In Focus — Managing Forests in Europe



Introduced tree species in European forests: opportunities and challenges

Frank Krumm and Lucie Vítková (eds.)



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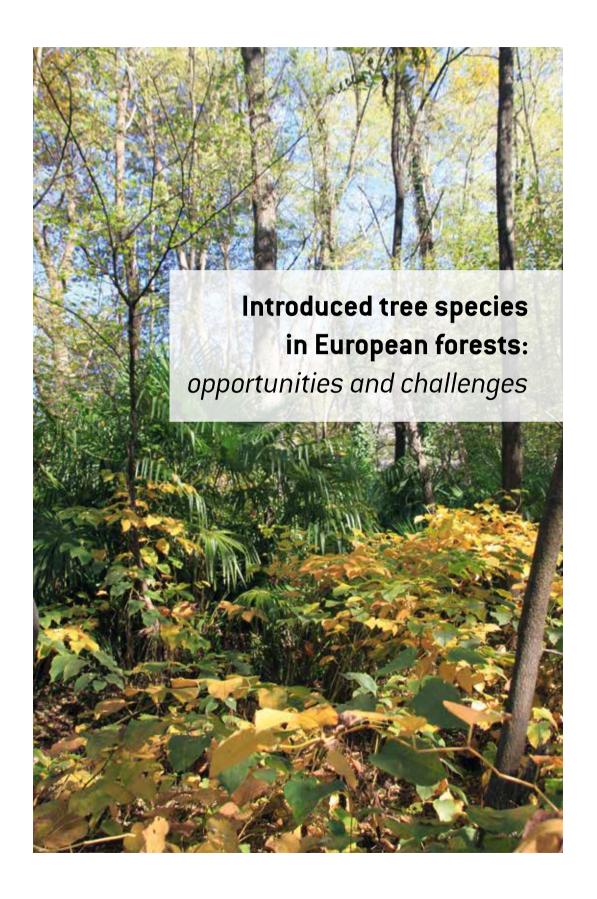
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2.5 Co-invasion of invasive trees and their associated belowground mutualists

Martin A. Nuñez, Nahuel Policelli and Romina D. Dimarco

The majority of trees need mutualistic associations to thrive and survive. This can be a fundamental limitation for their ability to colonise new areas and consequently invade them. While many non-native tree species may form associations with local mutualists that substitute those present in their native range, others, probably with a higher degree of specialisation invade along with their native range mutualists (co-invade). An example of this is the case of some figs (*Ficus* spp.); in the USA, these trees which have a highly specialised pollination system depending on particular species of wasps, became invasive only after their native pollinator had arrived (Richardson et al. 2000). Other examples can be found in many invasive trees that need belowground mutualists, like nitrogen-fixing symbionts and mycorrhizal fungi, to thrive in their new geographical range (e.g. Nuñez et al. 2009, Dickie et al. 2010). These soil mutualists have been found to play a key role on the invasion of numerous introduced tree species (Nuñez and Dickie 2014).

New technologies allowed researchers to understand and further appreciate the role of belowground organisms and how they can influence plant populations and communities.

Historically, researchers have had biases when studying mutualistic interactions since they were solely focused on the plant perspective with a strong emphasis on aboveground interactions (e.g. pollination). This has been, in part, due to our own view of the world from an aboveground perspective, and based on the paradigm that soil microorganisms are everywhere and are not dispersal limited (Peay et al. 2010). In the last few decades, new technologies have emerged, involving molecular tools, allowing researchers to understand and further appreciate the role of belowground organisms and how they can influence plant populations and communities. Given this historic absence of focus on the belowground aspect of the invasion process, we currently have many unanswered basic questions about plant invasion and their associated mutualisms. One example is the limited information we have on how mycorrhizal fungi are dispersed (Galante et al. 2011). In the last years there has been more research on this topic and hopefully soon, we will have a deeper understanding of the importance of invasive belowground biota for the success of tree invasions.

This chapter presents the current understanding of tree species invasions and their invasive belowground mutualists. The term invasive species (for both plants and their mutualists) will be used following an accepted classification (Blackburn et al. 2011), which does not include non-native species that were introduced to an area and never escaped from their introduced range – e.g. dwarf mountain pine (*Pinus mugo* Turra) or giant sequoia (*Sequoiadendron giganteum* (Lindl.) J.T. Bucholz) in Patagonia (Nuñez et al. 2011) and many commercial tree species. Mutualistic species only colonising tree species that have

never escaped plantations will also not be included – e.g. eucalypts (*Eucalyptus* spp.) in Spain (Diez 2005). All possible scenarios of tree invasion and their belowground mutualists, particularly focusing on the co-invasion process are addressed in this chapter.

The majority of invasive trees require belowground mutualists to successfully invade.

While most invasive tree species require belowground mutualists to successfully invade, other tree species do not need them. Invasions by species that are not dependent on mutualisms are not limited by absence of a mutualist (Figure 21). For example, invasive trees such as woody Proteaceae (Allsopp and Holmes 2001) do not associate with mycorrhizal fungi or nitrogen-fixing bacteria to colonise. Most of these plants have non-symbiotic nutrient uptake alternatives, such as cluster roots in the case of Proteaceae (Allsopp and Holmes 2001), and sometimes, they can successfully invade by disrupting existing mutualistic interactions of their competitors, therefore increasing their competitive ability (van der Putten et al. 2007, Meinhardt and Gehring 2012).

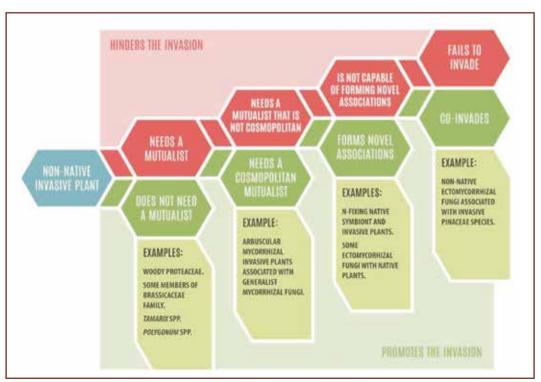


Figure 21. Four different strategies that allow plants to become invasive in relation to the presence or absence of soil biota. Some common examples are mentioned below each strategy.

Belowground mutualists can be cosmopolitan, establish a novel association or co-invade with tree species.

Three main strategies can be recognised in tree species requiring belowground mutualists (Dickie et al. 2010) (Figure 22).

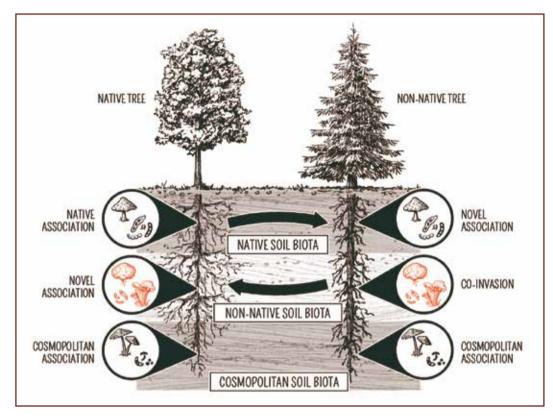


Figure 22. Diagram of the possible ways that native and non-native tree species havefor interacting with native, non-native and cosmopolitan soil mutualists. Co-invasion occurs when both, the plant and the mutualist, are non-native. Novel associations can occur with a native plant and a non-native symbiont, or with a non-native plant and a native symbiont. A special type of novel association is the "co-xenic" association where both plants and mutualists are non-native, but originate from distinct geographical ranges.

'Cosmopolitan' associations occur when there are introduced tree species and the mutualists are native to both the home range of the tree and the introduced range. These cosmopolitan associations are common between arbuscular mycorrhizal invasive plants that associate with generalist cosmopolitan mycorrhizal fungi – e.g. Chinese windmill palm (*Trachycarpus fortunei* (Hook.) H. Wendl) (Moora et al. 2011).

A second strategy involves the formation of '**novel**' associations and includes those introduced tree species that are capable of establishing novel associations with symbionts that are present in the introduced range but not in the native range (non-native tree, native symbiont). A reported example of this strategy is the case of native fungi from the Republic of Seychelles that form ectomycorrhizal symbioses with planted *Eucalyptus* spp. (Tedersoo et al. 2007). Another type of novel association occurs when an intoduced symbiont associates with native trees (native tree, non-native symbiont) as documented for the association between native southern beeches (*Nothofagus* spp.) trees and non-native *Amanita muscaria* (L.) Hook.) in New Zealand (Orlovich and Cairney 2004). A third type of novel association occurs when an introduced plant associates with a non-native symbiont but that do not share the same home range (co-xenic associations). An example is the

ectomycorrhizal fungi *Suillus luteus* (L.) Roussel from Europe colonising North American trees, such as ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson) and lodgepole pine (*P. contorta* Douglas ex Loudon), in South America (Hayward et al. 2015a).

The third strategy is '**co-invasion**' and seems to be at least as common as the occurrence of novel interactions (Figure 22). Co-invasion occurs when mutualists that are present in the native range of an introduced species are also introduced (intentionally or by accident) along with the introduced plant (Mikola 1990). Ectomycorrhizal Pinaceae species tend to co-invade more than other groups, although this tendency could be driven by the effort that has been made in introducing ectomycorrhizal symbionts due to the commercial importance of Pinaceae, and biases in research effort. After co-invasion, the mutualistic species can expand from their introduced host and form novel associations with native trees such as the economically important ectomycorrhizal fungi *Tuber indicum* Cooke & Massee, or the toxic *A. muscaria* and *A. phalloides* (Vaill. ex Fr.) Link (Dunk et al. 2012).

There are also exceptions to the above-mentioned strategies. Although many invasive nitrogen-fixing plants are able to generate novel interactions in their new range (Rodriguez-Echeverria et al. 2009), there is evidence that some may need to co-invade to successfully become invasive (Rodriguez-Echeverria et al. 2011). Something similar happens in the case of black locust (*Robinia pseudoacaccia* L.), a plant that associates with arbuscular mycorrhizal symbionts; black locust performs better with arbuscular mycorrhizal fungi from its native range (co-invade), despite being known to be promiscuous in associations as is general the case for arbuscular mycorrhizal plants species (Smith and Read 2008).

Not all soil mutualists have the capacity to invade.

There are numerous factors that can affect the invasive capacity of non-native soil organisms. Some mutualistic mycorrhizal fungi, for example, that produce high numbers of spores, and have the ability to disperse the spores by wind, water or local dispersal agents such as animals are likely candidates as invaders (Nuñez et al. 2013). Moreover, invasion can be facilitated if soil organisms can associate with an abundant plant species and/or a variety of plant species. The production of high number of propagules has also been shown to be associated with invasion (Peay et al. 2012). Previous studies have found that mycorrhizal fungi species with high production of spores tend to invade (e.g. *Rhizopogon* spp., *Suillus* spp.), while many species that are found associated to roots of planted trees are rarely, or never, found outside plantations (e.g. *Cortinarius* spp., *Inocybe* spp.) (Hynson et al. 2013, Hayward et al. 2015a). In general, the soil organisms that tend to invade are species that are found colonising the native range after a disturbance (Hayward et al. 2015a).

The invasion capacity of mutualists is also determined by their host specificity. If a mutualist has a high level of host specificity, but associates with a highly invasive tree species, then specificity is not a limitation for its invasion. This seems to be the case for several species that co-invade with pines, such as *Suillus* spp., which are highly invasive in the southern hemisphere (Hayward et al. 2015b). If the soil mutualist species has a low level of host specificity, it could thrive by forming novel associations in the invasive range with different tree species. This seems to be the case of arbuscular mycorrhizal fungi, some nitrogen-fixing bacteria, and some ectomycorrhizal species (Dunk et al. 2012).

New ecosystem functions may be created with co-invasion of certain species.

There are multiple impacts of co-invasions. One main effect is that it allows non-native tree species to invade. This could notably change ecosystems, for example by converting grassland into a forest. The absence of co-invaders could limit the growth and spread of invasive trees and also result in the failure of forestry plantations because of the absence of adequate ectomycorrhizal inocula. Non-native soil mutualists can also present novel enzymatic pathways for the invaded ecosystem that could include, for example, atmospheric nitrogen fixation (see Vitousek et al. 1987) and nutrient uptake from previously unavailable sources, such as organic forms by ericoid mycorrhizal or ectomycorrhizal fungi. This could have important impacts especially if such a function is new to the system. For example, the invasion of ectomycorrhizal fungi and their co-invasive plants on some oceanic islands like Hawai'i would represent an entirely novel ecosystem function, since there are no native ectomycorrhizal trees on some of these islands (Hynson et al. 2013).

Invading soil mutualists may also have impacts on native mutualists as the displacement of native plant species is the most obvious effect when non-native plants invade. Therefore, non-native mutualists could be expected to have the same effect. However, to date there is no strong evidence of this occurring (Nuñez and Dickie 2014). Some co-invasive mutualists (e.g. *Bradyrhizobia* associated with invasive acacias) have been found on native nitrogen-fixing plants (Rodriguez-Echeverria 2010). Also, *A. phalloides* originally associated with introduced tree species is now invading native plants in North America. However, studies on this topic showed no loss of ectomycorrhizal diversity in soil samples where *A. phalloides* was present (Wolfe et al. 2010).

If there is an impact by soil mutualists, it can result in a significant long term effect influencing future ecosystem trajectories.

Soil legacies tend to persist after the removal of introduced species and modify future plant communities and their native ecosystem function (Malcolm et al. 2008). As mentioned above, many effects of co-invasive mutualist can result insignificant long-lasting effects; however, co-invasive mutualists can also directly affect local plants and animals. Non-native *Bradyrhizobium* spp. colonise native legumes in parts of Europe and have notably less beneficial effects (i.e. nitrogen fixation) than native *Bradyrhizobium* species (Rodriguez-Echeverria et al. 2011). It is also important to note that some mycorrhizal fruiting bodies can be harmful to humans and animals if consumed. The highly toxic *A. phalloides* poisoned people in Australia and North America even resulting in some deaths (Trim et al. 1999).

The current understanding suggests that co-invasion of trees and their co-evolved symbionts is not a rare phenomenon, especially for ectomycorrhizas and nitrogen fixing symbioses, which are common for trees (e.g. Pinaceae, Fabaceae, Betulaceae, Myrtaceae) (Nuñez and Dickie 2014). The absence of a co-invader can limit the invasion of the tree and the associated soil organism since both must co-invade and in many cases are dispersed independently (Nuñez et al. 2009). In other soil mutualistic groups, such as arbus-

cular mycorrhizal fungi, the most important mutualistic group for invasive plant species (Figure 22), there is a relatively high promiscuity in terms of potential associations and wide fungal distribution (Tedersoo et al. 2014). For this reason, novel and cosmopolitan associations are common for many invasive plant species.



Management of invasive soil biota could be determinant for plant species invasions.

A more detailed understanding of symbiotic interactions and the co-invasion process can be important in order to better understand plant invasions. Lag times, very common in invasive trees (Richardson and Higgins 1998, Simberloff et al. 2010), can be explained by interactions with soil biota (e.g. late arrival of the co-invasive symbiont). Also, from a management perspective, once soil mutualists are widespread, their control or eradication can be challenging given the small propagule size, and the potential to persist in an inactive form for long periods (Bruns et al. 2009).

There are ways to minimise the potential impacts of co-invasive mutualists; for example, the introduction of highly invasive non-native soil biota into new areas should be avoided. Also there are some mutualists that mostly spread asexually and seldom produce spores and they could be considered ideal for introduction. As mentioned before, absence of a co-invader may result in limited growth or complete failure of an introduced species, and so in some cases deliberate introduction of a mutualist might be considered desirable. For some introduced tree species that rely mostly on co-invasive mutualists, it could be possible to use native soil symbionts (Moeller et al. 2015), or to minimise introductions of new, non-native symbionts without biosecurity measures (e.g. by restricting movement of soil or trees in pots). Where deliberate introduction of a mutualist is considered, the potential for invasion by the mutualist, and the possible negative effects of that invasion, must be considered. Management of invasive soil biota or the restoration of areas invaded by soil symbionts is a daunting task given their belowground habit, their microscopic size and their ability to persist for long periods (Dickie et al. 2016). Therefore, it is of fundamental importance to control the spread of soil symbionts to avoid the numerous detrimental effects co-invasion can have. Efforts to control the spread of invasive species might be wasted if managers are unaware of co-invasion as a determining factor in whether a plant species becomes invasive or not.

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