



Short communication

Reintroduction of threatened fungal species via inoculation



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ABSTRACT

Reintroduction of locally extinct species is increasingly applied as a conservation tool for re-establishing species within their historical ranges. Thus far, this option has however not been investigated for fungi other than lichens. A large fraction of wood-inhabiting fungal species have declined because of forest loss and fragmentation, in addition to a decrease in dead wood. Here, we show the results from an experiment carried out in southern Finland, which demonstrates that inoculation is an effective method for reintroducing threatened wood-inhabiting fungi. All selected red-listed fungal species successfully established in the inoculated logs as mycelia, and three out of the seven produced fruit-bodies. Success rate was greater when the strains were inoculated in early-decay logs, including species that usually fruit in late decay stages. Inoculation can provide an effective tool for reintroducing fungal species, as the source populations remain intact and it is possible to produce massive amounts of inoculation-units with relatively low cost. Reintroductions of fungi should however be preceded by a risk assessment of the species to be reintroduced, by using source populations from nearby localities, and they should be considered complementary to the primary target of increasing the amount of their habitat. Our results suggest that the reintroductions of threatened fungi via inoculation in combination with other conservation measures can have important bearings for forest conservation and restoration.

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1. Introduction

Reintroduction of threatened or locally extinct species is an important conservation tool for re-establishing species within their historical ranges (Seddon et al., 2007). Reintroductions and translocations have been carried out especially for animals (e.g. Kuussaari et al., 2015; Tosi et al., 2015) but also for plants (e.g. Weisenberger et al., 2014; Parthibhan et al., 2015). Many groups of fungi are highly vulnerable to anthropogenic changes such as habitat loss and fragmentation (Penttilä et al., 2006; Nordén et al., 2013), air pollution (e.g. Arnolds, 2001) and climate change (e.g. Kauserud et al., 2012). In spite of this, fungi have received limited emphasis in conservation biology (Heilmann-Clausen et al., 2015). For example, the potential of reintroducing threatened fungi has been not evaluated, except for lichens (see Lidén et al., 2004; Smith, 2014).

Experimental studies indicate that many fungi can be successfully introduced via inoculation. Fungal inoculations are routinely used to grow edible mushrooms (Hall et al., 2003), and to facilitate the growth of commercially important plants (e.g. Hart et al., 2015). Inoculations of wood-inhabiting fungi are used as a biological control tool against pathogenic fungi (e.g. Garbelotto and Gonthier, 2013) and as means for creating habitats for cavity breeding vertebrates (Filip et al., 2004). In a conservation context, the survival of threatened plant species has been facilitated by inoculations of mycorrhizal fungi (e.g. Zubek et al., 2009; Ferrazzano and Williamson, 2013). Furthermore, results from pilot studies suggest that some threatened fungal species can be successfully reintroduced to their habitats by inoculation (Venturella and Ferri, 1996; Pietka and Grzywacz, 2005).

Due to the drastic reduction of dead wood caused by forestry, many saproxylic species have diminished worldwide (Stokland et al., 2012). In particular, wood-inhabiting fungi have declined due to the reduction of natural forest areas and the loss of dead wood in managed forests (Junninen and Komonen, 2011). As a consequence, in Finland for

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example, over 40% of the polypore species have been red-listed according to the IUCN criteria (Rassi et al., 2010).

Many threatened wood-inhabiting fungi are dispersal limited (see Norros et al., 2012) and depend on landscape-level connectivity to retain viable populations (Penttilä et al., 2006; Nordén et al., 2013; Abrego et al., 2015). This decreases the efficiency of protected area networks, as small and isolated conservation sites hold less threatened species than they potentially could, some of the species being possibly absent simply due to dispersal limitation (Abrego et al., 2015). To counteract declines of saproxylic organisms, many restoration and conservation programs have focused on increasing the volume of dead wood in forests (Jonsson et al., 2005; Halme et al., 2013). However, the positive effect of dead-wood restoration for red-listed species has in many cases remained small (Pasanen et al., 2014) or realized only with long delay (Penttilä et al., 2013). Whether or not restored habitats are helpful for conserving species depends on whether the focal species are able to colonize them, which in turn depends on the proximity of the restoration areas to source populations (Kouki et al., 2012). In cases where natural colonization is unlikely, one alternative for re-establishing threatened species into restored and isolated protected sites is to artificially reintroduce them (Seddon et al., 2007).

The objective of the present study was to test the potential of inoculation as a tool for the reintroduction of red-listed wood-inhabiting fungal species. We developed laboratory and field protocols for inoculations, and tested their potential for fungal reintroduction by inoculating seven red-listed and regionally rare wood-inhabiting fungal species into a forest area in southern Finland, and by following their establishment success, both as mycelia and/or as fruit-bodies, for seven years after the reintroductions.

2. Materials and methods

Seven red-listed wood-inhabiting fungal species (Fig. 1) associated with Norway spruce (*Picea abies*) were selected for the reintroduction experiment with the criteria that i) the species had not been previously found from the reintroduction area, but were native species to the region (Appendix 1), ii) source populations were available within 300 km from the reintroduction area.

In autumn 2008, fungal fruit-bodies of the focal species were collected from various old-forest localities in southern and Central Finland (see Appendix 2 for the names of the localities and Appendix 3 for the stored voucher cultures). In the laboratory, we transferred small pieces of the fruit-bodies to agar plates to allow for mycelial growth and transferred the mycelia to *Picea abies* wood plugs (see Appendix 2 for details on the laboratory procedures).

The reintroduction area was located within Rörstrand, a spruce-dominated 80 ha natural-like forest abundant in dead wood, located in Sipoo, southern Finland. In Rörstrand, we delimited a 200 m × 200 m reintroduction area (coordinates: 60.45°N, 25.20°E), which had been intensively studied in our earlier work (e.g. Ovaskainen et al., 2013) but from which the focal species were not previously found. We selected randomly 100 spruce logs of 20–42 cm in diameter and representing decay classes 1–4 (range 1–5 from recently dead to very decomposed wood; Hottola and Siitonen, 2008). The numbers of selected logs in decay classes 1 to 4 was 19, 31, 34 and 16, respectively, and each log was marked to allow its monitoring.

In spring 2009, we drilled ten holes in each of the selected logs, five on the top part of the dead tree and five on the basal part, each 1 m apart from each other. We introduced one species into each drilling hole by inserting an inoculated wood plug. To each log, we inoculated 2–4 species to different randomly chosen drilling holes, using different strains of the same species if such were available. Each species was inoculated in total into 40 logs (Appendix 4).

For determining the absence of the focal species before the inoculations as well as their establishment success afterwards, all inoculated logs were surveyed for fruit-bodies in the autumns of 2008, 2009,

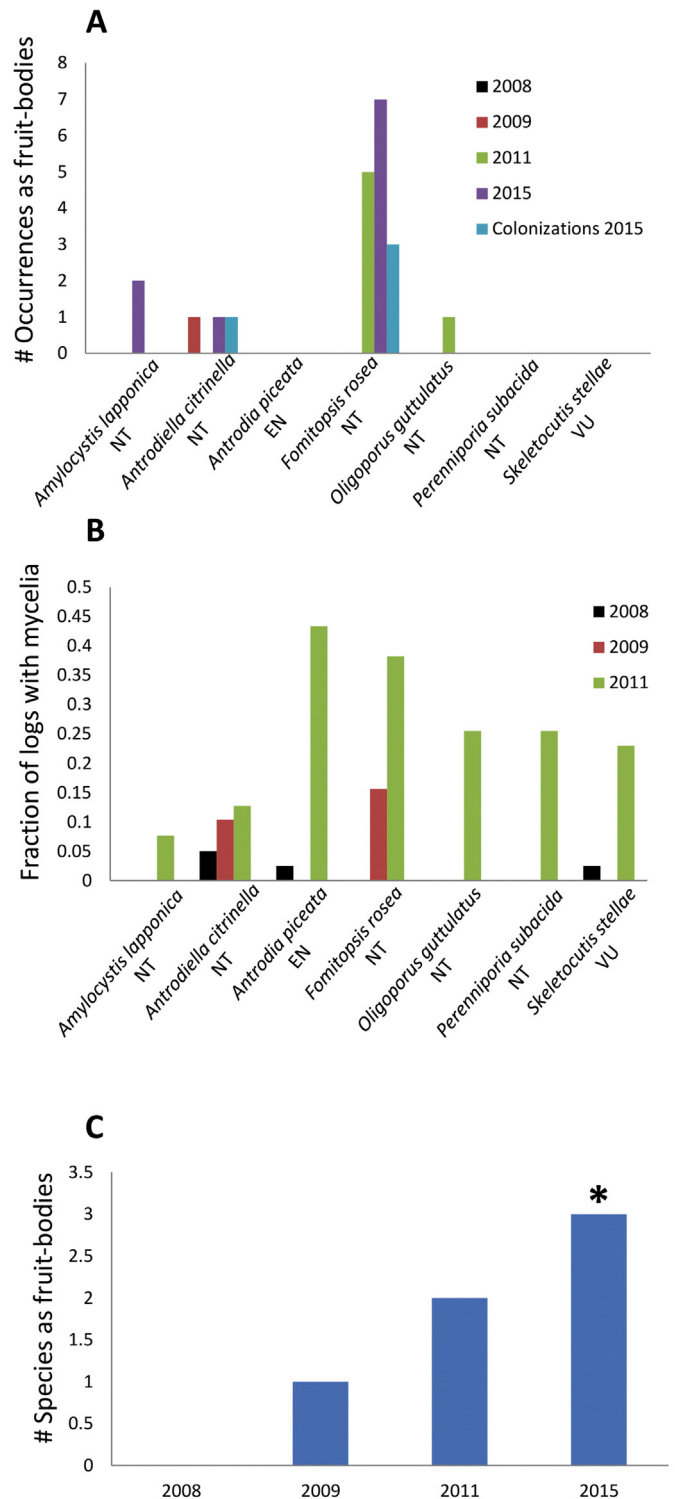


Fig. 1. Inoculation success rates for the species included in this study. **A** shows the number of logs in which each focal species was observed as fruit-bodies either as established individuals (fruit-bodies on inoculated logs) or as colonizations (fruit-bodies on non-inoculated logs). **B** shows the fraction of logs out of those logs to which the focal species was inoculated, in which each species was observed as mycelia. **C** shows the number of focal species that were recorded as fruit-bodies in each of the surveys. In Panel C, we have marked with an asterisk those cases in which the observed number of focal species was significantly greater than expected by the background colonization rate ($p = 0.01$ for 2015). For each focal species, the Finnish Red List categories according Rassi et al. (2010) are indicated in the figure (EN- Endangered, VU - Vulnerable, NT - Near threatened). The inoculations were carried out in the spring 2009.

2011 and 2015 and molecular samples were obtained in the autumns of 2008, 2009 and 2011. As detailed in Appendix 5, the DNA sample collection, DNA-extraction and sequencing were conducted as in [Ovaskainen et al. \(2013\)](#), and molecular species identification was conducted using the probabilistic taxonomical placement method of [Somervuo et al. \(2016\)](#). In 2015, non-inoculated spruce logs were surveyed for ca. 3 days in a 100 m buffer area to find fruit-bodies of the focal species to detect possible colonizations (we considered colonizations to have happened if a focal species was recorded in non-inoculated logs).

The additional strains that were not needed for the main experiment were used for inoculating 111 logs in another natural-like spruce forest (henceforth called additional reintroduction area; coordinates: 60.16°N, 24.01°E). As the inoculations in the additional reintroduction area followed a less rigorous study design than those in the main reintroduction area, we provide the description of the inoculation procedure as well as the results for the additional reintroduction area in Appendix 6.

To examine whether the observations of the reintroduced species could be attributed to the inoculations or they could have taken place through background colonization from surrounding areas, we acquired fruit-body data from 12 control forests that had been surveyed for other reasons (Appendix 7). The criteria for the control forests selection was that a) the forests should have been inventoried during the same period as the reintroduction areas (i.e. between years 2009 and 2015); b) they should be located within the Uusimaa province where the reintroduction areas were; c) the characteristics of the surveyed logs should be similar of those that were subject of study in the reintroduction areas (i.e. larger than 15 cm in diameter and between decay stages 2–4); d) the inventories should be based on single visits during the main period of fruit-body production. From the selected 12 control forests, we extracted the information about the log-level presence-absence data for the focal seven species. We applied a simulation approach to construct a null distribution for the number of observations for the logs in which the inoculations were conducted. We first randomized one of the control forests, and then subsampled logs either from the control forest or from the reintroduction area, so that their number was equal. From these logs, we counted the number of occurrences for each focal species, as well as the number of the focal seven species. We repeated the randomization 10,000 times, each time randomizing a new forest out of the 12 control forests. We computed an empirical p -value by examining in which fraction of the simulations the control forest had at least as many focal species as the reintroduction area. We used as threshold $p = 0.05$ to reject the null hypothesis that the observed number of focal species in the reintroduction areas could have been generated by a background colonization rate. This test is conservative, as it assumes that all observations from the control forests are new colonizations over the time span from inoculation to the secondary survey.

3. Results

All inoculated species established as mycelia, and three out of the seven species produced fruit-bodies in the inoculated logs ([Fig. 1](#)). There was high inter-specific variation in the establishment success, as for example *Fomitopsis rosea* was recorded in relatively high numbers as fruit-bodies and mycelia, whereas *Antrodia piceata* was not recorded as fruit-bodies but showed a high establishment success as mycelia. Two species were recorded as colonizations, i.e. they were found to fruit in logs to which the species were not inoculated ([Fig. 1A](#)). All inoculated species showed a time delay in their mycelial growth and fruiting, as the numbers of both kinds of occurrences increased with time since inoculation ([Fig. 1A–B](#)). Note that we recorded three of the species as mycelia already before the inoculations, though at much lower prevalence than after inoculations ([Fig. 1B](#)). Some of these occurrences are likely to relate to the inevitable uncertainty in molecular species identification: as we used 50% as the threshold probability for species identification, some false positives are to be expected (for more details, see Appendix 5). Further, some of the DNA may represent

monokaryotic mycelia incapable of producing fruit-bodies in our focal species, as merging of two compatible mycelia is required to make fruit-body production possible. In spite of these uncertainties, the drastic increase in the fraction of logs with DNA from the focal species in 2011 showed that the inoculations led to successful mycelial growth ([Fig. 1B](#)).

The inoculations that succeeded to produce fruit-bodies were generally conducted to logs in early decay stages: 37% of the logs in decay stage 1 resulted in successful inoculations, 19% in decay stage 2, 3% in decay stage 3, and 0% in decay stage 4 (Appendix 4).

The analyses comparing the occurrence rate of the focal seven species in the 12 control forests and the number of observations made in the reintroduction area showed that the number of focal species found in the final surveys in 2015 was greater than could be expected from the background colonization rate ([Fig. 1C](#)).

The results from the additional reintroduction area supported the results from the main reintroduction area (Appendix 6).

4. Discussion

Our results demonstrate that inoculation can be an efficient method for reintroducing red-listed wood-inhabiting fungal species, as all inoculated species established as mycelia and some of them produced reproductive structures in the inoculated logs. We recorded also colonizations outside the inoculated logs, which suggest that inoculations of individual logs can lead to the establishment of local populations. Nevertheless, the latter result is not conclusive, as we observed only a limited number of colonizations, and did not analyze genetically whether the individuals found outside the inoculated logs were derived from the inoculated individuals.

In line with previous findings, our results show that the fruiting of threatened wood-inhabiting fungal species mainly occurs after a long delay since mycelial colonization ([Ovaskainen et al., 2013](#)), which in our case corresponded to the time since the focal species were inoculated. Thus, it is possible that some of the inoculated wood-inhabiting fungal individuals may still fruit in the future, and in particular that colonizations to logs not inoculated will increase after several years.

While the numbers of inoculated individuals that successfully established were relatively low, we note that threatened wood-inhabiting fungal species are rare also in their natural ranges ([Berglund et al., 2011](#); [Nordén et al., 2013](#)). Even with low numbers of successfully established individuals, the numbers of focal species detected as fruit-bodies in the last survey since inoculation was significantly higher than expected from the background colonization rate. However, we note that our control-forest approach was not optimal. First, its results were conservative, as we assumed that all observations from the control forests were new colonizations. Second, we did not control for the potential influence of the disturbance generated by drilling the logs. Thus, a more rigorous way for conducting our experiment would have been to have control forests in which the logs would have been inventoried and drilled at the same time as when the species were inoculated, and which would have been then monitored for fungal colonizations at the same time as the inoculated sites. Another alternative for this would have been to genetically analyze whether the emerging fruit-bodies derived from the inoculated individuals.

In the case of animals and plants, reintroduction activities can cause negative impacts on source populations by removing individuals, and in the case of animals induce high levels of stress during the transportation and release of individuals (e.g. [Jenni et al., 2015](#)). In case of fungal reintroductions, such negative effects are expected to be negligible. In our study, the source individuals were sampled as fruit-bodies or parts of fruit-bodies, leaving the main part of the fungus (the mycelium) intact. Cultures obtained from fruit-bodies can be grown in the laboratory with relatively low cost to yield a potentially unlimited stock which can be stored alive as cryopreserved cultures until the reintroduction is to

take place (Homolka et al., 2006). These features enable one to use the populations from nearby locations as source populations (even if they are threatened themselves) as it is recommended by IUCN (2013). Consequently, we consider fungal translocation to have major potential to become a practical tool in large-scale restoration and conservation programs. For example, in Finland there is a goal to restore forested habitats in conservation areas with over 30,000 ha between the years 2014–2025 (Forest Biodiversity Programme for Southern Finland METSO 2014–2025). In order to make these restoration actions more effective, inoculations of locally extinct wood-inhabiting fungal species could be included, increasing the costs of the restoration actions only marginally but potentially increasing the conservation output considerably. If inoculations of threatened fungal species would be done at a large scale, the success rate reported here would be sufficient for reintroducing or reinforcing the populations of the species. We note that restoration generally produces dead wood in early decay stages, and that we recorded the highest colonization success in cases where the species were inoculated to logs in early decay stages. This is likely due to the fact that the interactions among resident species and colonizers are an important factor in determining colonization success, and that the number of fungal species competing for the resources generally increases with time (e.g. Holmer et al., 1997; Ottosson et al., 2014).

The overarching goal in reintroduction biology is to re-establish a species within its historical range where the species has gone extinct or is under extinction risk (Seddon et al., 2007; IUCN, 2013). Thus, as in the case of animals and plants, fungal reintroductions should be preceded with a risk assessment of the populations of the focal fungal species within the reintroduction area (see Pérez et al., 2012; IUCN, 2013). In the case of fungi, the most critical aspect in this context is the often limited knowledge of specific drivers of population dynamics and the large amount of unknown species (Halme et al., 2012). This makes it challenging in many cases to assess the population sizes and viability of the red-listed species in specific target areas. Additionally, in some cases, a spontaneous reestablishment of threatened wood-inhabiting fungi may happen after habitat-restoration (e.g. Bässler and Müller, 2010). Future research on reintroduction of species by inoculation should also consider intraspecific genetic variation, as in the present study the inoculated individuals belonged to a limited number of strains.

Our conclusion is that reintroducing a large number of threatened fungal species to multiple sites is feasible, but we emphasize that the protection and enlargement of existing high quality dead-wood rich habitats still remain the primary task in nature conservation, to save the source populations, to provide suitable species restoration sites and to prevent more species becoming threatened.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.biocon.2016.09.014>.

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