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Land use influences soil fungal community composition across central Victoria, south-eastern Australia

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ABSTRACT

Current theory expects that fungi, on the one hand, are spatially ubiquitous but, on the other, are more susceptible than bacteria to disturbance such as land use change due to dispersal limitations. This study examined the relative importance of location and land use effects in determining soil fungal community composition in south-eastern Australia. We use terminal restriction fragment length polymorphism (T-RFLP; primer pair ITS1-F–ITS4) and multivariate statistical methods (NMDS ordinations, ANOSIM tests) to compare relative similarities of soil fungal communities from nine sites encompassing three locations (ca 50–200 km apart) and four land uses (native eucalypt forest, *Pinus radiata* plantation, *Eucalyptus globulus* plantation, and unimproved pasture). Location effects were generally weak (e.g. ANOSIM test statistic $R \leq 0.49$) and were, in part, attributed to minor differences in soil texture. By contrast, we found clear and consistent evidence of land use effects on soil fungal community composition ($R \leq 0.95$). That is, soils from sites of the same land use grouped together in NMDS ordinations of fungal composition despite geographic separations of up to ca 175 km (native eucalypt forests) and 215 km (*P. radiata* plantations). In addition, different land uses from the same location were clearly separate in NMDS ordinations, despite, in one case, being just 180 m apart and having similar land use histories (i.e. *P. radiata* versus *E. globulus* plantation both established on pasture in the previous decade). Given negligible management of all sites beyond the early establishment phase, we attribute much of the land use effects to changes in dominant plant species based on consistent evidence elsewhere of strong specificity in pine and eucalypt mycorrhizal associations. In addition, weak to moderate correlations between soil fungal community composition and soil chemical variables (e.g. Spearman rank correlation coefficients for individual variables of 0.08–0.32), indicated a minor contributing role of vegetation-mediated changes in litter and soil chemistry. Our data provide evidence of considerable plasticity in soil fungal community composition over time spans as short as 6–11 years. This suggests that – at least within geographic zones characterised by more-or-less contiguous forest cover – soil fungal community composition depends most on availability of suitable habitat because dispersal propagules are readily available for colonisation after land use change.

1. Introduction

Spatial patterns in soil microbial composition provide clues to the factors that regulate soil biota and – given close feedbacks between above- and below-ground biota – to the factors that influence plant and ecosystem function (Ettema and Wardle, 2002; Wardle et al., 2004). At an ecosystem-level, the potential drivers of soil microbial patterns can be broadly classified as population processes (i.e. passive dispersal) or environmental factors (e.g. soil texture, topography, vegetation system; Ettema and Wardle, 2002). These are either constrained by location (e.g. proximity of dispersal propagules, soil parent material), or more widely distributed (e.g. broad vegetation type). Overlain are effects of disturbance, either through direct manipulation of the soil or through changes in plant community composition due to, for example, land use change (Ettema and Wardle, 2002; Hedlund et al., 2004).

A recent view argued that microbial eukaryotes such as fungi are ubiquitously distributed due to their great abundance, short generation times, and potentially high dispersal rates (Finlay, 2002). According to this view, fungal geographical distributions will mostly depend on availability of habitat since propagules are always available to take advantage of suitable conditions (Fenchel, 2003). This 'everything is everywhere' view was supported by evidence of global geographic ranges of some morphologically

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defined fungal 'species' (Taylor et al., 2006). However, recognition of fungal types using genetic rather than morphological methods, provided evidence of multiple phylogenetic species per morphological type (e.g. Pringle et al., 2005), and of previously unknown levels of endemism (Taylor et al., 2006). Further evidence of geographic limits in fungal distribution came from a DNA-based study of soil fungal patterns, which found consistent decreases in similarity of ascomycete fungi populations with distances ranging from 1 m to 100 km – indicating 'at least some geographical differentiation' (Green et al., 2004). Indeed, Hedlund et al. (2004) predicted that the less efficient dispersal and colonising abilities of fungi relative to bacteria – particularly mycorrhizal fungi – would render them susceptible to land use change involving habitat loss. Thus, we might expect that soil fungal community composition will vary according to both location and land use, and that these two effects might interact given that different locations can have different capacities for recolonisation after land use change (e.g. landscapes characterised by widespread clearing of native vegetation).

Studies comparing fungal composition among different soils have been largely equivocal on the relative contributions of land use effects (e.g. dominant plant species) and location effects (e.g. soil texture – usually land use independent; De Koning et al., 2003). For example, Klamer and Hedlund (2004) concluded herbaceous plant composition did not influence soil fungal communities, but acknowledged that their study excluded predominant arbuscular mycorrhizal fungi. Elsewhere, soil fungal community composition was found to vary among floristically distinct forest ecosystems, but the relative effects of dominant plant species (through, e.g. litter quality, soil surface chemistry) and the physical environment, were not examined (McLean and Huhta, 2002; Myers et al., 2001). Nonetheless, at least two studies (both based on phospholipid fatty acid analysis) indicated greater influence of land use (i.e. forest species; forest versus crop) than location effects (soil type) on soil fungal community composition (Burke et al., 2003; Leckie et al., 2004).

Impacts of exotic plantation establishment on the soil environment are a land use issue of enduring interest both in Australia and elsewhere. A limited number of studies relevant to soil fungi have indicated plantation establishment led to concomitant changes in soil processes and decreases in either soil fungal dominance (*Eucalyptus* plantation in India; Behera and Sahani, 2003), or ectomycorrhizal richness (*Pinus radiata* plantation in Ecuador; Chapela et al., 2001). More recently in Australia, comparisons using DNA- and RNA- based molecular techniques between single sites of native forest and adjoining plantations (*Araucaria cunninghamii* or *Pinus elliotti*), indicated that plantation establishment significantly altered soil fungal community composition (He et al., 2005; Bastias et al., 2007). These changes occurred over time spans of ca 12–22 (Chapela et al., 2001; Bastias et al., 2007) and 30 years (Behera and Sahani, 2003), which are roughly comparable with other indications of 25–30 years for fungal community recovery after disturbance (McLean and Huhta, 2002; Hedlund et al., 2004).

Using soils from four land uses (including native eucalypt forest and two types of plantations) across three distant locations in south-eastern Australia, we examined the relative importance of location and land use in determining soil fungal community composition. We used the PCR-based fingerprinting technique Terminal Restriction Fragment Length Polymorphism (T-RFLP) for its benefits over similar DNA-based techniques and its strength in comparative analyses (Marsh, 1999; Thies, 2007). Multivariate ordination techniques were used to compare patterns in soil fungal community composition among locations and land uses, and to examine relationships with a range of soil variables that reflect potential effects of location (particle size distribution) or dominant vegetation (e.g. carbon fractions). Related aims were to examine the generality of changes in soil fungal community composition with establishment of exotic plantations, and to give further indication of the time spans over which such changes occur.

2. Methods

2.1. Study locations

Nine study sites were established across three locations (A, B or C as below) in central Victoria, south-eastern Australia, with distances between locations of 175 km (A–B), 215 km (A–C) and 50 km (B–C). Sites encompassed four land uses – native eucalypt forest (four sites), *P. radiata* D. Don plantation (three), *Eucalyptus globulus* Labill. plantations (one), and unimproved pasture (one). To control for potential effects of major differences in soil texture on fungal composition (e.g. confounding soil type with location effects), we restricted site selection to a narrow soil texture range ('silt loams', USDA classification scheme; after Minasny and McBratney, 2001). In addition, we constrained the climatic range of each location by sampling only adjoining land uses or those within a geographic area of <20 km^2. This meant (as indicated above) that our sampling design did not involve all combinations of location and land use.

Location A is on the southern arm of the Delatite River approximately 130 km north-east of Melbourne, Victoria (37°9′S, 145°58′E). The area is characterised by moderate to steep slopes (13–27°), with elevations ranging from 400 m to 420 m a.s.l. ('above sea level'). Underlying parent materials of study sites are sandstones of Late Silurian to Early Devonian age (Thomas, 1947), with yellow podzolics being the predominant soil type (Rundle, 1977; classification of soils and approximate equivalents throughout as per Moore et al., 1983). The area receives about 860 mm of rain per year, most of it falling in winter (June–August). Mean monthly maximum temperatures range from 14 °C (July) to 29 °C (January).

Location B is a native eucalypt forest within the Wombat State Forest, 85 km north-west of Melbourne (37°29′S, 144°05′E). Slopes are moderate (<15°) with elevations ranging from 625 m to 640 m a.s.l. Soils are yellow podzolics derived from Ordovician sedimentary rocks (Tolhurst et al., 1992). The annual average rainfall is 925 mm falling throughout the year with mean monthly maximum temperatures ranging from 7 °C (July) to 22 °C (February).

Location C is situated near the township of Dereel, 105 km south-west of Melbourne (37°49′S, 143°45′E). The study area is flat with an elevation of 324 m a.s.l. Soils are brown sodsols derived from Ordovician marine and Neogene sediments (Robinson et al., 2003). The climate is temperate, with an annual rainfall of 688 mm and mean monthly maximum temperatures ranging from 11 °C (July) to 25 °C (February).

2.2. Study sites within locations

Two sites each were sampled in native eucalypt forest and second rotation *P. radiata* plantation (sites ca 0.25 ha) at location A. The native forest is open-forest (Specht, 1981) dominated by a mix of eucalypts, principally *Eucalyptus polyanthemos* Schauer, *Eucalyptus melliodora* Cunn. ex Schauer, *Eucalyptus goniocalyx* F. Muell. ex Miq. and *Eucalyptus macrorrhyncha* F. Muell. ex Benth. The second rotation pines were established in 1995 within a year of harvesting the first rotation pines, that were felled at 28 (site 1) and 36 years of age (site 2). Both second rotation pine sites were planted at densities of 900–1000 stems ha^{-1} and were not thinned. Prior to plantation establishment, these areas were farmland originally cleared in the 1840s.

Within location B, sites were part of a long-term burning experiment (see Tolhurst and Flinn, 1992) and soils were collected from a 19 ha area known locally as 'Barkstead'. Sites (ca 0.25 ha)