Forest Ecology and Management 285 (2012) 11–19

Contents lists available at SciVerse ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Landscape modulators and resource accumulation in a post-fire eucalypt woodland

Samantha K. Travers *, David J. Eldridge

Evolution and Ecology Research Centre, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia

ARTICLE INFO

Article history:
Received 22 May 2012
Received in revised form 8 August 2012
Accepted 10 August 2012
Available online 6 September 2012

Keywords:
Eucalyptus dumosa
Eucalyptus socialis
Fire
Leaf litter
Patch
Woody debris

ABSTRACT

In resource-limited environments patch development is a critical component of ecosystem function. Resource patches at both fine and broad scales are temporally dynamic, and the resources they provide change in response to broad-scale ecological disturbances such as fire. Here we consider temporal changes in perennial vegetation patches by measuring the fine-scale development of physical patch layers in response to a broad-scale abiotic process, fire. Until recently, such fundamental shifts in patch structure have, for the most part, been widely assumed and quantitatively ignored. Fundamental shifts in post-fire litter composition are important for predicting fire behaviour and may be useful in identifying the range of conditions or thresholds under which the arrangement of fuel components affects future fire behaviour. We describe the post-fire development of physical patch layers associated with two eucalypt mallee tree species (*Eucalyptus dumosa* and *Eucalyptus socialis*). We quantified tree, litter bed and canopy dimensions for sites with fire histories ranging from 4 to 42 years, focussing on the development of the sub-canopy litter bed. There were strong linear relationships between tree size and litter bed size with increasing time since last fire. After we accounted for tree and litter bed size, fire history still had a significant effect on the composition of the litter bed with sticks, seeds and fragments generally increasing and leaves generally decreasing with greater time since fire. There were no significant differences between the two tree species studied for any relationship with time since fire. Our results document the temporal, fine-scale changes in litter accumulation and composition following fire in a mallee woodland, indicating that substantial shifts in composition occur, likely affecting the flammability of the litter bed. More specifically, we have shed light on post-fire trends in litter accumulation, a fundamental component of patch development. This study provides us with a better understanding of fine-scale resource patch development, allowing us to predict shifts in resources at broader scales. By understanding how landscape modulators and their surrounding environment influence the development of patches, we are in a better position to predict how changes in these drivers are likely to affect ecosystem processes.

1. Introduction

Arid and semi-arid ecosystems function effectively by concentrating limited resources into discrete patches (Noy Meir, 1979; Ludwig et al., 1997). These nutrient- and water-rich resource patches can buffer surface temperatures and provide habitat for organisms (Whitford and Kay, 1999). The stark contrast in resource quality and quantity between the resource patch and the surrounding matrix can also significantly alter local species assemblages. Some resource patches are constructed by organisms that exploit, modify and concentrate resources. Examples include the resource-rich pits created by soil foraging animals (Whitford and Kay, 1999) and the resource patches that form around perennial vegetation (Shachak et al., 2008). Widespread fine-scale patch creation and development by dominant biota, such as perennial plants, can significantly alter landscape productivity and resource diversity at broad spatial scales (Ludwig et al., 1997), which, in turn, affects the abundance and diversity of patch-dependent biota (Shachak et al., 2008). Organisms that create and maintain resource patches and are dominant at broad scales are known as landscape modulators (*sensu* Shachak et al., 2008).

At broad scales, landscape patchiness and associated biodiversity are also driven by abiotic processes such as fire. Such broad-scale abiotic processes have long been recognised as major drivers of biodiversity (Bradstock et al., 2005). Current literature, however, suggests that fine-scale resource patches created and maintained by biota may be more important for maintaining biodiversity than those created and maintained by broad-scale abiotic processes such as fire (Loreau et al., 2001; Shachak et al., 2008). Fire can modify the spatial and temporal arrangement of broad- and fine-scale

Abbreviations: ANCOVA, Analysis of Covariance; N, nitrogen; PERMANOVA, Permutational Multivariate Analysis of Variance; SEM, Structural Equation Model.

* Corresponding author. Tel.: +61 2 9385 2194; fax: +61 2 9385 1558.
E-mail addresses: s.travers@unsw.edu.au (S.K. Travers), d.eldridge@unsw.edu.au (D.J. Eldridge).

0378-1127/$ - see front matter © 2012 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.foreco.2012.08.015

patches and affect their constituent biota for many decades after the event (Russell-Smith et al., 2010). In highly flammable communities, a regime of regular, natural fires of varying intensity and size can structure landscapes into a mosaic of different patches, each with different stages of recovery (Gill et al., 2003; Bradstock et al., 2005). Fire is, therefore, an important modulator of resources and resource patches, and in resource-limited environments such as semi-arid woodlands, this has dramatic effects on ecosystem structure and productivity (Noble, 1989; Cohn and Bradstock, 2000). At finer spatial scales, fire homogenises resource patches formed around trees, reducing resource diversity at the fine patch and inter-patch scales. However, this fine-scale loss of resource diversity is often short-lived due to the temporal dynamics of patches. Shachak et al. (2008) proposed that patches such as those associated with perennial vegetation are temporally dynamic and cycle through stages of resource contrast with their surrounding matrix. As patches develop, they become increasingly more complex, physically and chemically altering soil properties and providing a greater array of habitats and potential food sources for organisms across both small and large spatial scales. When patches decay through processes such as fire, resource contrast with the surrounding matrix is initially reduced, but develops again over time (Shachak et al., 2008).

The development of post-fire species assemblages is generally related to the extent to which patch types re-establish after fire. A range of patch types co-exist after fire, providing a multi-layered habitat for diverse groups of fauna. However, not all patch types co-exist at the same time. For example, over time a tree can create spatially complex patches, with multiple layers such as litter beds that develop rapidly on the soil surface, hollows that develop slowly in the canopy, and strips of bark on the trunk that develop at an intermediate rate. A classic example of such multi-layered resource patches occurs in Mediterranean woodlands where evergreen, sclerophyllous shrubs and trees are dominant at broad scales, creating and maintaining resource patches (Gabay et al., 2012). In Australia's Mediterranean climatic zones, mallee (*Eucalyptus* spp.) is the dominant vegetation community. Mallee trees have a growth form characterised by multiple stems that develop from a lignotuber root system. They are well adapted to periodic fires, and the stems resprout in as little as 2 weeks after fire (Noble, 1997). A range of fire histories typically occur across an entire landscape, resulting in a mosaic of multi-layered resource patches that vary in size and development. The physical elements of these multi-layered resource patches such as litter beds, canopy, trunks and arboreal bark strips also provide fuel for future fires.

Despite considerable debate on the importance of fire for mallee-dependent fauna (e.g. Driscoll and Henderson, 2008), many studies have demonstrated strong relationships between the post-fire recovery of mallee communities and a range of taxa (Clarke et al., 2010) such as reptiles (Caughley, 1985), birds (Woinarski, 1999), arthropods (Noble et al., 1990) and mammals (Kelly et al., 2010). Although there has been a significant focus on post-fire shifts in plant and animal assemblage in mallee communities, there are few data, to our knowledge, on the post-fire changes to these multi-layered resource patches that typify mallee communities (but see Haslem et al., 2011).

Our study examines the spatial and temporal changes in multi-layered resource patches after fire in mallee communities. We investigate resources at the scale of individual trees (*sensu* Shachak et al., 2008) using white mallee (*Eucalyptus dumosa* A. Cunn. ex J. Oxley) and red mallee (*Eucalyptus socialis* F. Muell. ex Miq.) as models of landscape modulators. We measure the spatial shift in resource patch size in response to fire history along a continuum of fire histories across the landscape. Given the identical structure of these two species, we did not expect to record differences in relationships between patch layers. However, given that litter fall can be species-specific (Miller and Urban, 1999) we compared them to test whether there was any species-dependent variation in the composition of the litter bed across the different fire histories. We expected that changes within the canopy and trunk of our mallee models would correspond with shifts in the environment of the sub-canopy patch. We quantified the dimensions of the physical patch elements, i.e. the tree and litter layer associated with our mallee trees across a range of fire histories, focussing on the spatial and compositional development of the litter patch (litter bed layer), quantifying and comparing litter bed dimensions and composition as a function of time since fire.

2. Methods

2.1. Field site

Our study was undertaken inside two large conservation areas, Tarawi Nature Reserve and Australian Wildlife Conservancy's Scotia Sanctuary in south western, New South Wales, Australia (33°43′S, 143°02′E). This area is semi-arid, receiving about 280 mm annual rainfall, however there are very few years in which this amount is actually received. Rainfall is highly irregular throughout the year and spatially variable across a scale of tens of kilometres. Winters are mild, with daily mean maximum temperature of 17 °C and a daily mean minimum temperature of 6 °C in July. Summer is typically hot with a January mean daily maximum temperature of 33 °C and a mean daily minimum of 19 °C (BOM, 2011).

Our study was conducted in a dune mallee community; a low open woodland located on long, low (relief to 7 m) east–west trending sand dunes. Dune mallee is generally dominated by an open overstorey of mallee (multi-stemmed) trees (*Eucalyptus gracilis* F. Muell, *E. dumosa*, *E. socialis*) and an understorey of scattered perennial hummock grasses (*Triodia scariosa* N. T. Burb. subsp. *scariosa*). However as mallee trees resprout from lignotuberous roots after fire, in recently burn sections mallee appear as hummock-to shrub-sized plants for approximately 10 years after fire. Individual trees grow as a cluster of stems, which may be isolated or clumped with other individuals, forming large connected litter layers. The perennial hummock grasses that dominate the inter-tree matrix are highly flammable and their role in fuel connectivity is well established (Noble, 1989, 1997). Shrub cover to 2 m is sparse on the dunes, with widely-spaced individuals of predominantly *Senna artemisioides* subsp. *filifolia* (Benth.) Randall and *petiolaris* Randell, and *Acacia burkittii* F. Muell. ex Benth (Keith, 2004). At our study site, the soils are mainly calcareous, brownish and siliceous sands sparsely capped with biological soil crusts.

2.2. Experimental design

In January 2011, we sampled nine areas with known fire histories ranging from 4 to 42 years since fire. All sampled areas were located within 20 km of each other, and were assumed to have burned under equivalent, relatively high intensity fires based on vegetation characteristics. More specifically the mallee vegetation at all sites had re-sprouted from lignotubers, rather than continuing growth from stems which existed before the fire which can happen after low intensity fires.

At each of our nine burn areas, we randomly selected 20 sites. At each site we measured two trees, one of each species (total $n = 360$). To minimise edge effects we did not sample within 30 m of the edge of a given burn area. Sampling was limited to *E. socialis* and *E. dumosa.* We identified these species based on leaf and bark traits, and fruits where possible. Due to size limitations of some burn areas we could not always find an equal number of