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Responses of flora and fauna in wet eucalypt production forest to the intensity of disturbance in the surrounding landscape

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ABSTRACT

In disturbance-dependent forest ecosystems, species associated with mature forest may maintain their ranges both by persisting in patches of mature forest and by recolonising patches regenerating after fire, harvesting or other disturbances. The null hypotheses are that these processes are both independent of the intensity of disturbance in the landscape surrounding those patches. These were tested in a 1120 km^2 region of tall, wet eucalypt forest in southern Tasmania, which provides a landscape-scale gradient in disturbance intensity shaped by past wildfires and post-European land-use.

For all 50 × 50 m cells in the region, a Landscape Disturbance Intensity (LDI) index was calculated based on the vegetation in the surrounding 0.5, 1.0 and 2.0 km-radius landscapes. The occurrence of species in three taxonomic groups – birds, vascular plants and flighted beetles – was then sampled in 28 plots (50 × 50 m) across the range of LDI in each of two forest age-classes – mature eucalypt forest (MAT) and 25–50 years-old silvicultural regeneration arising from clearfell harvesting (SILV).

In both MAT and SILV plots, the occurrences of many common species showed significant relationships with LDI. Most (> 80%) of those relationships reflected species that declined in occurrence with increasing LDI, i.e. were Landscape Disturbance-Sensitive (DS_L). However, there were contrasting patterns between the forest age-classes as well as among the three taxonomic groups in the proportion of common species that were DS_L. More plant and bird species were DS_L in SILV plots (15/49 and 9/27, respectively) than in MAT plots (4/49 and 1/27, respectively). The dominant fractions of the DS_L plant and bird species in SILV plots were classed as rainforest trees or shrubs in previous studies and birds that were associated with MAT plots rather than SILV plots in this study, i.e. species that were also sensitive to disturbance at the patch-scale. A similar number of the common beetle species were DS_L in MAT plots (29/234) as in SILV plots (35/234). Beetle species that were Patch Disturbance-Sensitive (DS_P) in this study were over-represented in the subset of DS_L species in MAT plots (9/29), but not in SILV plots (5/35).

We conclude that many DS_P species inhabiting mature forest stands are resilient to disturbance in the surrounding landscape, but their ability to recolonise regenerating forest stands can be diminished by disturbance at the landscape-scale. This highlights the role of vegetation structure at both patch and landscape-scales in the long-term viability of mature-forest-dependent species in production-forest landscapes.

1. Introduction

Ecological processes that sustain forest biodiversity operate across a range of scales in space and time (Lindenmayer and Franklin, 2002; Gustafsson and Perhans, 2010). These scales reflect the natural disturbance regime for the particular forest ecosystem (Kneeshaw and Bergeron, 2016). Accordingly, sustainable management of forest landscapes should aim to reflect these multi-scale processes. However, the different instruments through which management is applied are scale-dependent. For example, management at very large regional spatial

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scales (> 10^3 km^2), which span multiple ownerships and land uses, is usually co-ordinated by government and is typically reflected in networks of reserves (Fitzsimons et al., 2013; Barr et al., 2016). At the smaller scales of landscapes (10^1–10^2 km^2) and patches (10^{-1}–10^0 km^2), individual land owners/managers can undertake management with a degree of autonomy, but in accordance with legislation, regulations and codes of practice. The patch-scale equates to individual forest stands (typically < 50 ha) and trees within stands, and this is also the scale at which most plot-based measurements to characterise forest attributes are made (Duchesne and Ouimet, 2008; Bowman et al., 2014).

Modern forestry practices are evolving to better accommodate multi-scale ecological processes. A shift away from clearfelling towards retention forestry (Gustafsson et al., 2012) aims to cater for patch-scale processes. Informal protection of forest areas from harvesting, through retaining corridors / riparian buffers and leaving set-asides to protect habitat of sensitive species, aims to cater for processes operating at landscape-scales (Gustafsson and Perhans, 2010; Slade and Law, 2016). However, we need to understand the biological effects of management applied at both the patch- and the landscape-scale if we are to better articulate management goals (Angelstam et al., 2004), develop operational guidelines (Greater Fundy Ecosystem Research Group, 2005), and inform monitoring programs that review and refine management in an adaptive management framework (Bunnell et al., 2009).

Ecological effects of patch-level retention have been clearly demonstrated in boreal and temperate-forest ecosystems (Fedrowitz et al., 2014). That meta-analysis found consistent responses across taxonomic groups, with the impacts of retention forestry on forest-specialist species and open-area-specialist species being intermediate between impacts of not harvesting forest and of clearfells. In a cross-continental comparison, Baker et al. (2016) showed that retention provided both a "life-boating" effect, which maintained viable habitat that allowed forest-interior species to persist within harvest units, and a "forest-influence" effect, which assisted the earlier recolonisation of harvested areas by mature-forest species.

The landscape surrounding a patch has also been shown in a range of ecosystems to have ecological effects on species occupying patches (Mazerolle and Villard, 1999; Mori et al., 2017), and patches can be distinguished by the landscape context in which they occur. To date, much of the research into understanding the effect of landscape context on patch-level biodiversity has been carried out in patches of mature forest within production-forest or agricultural landscapes. In such patches, responses in species richness or abundance to the amount of residual mature forest in the surrounding landscape have been found in a number of studies (Radford et al., 2005; Betts et al., 2007; Lindenmayer et al., 2013; Cunningham et al., 2014), with these responses often being non-linear, although other studies found no strong relationships (Lindenmayer et al., 2005). The range of responses to landscape context shown by forest-dependent species resident in mature forest patches (including both increases and decreases in abundance) can be explained by differences in the natural disturbance regime of forest ecosystems (Drapeau et al., 2016), silvicultural regimes in the matrix that are unreflective of the natural disturbance regime (Betts et al., 2007), or dramatic alteration of the matrix habitat, e.g. conversion of forested landscapes to agriculture (Radford et al., 2005), in addition to simple differences in species ecology.

Chazdon et al. (2007) noted that the composition of the surrounding landscape is likely to be an important determinant of the rate at which mature-forest species recolonise forest areas recovering from disturbance, but the few studies on this give contrasting results. Selwood et al. (2009) and Gould and Mackey (2015) found landscape-context effects were minimal in chronosequences of revegetated areas previously cleared of native forests. However, Lindenmayer et al. (2013) reported a landscape-context effect (the effect of the severity of burn in the surrounding landscape) on populations of arboreal mammals in recently burnt areas. Similarly, Drapeau et al. (2016) reported strong landscape-context effects on the abundance of bird species recolonising early seral forests in forest landscapes that historically had high levels of mature forests, but fewer species responding to landscape-context in landscapes that had higher levels of natural disturbance and lower amounts of mature forest. Several studies in Scandinavian Boreal forests have also detected strong landscape context effects on beetles colonising coarse woody debris (Gibb et al., 2006; Kouki et al., 2012; Rubene et al., 2017).

In this work, a forested landscape in southern Tasmania shaped by past wildfires and a century of wood harvesting and associated forest management provided a pre-existing landscape-scale natural experiment, with a spatial gradient in forest age-class distribution and in the type and extent of historical disturbance. We use the term natural experiment *sensu* Diamond (1983) except that the landscape we study comprises both sites affected by human disturbance and sites affected only by natural disturbance, with the level of disturbance being the major independent variable for this work. The landscape surrounding different patches of eucalypt forest along this gradient has thus experienced differing levels of disturbance. This allowed us to examine how populations of species in patches of residual mature forest, and in patches of 25–50 years-old silvicultural regeneration, vary along the gradient of disturbance intensity in their surrounding landscapes. Our null hypotheses were that the capacity of species to persist in areas of mature forest, and to recolonise areas after timber harvesting, would be the same regardless of the intensity of disturbance in the landscape surrounding those areas. We test these for species in three taxonomic groups that have been well-studied in this landscape – vascular plants, birds and beetles. Further, we proposed that, if the null hypotheses were rejected, those species that respond to disturbance at the landscape-scale would respond in the same way to disturbance at the patch-scale.

2. Methods

2.1. Study area

The study was conducted in the Southern Forests Experimental Forest Landscape (SFEFL), a 32 km (E–W) × 35 km (N–S) region of Tasmania (Fig. 1). The SFEFL is anchored on the Warra Long-Term Ecological Research site – a member site of the Australian Supersite Network (http://www.tern-supersites.net.au).

The SFEFL is within the Temperate Climate Zone (Kőppen classification), with winter-dominated rainfall, mild to warm summer temperatures, and cool winter temperatures. There is a west–east gradient of decreasing rainfall and increasing temperatures across the SFEFL. Warra (Bureau of Meteorology station 097024), at the western edge of the landscape, has mean annual rainfall of 1738 mm with mean daily temperatures of 13.9 °C and 5.7 °C in January and July, respectively. Geeveston (Bureau of Meteorology station 94137), at the eastern edge of the landscape, has a mean annual rainfall of 894 mm with mean daily temperatures of 15.8 °C and 7.2 °C in January and July, respectively.

Laffan (2001) describes the geology and soils of the SFEFL, particularly those parts within the Warra LTER site. Jurassic dolerite forms the major ridges and peaks in the SFEFL. These are overlain by red or brown ferrosol soils. Permian sediments dominate the western valleys of the SFEFL, where they form mottled, brown kurosol soils. Triassic sediments dominate valleys in the eastern half of the SFEFL, where they form bleached, dystrophic, brown kurosol soils.

A large proportion of the SFEFL supports tall eucalypt forest which grades into rainforest in fire-protected situations, particularly in the high-rainfall western section, or into sub-alpine woodlands and non-forest communities (alpine moorlands in areas above 900 m altitude, and buttongrass moorlands on poorly-drained, peaty soils on Precambrian quartzite). Low eucalypt forests are restricted to the drier north-eastern section of the SFEFL, particularly on north-facing slopes. The tall eucalypt forests are dominated by one or two of three related