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How do heterogeneity in vegetation types and post-fire age-classes contribute to plant diversity at the landscape scale?

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ABSTRACT

Heterogeneity in environmental factors (e.g. soils) and disturbances (e.g. fire) are important drivers of plant diversity but the relative strength of their effects may be scale dependent. Given that fire regimes are often manipulated to maintain plant diversity at the landscape scale, detecting and disentangling fire from environmental effects at this scale is important. In SE Australia prescribed burning and wildfires have created mosaics of post-fire age-classes in vegetation ranging from moist forests to sclerophyllous heathlands along a gradient of decreasing productivity (rainfall and soil fertility). This provided us with an opportunity to investigate the effects of both environmental and disturbance heterogeneity on plant diversity at the landscape scale. Our survey units were mosaics (approx. 100 ha) of varying heterogeneity in the numbers of vegetation types (surrogate for environment) and post-fire age-classes (disturbance). As predicted, we found that plant diversity increased as the number of vegetation types in mosaics increased and as mean annual rainfall increased from heathlands to moist forests. There was also a weaker positive relationship between plant diversity and the number of post-fire age-classes in mosaics. The effect of post-fire age-classes on plant diversity was much stronger, however, when each vegetation type was considered separately, with species composition more sensitive to post-fire ages-classes in the moist forests at higher productivity compared with sclerophyllous heathlands at lower productivity. The effectiveness of mosaic burning in maintaining plant species diversity in environmentally diverse landscapes is therefore stronger at the small scale, within vegetation types, where the influence of environmental factors is minimised.

1. Introduction

Heterogeneity in environmental factors and disturbance regimes are both predicted to contribute to plant diversity within a landscape (Field et al., 2009; Huston, 1999; Sarr et al., 2005; Whittaker et al., 2001). Environmental factors, such as average rainfall, geology and topography, play a role in influencing the broad distribution of plant species and consequently determine the location and extent of vegetation types (Benayas and Scheiner, 2002; Forey et al., 2008). Within vegetation types, disturbances influence the abundances of individual species (Enright et al., 1994; Forey et al., 2008; Lavorel, 1999), and alter species diversity by increasing resource availability and changing competitive interactions (Huston, 1979). So, greater heterogeneity or complexity in environmental factors and disturbances is likely to increase species diversity.

Our ability to detect the effects of heterogeneity in environmental factors and disturbances on plant diversity may vary with scale (Sarr et al., 2005). At the landscape scale, which is commonly used for conservation planning, theory and empirical studies indicate the importance of environmental heterogeneity for species diversity (Currie and Paquin, 1987; O'Brien, 2000; Richerson and Lum, 1980; Sarr et al., 2005), but there is also some evidence that disturbances have influence at this scale (Whittaker et al., 2001). In contrast at smaller site scales, there is general agreement that non-equilibrium processes, like fire, influence species diversity through competition (Sarr et al., 2005; Whittaker et al., 2001). Given the uncertainty in the detectability of disturbances on plant species diversity in landscapes managed by fire, further research is warranted.

Fire is manipulated at landscape scales in many ecosystems to manage species diversity. For example, mosaic burning is currently

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used to create a ‘spatial patchwork’ of successional stages or post-fire age-classes to enhance plant diversity in a range of fire-prone landscapes (Bradstock et al., 2012; Burrows and McCaw, 2013; Parr and Andersen, 2006). The creation of post-fire age-classes is hypothesised to increase plant diversity by providing niches for species with different life history attributes to coexist (Parr and Andersen, 2006). Colonisers that grow and reproduce quickly after fire are likely to dominate in the earliest post-fire age-classes, when the vegetation is open and resources are plentiful. At intermediate post-fire age-classes, all plant species become reproductively mature and finally slow growing competitors with greater longevity are likely to dominate the older post-fire age-classes, when resources are more limited (Bazzaz, 1979; Connell and Slatyer, 1977). So variation in growth rates, time to reproductive maturity, competitive abilities and longevity determine species' successes and composition along a temporal continuum, and by representing this spatially, plant diversity is likely to be maximised (Parr and Andersen, 2006).

Although fire effects (e.g. post-fire age-classes) on plant diversity are often evident within single vegetation types (Alvarez et al., 2009; Capitanio and Carcaillet, 2008; Swanson et al., 2010), quantifying the effect of fire on plants at larger scales may be difficult due to the expected strong influence of environmental factors (Sarr et al., 2005). However, as both fire and conservation management often occur at landscape scales, disentangling disturbance effects from those of environmental factors is important. Effective use of mosaic burning for landscape scale management of plant communities requires an understanding of its relative contribution to plant diversity compared with environmental heterogeneity. There are a number of possibilities: firstly, diversity is strongly influenced by environmental factors and fire has little effect; secondly, fire contributes to diversity additively by creating more diversity over and above the background level, independent of environmental factors and; lastly, fire and environmental factors interact, so that the effect of fire on diversity depends on the underlying level of environmental heterogeneity. The likelihood of these scenarios in fire-prone landscapes is not well researched (Huston, 2003; Pausas and Austin, 2001; Sarr et al., 2005), and here we investigate the mechanisms that underpin these theoretical constructs.

The relative importance of disturbance, like fire, to plant diversity may also vary along a productivity gradient in the landscape. With the Dynamic Equilibrium Model, Huston (1979) proposed that competitive exclusion depends on both the rate of dominance and the disturbance regime. Although productive sites provide optimal conditions for colonization and growth for a broad suite of species, strong competitors can quickly eliminate poor competitors if disturbances are infrequent. By comparison, in less productive systems, colonization and growth occur more slowly, so competition occurs less rapidly or even incompletely and more species can coexist at lower disturbance frequencies. So, disturbance, like fire may be more important in maintaining species diversity at more productive sites in the landscape (de Bello et al., 2006; Huston, 2003; Odion and Sarr, 2007). Determining the applicability of the Dynamic Equilibrium Model to fire-managed landscapes can inform managers of the importance of fire to species diversity along a productivity gradient.

Vegetation is influenced by variation in a range of environmental factors and post-fire age-classes along a productivity gradient in our study area in the Great Otways National Park, south-eastern Australia (Cheal, 2010; Parsons et al., 1977; Pitt, 1981). Moist forests and sclerophyllous heathlands dominate at extremes of the productivity gradient: moist forests occur on fertile loams at high elevation and high rainfall and sclerophyllous heathlands occur on infertile sandy soils at low elevation and low rainfall. Moist forests burn infrequently (mean interval of 42 years) in extreme fire-weather conditions (Gill and Catling, 2002), which are typified by high temperatures, winds, and dryness. By comparison sclerophyllous heathlands burn more frequently under more moderate fire-weather conditions (mean interval of 16 years; Enright et al., 2012; Keith et al., 2002). Over the last three decades prescribed burning has been used to create a range of post-fire age-classes for both fuel reduction and ecological purposes in the vegetation along this productivity gradient (Department of Environment and Primary Industries, 2013). Further, major wildfires burned through large parts of the study area in 1939 and 1983. Together, the planned and unplanned fires have created land mosaics that vary in their degree of heterogeneity in relation to the number of vegetation types and post-fire age classes.

Our general aim was to determine if age-class heterogeneity increased plant species diversity over and above the expected increase due to heterogeneity in vegetation type. More specifically, we sought to quantify the relative importance and potential interactive effects of heterogeneity in vegetation types and post-fire age-classes in mosaics on plant species diversity along the productivity gradient (rainfall and soil fertility) in our study area. We used heterogeneity in vegetation types as a surrogate for environmental heterogeneity, while heterogeneity in post-fire age-classes were used to represent the effect of the fire regime. We hypothesised that at the landscape scale: 1/plant diversity (richness, Simpsons diversity, Sorensen turnover) would be positively related to heterogeneity in vegetation types and post-fire age-classes in mosaics; and 2/heterogeneity in post-fire age-classes will have greater effect on plant diversity at the higher end of the productivity gradient, where the moist forests are more sensitive to fire and conditions are more competitive. A secondary aim was to examine whether plant species compositions varied between post-fire age-classes at the smaller scale within each vegetation type. We hypothesised that 3/the effects of post-fire age-classes on plant diversity would be strong and easily detected at this scale.

2. Materials and methods

2.1. Study area

The study was undertaken in the Great Otway National Park (59,000 ha) in south eastern Australia (Fig. 1). The study area experiences a quasi-Mediterranean climate (mean annual minimum and maximum temperatures of 10.5 °C and 18.2 °C, respectively) with a mean annual rainfall of 693 mm in the north east and 1121 mm in the south west (Bureau of Meteorology, 2012, Appendix A). The vegetation grades from heathland, dominated by sclerophyllous shrubs with a scattered overstorey of *Eucalyptus* species (*E. obliqua*, *E. falciformis*) in the low lying, gently undulating north east (30–270 m a.s.l.) to moist forests with a canopy of *Eucalyptus* species (*E. obliqua*, *E. cypellocarpa*) and a moist understorey in the more elevated, dissected hills of the south west (200–650 m a.s.l.; Department of Sustainability and Environment, 2012).

Much of the study area was burned by large wildfires in 1939 and 1983, with smaller wildfires in the early to mid-1960s. Since 1980, prescribed fires have been used to burn relatively small areas (<400 ha) in all vegetation types for fuel reduction and ecological purposes (Department of Environment and Primary Industries, 2013).

2.2. Study design

Vegetation and fire maps were generated from spatial datasets in ArcMap 10 (ESRI, 2011). Vegetation types differed floristically and structurally and included heathland, tall mixed forest foothill forest, forby forest and moist forest, with increasing rainfall and