. & Ovaskainen, O. (2013). Specialist species of wood-inhabiting fungi struggle while generalists thrive in fragmented boreal forests. *Journal of Ecology*, 101, 701-712.

Nordén, J., Åström, J., Josefsson, T., Blumentrath, S., Ovaskainen, O., Sverdrup-Thygeson, A. *et al.* (2018). At which spatial and temporal scales can fungi indicate habitat connectivity? *Ecological Indicators*, 91, 138-148.

Norros, V., Karhu, E., Nordén, J., Vähätalo, A.V. & Ovaskainen, O. (2015). Spore sensitivity to sunlight and freezing can restrict dispersal in wood-decay fungi. *Ecology and Evolution*, 5, 3312-3326.

Norros, V., Penttilä, R., Suominen, M. & Ovaskainen, O. (2012). Dispersal may limit the occurrence of specialist wood decay fungi already at small spatial scales. *Oikos*, 121, 961-974.

Ovaskainen, O., Schigel, D., Ali-Kovero, H., Auvinen, P., Paulin, L., Nordén, B. *et al.* (2013). Combining high-throughput sequencing with fruit body surveys reveals contrasting life-history strategies in fungi. *Isme Journal*, 7, 1696-1709.

Parker, H., Nummi, P., Hartman, G. & Rosell, F. (2012). Invasive North American beaver *Castor canadensis* in Eurasia: a review of potential consequences and a strategy for eradication. *Wildlife Biology*, 18, 354-365.

Parrent, J.L., Garbelotto, M. & Gilbert, G.S. (2004). Population genetic structure of the polypore *Datronia caperata* in fragmented mangrove forests. *Mycological Research*, 108, 403-410.

Pasanen, H., Junninen, K. & Kouki, J. (2014). Restoring dead wood in forests diversifies wood-decaying fungal assemblages but does not quickly benefit red-listed species. *Forest Ecology and Management*, 312, 92-100.

Peay, K.G., Schubert, M.G., Nguyen, N.H. & Bruns, T.D. (2012). Measuring ectomycorrhizal fungal dispersal: macroecological patterns driven by microscopic propagules. *Mol Ecol*, 21, 4122-4136.

Peltoniemi, M., Penttilä, R. & Mäkipää, R. (2013). Temporal variation of polypore diversity based on modelled dead wood dynamics in managed and natural Norway spruce forests. *Forest Ecology and Management*, 310, 523-530.

Penttilä, R., Siitonen, J. & Kuusinen, M. (2004). Polypore diversity in managed and old-growth boreal *Picea abies* forests in southern Finland. *Biological Conservation*, 117, 271-283.

Perez, I., Anadon, J.D., Diaz, M., Nicola, G.G., Tella, J.L. & Gimenez, A. (2012). What is wrong with current translocations? A review and a decision-making proposal. *Frontiers in Ecology and the Environment*, 10, 494-501.

Pietka, J. & Grzywacz, A. (2005). In situ inoculation of larch with the threatened wood-decay fungus *Fomitopsis officinalis* (Basidiomycota) - experimental studies. *Polish Botanical Journal*, 50, 225-231.

Pietka, J. & Grzywacz, A. (2006). Attempts at active protection of *Inonotus obliquus* by inoculating birches with its mycelium. *Acta Mycologica*, 41, 305-312.

Pirttilä, A. & Frank, A. (2018). Endophytes of Forest Trees: Biology and Applications. Springer, p. 461.

Rajala, T., Tuomivirta, T., Pennanen, T. & Mäkipää, R. (2015). Habitat models of wood-inhabiting fungi along a decay gradient of Norway spruce logs. *Fungal Ecology*, 18, 48-55.

Rana, M.K. (2019). Mycoviruses infecting the forest pathogen *Heterobasidion annosum* - mutual interactions and host reactions. In: *Department of Forest Sciences*. University of Helsinki Helsinki.

Razgour, O., Forester, B., Taggart, J.B., Bekaert, M., Juste, J., Ibáñez, C. *et al.* (2019). Considering adaptive genetic variation in climate change vulnerability assessment reduces species range loss projections. 116, 10418-10423.

Read, H. (2000). *Veteran trees: a guide to good management*. English Nature, Peterborough.

Runnel, K., Tamm, H. & Lõhmus, A. (2015). Surveying wood-inhabiting fungi: Most molecularly detected polypore species form fruit-bodies within short distances. *Fungal Ecology*, 18, 93-99.

Samils, N., Vasaitis, R. & Stenlid, J. (2009). Impact of the biological control agent *Phlebiopsis gigantea* on its resident genetic structure in the Baltic Sea area. *Biocontrol Science and Technology*, 19, 263-276.

Seddon, P.J., Armstrong, D.P. & Maloney, R.F. (2007). Developing the science of reintroduction biology. *Conservation Biology*, 21, 303-312.

Seddon, P.J., Griffiths, C.J., Soorae, P.S. & Armstrong, D.P. (2014). Reversing defaunation: Restoring species in a changing world. *Science*, 345, 406-412.

Serfling, A., Wirsel, S.G.R., Lind, V. & Deising, H.B. (2007). Performance of the Biocontrol Fungus *Piriformospora indica* on Wheat Under Greenhouse and Field Conditions. 97, 523-531.

Smith, P.L. (2014). Lichen translocation with reference to species conservation and habitat restoration. *Symbiosis*, 62, 17-28.

Spirin, V., Nordén, J., Svantesson, S. & Larsson, K.H. (2016). New records of intrahymenial heterobasidiomycetes (Basidiomycota) in north Europe. *Nordic Journal of Botany*, 34, 475-477.

Spirin, V., Runnel, K., Vlasak, J., Miettinen, O. & Põldmaa, K. (2015). Species diversity in the *Antrodia crassa* group (Polyporales, Basidiomycota). *Fungal Biology*, 119, 1291-1310.

Spirin, V., Vlasak, J. & Miettinen, O. (2017). Studies in the *Antrodia serialis* group (Polyporales, Basidiomycota). *Mycologia*, 109, 217-230.

Tosi, G., Chirichella, R., Zibordi, F., Mustoni, A., Giovannini, R., Groff, C. *et al.* (2015). Brown bear reintroduction in the Southern Alps: To what extent are expectations being met? *Journal for Nature Conservation*, 26, 9-19.

Vasiliauskas, R., Larsson, E., Larsson, K.H. & Stenlid, J. (2005). Persistence and long-term impact of Rotstop biological control agent on mycodiversity in *Picea abies* stumps. *Biological Control*, 32, 295-304.

Weisenberger, L.A., Weller, S.G. & Sakai, A.K. (2014). Remnants of populations provide effective source material for reintroduction of an endangered Hawaiian plant, *Schiedea kaalae* (Caryophyllaceae). *American Journal of Botany*, 101, 1954-1962.

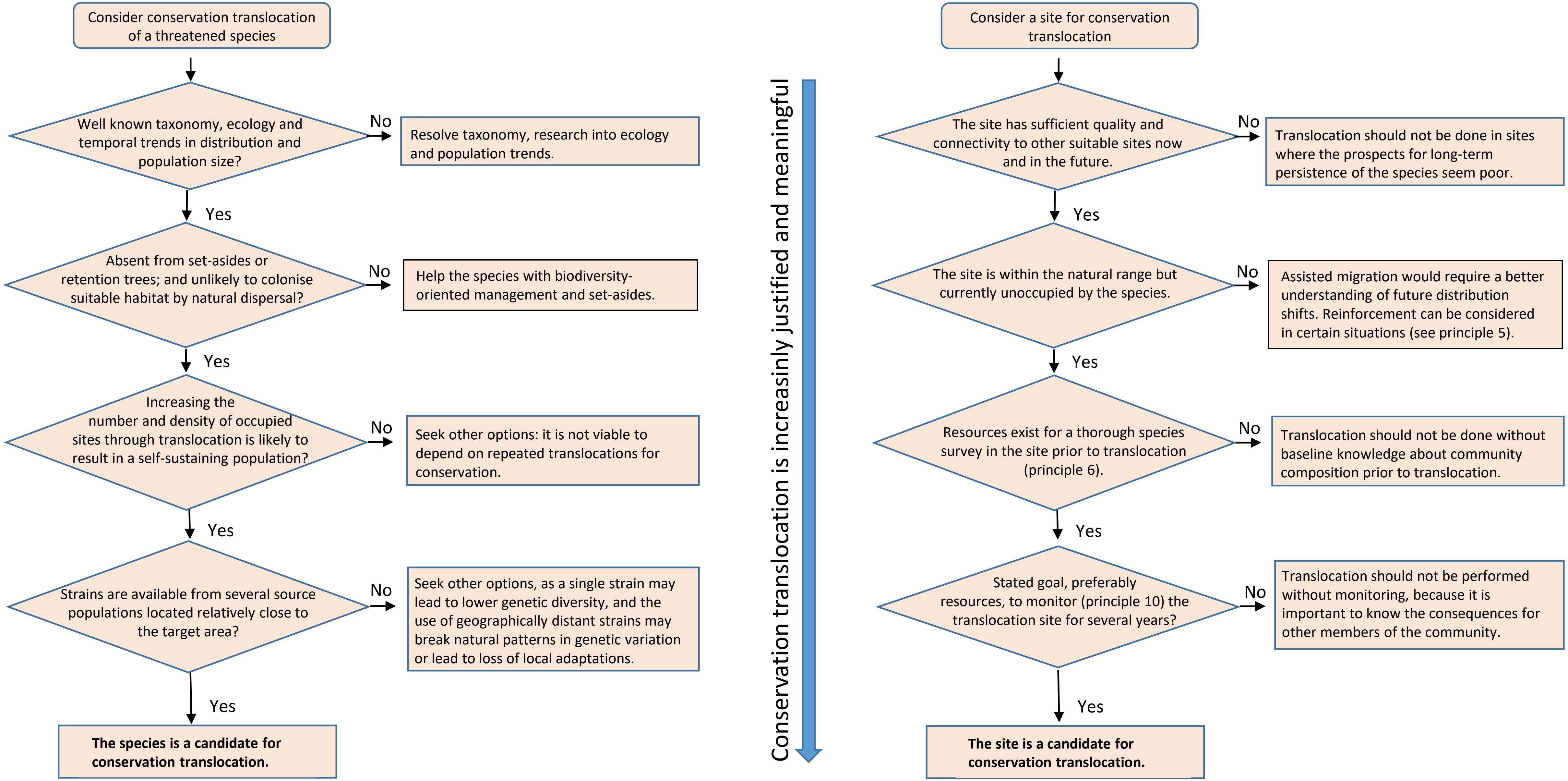
Zahn, G. & Amend, A.S. (2017). Foliar microbiome transplants confer disease resistance in a critically-endangered plant. *Peerj*, 5.

FIGURE LEGENDS

Figure 1. Flow charts to aid decision-making of suitability of threatened fungal species (left) and site selection (right) for conservation translocation. The necessity of conservation translocation must be carefully assessed prior to any translocation action.

Figure 2. Main research needs for ecologically sound and efficient fungal translocation and risk assessment, and methods suggested for filling these knowledge gaps.

Figure 1.



Consider conservation translocation of a threatened species

Well known taxonomy, ecology and temporal trends in distribution and population size?

No: Resolve taxonomy, research into ecology and population trends.

Yes: Absent from set-asides or retention trees; and unlikely to colonise suitable habitat by natural dispersal?

No: Help the species with biodiversity-oriented management and set-asides.

Yes: Increasing the number and density of occupied sites through translocation is likely to result in a self-sustaining population?

No: Seek other options: it is not viable to depend on repeated translocations for conservation.

Yes: Strains are available from several source populations located relatively close to the target area?

No: Seek other options, as a single strain may lead to lower genetic diversity, and the use of geographically distant strains may break natural patterns in genetic variation or lead to loss of local adaptations.

Yes: **The species is a candidate for conservation translocation.**

Consider a site for conservation translocation

The site has sufficient quality and connectivity to other suitable sites now and in the future.

No: Translocation should not be done in sites where the prospects for long-term persistence of the species seem poor.

Yes: The site is within the natural range but currently unoccupied by the species.

No: Assisted migration would require a better understanding of future distribution shifts. Reinforcement can be considered in certain situations (see principle 5).

Yes: Resources exist for a thorough species survey in the site prior to translocation (principle 6).

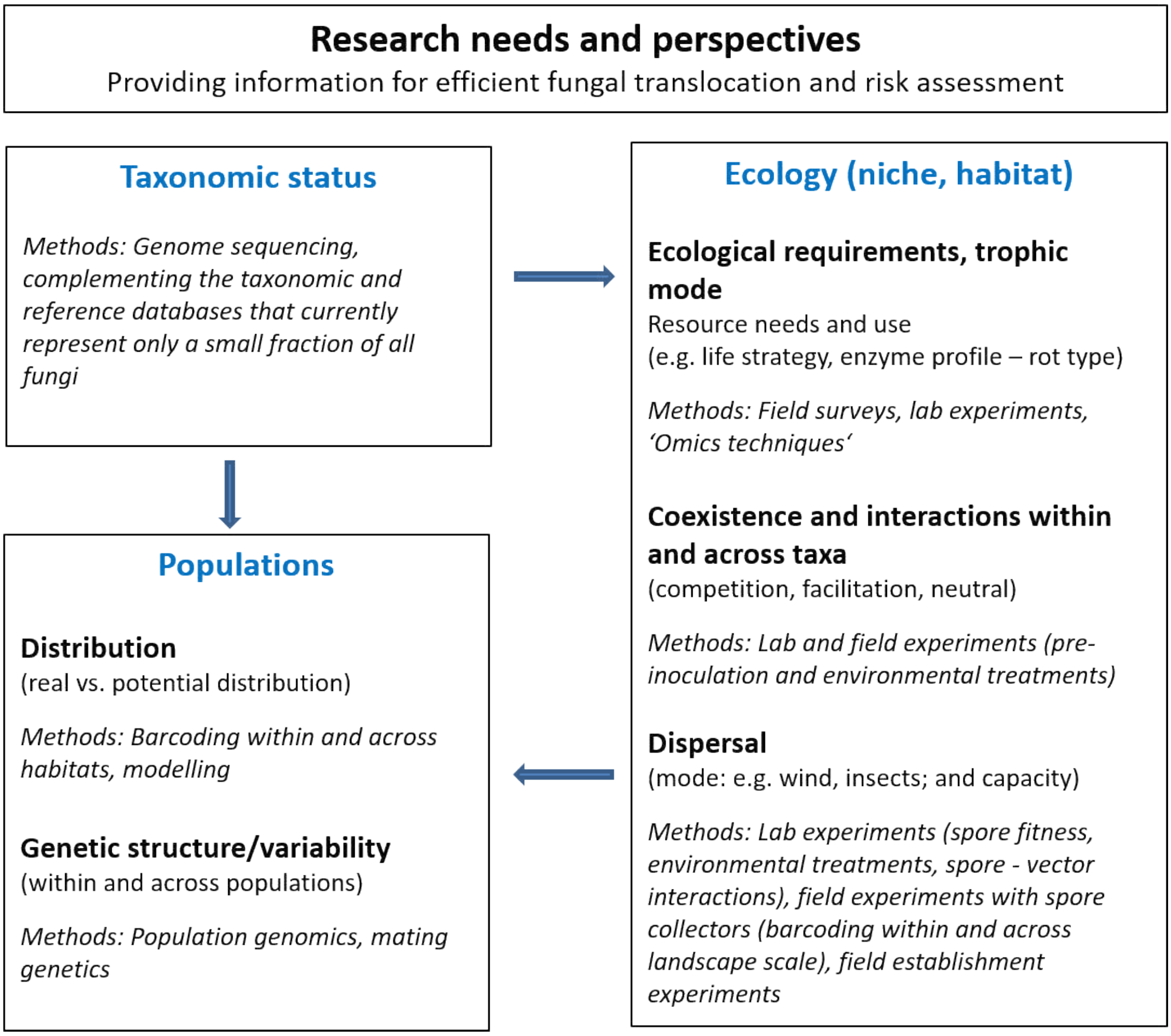
No: Translocation should not be done without baseline knowledge about community composition prior to translocation.

Yes: Stated goal, preferably resources, to monitor (principle 10) the translocation site for several years?

No: Translocation should not be performed without monitoring, because it is important to know the consequences for other members of the community.

Yes: **The site is a candidate for conservation translocation.**

Figure 2.



Research needs and perspectives

Providing information for efficient fungal translocation and risk assessment

Taxonomic status

Methods: Genome sequencing, complementing the taxonomic and reference databases that currently represent only a small fraction of all fungi

Populations

Distribution

(real vs. potential distribution)

Methods: Barcoding within and across habitats, modelling

Genetic structure/variability

(within and across populations)

Methods: Population genomics, mating genetics

Ecology (niche, habitat)

Ecological requirements, trophic mode

Resource needs and use

(e.g. life strategy, enzyme profile – rot type)

Methods: Field surveys, lab experiments, 'Omics techniques'

Coexistence and interactions within and across taxa

(competition, facilitation, neutral)

Methods: Lab and field experiments (pre-inoculation and environmental treatments)

Dispersal

(mode: e.g. wind, insects; and capacity)

Methods: Lab experiments (spore fitness, environmental treatments, spore - vector interactions), field experiments with spore collectors (barcoding within and across landscape scale), field establishment experiments

Table 1. Reported and ongoing translocation projects using red-listed wood-inhabiting fungi.

Fungal species	**Tree species**	**Type of wood**	**Type of inocula**	**Number of sites**	**Country**	**Year of inoculation**	**Purpose**	**Comments**	**Authors**
Laricifomes officinalis	*Larix polonica*	Standing living trees and dry stem sections	Wood chips	2	Poland	1999	Conservation	Successful establishment	Pietka & Grzywacz 2005
Inonotus obliquus	*Betula pendula*	Standing living trees and dry stem sections	Dowel	2	Poland	1999	Conservation	Unsuccessful establishment	Pietka & Grzywacz 2006
Hapalopilus croceus, Fistulina hepatica	*Quercus robur*	Standing living trees	Agar dowel	1	Sweden	1999-2000	Research	Ongoing	A. Dahlberg, A. Menkis, S. Sunhede, N. Jansson, D. Redr
Hericium coralloides, H. erinaceus	*Fagus sylvatica*	Felled logs	Dowel	2	UK	2002	Research	Successful establishment of *H. coralloides* in some logs. *H. erinaceus* not yet assessed.	Boddy et al. 2004
Hericium coralloides, H. erinaceus	*Fagus sylvatica*	Standing living trees	Dowel, large wood blocks, sawdust	3	UK	2002, 2018, 2019	Conservation	Ongoing	L. Boddy, M. Wainhouse, E. Gilmartin, I. Chedgy, P. Wald
Amylocystis lapponica, Antrodia piceata, Antrodiella citrinella, Fomitopsis rosea, Perenniporia subacida, Postia guttulata, Skeletocutis stellae	*Picea abies*	Fallen logs	Dowel	2	Finland	2009	Research	Successful establishment of all species. Three species produced fruit bodies	Abrego et al. 2016

Amylocystis lapponica, Antrodia piceata, Perenniporia subacida, Postia guttulata	*Picea abies*	Fallen logs	Dowel	1	Sweden	2011	Research	Ongoing	J. Nordén, B. Nordén
Phellinidium pouzarii	*Abies alba*	Felled logs	Wood chips	1	Germany	2016	Research	Ongoing	C. Bässler, H. Kellner
Amylocystis lapponica, Fomitopsis rosea, Phellopilus nigrolimitatus	*Picea abies*	Fallen logs	Dowel	10	Norway	2016	Research	Ongoing	J. Nordén, S. Maurice, H. Kauserud
Inonotus dryadeus	*Quercus robur*	Standing living trees	Dowel	2	Norway	2017	Conservation	Ongoing	S. Maurice, H. Kauserud
Pycnoporellus fulgens	*Picea abies*	Fallen logs	Dowel	3	Norway	2018	Conservation	Ongoing	J. Nordén, S. Maurice
9 species of red-listed spruce-living polypores (*Antrodia piceata, Antrodiella citrinella, Fomitopsis rosea,Perenniporia subacida, Physisporinus crocatus, Postia guttulata, Skeletocutis odora, Skeletocutis stellae, Steccherinum collabens)* and 10 red-listed pine and deciduous host species	*Picea abies, Pinus sylvestris, Populus tremula, Salix caprea*	Fallen logs and living *Salix caprea*	Dowel	15	Finland	2019/2020	Research	Ongoing	R. Penttilä, N. Abrego, S. Saine, O. Miettinen, R. Mäkipää, O. Ovaskainen
Antrodiella citrinella, Dentipellis fragilis, Fomitopsis rosea, Hericium flagellum, Phlebia centrifuga	*Abies alba,Picea abies, Fagus sylvatica*	Felled logs	Wood chips		Germany	2019/2020	Research	Ongoing	C. Bässler, H. Kellner