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Deforestation strongly affects soil seed banks in eucalypt forests: Generalisations in functional traits and implications for restoration

Trevor L. Meers [a,1], Neal J. Enright [b,2], Tina L. Bell [a,3], Sabine Kasel [c,*]

[a] Department of Forest and Ecosystem Science, University of Melbourne, Water Street, Creswick, Victoria 3363, Australia
[b] Geography Program, University of Melbourne, Parkville, Victoria 3010, Australia
[c] Department of Forest and Ecosystem Science, University of Melbourne, 500 Yarra Boulevard, Richmond, Victoria 3121, Australia

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ABSTRACT

We examined the potential role of the soil seed bank in restoration of an open eucalypt forest community following land-use change involving clearing of native eucalypt forest for grazing and subsequent abandonment, and for establishment of *Pinus radiata* plantation. We used plant functional traits responsive to disturbance and other traits associated with the capacity to re-colonise and form persistent seed banks as a means of assessing the effects of land-use change on soil seed banks. The soil seed bank and corresponding extant vegetation was surveyed within four replicated paired sites of fragmented native forest and abandoned farmland, and native forest and pine plantation. There was a significant difference in the composition of the soil seed bank for both land-use changes. Non-metric Multi-dimensional Scaling of plant attributes showed a clear separation of samples according to land-use type and between seed bank and extant vegetation. Cluster analysis of plant functional traits produced eight emergent groups. Phanerophytes were classified as either *Ant-dispersed shrubs and herbs*, *Ericoid heaths* or *Eucalypts*, perennial herbs were either *Vertebrate-dispersed species, Barochorous annuals and herbs* or *Small-seeded hemicryptophytes* and the remaining species were *Wind-dispersed species* or *Small-seeded annuals*. *Small-seeded annuals* dominated the soil seed banks and native phanerophytes with low specific leaf area, resprouting, ant-dispersal, large seed, and ericoid mycorrhizal and ectomycorrhizal associations formed a minor component of the soil seed bank for all land-use types. Sørensen Similarity between the vegetation and soil seed bank was low across all land-use types and was explained by the dominance of annuals in the soil seed bank and perennial species in the extant vegetation. Indicator species analysis revealed an increase in *Wind-dispersed species*, *Barochorous species* and *Small-seeded annuals* in the soil seed bank relative to extant vegetation. Trait associations include a therophyte life form (of predominantly introduced species) with high specific leaf area, small round seed, a seeder fire response, and arbuscular or non-mycorrhizal associations. Underlying axes in trait variation indicate seed banks were dominated by traits associated with the rapid acquisition of resources or the ability to respond rapidly to disturbance that provided for large and persistent stores of introduced ruderal species. In contrast, species excluded from the seed bank shared traits associated with the conservation of resources or ability to withstand environmental stress and were typical of native phanerophytes. These generalisable patterns in plant traits make it unlikely that eucalypt communities can be restored from the native soil seed bank alone.

1. Introduction

With increasing worldwide focus on restoration of degraded ecosystems (Chazdon, 2008; Choi et al., 2008) and improvement of biodiversity values in production landscapes (Brockerhoff et al., 2008; Scherr and McNeely, 2008), soil seed banks offer the potential to make a significant contribution to natural regeneration of vegetation communities (Bakker et al., 1996; Thompson et al., 1997; Grime, 2001). Whether the soil seed bank can assist restoration efforts depends, among other factors, on the richness and density of native species represented across successional groups, and of non-target or invasive species (Halpern et al., 1999; Willson and Traveset, 2000; Lang and Halpern, 2007). Thus, knowledge of the composition of soil seed banks and shifts in plant traits due to land-use change and associated disturbance regimes can help to guide management strategies designed to promote the

* Corresponding author. Tel.: +61 3 9250 6868; fax: +61 3 9250 6886.
E-mail address: skasel@unimelb.edu.au (S. Kasel).

[1] Current address: Greening Australia, 333 Bennetts Road, Norman Park, Queensland 4170, Australia.
[2] Current address: School of Environmental Science, Murdoch University, Murdoch, Western Australia 6150, Australia.
[3] Current address: Faculty of Agriculture, Food and Natural Resources, University of Sydney, Redfern, New South Wales 2015, Australia.

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germination of target species over non-target species. In turn, this will identify the need for more direct approaches to native species return such as broadcast seeding or planting (Yates and Hobbs, 1997; Standish et al., 2007; Prober and Smith, 2009).

Many forest species produce small quantities of short-lived seed. As such, the conditions in typical forest environments select for traits associated with high rates of seedling establishment at the expense of dispersal in space and time (Leishman and Westoby, 1994; Warr et al., 1994; Thompson et al., 1997; Hermy et al., 1999; Bossuyt and Hermy, 2001; Bossuyt and Honnay, 2008). This pattern is consistent with reports of low species similarity between the seed bank and extant vegetation of forested systems (Hopfensperger, 2007). In contrast, some authors have reported a relatively high component of late-successional species in the soil seed bank of certain forest types, explained by seed dispersal and dormancy characteristics of constituent species (Leckie et al., 2000) or disturbance regimes that provide for increased light availability, germination, and seed return to the soil (Mayer et al., 2004).

Soil seed banks associated with land-use change from native forest or with site degradation are often characterised by severe depletion of richness and abundance of native (especially woody) species. There is also a dominance of early successional species that persist in the soil seed bank or accumulate via dispersal (Warr et al., 1994; Halpern et al., 1999; Willson and Traveset, 2000; Roovers et al., 2006; Bossuyt and Honnay, 2008). This scenario is typical of soil seed banks in abandoned farmlands (Standish et al., 2007; Prober and Smith, 2009) and coniferous plantations that have replaced native forest (Halpern et al., 1999; Moles and Drake, 1999; Onaindia and Amezaga, 2000; Augusto et al., 2001). Moreover, early successional species are often dominated by introduced species so that the return of native species is contingent on establishment by other means (Amezaga and Onaindia, 1997; Moles and Drake, 1999; Wunderle, 1997; Hérault et al., 2005; Standish et al., 2007; Prober and Smith, 2009).

This study aimed to identify generalisable patterns in plant functional traits (*sensu* Violle et al., 2007) in response to land-use change and implications for the potential role of soil seed banks in restoration of native sclerophyll forest. We investigated two land-use change scenarios: clearing of native eucalypt forest for grazing and subsequent abandonment, and for establishment of *Pinus radiata* plantation. Earlier work examining the response of understorey vegetation to these two land-use change scenarios revealed a significant decline in the richness of native species, particularly ant-dispersed species (Meers et al., 2008, 2010b). Further, for abandoned farmland there was an increase in introduced annuals and vertebrate-dispersed species and a decrease in resprouters and clonal, non-rosette herbs relative to native forest (Meers et al., 2008). Both outcomes suggest that the soil seed bank may be compromised in terms of restoration potential.

We examined both the response of individual traits to land-use change and groups of species exhibiting correlations between a set of plant traits via emergent groups (*sensu* Lavorel et al., 1997). The application of emergent groups recognises that local and regional management variables apply to the whole plant, i.e. the combination of traits, rather than each trait separately. This approach provides results that are readily applicable to other regional areas and supporting different pools of species (Hérault et al., 2005). We address the following broad questions:

- Are there differences in the seed density and composition of the germinable soil seed bank following land-use change and, if so, what are they?
- How does the soil seed bank compare to extant vegetation?
- What is the potential of soil seed banks to contribute to the regeneration of native forest species?

2. Materials and methods

2.1. Study site

The Delatite Peninsula is located on the northern slopes of the Great Dividing Range in north-eastern Victoria, Australia (145° 58′ E, 37° 8′ S) and has a steeply dissected topography with altitude ranging from 300 to 500 m above sea level. Annual rainfall is approximately 850 mm and falls mainly in winter and spring (Bureau of Meteorology, 1887–2003). Mean monthly maximum temperature ranges from 12.0 °C in July to 29.0 °C in February, with corresponding mean monthly minimum temperatures ranging from 3.5 to 12.5 °C. Native vegetation consists of open eucalypt forest with a sparse understorey of sclerophyllous shrubs, grasses and herbs (Specht, 1981). Details about site history and land-use change are provided in Meers et al. (2008).

2.2. Site selection and survey

Soil seed bank and vegetation surveys were conducted in a series of replicated paired sites of (1) native forest and abandoned farmland and (2) native forest and pine plantation. The same paired sites were used previously for analysis of vegetation and plant functional traits (Meers et al., 2008, 2010b), but the research presented here represents the first report and interpretation of seed banks in relation to plant traits and disturbance regimes, and their comparison with extant vegetation. Sheep grazed the abandoned farmland until the late 1970s and pine plantations were mature stands 36–38 years old. Land-use history was consistent within each paired land use, such that both abandoned farmland and pine plantation were formerly native forest. Boundaries between land-use types were distinct and verified from archival material (see Meers et al., 2008, 2010b). Our previous research showed that the native forest adjacent to abandoned farmland had a greater component of introduced species compared to native forest adjacent to pine plantation (Meers et al., 2008, 2010b). Therefore, for the purposes of this study, native forest sites adjacent to abandoned farmland (AF) are referred to as ‘fragmented native forest’ (FNF), while sites adjacent to pine plantation (PP) are referred to as ‘native forest’ (NF). This distinction more accurately reflects a continuum of disturbance.

Paired sites were located 100 m from the land-use boundary to reduce the possible effect of short-distance dispersal events on vegetation composition (dispersal over a distance greater than 100 m is considered long-distance dispersal; Cain et al., 2000). A total of four paired sites were established for each comparison. Each site consisted of a 56 × 56 m plot within which three 7 × 7 m quadrats were randomly positioned. Pine sites were located within four separate compartments of pine plantation that ranged from 58 to 166 ha. Abandoned farmland sites were scattered within 3300 ha of abandoned farmland that formed a distinct land-use boundary with native forest. Both FNF and NF sites were located within state forest adjacent to Lake Eildon National Park that spans 27,750 ha.

Vegetation of all sites was surveyed in autumn 2004. For each quadrat, the projected foliage cover of extant understorey vegetation was estimated according to the Domin Scale (Kershaw and Looney, 1985). Soil samples were collected at the same time to provide an estimate of the soil seed bank using the seedling emergence method. For this, surface leaf litter was removed and 50 soil cores to 5 cm depth (diameter 6.84 cm) were randomly sampled from each quadrat and bulked to represent a surface area of 0.184 m^2. Soil samples were sieved to 5 mm, concentrating the seed in a smaller volume of soil (Bossuyt et al., 2000).

In fire-prone Mediterranean-type plant communities such as the open sclerophyll forests within this study, the application of