



The impact of spatial isolation and local habitat conditions on colonization of recent forest stands by ectomycorrhizal fungi



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ABSTRACT

Successful colonization of empty habitat patches depends both on the capacity of a species to reach the patch and its ability to establish and persist. Getting better insights into the various factors that affect colonization success is especially relevant in the context of restoration projects that aim at restoring biodiversity in newly created habitats like afforestation. While it is generally known that soil microbial communities play a key role in forest ecosystems, it remains largely unknown how they recover in recently restored forests on former agricultural land. Here, we used next-generation sequencing to investigate how spatial isolation and abiotic conditions affected the diversity and composition of ectomycorrhizal fungal communities in recent forest stands. Soil samples and roots of *Quercus robur* were sampled in ancient forest stands and recent stands both adjacent and spatially isolated from the ancient stands. Our results showed that ectomycorrhizal fungal community composition was affected by a combination of isolation and local soil conditions. Although communities of recently restored forest stands more resembled those of ancient stands when they immediately bordered ancient forest, there were still significant differences in community composition, most likely as a result of differences in edaphic conditions. Isolated stands had a significantly lower diversity and were mainly colonized by highly dispersive species. Overall, these results indicate that ectomycorrhizal fungal communities may develop faster in recent forest stands connected to ancient forest than in isolated stands, and that isolated stands may remain impoverished for many decades or even for indeterminate time.

1. Introduction

Anthropogenic activities over the last few centuries have severely reduced and fragmented natural habitats around the world (Meyer and Turner, 1992; De Keersmaecker et al., 2015; Lewis et al., 2015). The resulting decline in biodiversity has sparked many initiatives to mitigate biodiversity loss through restoring habitats on formerly agricultural and degraded land. The Bonn Challenge, for example, aims to restore 150 million hectares of degraded and deforested lands by 2020 (Bonn Challenge, 2011). However, whether species will be able to successfully colonize these newly created habitat patches remains to be seen (Huxel and Hastings, 1999).

Successful colonization of an empty habitat patch by a species depends both on its capacity to reach the patch and its ability to establish and persist (Palmer et al., 2008). Although recovery of biodiversity following afforestation has predominantly been studied on floral and faunal groups (Meli et al., 2017), most these studies indicate that many

species fail to colonize recently established forest patches and that full species recovery may therefore take several decades or even centuries (Flinn and Vellend, 2005; Hermy and Verheyen, 2007). Both dispersal limitation, i.e. the inability of an organism to travel large distances across a hostile landscape matrix, and recruitment limitation, i.e. the inability of an organism to establish and reach adulthood, have been considered to be important hurdles for forest biodiversity recovery following afforestation (Honnay et al., 2002; Verheyen et al., 2003; Flinn and Vellend, 2005; Baeten et al., 2008; Löhmus et al., 2014). Post-agricultural recent forests typically differ from ancient forests in terms of edaphic factors, which can enhance recruitment limitation (Verheyen and Hermy, 2001). The former generally have elevated soil pH and P levels, and lower soil organic matter, C and N concentrations (Hooker and Compton, 2003; Ritter et al., 2003; Falkengren-Grerup et al., 2006; De Schrijver et al., 2012; De Keersmaecker et al., 2013). These soil characteristics can both directly and indirectly (via microbiological processes) affect species establishment and survival (de la Peña et al.,

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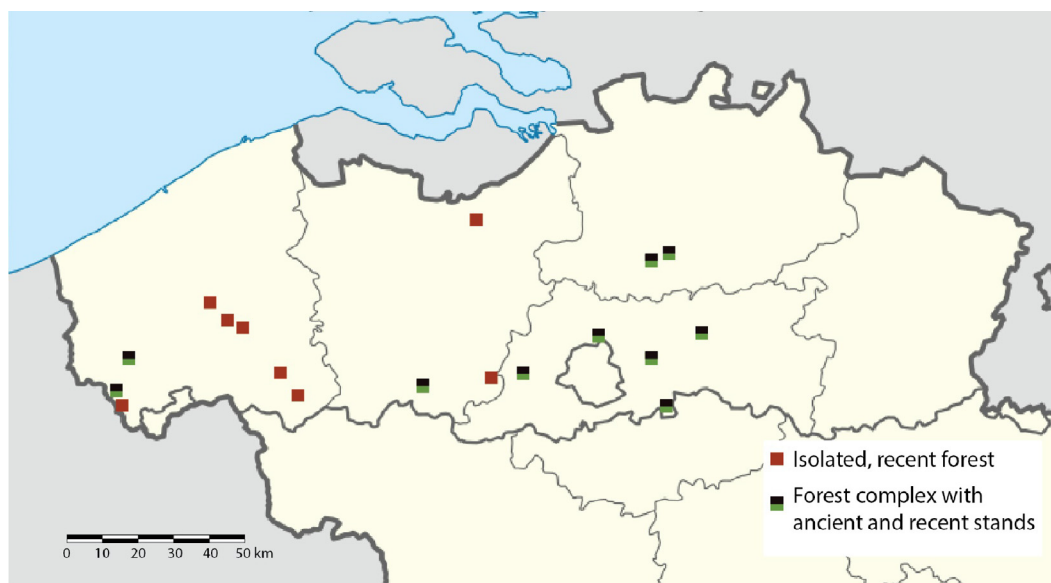


Fig. 1. Sampling took place in 18 forest complexes across the northern part of Belgium. In 10 forests both recent stands (< 45 years old) and ancient stands were sampled (black-green squares). The other 8 forests were recent forest stands (< 45 years old) isolated from ancient forest (red squares). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2016; Wooliver et al., 2016).

Whereas the factors that affect plant and animal species composition of ageing forests on former agricultural land have been relatively well studied (Flinn and Vellend, 2005; Hermý and Verheyen, 2007), much less is known about the recovery of the soil microbial communities (Sun et al., 2017). Yet, soil microbial communities play key roles in forest ecosystems, including regulating nutrient cycles and interacting with and connecting the root systems of plant species (Baldrian, 2017). One important functional group within the forest soil microbiome are ectomycorrhizal (EcM) fungi (Bahram et al., 2011; Tedersoo et al., 2012; Peay et al., 2016). As obligate symbionts of many dominant tree species in boreal and temperate forests, EcM fungi are indispensable components of forest ecosystems (Smith and Read, 2008). They mobilize inorganic nutrients from the soil and transfer them to their host in exchange for carbon (Read and Perez-Moreno, 2003), and they protect the host root system against pathogens, resulting in positive plant-soil feedbacks (Bennett et al., 2017).

Due to their small propagule size, enabling long-distance wind dispersal, and their mass propagule production, micro-organisms, including EcM fungi, have long been considered not to be dispersal-limited (Baas Becking, 1934; Finlay and Clarke, 1999). However, recent research has shown that effective dispersal of fungi may be more limited than expected (Peay et al., 2007, 2010, Norros et al., 2012, 2015). This is due to the strong decrease of the spore loads with distance from the fruiting body (Galante et al., 2011), and hence from the forest edge (Peay et al., 2012). Furthermore, EcM fungal spores have low germination rates in the absence of host roots, and even in the presence of host roots, they vary widely in how long they remain viable and retain their germination capacity (Ishida et al., 2008; Nara, 2009). After germination, the haploid mycelium of most EcM fungi need to fuse with another, sexually compatible haploid mycelium, in order to be able to establish and form functioning mycorrhiza (Horton, 2017). Additionally, some EcM fungi form below-ground fruiting bodies which depend on animals for dispersal (Colgan and Claridge, 2002). As a result, EcM fungal species can be expected to differ widely in their capacity to establish from spores (Newton, 1992), and pronounced differences in ectomycorrhizal fungal communities may arise between forest stands of different age and spatial isolation. As ectomycorrhizal fungi also differ in their capacity to, and preference for taking up different forms of soil nutrients (Erland and Taylor, 2002; Dickie et al.,

2013; Bogar and Peay, 2017), differences in edaphic factors (e.g. pH, soil moisture content, accumulation in soil organic material) between forests of varying age can also be expected to affect EcM fungal community composition.

Here we studied how spatial isolation and environmental conditions affected ectomycorrhizal fungal diversity and community composition in recently (< 50 years ago) afforested stands. For this purpose, we compared ectomycorrhizal fungal communities between isolated recent stands and recent stands adjacent to ancient forest with those of ancient forest stands in order to differentiate between effects of isolation and effects due to differences in soil conditions. We hypothesized that EcM fungal communities of isolated recent forest stands are less diverse and dominated by species that establish easily from spores due to dispersal limitation, while EcM fungal communities from recent stands adjacent to ancient forests have already accumulated more fungi, and are therefore more diverse and more similar to those of ancient forest. Nonetheless, we still expect that ectomycorrhizal fungal communities differ between connected recent stands and ancient stands due to differences in environmental conditions, affecting recruitment.

2. Material and methods

2.1. Study system and sampling

The study was conducted in Flanders (Northern Belgium), a region with traditionally a low amount of forest cover (11% in 2000) and a low degree of forest continuity (only 16% of the forested area in 2000 was continuously present at least since 1775) (De Keersmaecker et al., 2015). Climatic conditions within the study area show very little variation, with temperatures ranging from 10 to 11 °C and average yearly rainfall from 700 to 900 mm (www.meteo.be). We selected 17 recently established (between 18 and 45 years old) forest stands and nine ancient forest stands (continuous forest land use since at least 1775) (Fig. 1). Nine of the recent forest stands were adjacent to ancient forest, and 8 were isolated from ancient forests (minimum, median and maximum distance from ancient forest: respectively 219, 1901 and 7605 m). The recent forest stands were all homogeneous stands of *Quercus robur* planted on former agricultural land, while the tree layer of the ancient forest stands was dominated by *Q. robur*, with admixtures of other tree species (*Acer pseudoplatanus*, *Betula pendula*, *Castanea sativa*, *Fagus*

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