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Succession of mosses, liverworts and ferns on coarse woody debris, in relation to forest age and log decay in Tasmanian wet eucalypt forest

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ABSTRACT

In managed forest landscapes, understanding successional processes is critical to management for sustainable biodiversity. Coarse woody debris is a key substrate for forest biodiversity, particularly because it undergoes complex succession reflecting the effects of changes in both forest structure and substrate characteristics. The present study used a chronosequence approach to investigate succession of mosses, liverworts and ferns on coarse woody debris following clearfell, burn, sow native forest silviculture in wet eucalypt forest in Tasmania, focussing on discriminating between the effects of forest age and log decay. It also compared successional processes following wildfire with those following clearfell, burn, sow silviculture. Forest regenerating after the latter form of regeneration showed clear ecological succession up to 43 years (the limit of available sites), characterised by increasing diversity and cover, and clearly delineated specialisation among species with regard to successional stage. Analyses of subsets of the full data-set indicated that the effects of forest age dominated this succession, with minimal effects of substrate change independent of forest age. Analysis of within forest microenvironments were consistent with the inference that microenvironmental changes related to forest age drive major successional changes in these forests. Comparative analysis indicated similarity between successional states in post-wildfire and post- clearfell, burn, sow regeneration after 43 years for logs of the same decay stages, and continuing succession on post-wildfire sites to at least 110 years. Overall, these data suggest that management to sustain fern and bryophyte diversity should ensure that areas of forest beyond 110 years are represented in the landscape at appropriate spatial scales.

1. Introduction

Planning to ensure sustainability of biodiversity in forest ecosystems managed for wood or pulp production requires an understanding of both the underlying ecological processes underpinning the natural dynamics of these systems and how these processes differ between managed and unmanaged systems. These factors are particularly salient considering that managed forests can support major components of regional biodiversity (Lindenmayer and Franklin, 2002; Pharo and Lindenmayer, 2009). This is most important in 'native forest' approaches to forestry, where native species are exploited using more-or-less natural regeneration.

Ecological succession is a key process underpinning the biodiversity consequences of managing native forests in many temperate parts of the world. In these systems, exploitation of many forests for wood and pulp involves major disturbance and regeneration that, in some ways, resembles the natural successional processes of these forests. For example, the wet eucalypt forests of South-Eastern Australia are largely dependent on intense wildfire for natural regeneration (Wells and Hickey, 1999), and there is evidence that clearfell, burn and sow (CBS) silviculture in these economically important forests resembles these natural processes in many ways (Attiwill, 1994), although there can be some clear differences. Thus, Ough (2001) showed that, 10 years after the regeneration fire, the structure and composition of post-wildfire forest can differ significantly from post-CBS forest in Victoria, Australia. In contrast, Hickey (1994) showed that in older regenerating forests in Tasmania differences were smaller – the vascular plant floristic composition of these two forest types were similar, except for a reduced representation of epiphytic ferns in the post-CBS regenerating forests. Because forest succession involves progressive replacement of taxa through time within forests, landscape level biodiversity of managed forests depends on the presence of appropriate representation of forests at different successional stages at any given future time. The determination of the appropriate forest ages, and the size and number of patches of these

Abbreviations: CBS, clearfell, burn and sow; CWD, coarse woody debris; NMDS, non-metric multidimensional scaling.

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forest ages, is clearly dependent on understanding the successional processes in managed forests and their natural counterparts.

Coarse woody debris (CWD), representing logs and other relatively large pieces of dead wood (Woldendorp et al., 2004), is ecologically important and well-studied in forests. Within forests, it provides essential habitat for wood-inhabiting fungi and saproxylic beetles, a substrate for plants, and shelter for vertebrates (Davis et al., 2010; Grove, 2002; Harmon, 1986; Heilmann-Clausen et al., 2005; Lindenmayer et al., 1999; Pharo and Blanks, 2000). It provides an ecologically diverse range of substrates due to the variation in fragment size and structure. Sizes range from ~10 cm to metres in diameter and from centimetres to tens of metres in length (Ashton, 1986; Woldendorp and Keenan, 2001). Fragments of CWD also change as decay transforms them from a state very similar to that in living trees to being virtually unrecognisable as wood. These changes have consequences for plant communities growing on them (Söderström, 1988). The time scale of these decay processes varies according to forest type and fragment size, but in the focus of the present study, medium-large sized logs in Tasmanian wet eucalypt forests, this process typically takes many decades (Grove et al., 2009).

In mid to high latitude forests, ferns, mosses and liverworts are typically the main plant groups that grow on CWD. These plants are important in forest ecosystems because they contribute to forest structure, moisture dynamics, forest humidity, nutrient cycling and provide habitat for other organisms (Turner and Pharo, 2005). They make a significant contribution to plant diversity in boreal and temperate forests where they occur on a variety of substrates including trees, rocks, soil and CWD (Cole et al., 2008; Rudolphi, 2007; Turner and Pharo, 2005).

Both macro- and microhabitat factors are important in determining the distribution of ferns, mosses and liverworts in forest ecosystems (Pharo and Beattie, 2002; Vitt and Belland, 1997). Thus, Crites and Dale (1998) found that species tended to colonise CWD in the middle and late stages of decay, and were more abundant on logs in advanced stages of decay and of large diameter. Such logs provided a greater array of suitable substrate patches than smaller and less decayed logs. Similarly, Botting and DeLong (2009) showed continuous succession of mosses and liverworts associated with increasing decay in British Columbia. Opening the canopy of northern hardwood forests changes the bryophyte flora from a closed-forest composition to one more typical of open forests (Paltto et al., 2008; Shields et al., 2007). On a macrohabitat scale, the diversity and structural complexity of habitats contributes to the abundance and quality of potentially suitable substrates. This in turn provides a diversity of habitats within and between substrate types that allow a diversity of species from a variety of functional groups to occur. As a result, successional patterns of ferns, mosses and liverworts on CWD in forest can be a combination of two processes – whole-forest succession (dependent on changes in mesoclimatic conditions and rates of arrival of propagules) and substrate succession (dependent on the rates of log decay and characteristics of logs at different stages of decay).

This study aimed to identify the patterns of ecological succession of ferns, mosses and liverworts growing on CWD in managed wet eucalypt forests of Southern Tasmania and compare them with their naturally regenerated counterparts. Previous work has indicated that post-wildfire bryophyte succession in these forests involves major compositional changes and increases in diversity to at least 108 years (Hodge et al., 2009). Also, in a broad scale survey, Turner and Kirkpatrick (2009) suggested that the forest regenerating 33–39 years after clearfell, burn and sow (CBS) silviculture in this region differed in floristic composition from similar aged forest after wildfire, with most of the floristic differences being among bryophytes. Southern Australian wet eucalypt forest is not only economically important (providing a major source of pulp for paper-making, structural timber and craft timber), but also has long been considered a model system for forest succession, starting with the seminal works of Gilbert (1959) and Jackson (1968).

We used a chronosequence-type approach to test for the presence of significant successional patterns after CBS silviculture. This involved selecting sites of different times since disturbance but as closely matched as possible in all other characteristics. Utilising these sites, we posed several questions: Does species richness and composition of ferns, mosses and liverworts growing on CWD change over time? Is there discrimination between the effects of whole-forest processes and those of substrate succession? To answer this question, we tested for association with microclimate, substrate decay stage and substrate water content. Does, as proposed by Turner and Kirkpatrick (2009), ecological succession of fern, moss and liverwort on CWD after CBS silviculture differ from that after natural wildfire?

2. Materials and methods

2.1. Study sites and sampling

Data related to the bryophytes and ferns growing on coarse woody debris were collected from 22 sites (16 sites regenerating after CBS silviculture and six regenerating after natural wildfire) in the Warra Long Term Ecological Research site (http://www.warra.com/warra/about.html) and nearby areas in the Arve Valley, Southern Tasmania (Fig. 1; Supplementary materials Table S1).

Data was collected from four ages of forest regenerating following CBS silviculture and sites regenerating after natural wildfire. There were four post-CBS sites in each of four age classes: 43 ± 1, 32 ± 1, 20 ± 1 and 8 ± 1 years after the regeneration burn. There were three post-wildfire sites of each of three ages: 43, 75 years and old growth (greater than 110 years post-wildfire). Suitable post-wildfire sites of comparable age to the younger post-CBS (32, 20 and 8 years) sites are not available in this region (Turner et al., 2009). All sites were characterised by wet eucalypt forest dominated by *Eucalyptus obliqua*, had soils overlying Jurassic dolerite, and a southerly to easterly aspects (as defined as between 67.5° and 205.5° true).

The monthly temperature at Warra for the 12 month period from April 2008 until March 2009 ranged from a mean maximum of 18.9 °C in February to mean minimum of 1.3 °C in July, and the monthly rainfall ranged from 64 mm in May to 286 mm in September (data provided by the Australian Bureau of Meteorology). Microclimatic measurements were taken from one data logger in each of the post-CBS sites, over a period from mid winter to early autumn (detailed methods and results are given by Browning, 2009).

2.2. Log characteristics and floristic sampling

At each site, a single transect was used for log sampling. A specialised transect method that sampled relatively small total areas in each site was used to minimise the effects of within site environmental gradients. This transect initially ran perpendicular to the coupe edge then turned at right angles, alternating left and right, every 50 m. Logs sampled were at least 10 cm in diameter, bore cut ends indicating that they were generated in the clearfell, burn and sow harvesting event, and to eliminate edge effects, were at least 30 m from the coupe edge or other major ecological boundaries. To minimise the effects of different coupe sizes, transects were terminated after approximately 150 m. In all coupes, between 10 and 20 logs were sampled. The logs were categorised into decay stages (Table 1). Moisture content was measured in each log on each of two