



Temporal persistence of edge effects on bryophytes within harvested forests



Thomas P. Baker^{a,b,c,*}, Susan C. Baker^{a,b,c}, Patrick J. Dalton^a, Nicholas M. Fountain-Jones^a, Gregory J. Jordan^a

^a School of Biological Sciences, University of Tasmania, Private Bag 55, Hobart, Tasmania 7001, Australia

^b ARC Centre for Forest Value, University of Tasmania, Private Bag 55, Hobart, Tasmania, Australia

^c Forestry Tasmania, Research and Development Branch, GPO Box 207, Hobart, Tasmania 7001, Australia

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ABSTRACT

For the management of forest harvesting it is important to understand the processes that impact the re-colonisation of disturbed forests. Edge effects into disturbed forests have been identified as having important impacts on the re-colonisation of both flora and fauna. In a study system located in southern Tasmania, we investigated whether bryophyte colonisation of harvested forests was impacted by edge effects from a standing mature forest (forest influence) and if this effect persisted through time. We tested this by placing transects across a mature/regeneration forest boundary, then recording bryophyte community composition from the ground and coarse woody debris at set distances from the edge. A chronosequence of harvested forest ages (~7, ~27 and ~45 years post harvesting) was used to determine if forest influence persisted through time. Models generated by non-linear canonical analysis of principal coordinates (NCAP) predicted the depth of forest influence, and 'distances among centroids' inferred the magnitude of forest influence.

Results showed that bryophyte composition in regeneration forests responded to distance from a mature edge. Locations closer to a mature edge had greater similarity in community composition with mature forests. This study also showed that the response of bryophytes to forests influence persisted though time, even after canopy closure. Overall, mature forest species tended to be aided and early seral species restricted by forest influence. However, responses were species-specific and varied with forest age. The colonisation success of mature forest associated species was improved by forest influence; these species are typically at most at risk of being eliminated after disturbance. This result highlights the need to consider edge effects in management. The impact of forest influence on bryophytes therefore has the potential to be used in the design of areas to be harvested.

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1. Introduction

In the last few decades, retention forestry techniques, which retain elements of mature forests within harvested areas, have come to the fore as ways to conserve biodiversity and support the redevelopment of pre-harvest communities (Gustafsson et al., 2012; Lindenmayer et al., 2012). In addition, forest influence (edge effects that occur in the harvested matrix near uncut forest (Mitchell and Beese, 2002)), have been shown to aid the re-colonisation of pre-disturbance communities of beetles, fungi, vascular and non-vascular plants (Tabor et al., 2007; Outerbridge

and Trofymow, 2009; Baker et al., 2013b; Fountain-Jones et al., 2015). Therefore, the development of harvesting techniques that can increase the area under forest influence is seen as beneficial. Aggregated retention is a common form of retention forestry that increases the area under forest influence (Baker and Read, 2011). To improve implementation and conservation outcomes of techniques such as this it is important to understand the impacts of forest influence on various taxa and the persistence of the effects through time.

Two dominant factors drive the effects of forest influence on communities; firstly retained forests act as sources of propagules/dispersal units for species which do not survive the disturbance, and secondly, the presence of a mature edge can impact environmental conditions of the regeneration forest (Ries et al., 2004; Baker et al., 2013a) and thus indirectly affect species' distributions. Bryophytes (mosses, liverworts and hornworts) are

* Corresponding author at: School of Biological Sciences, University of Tasmania, Private Bag 55, Hobart, Tasmania 7001, Australia.

E-mail addresses: tpbaker@utas.edu.au (T.P. Baker), Sue.Baker@forestrytas.com.au (S.C. Baker), p.j.dalton@utas.edu.au (P.J. Dalton), nfountainjones@gmail.com (N.M. Fountain-Jones), greg.jordan@utas.edu.au (G.J. Jordan).

known to respond to forest influence and are important to study as they play crucial roles in many aspects of forest ecosystems, such as the uptake and storage of nutrients and soil hydrological processes (Brasell and Mattay, 1984; DeLuca et al., 2002; Lindo and Gonzalez, 2010). These factors give bryophytes the potential to be good indicators of mature forest integrity (Frego, 2007) and provide a useful set of species to study the impacts of forest influence. Bryophyte species richness can equal, and often exceed, the richness of vascular plants in some Australian systems (Jarman and Kantvilas, 1995; Pharo and Blanks, 2000; Dynesius and Zinko, 2006). This makes bryophytes an important component of the forest system in terms of diversity.

Managed forests can have lower bryophyte richness than unmanaged forests (Paillet et al., 2010) and differ in their community compositions, thus proactive management may be required to address these differences. There is some empirical evidence that forest influence aids re-colonisation of mature forest bryophytes (Caruso et al., 2011; Baker et al., 2013b), although Hylander (2009) has shown no benefit. While some bryophytes can disperse long distances (Miller and McDaniel, 2004; Sundberg, 2013; Lönnell et al., 2014), the dispersal capacity of species that rarely or never produce spores is often very limited (Miles and Longton, 1992; Kimmerer, 1994; Frey and Kürschner, 2011). The increased proximity to propagule sources associated with forest influence may therefore increase the probability of re-colonisation of disturbed sites, especially for dispersal limited species. However, temporal aspects of re-establishment must be considered, since short distance dispersal may not be limiting over longer time spans. However, the impact of dispersal distance is complicated by the ability of some species to colonise from others sources e.g., the soil propagule bank (Ross-Davis and Frego, 2004), although this may be rare following intense regeneration burns that occur in Tasmanian forests. Additionally, bryophyte establishment and growth is limited by microclimate (Busby et al., 1978; Hanslin et al., 2001; Stewart and Mallik, 2006), particularly during germination (Wiklund and Rydin, 2004). Since the microclimate of harvested forests varies with distance from a mature forest edge (Davies-Colley et al., 2000; Godefroid et al., 2006; Baker et al., 2014), locations under forest influence may provide better re-establishment conditions for bryophytes.

The impact of forest influence on bryophyte re-colonisation may vary with time since disturbance and seral stage affiliation of the species involved. Bryophytes re-colonising immediately after disturbance typically have high dispersal capacities and are tolerant of variable microclimatic conditions (During, 1979; Heinken and Zippel, 2004). Such species may either be little affected by forest influence or even negatively affected near edges. Reduced growth near edges has been observed in some North American pine species (Coates, 2000; York et al., 2003), but this has not previously been investigated for bryophytes. In contrast, many old-growth forest species have limited dispersal ability (During, 1979; Kimmerer, 1994) and are sensitive to microclimate (Busby et al., 1978; Stewart and Mallik, 2006). While these traits may result in high responsiveness to forest influence, mature forest species typically re-colonise during the later stages of forest succession when the magnitude of microclimatic forest influence is diminished (Baker et al., 2014). Therefore, there may be an interesting interaction between species seral stage and the strength of forest influence that impacts on the effect of forest influence persisting through time. However, the persistence of forest influence is relatively unstudied across all taxa, and to our knowledge, has only been addressed in bryophytes by a single study from Lithuania (Marozas et al., 2005).

This paper examines how forest influence impacts bryophyte community composition in forests regenerating after harvesting and assesses which species are the most impacted. It also

determines whether forest influence on bryophytes persists through time. Our specific predictions are that:

- (1) Bryophytes communities within harvested forests will be more similar to mature forest communities with increased proximity to a mature forest edges (forest influence).
- (2) Forest influence patterns in bryophyte communities will persist through time.
- (3) Seral stage (early colonisers vs. interior forest species) will determine species response to forest influence.

2. Methods

2.1. Study sites

This study was conducted in southern Tasmania, Australia (Appendix 1). Four sites in each of three age classes of regeneration forest were selected: “~7 year old regeneration forests” were harvested between 2002 and 2007; “~27 year old regeneration forests” were harvested between 1983 and 1989 and “~47 year old regeneration forests” were harvested between 1966 and 1972. All sites were regenerating following clearfell, burn and sow silviculture, which involved the use of heavy machinery to harvest all major trees, after which the debris was subjected to a high intensity broadcast fire and the area sown with locally-sourced *Eucalyptus* seed. Areas next to the edge (~10 m) were usually cleared of all vegetation by machinery to create a firebreak to contain the regeneration burn. This resulted in greater soil compaction; therefore these areas were not studied. All sites were undisturbed before harvesting, underwent the same harvesting process and were classed as the same forest type as the adjacent mature forest prior to harvesting. We therefore assume that presence of mature forest species represents recolonisation.

All sites were bordered on at least one edge by mature (undisturbed) forest which contained emergent *Eucalyptus obliqua* and/or *Eucalyptus regnans* over a rainforest understorey dominated by *Nothofagus cunninghamii* and/or *Atherosperma moschatum*. Species such as *Eucryphia lucida*, *Phyllocladus aspleniifolius* and *Anodopetalum biglandulosum* were also common. Mature forests were selected which had not been previously harvested and were undisturbed by wildfire for at least 70 years. Examined edges were selected that did not show any apparent damage to the mature forest from escaped regeneration burns or wind.

2.2. Experimental design

Within each site, three transects were established running perpendicular to the mature/regeneration boundary (Appendix 1). Transects were placed randomly, although they were a minimum of 50 m from other transects and roads. Transects ran 35 m from the boundary into the mature forest to 200 m from the boundary on the harvested side. On each transect, seven 10 × 10 m plots were marked; two within the mature forest centred at –35 m and –15 m from the boundary (‘–’ indicates a mature forest plot), and five in the regeneration forest at 15, 35, 70, 120 and 200 m from the boundary (see Baker et al. (2014) for transect layout). This resulted in 21 plots per site, six in mature forest and 15 within the harvested unit. Two of the mature forest plots from a single ~27 year old site were not sampled due to disturbance during the sampling period; resulting in a total of 250 surveyed plots.

2.3. Bryophyte sampling

The occurrence of bryophyte species within each plot was assessed between January 2012 and May 2013. In each plot, bryophyte community composition was sampled on two substrates:

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