



## Similar biodiversity of ectomycorrhizal fungi in set-aside plantations and ancient old-growth broadleaved forests



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### ARTICLE INFO

#### Article history:

Received 11 September 2015

Received in revised form 27 November 2015

Accepted 3 December 2015

Available online 18 December 2015

#### Keywords:

Ectomycorrhizal fungi

Oak

Old-growth

Overmature

Planted forest

Set-aside

Species richness

Sporocarp

### ABSTRACT

Setting aside overmature planted forests is currently seen as an option for preserving species associated with old-growth forests, such as those with dispersal limitation. Few data exist, however, on the utility of set-aside plantations for this purpose, or the value of this habitat type for biodiversity relative to old-growth semi-natural ecosystems. Here, we evaluate the contribution of forest type relative to habitat characteristics in determining species richness and composition in seven forest blocks, each containing an ancient old-growth stand (>1000 yrs) paired with a set-aside even-aged planted stand (ca. 180 yrs). We investigated the functionally important yet relatively neglected ectomycorrhizal fungi (EMF), a group for which the importance of forest age has not been assessed in broadleaved forests. We found that forest type was not an important determinant of EMF species richness or composition, demonstrating that set-aside can be an effective option for conserving ancient EMF communities. Species richness of above-ground EMF fruiting bodies was principally related to the basal area of the stand (a correlate of canopy cover) and tree species diversity, whilst richness of below-ground ectomycorrhizae was driven only by tree diversity. Our results suggest that overmature planted forest stands, particularly those that are mixed-woods with high basal area, are an effective means to connect and expand ecological networks of ancient old-growth forests in historically deforested and fragmented landscapes for ectomycorrhizal fungi.

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### 1. Introduction

High structural diversity and long continuity of old-growth forests make them irreplaceable biodiversity resources (Gibson et al., 2011; Spake et al., 2015). Planted or regenerated forests of relatively young and even age now constitute 73% of total forest cover in Europe (San-Miguel-Ayanz et al., 2011). Throughout Europe, timber-orientated forest management has shortened forest stand development to just 10–40% of the potential lifespan of dominant tree species (Bauhus et al., 2009; Barbati et al., 2012). These forests consequently lack the continuity and many of the structural attributes typical of old-growth forests, including high variation in tree size, the presence of large dying trees and irregular gap size and distribution (Bauhus et al., 2009).

Concern about the global decline of old-growth forest and the associated loss of biodiversity has motivated initiatives to increase the area of protected old-growth (CBD, 2011). Although strict protection of natural forests will likely remain a conservation priority throughout the world, management options increasingly recognise the additional potential for other types of forests to support biodiversity (Gibson et al., 2011; Putz et al., 2012). Presently, there is much interest in the setting aside of overmature planted stands as a means of preserving species associated with old-growth forests (Humphrey, 2005; Lassauce et al., 2013). Set-aside is a topical forest management strategy in Europe, where countries generally have a greater area of even-aged planted forests approaching biological maturity than old-growth forest (Barbati et al., 2014). The ageing of even-aged forest stands is a continuous process in which small-scale disturbances shape forest structural diversification (Barbati et al., 2012), with consequences for biodiversity conservation, carbon storage and the ways energy, gases and nutrients are cycled through the forest (Parker et al., 2004).

Species associated with old-growth forest are predicted to accumulate over time in set-aside in response to the increasing structural diversification as a forest ages. The temporal continuity and ever-

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enriching diversity of resources particularly favours colonisation by the dispersal-limited species characteristic of old-growth forest (Norden and Appelqvist, 2001). Indeed, several studies of dispersal-limited groups have demonstrated that ecological communities from older forests are generally, but not invariably, richer than those of more recent forests. For example, Peterken (1974) and Rose (1974) showed that the occurrences of certain vascular plants and epiphytic lichens could distinguish ancient semi-natural forests (old-growth forest that has been continuously wooded since 1600 A.D.) from more recent, secondary forest stands. Whilst differences in species composition between ancient and more recent forests can be attributed to differences in stand structure and microhabitat composition, many studies emphasise the importance of time per se; evidenced by certain species being absent from young forests despite the presence of suitable habitats (Norden and Appelqvist, 2001). For example, many cyanobacterial macrolichens are rare in recent stands even if seemingly suitable substrate is available (Kuusinen, 1996). It is therefore thought to be the longer residence time that is important in allowing dispersal limited species to reach and establish in a habitat (Norden and Appelqvist, 2001).

Despite the perceived importance of overmature planted forest in supporting old-growth forest communities, empirical data are lacking on their relative biodiversity values for many taxonomic groups (Sverdrup-Thygeson et al., 2015). A recent meta-analysis synthesising species richness relationships with stand age in temperate and boreal forests demonstrated functional group-specific responses to stand age, owing to specific dependencies on resources or environmental conditions that become available at different times during succession (Spake et al., 2015). This synthesis showed that species richness in planted and regenerating forests can eventually achieve equivalence to old-growth forests for some functional groups, including epiphytic lichens and fungi. Compositional differences have yet to be investigated, however, and the potential for planted forests to support old-growth forest communities remains poorly understood. Here we investigate empirically the value of planted, economically overmature forests to ectomycorrhizal fungal communities, relative to ancient old-growth forest in the New Forest National Park, UK.

Ectomycorrhizal fungi (EMF) comprise a functional group that forms mutualistic associations with most economically and ecologically important temperate tree species (Smith and Read, 2008). Approximately 90% of species rely on mycelial networks intimately connected with their roots, ectomycorrhizae, for the uptake of water and N, P, and other minerals from soil (Heilmann-Clausen et al., 2014). EMF form a highly diverse biota in boreal and temperate forests, which is sensitive to natural and anthropogenic disturbances, such as nitrogen deposition (Barker et al., 2013; Suz et al., 2014). High EMF diversity is important both to the vigour of individual hosts and to the functioning of the forest ecosystem. At the individual level, the diverse capacities amongst EMF species for mobilising nutrients from soil mineral and organic matter (Nygren et al., 2007) insure a host tree against environmental stresses (Courty et al., 2010). At the ecosystem level, EMF are not only important for nutrient cycling, but high EMF diversity can facilitate resistance to disease and drought (Kernaghan, 2005), and contribute to net primary productivity, mineral weathering and soil carbon storage (Smith and Read, 2008).

Whilst the relative biodiversity value of ancient old-growth and more recent secondary forest has been established for groups including vascular plants and epiphytic lichens (Rose, 1974; Peterken, 1974), we still lack sufficient empirical assessments of the relative biodiversity value of planted and old-growth forest for EMF. To date, studies have reported only from coniferous forest in North America (e.g. Kranabetter et al., 2005; Twieg et al., 2007), where they show that EMF exhibit much lower species richness in young secondary forests. Meta-analysis of these studies shows an average time of 90 years to recover EMF richness to old-growth values (between 45 years to unrecoverable at 95% prediction limits: Spake et al., 2015). No previous study has

examined EMF-stand age relationships in broadleaved forests with a statistically robust study design. Dispersal limitation is important in structuring EMF communities, despite the fact that fungal fruit bodies produce large numbers of spores with high potential for long distance travel (Peay et al., 2010). Indeed, red-lists and field observations suggest that numerous species are likely to be confined to old-growth forests due to infrequent dispersal (Dickson and Leonard, 1996; Senn-Irlet et al., 2007).

In historically deforested regions such as the UK, where the proportion of forest has declined to just 12% of total land area, ~80% of this forested area is planted and just 5% is classified as ancient (UK National Ecosystem Assessment, 2011), the setting-aside of planted forests presents a particularly pertinent opportunity for increasing the area of forest that can support the biodiversity and functions that characterise old-growth forests (Bauhus et al., 2009). The aims of this study were to (1) compare EMF biodiversity and species associations amongst overmature planted and ancient old-growth forest stands; and (2) determine what stand characteristics explain the differences in species richness and composition in order to identify opportunities for enhancing EMF diversity in overmature planted stands.

## 2. Methods

### 2.1. Study area

The study area was located in the New Forest National Park in southern England, UK (Figure A1.1). The New Forest lies within the Warm Dry climatic zone (Pyatt et al., 2001), with mild winters and warm summers. Temperatures range from 2.3 °C (mean February minima) to 20.8 °C (mean July maxima). Annual precipitation is 760 mm. Soils are mainly brown earths above Barton clays and Chama sands overlying Tertiary gravels. The old-growth forests in this study are ancient sensu Peterken (1977), in that they have originated before a threshold date of 1600 A.D.; a time before which secondary forests were rarely established through planting. In fact, the New Forest's ancient forests include remnants of post-glacial forest that have never been completely cleared (Tubbs, 2001), and the ancient stands under study all had stand continuity of >1000 years. They are also deemed semi-natural, in that they have been selectively felled for timber in the past, but allowed to regenerate naturally, without any major tree removal since the mid-20th century. The canopies of the ancient and planted stands under study are dominated by English oak (*Quercus robur*), sessile oak (*Quercus petraea*) and beech (*Fagus sylvatica*) with the understorey consisting largely of holly (*Ilex aquifolium*) (Tubbs, 2001).

The plantations under study were on average 180 years old. Plantation ages were considered equal to the number of years since planting (Table A1.1; Appendix A2). Plantations were established following clear-cutting of partially forested (deer parks) to completely forested grounds. All sites likely underwent the same preparation procedure following clear-cutting, involving the upturning of soil and trench formation for water drainage (see Appendix A2 for a detailed description). The management histories of the ancient old-growth stands under study were elucidated using historic maps, Forestry Commission management plans, pollen records and consultation with local experts. The stand ages refer to the oldest record available indicating that the site was forested (Table A1.1), and since then have not experienced major tree removal.

### 2.2. Study design

In order to compare EMF communities in overmature planted set-asides and ancient old-growth forest communities, locations were selected that paired forest types in a randomised block design (Hurlbert, 1984). Seven forest locations containing both a planted stand and an ancient stand were identified. In order to minimise extraneous variation, paired stands were matched for canopy species (oak dominated), elevation and underlying geology, and separated

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