



Variation in soil microbial communities associated with critically endangered Wollemi pine affects fungal, but not bacterial, assembly within seedling roots

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ABSTRACT

The critically endangered Wollemi pine (*Wollemia nobilis* W. Jones, K. Hill & J. Allen) has very low levels of recruitment in the wild. Wollemi pine grows on shallow soils of poor nutrient status and high acidity and is likely to be highly dependent on microorganisms such as mycorrhizal fungi and other microorganisms that contribute to nutrient cycling in soils. The microbial communities present in soil around wild Wollemi pine and the specificity of subsequent assembly in seedling roots has never been assessed. We analysed soil fungal and bacterial communities associated with wild Wollemi pine and neighbouring co-dominant, coachwood. Root-associated assemblages in seedlings were evaluated in the presence of inoculum collected from under Wollemi pine or coachwood (*Ceratopetalum apetalum*) in the field. Variation partitioning revealed that fungal and bacterial community assembly in soil were associated with different processes, with fungi more strongly influenced by spatial factors and bacteria influence equally by spatial and edaphic factors. Variation in soil microbial communities in the wild affected fungal, but not bacterial assembly in roots of Wollemi pine seedlings. Wollemi pine recruited a distinct bacterial community in its roots regardless of soil origin.

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1. Introduction

Wollemi pine (*Wollemia nobilis* W. Jones, K. Hill & J. Allen) is one of Australia's rarest tree species and is listed as critically endangered (Thomas, 2011). There are fewer than 100 Wollemi pines remaining in four stands in Wollemi National Park, Australia (Benson and Allen, 2007; NSW Department of Environment and Conservation, 2006a). Individuals within this population have been shown to have very low genetic variation (Peakall et al., 2003). Wollemi pine is an important conservation target as it has both taxonomic and cultural significance due to a long pollen and fossil history (Brodribb and Hill, 1999; Chambers et al., 1998; Macphail et al., 1995), has a high adaptability to cultivation (Trueman et al., 2007) and holds intrigue as 'the dinosaur tree' and

as a 'living fossil' (Offord, 1996). Rates of seed germination for Wollemi pine are highly variable in the wild, ranging from no germination in some years up to 60 seedlings in others (Zimmer et al., 2013). In the wild, recruitment bottlenecks exist during the transition from seedlings to juveniles, in particular it has been observed that growth and establishment of Wollemi pine seedlings is suppressed. Zimmer et al. (2013) found that in the wild, Wollemi pine seedling survival is low (65% die within their first year) but that survival of established juveniles is high, with 44% of established juveniles surveyed surviving a 16-year monitoring period.

The mechanism causing the observed bottleneck is unknown. Seedlings exist in the deep shade of adult trees and it has been hypothesised that low light availability, burial by litter, con- and heterospecific competition, soil pH, pathogens and a lack of beneficial microbial partners may be potential causes for this recruitment bottleneck (Offord et al., 1999). The remnant population grows on shallow soils of poor nutrient status and high acidity and are threatened by pathogens (Jones et al., 1995; NSW Department of Environment and Conservation, 2006a), suggesting that soil and endophytic microbial communities may be important

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for mediating interactions with the biotic and abiotic environment. To date, investigations into rhizosphere microbiota associated with Wollemi pine has focused on a limited survey of root-associated mycorrhizal fungi (McGee et al., 1999) with minimal focus on free-living fungi, endophytes and bacteria in the rhizosphere. The microbial community may improve plant growth and nutrition via mycorrhizal symbiosis (Smith and Read, 1997); improve resilience to environmental stresses such as drought, salinity and heat stress (Augé, 2001; Borowicz, 2001; Rodriguez et al., 2008) and help protect against soil pathogens (Azcón-Aguilar et al., 1997). The soil microbial community can also have detrimental impacts on a plant, for example, if plant pathogens are present (Bell et al., 2006; Bever, 1994; Mills and Bever, 1998; Packer and Clay, 2000). Altered plant growth and survival as a result of the microbial community can then impact plant community composition (Bever et al., 2010; Bever, 2003).

Wollemi pine grows in a dynamic system alongside other tree species such as coachwood (*Ceratopetalum apetalum*), Sassafras (*Doryphora sassafras*) and Lilly Pilly (*Acmena smithii*) with an understorey dominated by ferns such as *Blechnum cartilagineum* and *Sticherus flabellatus* var. *flabellatus* (Benson and Allen, 2007). Coachwood is a dominant tree species at the wild Wollemi pine site and on average has higher percentage coverage than Wollemi pine (Benson and Allen, 2007) and is known to form both ectomycorrhizal and arbuscular associations (McGee and Furby, 1992), which both differ morphologically to those which have been observed in Wollemi pine (McGee et al., 1999). Microbial communities can differ in soils under different plant species, with the effect of plant species occasionally being stronger than other important drivers such as soil type (Grayston et al., 1998; Urbanová et al., 2015), which will mediate the establishment of microbial communities within roots. Relationships between the microbial community composition and different drivers such as plant species or environmental variables can inform what roles these drivers play in determining the assembly of functionally important communities (Legendre et al., 2005; Peres-Neto et al., 2006).

Given the lack of information regarding the composition of soil- and root-associated microbial communities for Wollemi pine, which may constrain recovery efforts for the species, we engaged upon a survey of these communities and an experimental test of

their host specificity. The present study aims to address the following questions: (i) does Wollemi pine assemble a distinct microbial community in its own soil compared to soil of neighbouring co-dominant coachwood? (ii) What are the most important drivers of microbial community assembly in soil at the wild Wollemi pine site? and (iii) Does the origin of soil (con- or hetero-specific) influence the assembly of root microbial communities in Wollemi pine and neighbouring Coachwood? We hypothesise that Wollemi pine will harbour a species-specific microbial community in the wild due to plant species-specific changes to the soil microenvironment and that changes in the soil microbial community composition will influence the subsequent assembly of root microbial communities of seedlings.

2. Methods

2.1. Soil sampling for assessment of edaphic properties and soil microbial communities

Access to the wild Wollemi pine site is restricted as it is declared critical habitat (NSW Department of Environment and Conservation, 2006b). Soil sampling was conducted by an authorised member of the Wollemi pine Recovery Team to ensure that existing site management was not compromised.

Approximately 200 g of soil was sampled from three separate locations under the canopy of six adult Wollemi pine and eight adjacent coachwood (42 independent samples). All samples were received at Hawkesbury Institute for the Environment three days after collection in the remote field site and were processed immediately to limit changes between sample collection and data collection (although some disturbance intolerant species may still have been affected). For each of the 42 samples, three 1.5 mL soil samples were frozen at -80°C for molecular analysis. Remaining soil was air dried at 70°C for three days and analysed for pH, carbon (C), nitrogen (N), available phosphate (PO_4), air-filled porosity (AFP) and total water holding capacity (TWHC).

pH was measured on a soil: water slurry (1:1) using a S20 SevenEasy pH Meter (Mettler Toledo, Columbus, OH, USA). 200 mg of soil that had been ground in a Mixer Mill MM 400 (Retsch, Haan, Germany) was used to analyse carbon and nitrogen

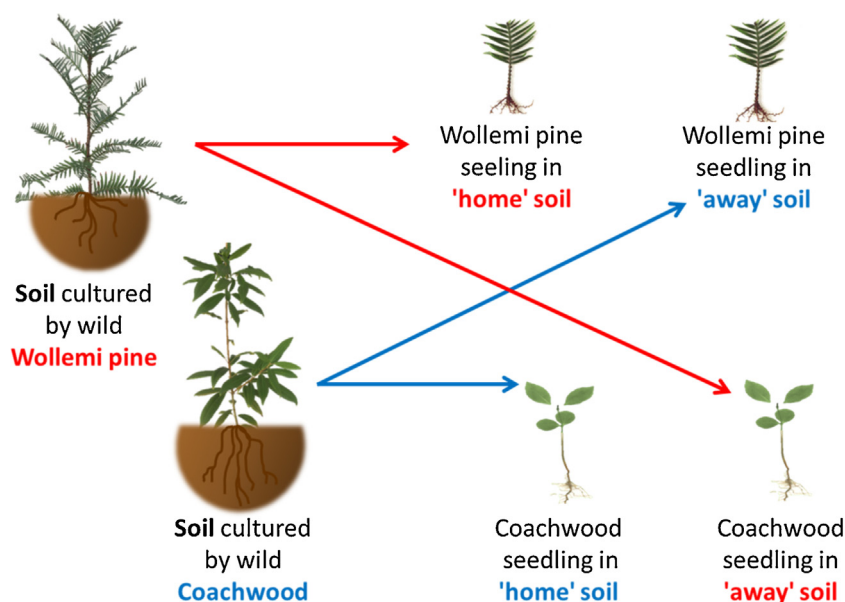


Fig. 1. Reciprocal inoculation experimental set-up. Soil was sampled in triplicate from underneath six adult Wollemi pine and eight adult Coachwood in the wild (total 42 samples). A small amount of this soil (containing native microbial communities) was used to inoculate seedlings of these species so that both were growing in their 'home' (conspecific) and 'away' (hetero-specific) soil.

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