

# The role of mycorrhizal fungi in plant invasions

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New Zealand is a country dominated by invasive plants. Since the arrival of Māori (1280-1300), and particularly Europeans some 500 years later, more than 24,000 alien species of plants have become established (Duncan and Williams 2002). Of those 24,000 established alien plants, more than 2500 have become invasive. This is a remarkable number given that New Zealand has only around 2400 native plant species – there are now more invasive alien than native plant species (and 10× more alien species than native overall).

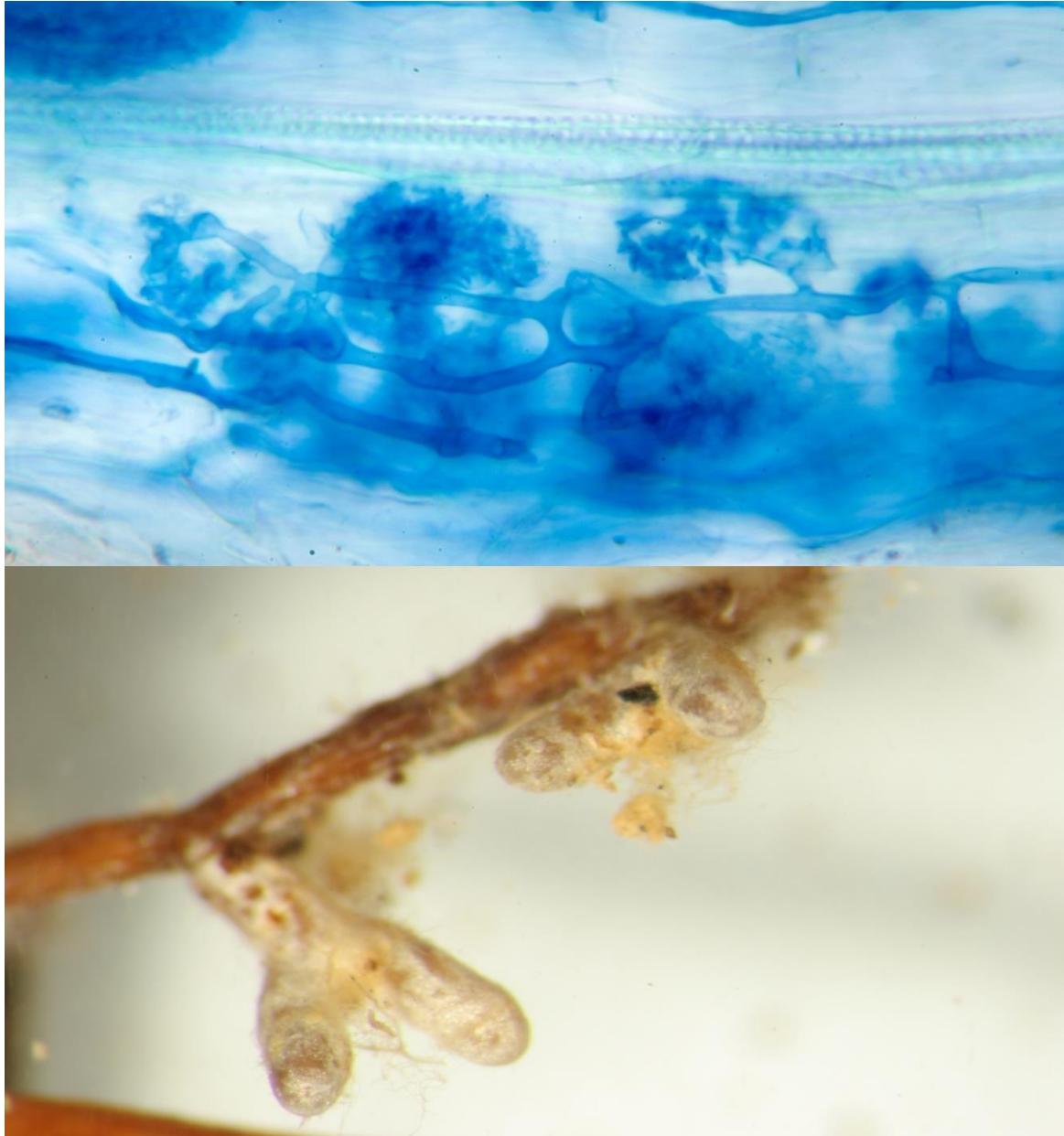
All plants are hosts to a wide range of co-evolved beneficial and harmful organisms, but the process of being introduced can result in non-native plants leaving behind many of these mutualists and antagonists (Diez et al. 2010; Dickie et al. 2017). This can give introduced plants an advantage over native plants: while native plants struggle with herbivores, pathogens, and parasites many introduced plants do not. This process, called "enemy release" by ecologists, is believed to play a role in allowing invasive plants to establish and spread. However, just as a loss of specialised enemies may benefit plants, a loss of specialised mutualists may be an important limitation (Nunez et al. 2009; Nunez and Dickie 2014). Plants rely on a wide range of mutualists for pollination, seed dispersal, nitrogen fixation, nutrient uptake, and herbivore defence. When introduced to a new range, these mutualists may be left behind, reducing the ability of a plant to establish, survive and grow. Better understanding of this process may help both manage existing plant invasions and prevent new ones.

## The mycorrhizal side of invasions

Perhaps the most widespread plant-fungal mutualisms are "mycorrhizas" in which fungi colonise plant roots. The vast majority (94%) of plants rely on these beneficial fungi for their normal growth, with the plant supplying the fungus with an abundant source of carbon and the fungus, in turn, providing the plant with mineral nutrients and other benefits (pathogen protection, water uptake). Mycorrhizal nutrient uptake is the most common way plants acquire nutrients, and can be responsible for up to 100% of plant phosphorus uptake (Smith and Read 2008).

Around 76% of invasive plants in New Zealand rely on one type of mycorrhizas, known as "arbuscular mycorrhizas" (Fig. 1, p. 6). The fungi that form arbuscular

mycorrhizas are inconspicuous, reproducing through relatively small, soil-borne spores. There are relatively few known fungi that form arbuscular mycorrhizas, with 350 to 1000 defined species (Davison et al. 2015). With so few species, it is not surprising that many arbuscular mycorrhizal fungi have very large (cross-continental) scale natural distributions, and while different plant hosts do support different fungal communities, strict host-specificity is rare (Davison et al. 2015; Martinez-Garcia et al. 2015).



**Figure 1.** The two dominant types of mycorrhizal associations are arbuscular mycorrhizas (top) and ectomycorrhizas (bottom). The *Buddleja davidii* root in the top photograph has been cleared and stained to reveal the characteristic branching (“tree-like”) structure known as an "arbuscule" where nutrient exchange between plant and fungus occurs, and the thicker fungal hyphae. In ectomycorrhizas, as shown in *Pinus contorta* (bottom), fungal hyphae wrap around the outside of roots and penetrate between, but not into, plant cells.

As host-specificity of arbuscular mycorrhizal fungi is low, invasive arbuscular mycorrhizal plants generally have few problems finding partners and forming the mycorrhizal associations they need, as shown for invasive grasses (Johansen et al. 2017). The main exceptions would be in ecosystems where there are no established arbuscular mycorrhizal plants, such as very low diversity mountain beech forest (*Fuscospora cliffortioides*). The southern beeches do not form arbuscular mycorrhizas, and hence the invasion of tussock hawkweed (*Hieracium lepidulum*) into such forests may be limited by a lack of available arbuscular mycorrhizas. By contrast, where arbuscular mycorrhizal plants have previously established, they can then provide a source of inoculum and hence facilitate hawkweed invasion (Spence et al. 2011).

### **Ectomycorrhizas and tree invasions**

A much less common type of mycorrhizas are known as ectomycorrhizas (see Fig 1, p. 6), which are formed by only around 2% of land plants. While relatively small in number, the plants that form ectomycorrhizas include many dominant forest trees. Among invasive woody plants, ectomycorrhizas are formed by wilding pines (*Pinus*), Douglas-fir (*Pseudotsuga*), willow (*Salix*), and alder (*Alnus*), as well as many less-invasive alien trees such as oaks (*Quercus*), eucalypts (*Eucalyptus*), birch (*Betula*), and poplar (*Populus*). Among native species, only the beeches (*Fuscospora* and *Lophozonia*), manuka and kanuka, and *Pomaderris* form ectomycorrhizas (Warcup 1980; Orlovich and Cairney 2004)

The fungi involved in ectomycorrhizas are entirely distinct from the fungi involved in arbuscular mycorrhizas. Ectomycorrhizal fungi are incredibly diverse, including an estimated 20 000 to 25 000 species of fungi from 66 lineages spanning three phyla of fungi (predominantly Basidiomycota and Ascomycota, along with some Mucoromycota) (Tedersoo et al. 2010). Many ectomycorrhizal fungi produce large mushrooms in a brilliant array of colours and forms (Fig. 2, p. 8), while others produce less conspicuous fruiting bodies. Unlike arbuscular mycorrhizal fungi, ectomycorrhizal fungi show a high level of endemism in New Zealand. Ectomycorrhizal fungi can also show host specificity, with some fungi only associating with, for example, pine trees (including most *Suillus*), alders (the fungus *Alnicola*), or birch (birch bolete, *Leccinum scabrum*).

Host specificity of fungi presented a unique challenge to the establishment of pine trees in New Zealand and elsewhere in the southern hemisphere. When pine trees, Douglas-fir, alder, willows and other ectomycorrhizal species were first planted in the southern hemisphere, establishment and growth were frequently poor (Gilmour 1958). The failure of early plantings played a large role in scientific recognition of the importance of mycorrhizal fungi to plants. Once the importance of a lack of mycorrhizal fungi was recognised, active inoculation programs were developed, with government forestry researchers promoting the spread of ectomycorrhizal fungi in order to enhance alien tree establishment as late as the 1970s and 80s (Ledgard 1976).



**Figure 2.** Some examples of native (a - d) and alien (e - h) ectomycorrhizal fungi, including the native species (a) *Amanita pekeoides*, (b) *Porphyrellus formosus*, (c) *Cortinarius* sp., and (d) *Octaviania* sp.; and the alien species (e) *Boletus edulis*, a choice edible fungus growing on native beech, (f) *Tricholoma terreum*, (g) *Amanita muscaria*, and (h) *Suillus luteus*.

## The arrival and spread of mutualists

The ectomycorrhizal fungi that are now widespread on pines, birches, willows and alders were probably primarily introduced by happenstance on living plant roots. Transport of living plants was remarkably common in the 1800s, and each plant likely brought along fungi on its roots and in the surrounding soil. For example, it is quite likely that the choice edible ectomycorrhizal fungus *Boletus edulis* (porcini, cepes), currently found primarily in and around Christchurch, was brought from the UK to New Zealand on the roots of large living oak trees that were planted in Hagley Park (Herriott 1919).

Pines may have taken a circuitous route to arriving in New Zealand. Radiata pine was introduced to New Zealand by at least 1859 as a seedling transplanted from Australia (<https://teara.govt.nz/en/photograph/16831/radiata-pine-at-mt-peel-station>), although there may have been earlier introductions (Sutton 2011). The source of the Australian populations may have been from seedlings transplanted from Britain (Fielding 1957), where radiata pine had been introduced in 1833 (Green 1954). The movement of seedlings with associated soils was likely a main source of fungal inoculum. One of the curious results of this circuitous introduction route is that invasive North American *Pinus contorta* in New Zealand seem to associate with a number of fungi from Europe, including *Suillus luteus*.

In some cases, deliberate efforts to spread ectomycorrhizal inoculum have taken place. In 1939, R J Lawrence, a Forest Ranger with knowledge of mycorrhizal activity, theorised that the poor health of Douglas-fir in the Nelson area was due to a lack of suitable symbiotes in most local nurseries (Lawrence 1945). Lawrence transported forest floor material from a successful Douglas-fir stand in Hanmer Springs and applied it to various Nelson Douglas-fir stands with the express intention of introducing suitable mycorrhiza, thereby improving the health and growth of the trees (Gilmour 1958). Lawrence was subsequently involved in several other trials in the Canterbury region that explored the impact of incorporating litter from well-performing local Douglas-fir stands into nursery seedbed soil. This research also indicated the positive impact of this putative mycorrhizal introduction on the later growth of the Douglas-fir seedlings generated from these trials (Lawrence 1945). This early work culminated in a significant trial set up to improve Douglas-fir establishment in Otago in the 1950s. Assessments of root morphology across healthy and poor performing trees indicated mycorrhizal presence was a key factor in good growth, and this factor was determined by the nursery that supplied the trees (Gilmour 1958). Forest floor material was then introduced to a nursery that was producing poorly performing stock; subsequent seedling crops from that nursery were observed to be colonised by suitable mycorrhiza, and performed well in the field. Other introductions have used fungal sporocarps, particularly of *Rhizopogon parksii* which was systematically introduced into Douglas-fir nurseries in the 1980s to enhance the establishment of Douglas-fir plantations (Davis 2008). Deliberate spread of fungal sporocarps and forest floor material as inoculum played a large role in establishing the New Zealand forest industry, but also contributed substantially to the success of both pine and Douglas-fir as invasive species.

Once mycorrhizal fungi were established into tree nurseries, the widespread planting of pine seedlings, often by researchers (Ledgard and Baker 1988), into high-country grasslands led to the initial introduction of non-native ectomycorrhizal fungi to these ecosystems. Ectomycorrhizal fungi produce abundant sporocarps (mushrooms), each one of which can contain millions to billions of fungal spores. Curiously, although the general expectation might be that wind would be the primary dispersal agent of these fungi, it actually appears that mammals, including Australian brush-tailed possums (*Trichosurus vulpecula*) and red deer (*Cervus elaphus*), are vital dispersal agents. These mammals seek out and consume fungal sporocarps of both native and alien fungi, but work by Wood and colleagues demonstrates that they are only effective dispersal agents for alien fungi (Wood et al. 2015). As a result of repeated introductions and subsequent spread, alien mycorrhizal fungi are now widespread in many areas. As a result, a lack of mycorrhizal inoculum no longer precludes tree invasion in many areas (Davis and Smaill 2009; Dickie et al. 2014b).

While most fungal introductions are inadvertent, there have been a few deliberate introductions (Schwartz et al. 2006). These include ectomycorrhizal truffle species and other edible species, as well as mycorrhizal inoculum products (including both arbuscular and ectomycorrhizal fungi).

### **Invasive plants and fungi transform ecosystems**

The invasion of ectomycorrhizal trees such as wilding pines, alders, and willows in most cases represents a shift from arbuscular mycorrhizal dominance (native grasses and many native shrubs) to ectomycorrhizal dominance. It has long been recognised that arbuscular mycorrhizal and ectomycorrhizal vegetation drive fundamentally different ecosystem processes (Read 1991; Lambers et al. 2008; Dickie et al. 2015). In particular, ectomycorrhizal fungi have a much greater ability to directly access organic nutrients than arbuscular mycorrhizal fungi. Over long time periods, this direct nutrient uptake can lead to a short-circuiting of the nitrogen cycle, build-up of organic carbon, and reduced plant diversity (Orwin et al. 2011; Phillips et al. 2013; Dickie et al. 2014c). However, long-term outcomes of changes in mycorrhizal status may not be particularly relevant to invasions.

The short-term soil ecosystem effects of ectomycorrhizal plant invasions are profound, but often opposite to longer-term predictions. In the short-term, the invasion of pines is associated with a substantial loss, rather than gain, of soil carbon and an increasing availability of both nitrogen and phosphorus (Chen et al. 2000; Chapela et al. 2001; Dickie et al. 2014a; Dickie et al. 2014b). These changes may reflect the novel enzymatic capabilities of ectomycorrhizal fungi, potentially releasing nutrients from soil organic compounds that have accumulated over extended time periods. There are also very large shifts in the rate of nutrient cycling. Decomposer communities in native grasslands tend to be fungal dominated, resulting in relatively slow cycling of nutrients. Following the invasion of ectomycorrhizal wilding conifers, these systems shift into a bacterial dominated state (Dickie et al. 2011; Dickie et al. 2014b). Bacteria are much more susceptible to predation than

fungi, hence bacterial dominated soils tend towards much faster nutrient cycling (Wardle 2002), further contributing to a higher availability of nitrogen and phosphorus following tree invasion.

Changes in belowground ecosystems have profound implications for restoration. At present, most efforts to control plant invasions focus nearly entirely on killing invasive plants. This is a necessary first step, and sufficient to play an important role in preventing further spread. However, simply killing and removing invasive plants does little to reverse changes in soil functioning and hence does not restore the local ecosystem. Rather, areas where invasive ectomycorrhizal trees have been removed tend to be rapidly dominated by invasive alien grasses (Dickie et al. 2014b). While grass dominance may partially reflect high seed availability and an ability to rapidly colonise disturbances, soil bioassays demonstrate that soil legacies of invasive trees are playing a major role (Dickie et al. 2014b). Invasive ectomycorrhizal plants also build up fungal inoculum over time, which can be highly persistent (Bruns et al. 2009). This suggests that over time, removal of invasive trees will lead to invasion by non-native grasses, which are then re-invaded by invasive trees, resulting in a potentially endless cycle of tree invasion, control, and reinvasion.

### **Restoring ecosystems rather than killing trees**

At present, millions of dollars are being spent annually on controlling tree invasions using herbicide and other treatments to attempt to eradicate the invasion and restore native grasslands. Whether long-term eradication can be achieved remains to be seen, but better management of ecosystem legacies of pines will be required if native grasslands are to be restored. Further, this strategy will require an ongoing investment of considerable resources to prevent any pines from reaching seeding age if long-term eradication is to be achieved.

Given the difficulty in restoring native ecosystems following invasion, is it worth continuing to try? There are certainly some who have argued that invasive plants are a positive change to our ecosystems, and advocate for simply accepting them as part of the new normal. Invasive plants do provide positive ecosystem services (Dickie et al. 2014a), including fixing a substantial amount of carbon (Dickie et al. 2011), and some would argue that invasive species add to the diversity of plants in New Zealand. Nonetheless, while invasive species may add to species numbers at a national scale, this comes at a high cost to species diversity at a local scale, and the loss of iconic New Zealand landscapes.

There may be a third possibility that doesn't require accepting pine dominance of landscapes, but also reduces future reinvasion. We might consider whether the time of the New Zealand tussock grasslands is simply past. Many of these grasslands were forest before Māori and particularly European settlement (Hobbs et al. 2006), and the suitability of climatic conditions in these grasslands for forest is clearly evident in the success of tree invasions. Management to restore these ecosystems to native forest might provide a much longer-term solution than trying to maintain grasslands. Doing so might require careful planting of native species either before or after removing

invasive trees, and incur substantially higher costs than simply spraying herbicide from a helicopter. Nonetheless, establishing a tall native woody cover is perhaps the only strategy that would limit the ability of pines to reinvade. This approach would not prevent Douglas-fir invasion, given its high shade tolerance, but could greatly reduce most of the other invasive pine species.

### **Biosecurity implications**

Given what we now know about the role of mutualisms in plant invasion, there are some ways in which we may be able to reduce future invasions. Firstly, it is important to recognise that a plant species that is not currently invasive could become invasive if a particular fungus arrives. Risk assessments need to consider the possibility that plant phenotypes are a function not only of physiology, but also of ecological interactions. For example, *Eucalyptus* was present for a considerable time in Spain before becoming invasive, and some have suggested that late arriving co-invading Australian ectomycorrhizal fungi may be driving that invasion (Diez 2005; Dickie et al. 2016). Given the risk, it might be prudent to monitor the 220 species of introduced *Eucalyptus* in New Zealand to ensure that a late-arriving fungus doesn't drive a similar transition here.

Very few fungi were deliberately introduced to New Zealand, with most arriving on soils and roots of plants. Live plant imports are well recognised as a source of pathogen and insect invasions (Liebhold et al. 2012), but also represent a major pathway for mycorrhizal fungal invasions. Botanic gardens (Hulme 2011), urban plantings, and forestry trial sites may have particularly high levels of non-native fungi present. Managing soil movements from these sites may help delay future invasions. In some cases, such as the highly poisonous *Amanita phalloides*, eradication of currently limited populations should be considered (Dickie et al. 2016).

Lastly, ongoing efforts to import new species of mycorrhizal fungi should be viewed with extreme caution. There are a number of mycorrhizal inoculum products that are sold overseas and applications are periodically made for permission to import to New Zealand. In general, these products contain fungal species that have been selected for high spore production for ease of production (Schwartz et al. 2006; Vellinga et al. 2009). The value of mycorrhizal inoculum products is often unclear, and at least in the context of New Zealand restoration projects native fungi may provide stronger benefits (Williams et al. 2012). Conversely, the risks of introducing new fungi may be considerable, given the history of non-native fungi facilitating weed invasions.

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## **Branch River - the catchment of greatest vegetation change?**

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Back in the 1970s and 80s I used to spend a fair bit of time in the Branch catchment in South Marlborough. This river drains into the Wairau River alongside SH63, which runs from Blenheim up to St Arnaud. Being remote and rugged, with a demanding river crossing and 4WD track through original beech forest to reach the main hut (Grieg's), it was always an attractive destination for a young man keen on the backcountry and 'hunting, shooting and fishing'. It is also home to a fascinating tale of major vegetation change over a relatively short period of time. In his 1996 book *Steepland Forests*, Peter McKelvey describes the Branch catchment work as "easily the largest purely protective reforestation project in the NZ mountainlands". Much of the following is extracted from Peter's book, aided by the results of research trials in which I was involved.

Originally the Branch catchment was densely forested up to a timber line at about 1500 m. The dominant forest species were red and mountain beech, with areas of kanuka and shrubland (mainly *Carpodetus*, *Pittosporum*, *Cassinia* and *Senecio* species). Above 900 m there is increasing grassland dominated by *Rytidosperma setifolium* and *Festuca matthewsii* / *Poa colensoi*, with areas of *Chionochloa australis* (carpet grass) or *C. pallens* (snow grass). The most extensive vegetation clearances took place about the turn of the century, with the last major fires between 1917 and 1920. It is likely that forest destruction through burning had been underway for several centuries before that, but the prospect of grazing sheep accelerated it in the early 1900s. The end result was thousands of hectares of largely bare, erosion-prone slopes. I have slides taken in the early 1970s of huge areas of such steep land, with the most obvious above-ground feature being the widely scattered spars of large burnt beech trees. The only wildlife seen was rapidly retreating goats, hares and the occasional chamois. So open was the country that it was hard for even a fit, keen young man to get within assured rifle range.