THE IMPORTANCE OF MANAGING AND CONSERVING LARGE OLD TREES: A CASE STUDY FROM VICTORIAN MOUNTAIN ASH FORESTS

DAVID LINDENMAYER

Fenner School of Environment and Society, The Australian National University, Canberra, ACT, 2601 Correspondence: David.Lindenmayer@anu.edu.au

Abstract: Large old trees are critical structures in the Mountain Ash forests of the Central Highlands of Victoria. They perform many critical ecological and other roles. Populations of these trees are also in serious decline. A range of key management strategies is needed to arrest the decline of existing populations of large old trees and instigate population recovery. In particular all existing large old trees need to be properly protected with adequate buffers of uncut forest. In addition, all stands of old-growth forest, irrespective of their size, need to be protected to ensure they are not logged. The size of the old-growth estate also must be expanded so that it encompasses at least 30%–50% of the distribution of Mountain Ash. Finally, the recruitment of new cohorts of large old trees is critically important to replace existing trees when they are lost. To achieve this, large areas of existing regrowth forest that regenerated after the 1939 fires need to be excluded from logging and grown through to an old-growth stage. Implementation of altered management in Mountain Ash forests is urgent, as delays in policies will exacerbate the decline of this significant population of large old trees in south-eastern Australia.

Keywords: Stags, logging, fire, climate change, Central Highlands of Victoria

INTRODUCTION

Large old trees are among the biggest and longest-living organisms on earth and occupy a revered position in the human psyche, appearing often in iconography, art, books, films and other cultural expressions (Blicharska & Mikusinski 2014). Large old trees also play numerous key ecological and ecosystem roles and have a major influence on hydrological regimes, nutrient cycles, disturbance regimes, and the distribution and abundance of populations of their own and other species (Lindenmayer et al. 2014b).

Populations of large old trees are susceptible to a wide range of threats and their conservation poses enormous challenges for resource managers (Lindenmayer et al. 2014b; Lindenmayer & Laurance 2016). Some of the ecological roles of, threats to, and conservation challenges associated with large old trees are well illustrated in the wet ash-type eucalypt forests in the Central Highlands of Victoria. The large old trees in this ecosystem, and in particular, Mountain Ash (*Eucalyptus regnans*) trees are the focus of the remainder of this short paper. However, large old trees in other ecosystems in Victoria are also in rapid decline, such as those dominated by Alpine Ash (*E. delegatensis*) (Lindenmayer et al. 2016) and River Red Gum (*E. camaldulensis*) (Newton-John 1992).

CASE STUDY OF LARGE OLD TREES IN VICTORIAN MONTANE ASH FORESTS

Mountain Ash trees are the tallest flowering plants on the earth, with trees exceeding 100 metres in height and 34 metres in girth having been recorded in the Central Highlands of Victoria (Ashton 1975). Mountain Ash typically occurs in monotypic stands, although at low elevations it occurs with Mountain Grey Gum (Eucalyptus cypellocarpa), Messmate (E. obliqua), and Red Stringybark (E. macrorhyncha). At higher elevations, Mountain Ash stands also support Alpine Ash (E. delegatensis) and Shining Gum (E. nitens) trees. Mountain Ash typically occupies a different bioclimatic niche relative to these other tree species (Lindenmayer et al. 1996). For example, Mountain Ash stands occupy locations with higher values for the minimum temperature of the coldest month and the mean temperature of the coldest quarter compared with the other eucalypt taxa listed above (Lindenmayer et al. 1996; Lindenmayer 2009). Recent work has shown that the abundance of large old Mountain Ash trees is greatest in a subset of the overall environmental niche occupied by the species (Lindenmayer et al. 2016). In particular, wet areas (as reflected by high values for topographic wetness), as well as places on steep slopes with either an easterly or westerly aspect, support significantly more large old trees than elsewhere in forest landscapes dominated by Mountain Ash (Lindenmayer et al. 2016).

Ecological and other roles of Mountain Ash trees in the Central Highlands of Victoria

Large old Mountain Ash trees have a wide range of key ecological and other values. Their value as habitat for numerous cavity-dependent mammals and birds has been well documented, including critically endangered animals such as Leadbeater's Possum (*Gymnobelideus leadbeateri*) (Lindenmayer et al. 1991b; Lindenmayer 2009; Lindenmayer et al. 2014a). They also are important habitat for many other species, including reptiles and plants (Pharo et al. 2013; Lindenmayer et al. 2015).

Large old Mountain Ash trees have a wide range of other important ecological values. For example, they produce significantly more flowers than younger Mountain Ash trees, with likely corresponding impacts on animals dependent on flower-based resources. Many species of large old trees produce massive seed crops, with positive relationships between increasing tree size with allocation to reproduction being a widespread phenomenon globally (Wenk & Falster 2015). Mountain Ash appears to follow this pattern and recent work has indicated that, following wildfire, the prevalence of germinants and seedlings is significantly greater in burned old growth stands than in forests that were of younger age at the time of fire (Smith et al. 2013; Smith et al. 2016). Large old trees have critical roles in nutrient cycling, particularly the carbon cycle. Keith et al. (2009) suggested that Mountain Ash forests are the most carbon-dense forests on earth. They store vast amounts of carbon, particularly when they have not been disturbed by industrial logging (Keith et al. 2014). As in many forest types globally, large old trees contribute a significant proportion of the total carbon biomass stored in individual forest stands. Moreover, work by Koch et al. (2015) demonstrated that the largest and oldest trees continue to accumulate very large amounts of biomass right up to the time of apical crown collapse, even though these trees are often also the most decayed individuals.

Large old trees are critical in hydrological cycles, with much of the water for the city of Melbourne derived from water catchments dominated by Mountain Ash forests or other ash-type eucalypts (Viggers et al. 2013). There are well-established positive relationships between the age of stands and the water yield (Langford et al. 1982; Vertessy et al. 2001). That is, catchments dominated by old-growth forests produce significantly more water than those where the forest cover is primarily young forest (O'Shaughnessy & Jayasuriya 1991).

Mountain Ash forests have significant cultural values, and large old trees in these forests have featured in many



Figure 1: 'Near Fernshaw' by Louis Buvelot.

artworks, both historic and contemporary. The painting 'Near Fernshaw' that the Swiss artist Louis Buvelot created in 1873 is one of several classic landscape works depicting Mountain Ash forests (Figure 1). Large old trees also feature in many written historical accounts of the lives of white settlers in Mountain Ash forests, including those of extensive past timber cutters (e.g. Houghton 1986; Evans 1994). There are also classic historical photographs of large old trees, such as the now collapsed Furmston Tree surrounded by the entire townsfolk of Fernshaw (Figure 2).

Tourism has always been important in the Central Highlands region, with towns such as Marysville having a long connection with the tourism industry. Large old trees are key attractions in Mountain Ash forests. Current extraordinary individual trees with high visitation rates include the Kalatha Giant in Toolangi State Forest, the



Figure 2: Furmston tree. Image from the State Library of Victoria.

Big Tree in the Tall Trees Reserve at Cambarville, east of Marysville, and the Ada Tree in Powelltown State Forest.

Mountain Ash trees are used extensively in the production of paper as well as some timber products (Flint & Fagg 2007), although recent analyses based on formalised international environmental accounting procedures indicate the economic value of forest for water and tourism far exceed the value of the forest for paper and timber (Keith et al. 2016).

Threats to populations of large old trees in the Central Highlands of Victoria

Populations of large old trees are in serious decline in the Mountain Ash forests of the Central Highlands of Victoria. Recent analyses have indicated that 41% of large old trees first measured on 166 long-term monitoring sites in 1997

had collapsed by 2015 (Lindenmayer et al. 2016). Current, empirically-based projections (based on the unlikely assumption of no fire and no logging in the next five decades) suggest that the abundance of large old trees will decline from an average of seven trees per hectare in 1997 to less than one per hectare by 2065 (Lindenmayer et al. 2015). Indeed, given this level of decline and that large old trees are keystone structural attributes (sensu Tews et al. 2004) in Mountain Ash forests, recent IUCN Ecosystem Assessment protocols (see Keith et al. 2013) indicate that Mountain Ash forests should be formally classified as Critically Endangered (Burns et al. 2015).

Many, often interacting, natural and human factors (see Figure 3) are driving the well-documented collapse in populations of large old trees in Mountain Ash forests. Past and present logging is a major driver of decline. Clearfelling is the predominant form of logging in Mountain Ash forests (Lutze et al. 1999; Lindenmayer et al. 2015) and large old trees are generally not cut down in these operations. However, many hundreds of large old trees are destroyed annually by the high-intensity burns lit to regenerate logged forests after clearfelling (Lindenmayer et al. 2015). In addition, the clearfelling of forests increases the susceptibility of retained trees to collapse through exposure and blowdown (Lindenmayer et al. 1997). Notably, recent empirical work indicates that abundance of collapsed large old trees is highest in young forests that have been subject to past logging (Lindenmayer et al. 2016). A further effect of logging is that harvesting removes trees before they reach an age where they can become large old trees; that is, it impairs the recruitment of new cohorts of large old trees (Lindenmayer et al. 2012). Finally, logging increases the risk that future fires in Mountain Ash forests will be crown-scorching conflagrations that kill or even completely consume large old trees (Taylor et al. 2014). The landscape-wide effects of logging operations on the abundance of large old trees in Mountain Ash forests have been quantified in recent analyses, which indicate that forests in unlogged protected areas support significantly greater numbers of such trees than areas in wood-production forests (Lindenmayer et al. 2016).

Fire is another driver of decline in populations of large old trees in Mountain Ash forests. Large old dead trees are significantly less abundant on sites that have been burned (Lindenmayer et al. 2016), with dead trees often completely consumed by fire. In addition, burned sites can be subject to post-fire salvage logging which has been shown to further elevate rates of loss of large old trees (Lindenmayer & Ough 2006). The effects of fire on large old tree populations are magnified by the status of the forest at the time it is burned. For example, young forests tend to burn at higher severity than old forests (Taylor et al. 2014) and this can have negative effects on scattered large old trees that occur in stands dominated primarily by younger trees that are created by logging operations. Conversely, fire in old-growth stands can kill or badly damage large old trees, but nevertheless create a pulse of trees which, if they remain standing, continue to store large amounts of carbon as well as eventually become suitable habitat for cavity-dependent fauna.

The development of industrial human infrastructure is a threat to large old trees in Mountain Ash forests. For example, the construction of fire breaks in Mountain Ash forests has led to the destruction of numerous large old trees (see Lindenmayer et al. 2015). Similarly, roads constructed to facilitate logging operations also can have a direct negative impact on large old trees through forest clearing.

Climate change is a significant threat to the occurrence and abundance of large old trees in Mountain Ash forests. Previous modelling has indicated that altered rainfall and temperatures associated with climate change will reduce the area supporting suitable environments where the species can grow (Lindenmayer 1989; Mackey et al. 2002), especially given the relative narrow bioclimatic domain in which the species occurs. Large old trees may be particularly susceptible to changes in environmental regimes as global analyses suggest that intra-specific competitive pressures mean that these trees often operate at the margins of their physiological drought tolerance (Choat et al. 2012).

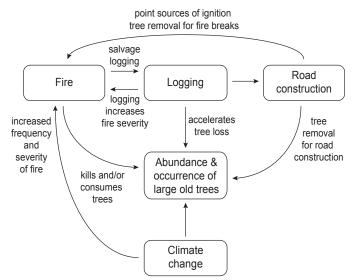


Figure 3: Interacting drivers of large old tree decline in the Mountain Ash forests of the Central Highlands of Victoria.

Indeed, during the period 2004–2011, almost 25% of large old living trees on long-term monitoring died on sites that remained unburned by the 2009 wildfires (Lindenmayer et al. 2012). Much of this period spanned the Millennium Drought, characterised by extreme temperatures and limited rainfall, and such widespread patterns of large old tree mortality were ten times the expected background rates for these cohorts of trees.

There can be important interactions between some of the key drivers of decline of large old trees in Mountain Ash forest. Interrelationships between logging and the risk of elevated fire severity in young forests regenerating after harvesting have been discussed above (see also (Lindenmayer et al. 2009a; Taylor et al. 2014). Logging following fire (i.e. salvage logging) is another important interrelationship between drivers of decline of populations of large old trees (Lindenmayer et al. 2008). There are also interactions between logging, fire and the development of human infrastructure, as roads need to be constructed to facilitate harvesting operations and this can, in turn, not only lead to the direct removal of trees but also increase potential point sources for fire ignitions by arsonists (although roads are also important for fire suppression efforts). Some drivers of large old tree loss interact with the effects of climate change. For example, relationships between increasing temperatures, reducing rainfall and the increased prevalence and severity of wildfires are well established for south-eastern Australia (Williams et al. 2009; Cary et al. 2012).

Challenges to the management and conservation of large old trees in the Central Highlands of Victoria

The conservation of large old trees in Mountain Ash forests represents a significant challenge for forest, wildlife and reserve managers. This is because many things need to be done to arrest and then reverse the current trend of rapid population decline. The three most important actions are briefly outlined below.

First, all remaining large old trees must be adequately protected. This means not only preventing them from being cut down (this is still occurring in some places), but also buffering them from logging in the surrounding landscape. Buffers of uncut forest measuring 100 metres in radius have been proposed to protect each individual large old tree (Lindenmayer et al. 2013). Such protection measures are critical because it takes so long (centuries) to replace large old trees if they are lost. The focus on strategies to protect all existing large old trees must not be diverted by attempts to replace some of the key ecological roles of large old trees with 'engineering-style' solutions for which medium- to long-term effectiveness remains unknown. The provision of cavities for hollow-dependent fauna through the establishment of nest boxes is an example (Lindenmayer et al. 2009b) and the attention given to them is ecologically nonsensical - and cost-ineffective (see McKenney & Lindenmayer 1994), while large old trees continue to be lost as a result of direct human management actions, including logging.

Second, all areas of old growth need to be protected as this is where the abundance of large old trees is greatest in Mountain Ash forests (Lindenmayer et al. 1991a; Lindenmayer et al. 2016). Old growth protection must include small patches of old forest (such as those less than 1 ha in areas) but which are currently at risk of being logged. Moreover, the marginal value of large old trees, particularly for biodiversity, may be higher where these trees are limited in abundance (Fischer et al. 2010). The protection of all areas of old growth forest, irrespective of the area of such stands, is particularly critical in Mountain Ash forests given that the current area of old growth is just 1.16% of the entire forest estate or 1/30th-1/60th of what it was historically (i.e. prior to white settlement) (Lindenmayer et al. 2015). Indeed, given the limited size of the old-growth estate, a crucial forest management strategy must be to undertake extensive ecosystem restoration and regrow large and continuous areas of old growth Mountain Ash forest (Lindenmayer et al. 2013). This has other key advantages; for example, a larger old growth estate will have fire suppression benefits as well as creating potentially suitable post-fire habitat for animals such as Leadbeater's Possum (Lindenmayer et al. 2013; Lindenmayer et al. 2015). In addition, an increased old growth forest estate would have major ecosystem service benefits (Lindenmayer et al. 2015) such as increased levels of carbon storage (Keith et al. 2014) and water production (Vertessy et al. 2001; Viggers et al. 2013).

A major strategy for recovering populations of large old trees is to ensure adequate recruitment of new cohorts of such trees (Gibbons & Lindenmayer 1996). Logging can significantly impair the recruitment process in wood production forests (Lindenmayer et al. 2012). In Mountain Ash forests, the next nearest stands of old growth forest (and hence cohorts of large old trees) are the areas of 76year old regrowth stands that regenerated after the 1939 Black Friday wildfires. There is a critical need to exclude logging from extensive areas of 1939-aged Mountain Ash forest to not only better conserve existing large old trees in these forests, but also to recruit new cohorts of large old trees as well as significantly expand the old growth forest estate (Lindenmayer et al. 2015).

Acknowledgements

I thank Bjarne K Dahl Trust and especially Bram Mason and Bill Birch for encouraging me to write this short summary paper. This article is based on several other earlier and longer papers. Collaborations with Wade Blanchard, David Blair, Lachlan McBurney and Bill Laurance were critical in the development of that earlier work.

References

- Ashton, D.H., 1975. The seasonal growth of *Eucalyptus* regnans F. Muell. Australian Journal of Botany 23: 239–252.
- Blicharska, M. & Mikusinski, G., 2014. Incorporating social and cultural significance of large old trees in conservation policy. *Conservation Biology* 28: 1558–1567.
- Burns, E.L., Lindenmayer, D.B., Stein, J., Blanchard, W., McBurney, L., Blair, D. & Banks, S.C., 2015. Ecosystem assessment of mountain ash forest in the Central Highlands of Victoria, south-eastern Australia. *Austral Ecology* 40: 386–399.
- Cary, G.J., Bradstock, R.A., Gill, A.M. & Williams, R.J., 2012. Global change and fire regimes in Australia. In *Flammable Australia: Fire Regimes, Biodiversity and Ecosystems in a Changing World*, R.A. Bradstock, A.M. Gill & R.J. Williams, eds. Melbourne, CSIRO Publishing, pp. 149–169.
- Choat, B., Jansen, S., Brodribb, T.J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S.J., Feild, T.S., Gleason, S.M., Hacke, U.G., Jacobsen, A.L., Lens, F., Maherali, H., Martinez-Vilalta, J., Mayr, S., Mencuccini, M., Mitchell, P.J., Nardini, A., Pittermann, J., Pratt, R.B.,

Sperry, J.S., Westoby, M., Wright, I.J. & Zanne, A.E., 2012. Global convergence in the vulnerability of forests to drought. *Nature* 491: 752–755.

- Evans, P., 1994. *Rails to Rubicon: A history of the Rubicon Forest.* Light Railway Research Society of Australia, Melbourne.
- Fischer, J., Stott, J. & Law, B.S., 2010. The disproportionate value of scattered trees. *Biological Conservation* 143: 1564–1567.
- Flint, A. & Fagg, P., 2007. Mountain Ash in Victoria's State Forests. Department of Sustainability and Environment, Melbourne.
- Gibbons, P. & Lindenmayer, D.B., 1996. Issues associated with the retention of hollow-bearing trees within eucalypt forests managed for wood production. *Forest Ecology and Management* 83: 245–279.
- Houghton, N., 1986. *Timber Mountain*. Light Railway Research Society of Australia, Melbourne.
- Keith, H., Mackey, B.G. & Lindenmayer, D.B., 2009. Re-evaluation of forest biomass carbon stocks and lessons from the world's most carbon-dense forests. *Proceedings of the National Academy of Sciences* 106: 11635–11640.
- Keith, D.A., Rodríguez, J.P., Rodríguez-Clark, K.M., Nicholson, E., Aapala, K., Alonso, A., Asmussen, M., Bachman, S., Bassett, A., Barrow, E.G., Benson, J.S., Bishop, M.J., Bonifacio, R., Brooks, T.M., Burgman, M.A., Comer, P., Comín, F.A., Essl, F., Faber-Langendoen, D., Fairweather, P.G., Holdaway, R. J., Jennings, M., Kingsford, R.T., Lester, R.E., MacNally, R., McCarthy, M.A., Moat, J., Oliveira-Miranda, M.A., Pisanu, P., Poulin, B., Regan, T.J., Riecken, U., Spalding, M.D. & Zambrano-Martínez, S., 2013. Scientific foundations for an IUCN Red List of Ecosystems. *PLOS One* 8: e62111.
- Keith, H., Lindenmayer, D.B., Mackey, B.G., Blair, D., Carter, L., McBurney, L., Okada, S. & Konishi-Nagano, T., 2014. Managing temperate forests for carbon storage: impacts of logging versus forest protection on carbon stocks. *Ecosphere* 5(6): Art. 75. [online] http:// dx.doi.org/10.1890/ES1814-00051.00051.
- Keith, H., Vardon, M., Stein, J., Stein, J. & Lindenmayer, D.B., 2016. Experimental Ecosystem Accounts for the Central Highlands of Victoria. Fenner School of Environment and Society, The Australian National University, Canberra. Available at: http://fennerschoolassociated.anu.edu.au/documents/Ecosystem_ Accounts_full_report_v1.pdf.
- Koch, G.W., Sillett, S.C., Antoine, M.E. & Williams, C.B., 2015. Growth maximization trumps maintenance of leaf conductance in the tallest angiosperm. *Oecologia* 177: 321–331.
- Langford, K.J., Moran, R.J. & O'Shaughnessy, P.J., 1982. The Coranderrk Experiment — the effects of roading

and timber harvesting in mature Mountain Ash forest on streamflow and quality. In *The First National Symposium on Forest Hydrology*, E.M. O'Loughlin & L.J. Bren, eds. Institution of Engineers, Canberra, pp. 92–102.

- Lindenmayer, D.B., 1989. *The Ecology and Habitat Requirements of Leadbeater's Possum*. The Australian National University, Canberra.
- Lindenmayer, D.B., 2009. Forest Pattern and Ecological Process: A Synthesis of 25 Years of Research. CSIRO Publishing, Melbourne.
- Lindenmayer, D.B., Cunningham, R.B., Nix, H.A., Tanton, M.T. & Smith, A.P., 1991a. Predicting the abundance of hollow-bearing trees in montane ash forests of southeastern Australia. *Australian Journal of Ecology* 16: 91–98.
- Lindenmayer, D.B., Cunningham, R.B., Tanton, M.T., Smith, A.P. & Nix, H.A., 1991b. Characteristics of hollow-bearing trees occupied by arboreal marsupials in the montane ash forests of the Central Highlands of Victoria, south-east Australia. *Forest Ecology and Management* 40: 289–308.
- Lindenmayer, D.B., Mackey, B. & Nix, H.A., 1996. Climatic analyses of the distribution of four commerciallyimportant wood production eucalypt trees from southeastern Australia. *Australian Forestry* 59: 11–26.
- Lindenmayer, D.B., Cunningham, R.B. & Donnelly, C.F., 1997. Decay and collapse of trees with hollows in eastern Australian forests: impacts on arboreal marsupials. *Ecological Applications* 7: 625–641.
- Lindenmayer, D.B. & Ough, K., 2006. Salvage logging in the montane ash eucalypt forests of the Central Highlands of Victoria and its potential impacts on biodiversity. *Conservation Biology* 20: 1005–1015.
- Lindenmayer, D.B., Burton, P.J. & Franklin, J.F., 2008. Salvage Logging and its Ecological Consequences. Island Press, Washington DC.
- Lindenmayer, D.B., Hunter, M.L., Burton, P.J. & Gibbons, P., 2009a. Effects of logging on fire regimes in moist forests. *Conservation Letters* 2: 271–277.
- Lindenmayer, D.B., Welsh, A., Donnelly, C.F., Crane, M., Michael, D., MacGregor, C., McBurney, L., Montague-Drake, R.M. & Gibbons, P., 2009b. Are nest boxes a viable alternative source of cavities for hollow-dependent animals? Long-term monitoring of nest box occupancy, pest use and attrition. *Biological Conservation* 142: 33–42.
- Lindenmayer, D.B., Blanchard, W., McBurney, L., Blair, D., Banks, S., Likens, G.E., Franklin, J.F., Stein, J. & Gibbons, P., 2012. Interacting factors driving a major loss of large trees with cavities in an iconic forest ecosystem. *PLOS One* 7: e41864.
- Lindenmayer, D.B., Blair, D., McBurney, L., Banks, S.C., Stein, J.A.R., Hobbs, R.J., Likens, G.E. & Franklin,

J.F., 2013. Principles and practices for biodiversity conservation and restoration forestry: a 30-year case study on the Victorian montane ash forests and the critically endangered Leadbeater's Possum. *Australian Zoologist* 36: 441–460.

- Lindenmayer, D.B., Barton, P.S., Lane, P.W., Westgate, M.J., McBurney, L., Blair, D., Gibbons, P. & Likens, G.E., 2014a. An empirical assessment and comparison of species-based and habitat-based surrogates: a case study of forest vertebrates and large old trees. *PLOS One* 9: e89807.
- Lindenmayer, D.B., Laurance, W., Franklin, W.F., Likens, G.E., Banks, S.C., Blanchard, W., Gibbons, P., Ikin, K., Blair, D., McBurney, L., Manning, A.D. & Stein, J.A.R., 2014b. New policies for old trees: averting a global crisis in a keystone ecological structure. *Conservation Letters* 7: 61–69.
- Lindenmayer, D.B., Blair, D., McBurney, L. & Banks, S., 2015. *Mountain Ash: Fire, Logging and the Future of Victoria's Giant Forests.* CSIRO Publishing, Melbourne.
- Lindenmayer, D.B., Blanchard, W., Blair, D., McBurney, L. & Banks, S.C., 2016. Environmental and human drivers of large old tree abundance in Australian wet forests. *Forest Ecology and Management* 372: 226– 235.
- Lindenmayer, D.B. & Laurance, W.F., 2016. The unique challenges of conserving large old trees. *Trends in Ecology and Evolution* 31: 416–418.
- Lutze, M.T., Campbell, R.G. & Fagg, P.C., 1999. Development of silviculture in the native State forests of Victoria. *Australian Forestry* 62: 236–244.
- Mackey, B., Lindenmayer, D.B., Gill, A.M., McCarthy, M.A. & Lindesay, J.A., 2002. Wildlife, Fire and Future Climate: A Forest Ecosystem Analysis. CSIRO Publishing, Melbourne.
- McKenney, D.W. & Lindenmayer, D.B., 1994. An economic assessment of a nest-box strategy for the conservation of an endangered species. *Canadian Journal of Forest Research* 24: 2012–2019.
- Newton-John, J., 1992. Arboreal Habitat Hollows in River Red Gum (E. camaldulensis) in the Barmah Forests. University of Melbourne, Melbourne.
- O'Shaughnessy, P. & Jayasuriya, J., 1991. Managing the ash-type forest for water production in Victoria. In *Forest Management in Australia*, F.H. McKinnell, E.R.

Hopkins & J.E.D. Fox, eds. Surrey Beatty and Sons, Chipping Norton, pp. 341–363.

- Pharo, E.J., Meagher, D.A. & Lindenmayer, D.B., 2013. Bryophyte persistence following major fire in eucalypt forest of southern Australia. *Forest Ecology and Management* 296: 24–32.
- Smith, A.L., Blair, D., McBurney, L., Banks, S.C., Barton, P.S., Blanchard, W., Driscoll, D. A., Gill, A.M. & Lindenmayer, D.B., 2013. Dominant drivers of seedling establishment in a fire-dependent obligate seeder: climate or fire regimes? *Ecosystems* 17: 258–270.
- Smith, A.L., Blanchard, W., Blair, D., McBurney, L., Banks, S.C., Driscoll, D.A. & Lindenmayer, D.B., 2016. The dynamic regeneration niche of a forest following a rare disturbance event. *Diversity and Distributions* 22: 457–467.
- Taylor, C., McCarthy, M.A. & Lindenmayer, D.B., 2014. Non-linear effects of stand age on fire severity. *Conservation Letters* 7: 355–370.
- Tews, J., Brose, U., Grimm, V., Tielborger, K., Wilchmann, M., Schwager, M. & Jeltsch, F., 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography* 31: 79–92.
- Vertessy, R.A., Watson, F.G.R. & O'Sullivan, S.K., 2001. Factors determining relations between stand age and catchment water balance in mountain ash forests. *Forest Ecology and Management* 143: 13–26.
- Viggers, J.I., Weaver, H.J. & Lindenmayer, D.B. 2013. Melbourne's Water Catchments: Perspectives on a World Class Water Supply. CSIRO Publishing, Melbourne.
- Wenk, E.H. & Falster, D., 2015. Quantifying and understanding reproductive allocation schedules in plants. *Ecology and Evolution* 5: 5521–5538.
- Williams, R.J., Bradstock, R.A., Cary, G.J., Enright, N.J., Gill, A.M., Liedloff, A.C., Lucas, C., Whelan, R.J., Andersen, A.N., Bowman, D.J., Clarke, P.J., Cook, G.D., Hennessy, K. J. & York, A., 2009. *Interactions Between Climate Change, Fire Regimes and Biodiversity in Australia: A Preliminary Assessment*. Department of Climate Change and Department of the Environment, Water, Heritage and the Arts, Canberra.