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Commentary

Introduced tree species released from negative soil biota

In spite of some recent suggestions that ecologists pay too much attention to introduced exotic species (Davis *et al.*, 2011), exotics undeniably invoke many environmental and economic problems worldwide. The primary causes of species introductions are trade, transport and tourism, which make species cross geographical barriers that prevent natural dispersal of their enemies. However, it is true that relatively few introduced species have become a pest in their new range, which complicates the search for general mechanisms driving invasiveness: how to derive patterns from a minority? One species that has benefitted well from human introductions is *Pinus contorta*, a pine species that is native to western North America (Fig. 1). In this issue of *New Phytologist* Michael Gundale and colleagues from the Swedish Agricultural University at Umeå (Gundale *et al.*, 2014a, pp. 415–421) provide evidence that introduction of *P. contorta* in Sweden has released the species from growth-reducing soil biota. They therefore provide support for a mechanism, release from soil-borne pathogens, which is increasingly proposed, but still lacks important evidence.

> *'One of the intriguing issues with exotics concerns the general observation that only a minor fraction of all introduced species becomes invasive in the new range.'*

The role of soil biota in plant invasion has been pointed at more than a decade ago (Klironomos, 2002), but rigorous tests require information from both the native and the introduced range (Hierro *et al.*, 2005). The first study doing so was carried out on *Prunus serotina* (black cherry) (Reinhart *et al.*, 2003), but in that and subsequent studies it has been impossible to link the populations in the introduced range to original populations in the native range. As foresters keep track well of the history of their forest stands, it was possible for Gundale *et al.* (2014a) to exactly relate source and sink populations. They could trace back 16 experimental *P. contorta* populations from Sweden to four original populations in British Columbia: each source population from Canada led to four populations in Sweden. Both seeds and soil were collected from the native and nonnative regions to carry out two experiments in a glasshouse in Sweden.

In the first experiment, it was established that both plant origins produced *c.* 43% more biomass in Swedish than in Canadian forest soil, whereas pH and ammonium availability were highest in Canadian soil. Effects of soil origin were half as strong as effects of artificial fertilization. In the second experiment, soil sterilization by gamma-irradiation removed the difference between biomass production of *P. contorta* in Canadian and Swedish soil, suggesting that absence of soil-borne pathogens may be the driver of superior growth in soil from the introduced range. Inoculation of the sterilized soil with living soil, which contains soil biota including pathogens, symbionts, and decomposers, resulted in plants producing 62% more total biomass in Swedish than Canadian soil. This is pretty strong evidence that soil biota caused the growth differences between native and nonnative soil. The absolute evidence would require further teasing apart of the contributions of soil pathogens, mutualistic symbionts and decomposers, as well as the various species involved. Those tests will be essential in order to determine the cause of enhanced growth in soil from the introduced range, however, such studies are an extreme challenge, if not the ultimate nightmare, to ecologists (De Rooij-van der Goes, 1995; Morriën & van der Putten, 2013).

Novel molecular techniques will definitely be indispensable in enhancing our current insights into the dazzling complexity of microbial communities underground. Gundale *et al.* (2014a) have not made use of molecular-based methods to qualify the soil communities in the native and introduced range soils. Application of T-RFLP or 454 pyrosequencing might have shown how patterns of bacteria, fungi and mycorrhizal fungi differed between both ranges. Nevertheless, demonstrating which causal factors drive the observed patterns would also require experimental tests based on isolation, culturing and inoculation studies. Such an approach involves several problems. First, many soil microbes are non-cultivatable and second, testing possible involvement of tens of species already is immensely demanding in terms of possible combinations that need to be explored (De Rooij-van der Goes, 1995). Therefore, the growth experiment-based evidence provided by Gundale *et al.* (2014a) is among the best that can be provided currently, whereas a future challenge will be to develop new approaches that enable teasing apart of belowground communities, and testing how individuals alone, and in communities, might explain the observed patterns in plant performance between the native and introduced ranges.

Another unprecedented aspect of the study by Gundale *et al.* (2014a) is that they were able to compare responses to soil biota of populations of *P. contorta* between the two ranges, as the source populations had been carefully documented. Difference in tree provenance had a much lower effect on biomass production than soil inoculation or fertilization (Gundale *et al.*, 2014a), suggesting that native and introduced seed provenances from the two ranges differ far less with respect to impacts on plant performance than soil biota. That result is understandable in this context, as the trees have been introduced by humans and tree evolution might be a slow

Fig. 1 (a) *Pinus contorta* in British Columbia, Canada (the native range); (b) in Sweden (the nonnative range); (c, d) in a glasshouse experiment testing effects of soil, nutrients, and seed provenance; (e) Coyhaique, Chile (nonnative range); and (f) New Zealand (nonnative range). Photographs courtesy of Michael Gundale (a–d), Martin Nuñez (e) and Ian Dickie (f).

process in planted forests. Nevertheless, the question to what extent plant–soil biota interactions can be subject to evolution, and whether they can play a role in the evolution of introduced populations is still wide open. Several studies in native ranges of herbal or woody plant species have pointed towards considerable genotype-specific effects of plant–soil biota interactions (Lau & Lennon, 2011; Schweitzer *et al.*, 2014). The growing awareness that plant–soil feedback interactions are driving spatio-temporal plant dynamics in many ecosystems makes evolutionary aspects of plant–soil interactions an important avenue that might lead to exciting future viewpoints.

One of the intriguing issues with exotics concerns the general observation that only a minor fraction of all introduced species becomes invasive in the new range. This observation does not match very well with the notion that many invasive plant species are early successionals and that early successionals especially can develop soil pathogenic activity in their native range (Kulmatiski *et al.*, 2008). There are many reasons why not more introduced plant species become highly invasive in the introduced range. One possibility is that negative plant–soil feedback may correlate with low plant abundance, but that it is not a major cause of plant abundance control. Another possibility is that in the new range abundance of the introduced plant species is limited by other factors, for example the lack of suitable beneficial soil biota, pollinators, or abundance control by aboveground biota, such as limited numbers of pollinators, over-exploitation by generalist herbivores, or seed dispersers. There are relatively few field studies on plant–soil biota interactions (Casper & Castelli, 2007) and a challenge for future research is to quantify, in the field, the contribution of plant–soil feedback interactions relative to other factors that influence plant population development and community composition.

A pivotal question will be what use can be made of the awareness that introducing exotic plant species may result in their release from native soil-borne enemies. One option could be that the soil pathogens from the native range become artificially co-introduced in order to control the invasive hosts. This is well known for ectomycorrhizal fungi and other root symbionts (Nuñez & Dickie, 2013). However, let us hope that the researchers in Umeå will have discarded the soil samples from Canada according to the prescribed regulations, because introducing soil pathogens from the native range, such as parasitic *Armillaria* fungi, might be devastating to the invaded ecosystems (Karlman, 2001). The example of the introduced soil pathogen *Pythium cinnamomi* in Australia, which eliminates entire native forest communities, is a horror story that should be avoided by all means. It would be interesting to explore further how, and how fast, introduced plant species in the new range become colonized by natural soil-borne enemies (Dostál *et al.*, 2013), which might lead to future studies showing how soil management of the invaded range might help prevent, or control invasiveness of exotic plant species.

Introduced exotic species can be a real pain for local biodiversity, ecosystem functioning and the services that humans derive from ecosystems, but they also provide opportunities for ecologists to learn more about factors that may control abundance of individual species in natural and managed ecosystems. The contribution of the study by Michael Gundale and colleagues (Gundale *et al.*, 2014a) is that it firmly demonstrates that introducing *P. contorta* from Canada into Sweden has liberated the trees from soil-borne pathogenicity. This result should create awareness among Swedish foresters that managing the biotic and abiotic conditions of their forest soils might make the difference between a useful species or an exotic invader. Potential threats of this species are well documented in several places, including South America (Gundale *et al.*, 2014b) and New Zealand (Nuñez & Dickie, 2013) (Fig. 1). The results by Gundale *et al.* (2014a) will stimulate ecologists to further understand the role of soil biota in natural and semi-natural ecosystems, which will ultimately provide spin-offs for managing agro- and forest ecosystems in a more sustainable way.

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