



Effects of host species, environmental filtering and forest age on community assembly of ectomycorrhizal fungi in fragmented forests

Margaux Boeraeve*, Olivier Honnay, Hans Jacquemyn

Department of Biology, Plant Conservation and Population Biology, KU Leuven, B-3001, Leuven, Belgium

ARTICLE INFO

Article history:

Received 30 March 2018

Received in revised form

30 July 2018

Accepted 6 August 2018

Corresponding Editor: Karina Engelbrecht Clemmensen

ABSTRACT

Understanding the assembly of biological communities in space and time is a major goal in community ecology. While most studies have focused on community assembly patterns in macro-organisms, there are comparatively few studies on micro-organisms. Here, we investigated how communities of ectomycorrhizal (EcM) fungi assemble in fragmented forests. We used a space-for-time substitution as an alternative for long-term studies to investigate variation in EcM fungal communities in three host species collected from 41 forest patches of different ages. Metabarcoding of root samples revealed that community composition was affected by a combination of host plant, soil variables, and forest age. While there were no clear effects of forest age on EcM fungal communities in early-successional tree species alder and hawthorn, forest age did affect the EcM fungal communities in hazel, which is typically associated with ancient forest. EcM fungal communities in early-successional species were affected mostly by soil conditions.

© 2018 Elsevier Ltd and British Mycological Society. All rights reserved.

1. Introduction

A major goal in ecology is to explain patterns of species diversity and community composition. The importance of both local and regional processes in structuring natural communities is well documented, and a large number of hypotheses (for a list of 120 different hypotheses see Palmer, 1994) have been put forward to explain the occurring variation in species richness and community composition (e.g. Zobel, 1992; Schluter and Ricklefs, 1993; Huston, 1994; Weiher and Keddy, 1995; Roughgarden, 2009). In an attempt to unify the various theories that have aimed at conceptualizing community ecology, Vellend (2010) recognized four key processes: selection among species, drift, speciation and dispersal (see also Vellend (2016)). These processes are analogous to the four central processes in population genetics theory, *i.e.* selection within species, drift, mutation, and gene flow. While Vellend's framework originally focused on macro-organisms such as animals and plants, it can also be applied to microbial communities (Nemergut et al., 2013). Micro-organisms have generally been considered to have very high dispersal capacities (Finlay and Clarke, 1999; Finlay, 2002; Darcy et al., 2011) and therefore to be latently present

around the globe, appearing wherever environmental conditions are suitable (Baas-Becking's hypothesis (1934): 'everything is everywhere, but the environment selects'). Micro-organisms were thus assumed not to be dispersal limited and only to be affected by selection through abiotic filtering. However, recent studies have shown that this is not necessarily the case (e.g., Martiny et al., 2006, 2011), and that the relative effects of environmental factors on community composition vary across spatial and temporal scales (Nemergut et al., 2013).

Ectomycorrhizal (EcM) fungi represent an important ecological group, both ecologically and economically. They are made up of microscopic structures (hyphae), produce spores and therefore can be categorized as micro-organisms, notwithstanding the large genet size or fruit bodies of some species (Bergemann and Miller, 2002; Boddy and Jones, 2007). Although they associate with only a small proportion of plant species (ca. 2%), EcM are the dominant mycorrhizal type in temperate, boreal and some tropical forests (Smith and Read, 2008; Brundrett, 2009; Tedersoo et al., 2010; van der Heijden et al., 2015). As root symbionts, they increase nutrient uptake of their hosts, provide protection against soil pathogens (Bennett et al., 2017), and therefore are critical to the structuring of plant communities. However, how ectomycorrhizal communities disperse and assemble in current-day landscapes remains poorly understood (Horton, 2017). Particularly in landscapes that consist of habitat patches of different age, land use history and local growth

* Corresponding author.

E-mail address: margaux.boeraeve@kuleuven.be (M. Boeraeve).

conditions, little is known about how ectomycorrhizal communities assemble in space and time and how this is affected by environmental variables (Bahram et al., 2015). Previous research has shown that, although these root-associated symbionts show large differences in dispersal capacity, even highly dispersive species show rapidly decreasing spore loads with increasing distance from source patches (Peay et al., 2012). As a consequence, EcM fungal communities in newly established habitats may be highly affected by dispersal limitation (Peay et al., 2010) and it is therefore not unlikely that spatial isolation and overall landscape connectivity contribute to EcM fungal community assembly (Peay and Bruns, 2014; Vannette et al., 2016; Boeraeve et al., 2018).

Apart from dispersal, selection, both through biotic interactions and environmental filtering, may affect the assembly of EcM fungal communities. Obviously, the main selecting agent is the presence of a suitable host (Ishida et al., 2007; Buée et al., 2011; Urbanová et al., 2015; Vincenot and Selosse, 2017). While most EcM plant species associate with a broad range of phylogenetically diverse EcM fungi, EcM fungi vary greatly in their host range (Molina et al., 1992; Smith and Read, 2008; van der Heijden et al., 2015). For example, *Laccaria amethystina* and *Tricholoma scalpturatum* are species with a very broad host range (Roy et al., 2008; Christensen and Heilmann-Clausen, 2013), while species such as *Tricholoma cingulatum* (*Salix*), *Lactarius pyrogalus* (*Corylus*) and *Cortinarius ammophilus* (*Salix repens*) only associate with one genus or even one single species (Arnolds and Kuyper, 1995; Heilmann-Clausen et al., 2000). Furthermore, EcM fungi do not only interact with their host, but also with other soil organisms, including other EcM fungi (Kennedy, 2010), saprotrophic fungi (Cairney and Meharg, 2002), soil fauna (Anslan et al., 2018), and soil bacteria (Kluber et al., 2011; Barbieri et al., 2012), and priority effects can have a major impact on final community composition by altering competitive interactions between EcM fungi (Kennedy et al., 2009). Apart from biotic interactions, abiotic factors such as soil moisture, nutrient availability and pH also affect EcM fungal community composition (Suz et al., 2014; Erlandson et al., 2015).

The general aim of this study was to (i) investigate patterns of ectomycorrhizal fungal community composition in forest patches of different age which occur as islands in an agricultural landscape matrix, and (ii) assess the relative importance of dispersal limitation and selection through both biotic interactions with the host plant and abiotic filtering in the assembly of EcM communities. We hypothesized that, if ectomycorrhizal fungi are dispersal limited, EcM community composition is significantly affected by forest age, with the youngest forest patches being dominated by species with high dispersal capacities, while the communities of older forest patches also comprise more slowly dispersing species. If, on the other hand, local environmental conditions or host type are the main factors determining ectomycorrhizal community assembly, differences in ectomycorrhizal communities are mainly caused by biotic and abiotic factors, and to a lesser extent by the dispersal capabilities of the fungi. To test these predictions, we used amplicon sequencing of the ITS1 rDNA region using Illumina MiSeq to identify the EcM community composition of three different host tree species that were sampled across a set of 41 fragmented forest patches of different age and covering a gradient in abiotic factors.

2. Materials & methods

2.1. Study species

Three different tree species that display different affinities to ancient forests were selected to investigate patterns of community assembly of ectomycorrhizal fungi in fragmented forest patches. Whereas alder (*Alnus glutinosa*) shows no specific

affinities to forest age and can rapidly colonize newly established forest patches, hazel (*Corylus avellana*) is considered a typical ancient-forest plant species that only colonizes forest patches late in the succession stage (Honnay et al., 1998; Hermy et al., 1999). Although hawthorn (*Crataegus monogyna*) may show higher abundance in ancient forest (Dupouey et al., 2002), it is usually not considered a typical ancient-forest species in our study region (Hermy et al., 1999; Jacquemyn et al., 2003). Moreover, the three species are known to differ in the specificity of their EcM communities. While the EcM fungi associated with *Alnus* are highly specialized (Rochet et al., 2011), *Corylus* has only a few (known) specialist fungi (e.g. *L. pyrogalus* (Heilmann-Clausen et al., 2000)). For the third host species, hawthorn (*C. monogyna*), the specificity of EcM interactions is unknown, although previous research has shown that the species does form associations with EcM fungi (Newton and Haigh, 1998).

2.2. Study area

Sampling took place in 41 forest fragments located in central Belgium, 20 km east of Leuven (50°51'60"N, 4°56'50"E), in a study area of c. 50 km² (Fig. S1, see Jacquemyn et al. (2003) for more details). The forests in this study vary from wet forests on loamy, poorly drained soils classified as Alno-Padion forests in the valley of the river Velpe and its tributaries to forests on the hills bordering the valley with sandy loam, well drained, acidic soils that belong to the Quercion alliance. Based on nine historic topographic maps, the oldest one going back to 1775, the age of each of the selected forest fragments was determined and they were assigned to four age classes: <50, 50–100, 100–200 and >200 years old (Jacquemyn et al., 2001).

2.3. Sampling

Forests were selected evenly over the gradient in environmental characteristics (from wet, loamy soils to dry, sandy loam soils) and over the four age classes. Tree species composition generally varied with soil conditions, but sampling was conducted in such a way that variation in tree species composition within sampling plots was minimized. In the wettest forests, the tree layer consisted mostly of *Populus x canadensis* (AM and EcM), *Fraxinus excelsior* (AM), *A. glutinosa* (AM and EcM) and *Quercus robur* (EcM) and in the drier forests the tree layer was made up mostly from *Q. robur* (EcM), *Betula pendula* (EcM) and *Sorbus aucuparia* (EcM). In each forest fragment, a plot of 10 by 10 m was established in which root samples from one individual of alder (*A. glutinosa*), hazel (*C. avellana*) and hawthorn (*C. monogyna*) were taken. Plots were established 10 m away from the forest edge to exclude edge effects. As not every host was present in every forest, in some plots only one or two hosts were sampled. As alder was only found in the wettest forests, it was sampled only 20 times, while hazel and hawthorn were sampled 40 times. Root samples were taken by digging along a large root starting from the base of the tree towards the finest roots to ensure the sampled roots were from the selected host plant. The fine roots were visually inspected and 10 roots of around 5 cm were put in paper bags with silica gel. This was repeated three times on one tree, to better represent the diversity within one individual tree. All fine roots were collected within a 2 m radius of the tree and within the upper 20 cm of the soil and pooled in one sample per tree. Overall, we collected 20 pooled root samples from alder, and 40 pooled root samples from hawthorn and hazel resulting in a total of 100 root samples (Table 1).

Additionally, five soil samples for chemical analysis were randomly taken in each plot, pooled in a plastic bag and stored on ice. Samples were stored up to 4 days before processing.

Download English Version:

<https://daneshyari.com/en/article/11030860>

Download Persian Version:

<https://daneshyari.com/article/11030860>

[Daneshyari.com](https://daneshyari.com)