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Key perspectives on early successional forests subject to stand-replacing disturbances

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Abstract

In forests subject to stand-replacing disturbances, early successional stands can provide important habitats for a range of species not typically present in long-undisturbed areas. Compared to old-growth forests, the habitat values of – and key ecological processes in – early successional forests have been less studied, perhaps due to a perception that early successional forests revert to a homogenous "clean slate" following stand-replacing disturbances. In this paper, we draw on 36 years of long-term research in the Mountain Ash (*Eucalyptus regnans*) and Alpine Ash (*Eucalyptus delegatensis*) forests of south-eastern Australia, together with examples from elsewhere around the world, to show that not all kinds of early successional forests are created equal. We argue that the ecological values of early successional forests can be profoundly affected by six inter-related factors: **(1)** The evolutionary context and environmental domain of a given ecosystem. **(2)** Successional stage and condition of a forest stand prior to disturbance. **(3)** Disturbance intensity, severity and type (e.g. wildfire versus clearcutting). **(4)** Post-disturbance conditions including climate and weather. **(5)** Post-disturbance management (e.g. salvage logging) which can have significant impacts on biological legacies. And, **(6)** The relative spatial extent and spatial arrangement of early and late successional forest across a landscape. These factors can influence ecological values directly, or through effects on the types, amount and spatial patterns of biological legacies present in early successional forest. We present a conceptual model highlighting the inter-relationships between these factors and illustrate its use through a detailed case study.

Strategies to improve the management of early successional forests include: **(1)** Identifying the species associated with post-disturbance environments and the reasons why they occur in such environments. **(2)** Understanding the types, numbers, and spatial patterns of biological legacies that remain after natural disturbance. **(3)** Identifying critical areas that should be excluded from logging or other human disturbance. **(4)** Limiting the extent of post-disturbance activities like salvage logging that undermine the ecological values of, and ecosystem processes in, early successional forests. And, **(5)** Balancing the relative amounts of early successional versus late successional forest in a given landscape or region to ensure that a variety of forest types are present at any given time, and that critical biological legacies are retained. Paradoxically, ensuring that landscapes support extensive areas of late successional forest is critical so that future early successional forests are not devoid of the biological legacies necessary for ecosystem function and recovery.

Keywords: Late successional forest, biological legacies, biodiversity, natural disturbance, wildfire, clearcutting, salvage logging, Mountain Ash forests, Alpine Ash forests, landscape traps.

1. Introduction

Natural disturbance is an inherent part of forest ecosystems (Noble and Slatyer 1980; Attiwill 1994; Frelich 2005; Thom and Seidl 2016; Sommerfeld et al., 2018). Succession following disturbance is also a key part of vegetation dynamics in all forest ecosystems (Noble and Slatyer 1980; Slik et al., 2002; Pulsford et al., 2016; Chang and Turner 2019). Indeed, a huge literature has developed around succession as part of vegetation theory (Frelich 2005; Johnson and Miyanishi 2008; Pulsford et al., 2016; DellaSala et al., 2017). While much discussion of forest conservation has focused on intact old growth (or late successional) forest (Franklin et al., 1981; Watson et al., 2018), early successional environments are increasingly recognised as being important for biodiversity (Hutto 2008; Swanson et al., 2011; Swanson et al., 2014). Some species are strongly associated with the initial stages of post-disturbance recovery and are rare or even entirely absent from other, older, stages of development (Heyborne et al., 2003; Hutto 2008; Swanson et al., 2011; Hutto et al., 2016). Nevertheless, the habitat values of, and key ecological processes in, early successional forests have received limited study in many ecosystems (Hutto 1995; Swanson et al., 2011; Swanson et al., 2014). Indeed, many of the temporal and spatial factors that promote or undermine the ecological values of early successional environments remain poorly understood.

In this paper, we discuss key factors affecting the ecological values of early successional forests subject to stand-replacing natural disturbances. Our particular focus is on forests where the dominant disturbances are wildfire and logging, given the considerable challenges of managing these ecosystems to both conserve biodiversity and maintain timber harvesting operations (Simon et al., 2002; Van Wilgenburg and Hobson 2008; Keeley and Pausas 2019). Early successional forests are sometimes perceived as being homogenous and viewed as a "clean slate" following stand-replacing disturbances (Noble and Slatyer 1980). However, not all early successional forest ecosystems are created equal. Between-stand variation in the habitat and other ecological values of early successional forests can occur for a range of reasons that we explore in detail below.

One key element influencing the ecological attributes of disturbed forest is the type, number and spatial pattern of biological legacies carried over from a previous stand to a post-disturbance regenerating stand (Franklin and MacMahon 2000; Dale et al., 2003; Swanson et al., 2011; Donato et al., 2012). Biological legacies are broadly defined as: *the living and dead structures and organisms remaining after disturbance that can influence the recovery of the post-disturbed environment* (Franklin et al., 2000). They can include living and dead trees, shrubs and other plants, living animals, animal carcasses, seeds, spores, fungi, eggs and soil communities (Franklin et al., 2000; Stahlheber et al., 2015). Biological legacies can have profound effects on habitat suitability of early successional stands for many species (Hutto et al., 2015) as well as influence ecosystem processes like carbon storage and nutrient cycling (Harmon et al., 1986; and see Keith et al., 2014a). Indeed, some species may continue to persist within disturbed areas only because of the legacies remaining after disturbances (Hutto 1995; Franklin and MacMahon 2000; Swanson et al., 2011). Where species are extirpated by fire or logging, the ongoing presence of biological legacies also may facilitate rapid colonization of disturbed sites, relative to areas where biological legacies are rare (Franklin et al., 2000; Hutto 2008). The available evidence suggests that effects of biological legacies are both important and widespread, with several reviews documenting the many species that are strongly associated with legacies – such as deadwood – that can be created by natural disturbances (e.g. Fischer and McClelland 1983; Harmon et al., 1986; Rose et al., 2001; Lindenmayer and Franklin 2002; Thorn et al., 2017; Thorn et al., 2018).

A variety of landscape and site-level factors can strongly influence the ecological values of early successional forests, both through effects on biological legacies, and via more direct pathways (Donato et al., 2012). First, the evolutionary and environmental context of a given ecosystem constrain the spatiotemporal availability of habitats within which a suite of early successional species may occur and evolve (Hutto et al., 2015). Second, the pre-disturbance age of a perturbed forest (as reflected by the time elapsed since the previous fire) will have a substantial influence on the ecological values of the post-disturbance forest (e.g. (Raphael and Morrison 1987; Smucker et al., 2005; Saab et al., 2007; Kemp et al., 2019); effects which will be manifested through the biological legacies carried from a pre-disturbance stand to a post-disturbance stand (ecological continuity). Disturbances in late successional forests will often produce more biological legacies (including seeds) than where early successional forests are disturbed. In addition, many biological legacies (e.g. standing dead trees) that are created when late successional forests burn will be larger, and persist longer than, legacies created following disturbance in a younger forest. This provides a continuity of complexity when early successional habitats are created from the disturbance of late successional stands (Franklin et al., 2000; Donato et al., 2012). Third, disturbance type will have a fundamental influence. For example, areas regenerating after high-intensity clearcut logging will generally support fewer biological legacies relative to stands recovering following natural disturbances such as wildfire (McLean et al., 2015; Kemp et al., 2019; Turner et al., 2019). Fourth, post-disturbance conditions such as drought, temperature and wind speeds can affect the survival and persistence of legacies such as seeds, fungal spores and standing trees, as well as the growth and survival of recovering and recolonising species. Fifth, post-disturbance management practices such as salvage logging (Thorn et al., 2017; Leverkus et al., 2018), or repeated natural disturbances at short intervals, can erode the ecological values of early successional forest, in part through undermining the important roles and functions provided by biological legacies. Finally, the relative spatial extent of early and late successional forest across a landscape can influence key ecological processes and ultimately the habitat values and sizes of populations of biota in early successional forests.

We propose a conceptual model that highlights the inter-relationships between the key factors which influence the habitat values and ecosystem processes within early successional forests (Fig. 1). We illustrate the effects of these factors using examples from a range of forest types around the world where stand-replacing disturbances occur. We draw extensively on insights from 36 years of long-term research and monitoring in the Mountain Ash (*Eucalyptus regnans*) and Alpine Ash (*Eucalyptus delegatensis*) forests of the Central Highlands of Victoria, south-eastern Australia. The primary forms of natural and human disturbance in these forests are wildfire and clearcut logging, respectively (Flint and Fagg 2007; Taylor et al., 2014). Such stand-replacing disturbance dynamics in Mountain Ash and Alpine Ash forests are similar to those which characterize a wide range of other wet forest types globally (Frelich 2005; Sommerfeld et al., 2018) (e.g. Douglas-Fir [*Pseudotsuga menziesii*] (Franklin et al., 2002; Phalan et al., 2019) and boreal forests (Burton et al., 2003; Bergeron et al., 2006)). However, stand-replacing forest dynamics are uncommon in the majority of other forest ecosystems within Australia where dominant trees survive fire through recovery mechanisms such as epicormic growth and/or growth from lignotubers (Chattaway 1958; Bradstock et al., 2012).

2. Background – empirical studies in Mountain Ash and Alpine Ash forests

The insights we outline in this paper are derived from long-term studies in the Mountain Ash and Alpine Ash forests of the Central Highlands of Victoria, in south-eastern Australia. This 60 km x 80 km area is approximately 100 km north-east of Melbourne. Mature trees in Mountain Ash forest commonly reach heights of ~ 65+ metres (Ashton 1975).

Alpine Ash is also a spectacular tree with mature individuals approaching 60 metres in height (Boland et al., 2006). Both species in the Central Highlands region are obligate seeders, meaning that wildfires often kill trees and the forest regenerates from canopy stored seed (Smith et al., 2014), typically creating even-aged cohorts of trees (Ashton 1981). Parts of the Central Highlands region has been subject to a series of wildfires in the past century including those in 1926, 1932, 1939, 1983, 2009 and, most recently, 2019 (Lindenmayer et al., 2019a).

Clearcutting is the primary form of human disturbance in Mountain Ash forests (Flint and Fagg 2007) and, like wildfire, creates even-aged cohorts of post-disturbance regeneration. The nominal rotation time between clearcutting operations is 80 years, although analyses of government mapping shows much of the potentially loggable forest has been harvested well before this age (Keith et al., 2017). Prior to the deployment of clearcut harvesting, Mountain Ash and Alpine Ash were subject to widespread selective harvesting with substantial amounts of timber cut from these forests over the past 120+ years (Griffiths 2001). Indeed, approximately a century ago, over 240 sawmills operated in the Central Highlands region (Commonwealth of Australia and Department of Natural Resources and Environment 1997). Now just six sawmills operate in our study region.

Currently, late successional Mountain Ash and Alpine Ash forest is uncommon. An estimated 98% of the Mountain Ash estate and 99.5% the Alpine Ash estate comprises forest with an overstorey that is <80 years old (Lindenmayer and Sato 2018). In the case of Mountain Ash forests, late successional forest (exceeding 120 years old) may have comprised up to 30-60% of the estate at the time of European settlement and prior to the onset of widespread logging operations and recurrent wildfires (Lindenmayer and McCarthy 2002).

Between 1983 and 2019, we established 181 long-term field sites as well as 100 logging experiment sites throughout the Mountain Ash and Alpine Ash forests in the Victorian Central Highlands region. These sites spanned a range of forest age classes ranging from 10 to 300+ years old at the time they were established. They also span a wide range of environmental conditions, including sites on steep slopes and flatter terrain, at low and high elevations, and areas subject to different numbers of disturbance events. Approximately half of our sites burned in a major wildfire in 2009. These sites have been the target of studies of mammal, bird and plant responses to disturbance, as well as investigations of carbon storage and nutrient cycling, providing detailed insights into the biodiversity and other ecological dynamics of early succession.

Large wildfires and logging are stand-replacing disturbances in Mountain Ash and Alpine Ash forests, and biological legacies are therefore critical to the ecological value of early successional stages of these forests. Biological legacies that persist on burned sites after high-severity fire include: **(1)** Large old living and standing dead hollow-bearing trees (Lindenmayer et al., 2016; Lindenmayer et al., 2018a). **(2)** Fallen trees and coarse woody debris (Lindenmayer et al., 1999b). **(3)** Large old tree ferns that can exceed 350 years of age (Mueck et al., 1996; Blair et al., 2017). **(4)** Resprouting vascular plants (e.g. Musk Daisy Bush [*Olearia argophylla*]) (Blair et al., 2016). **(5)** An array of species of bryophytes (Pharo et al., 2013). **(6)** Plant seeds, fungal spores, nutrients and other components that persist within the soil (Bowd et al., 2019). And, **(7)** Living animals such as the Mountain Brushtail Possum (*Trichosurus cunninghami*), Bush Rat (*Rattus fuscipes*) and Agile Antechinus (*Antechinus agilis*) (Banks et al., 2011a; Banks et al., 2011b). Several of these biological legacies are known to affect the occurrence of rare or endangered species that use Mountain Ash and Alpine Ash forests. For example, our field data shows that the Critically Endangered Leadbeater's Possum (*Gymnobelidues leadbeateri*) can sometimes colonize forest within a decade of a major disturbance (Lindenmayer et al., unpublished data) if the regenerating stands support sufficient numbers of large old hollow-bearing trees for denning and nesting (Lindenmayer et al., 1991b). This species, and other cavity-dependent taxa, are generally absent from early successional forests if biological legacies like large old trees do not occur (Lindenmayer et al., 1991b; Lindenmayer et al., 2014a). In such places, it may be 170+ years before trees eventually develop the kinds of cavities that will provide potentially suitable habitat for hollow-using animals (Lindenmayer et al., 2017a). Hence, the presence of biological legacies can accelerate post-disturbance colonization by some species by up to 160 years.

3. Factors influencing ecological values of early successional forests

As described in our conceptual model (Fig. 1), we suggest that six factors influence the ecological values of early-successional forest, both directly, and through effects on biological legacies. Below we describe these factors and their interactions in detail.

3.1 Evolutionary boundaries for early successional forests and associated biota

We suggest that the assemblage of early successional species in any given ecosystem will be shaped by the evolutionary context of that environment. That is, the prevalence of early successional specialist species will be associated with opportunities for the evolutionary development of such species (Poisot et al., 2011). These opportunities will likely be maximized where early successional forests are spatially extensive, persist for prolonged periods (before canopy closure), recur frequently, or all of these. They also may be more prevalent where adjacent open habitats such as grassland or shrubland (which may provide similar niche space to early successional forest) act as source populations of early successional specialist species. Conversely, we suggest few early successional specialists are likely to evolve in narrowly distributed forest ecosystems where stand-replacing disturbances are spatially and temporally rare (Poisot et al., 2011), and where neighbouring habitats are not open, or prone to stand-replacing disturbances.

Early successional specialists are rare in Mountain Ash and Alpine Ash forests. This paucity of early successional specialists is in marked contrast to many other forest ecosystems prone to stand-replacing disturbances, where early successional species can be relatively common (Swanson et al., 2014; Hutto et al., 2015). These include upland forests of south-eastern USA, the Douglas-Fir forests of the Pacific Northwest of the USA, and the boreal forests of Canada and elsewhere in the Northern Hemisphere (Angelstam 1998; Burton et al., 2003; DeGraaf et al., 2003; Klaus et al., 2010a; Klaus et al., 2010b; Swanson et al., 2011; Swanson et al., 2014). Of the more that 70 bird species inhabiting Mountain Ash and Alpine Ash forests, populations of only one species, the Flame Robin (*Petroica phoenicea*), increases significantly in recently burned areas (Lindenmayer et al., 2014b; Lindenmayer et al., 2019b). For the mammal community which comprises ~20 species, only the exotic House Mouse (*Mus musculus*) is common in early successional forests and is almost never recorded in older forests (Lindenmayer et al., 1994a).

In Mountain Ash and Alpine Ash forests, the natural fire regime is a high-severity stand-replacing conflagration on average every 107 years (McCarthy et al., 1999), but the time from disturbance to canopy closure of the regenerating stand is just 2-3 years (Blair et al., 2016). It seems somewhat paradoxical that a forest ecosystem which supports the world's tallest flowering plants and is subject to stand-replacing fire can be characterized by canopy closure within three years of a major perturbation. The reasons for the evolution of such dynamics remain unknown, but are likely related to high growth rates and reproductive output in ash species. Relative to many other areas in Australia that are dominated by other kinds of eucalypt forests, Mountain Ash forests grow in areas characterized by high levels of rainfall and deep fertile soils, which can promote rapid tree growth (Ashton 1975; Lindenmayer et al., 1996). A related explanation may be that Mountain Ash trees can produce prolific amounts of seed, especially mature and old trees. High seed production and high rates of post-disturbance germination, coupled with conditions conducive to rapid tree growth, may therefore result in extreme competition for light, leading to rapid canopy closure (and subsequent mortality of sub-dominant trees). In this sense, Mountain Ash functions both as a pioneer and a late successional tree species.

The broader regional context of response strategies to disturbance also may explain the paucity of early successional specialists in Mountain Ash and Alpine Ash forests. Ecosystems adjacent to Mountain Ash and Alpine Ash forest are forests dominated by eucalypts that do not exhibit stand-replacing disturbance dynamics. Rather, many canopy trees and understory plants damaged by fire are not killed, and resprout rapidly from epicormic buds in the trunk, or from underground lignotubers, thereby skipping the conventional early successional stage of a stand replacing forest. Such areas would therefore be unlikely to provide a source of early successional specialist species to disperse into adjacent Mountain Ash and Alpine Ash ecosystems.

3.2 Effects of pre-disturbance stand conditions on the ecological values of early-successional forest

Many between-stand differences in the ecological value of early successional forests are underpinned by differences in the quantity, type and spatial distribution of biological legacies from the previous stand (Franklin et al., 2000). The prevalence and type of biological legacies can, in turn, be strongly affected by the age and condition of a forest at the time of a disturbance (Donato et al., 2012; see Fig. 2). For example, the effects of disturbance in a young forest may be markedly different to the effects of a similar kind of disturbance in an old forest. (Hutto 1995) showed that in North America, pre-fire stand conditions had substantial impacts on stand suitability post-fire for species such as the Black-backed Woodpecker (*Picoides arcticus*). In Mountain Ash and Alpine Ash ecosystems, early successional forests that develop in areas which were previously late successional stands will support more fire-damaged large old trees than early successional stands regrowing where young stands were perturbed. Larger, older trees at the time of a fire also have a greater chance of surviving fire (Lindenmayer et al., 1991a) and contribute to the development of stands characterized by multiple age cohorts of trees (Lindenmayer and McCarthy 1998). In addition, the fire-damaged trees in burned late-successional forests will be larger in diameter than fire-killed trees in young burned stands. Large diameter dead trees remain standing for significantly longer than small diameter dead trees (Lindenmayer et al., 1997). Such differences matter because the prevalence of large old trees and long-lived tree ferns are key components of habitat suitability for a range of faunal species in Mountain Ash and Alpine Ash ecosystems (Lindenmayer et al., 1994b; Lindenmayer et al., 2014a). Similarly, after a large wildfire in 2009, sites that were previously long-unburnt had greater soil nutrients than younger forests (Bowd et al., 2019). In another example, the abundance of germinants following wildfire in Mountain Ash forests is significantly lower when a young stand has been burned in comparison to areas that were previously late successional forests when burned (Smith et al., 2014). It is likely that greater flowering and seed production in large old trees relative to smaller, younger trees (Ashton 1975; Wenk and Falster 2015), as well as differences in soil nutrients underpin such differences in germination dynamics following wildfire.

The condition of a stand prior to a disturbance also can affect early successional forests by influencing the severity of the disturbance that occurs (Fig. 1). For example, young regenerating forests with densely spaced trees can be at significantly greater risk of reburning at higher severity than late successional stands (Thompson et al., 2007). Conversely, fire severity is typically lower in late successional stands (e.g. Zald and Dunn 2017). Such kinds of relationships between stand age and the probability of crown-scorching wildfire have been documented for both Mountain Ash forests (Taylor et al., 2014) and Alpine Ash forests (Zylstra 2018). This, can, in turn, influence the types and abundance of biological legacies in disturbed stands.

In summary, stand conditions prior to a disturbance can have profound effects on the severity of a disturbance and, in turn, the characteristics of a post-disturbance stand, especially the prevalence of biological legacies like large old trees and long-lived understorey elements (e.g. tree ferns) (Fig. 2).

3.3 Effects of the type, severity and timing of disturbance

The severity of disturbance can have profound impacts on the ecological value of, and ecological processes in, early successional forests. High-severity disturbances such as wildfires will (by definition; *sensu* Keeley, 2009) consume more of the original stand than low-severity disturbances, typically leaving fewer biological legacies (although large quantities of deadwood can be produced). However, even high-severity fires may consume less than 20% of the biomass of a pre-disturbance stand (Keith et al., 2014a). Disturbances that are largely non-consumptive like windstorms will typically leave behind more legacies than perturbations such as wildfires (Lindenmayer and Franklin 2002). Floods can bring significant extra inputs to forest environments such as sediment and coarse woody debris which can reshape such perturbed ecosystems (Gregory 1997; Major et al., 2019). Variation in the severity of disturbances also can have marked impacts on the biodiversity that can persist in early successional forest (Smucker et al., 2005; Kotliar et al., 2007; Fontaine and Kennedy 2012; Rush et al., 2012; Hutto and Patterson 2016).

Studies of Mountain Ash and Alpine Ash forests have revealed marked differences in the responses of different groups of biota to fires of low, moderate and high severity. These include birds (Lindenmayer et al., 2014b), arboreal marsupials (Lindenmayer et al., 2013b), and large old trees (Lindenmayer et al., 2012). Stands of Mountain Ash and Alpine Ash subject to low to moderate severity wildfire can leave behind fire-scarred large trees, some of which may survive a conflagration, leading to the development of multi-aged stands (Lindenmayer and McCarthy 1998). Such stands can become, in turn, important areas for biodiversity. For example, they typically support the highest diversity of arboreal marsupials (Lindenmayer et al., 1991b).

The type of disturbance can have a marked effect on early successional forest ecosystems. For example, fire-generated early successional forest has some fundamentally different stand structural and plant species compositional characteristics relative to early successional forest regenerating after logging operations (Hutto 1995; Lindenmayer and Franklin 2002; McLean et al., 2015; Hutto et al., 2016) In the case of Mountain Ash and Alpine Ash forests, wildfires consume approximately 11-14% of the above-ground biomass on a site (Keith et al., 2014a). In contrast, 40% of the biomass of the original stand is taken off-site as logs during harvesting operations, with a further 30% volatized in high-intensity fires lit to promote the regeneration of cutblocks (Keith et al., 2014b). Differences between fire and logging can have other effects on post-disturbance stand conditions in Mountain Ash and Alpine Ash forests. These include differences in: **(1)** Soil nutrients and the structural attributes of soils (Bowd et al., 2019). **(2)** Plant community composition, especially resprouting and on-site seeding taxa (Blair et al., 2016; Bowd et al., 2018). As an example, there is a 96% reduction in the abundance of tree ferns in logged areas relative to burned forests (Blair et al., 2016) and this affects food sources for animals (Lindenmayer et al., 1994b) as well as substrates for epiphytic plants (Pharo et al., 2013).

3.4 The influence of post-disturbance environmental conditions

The ecological values of early successional forests can be strongly influenced by environmental conditions such as weather and climate during the post-disturbance recovery (Kemp et al., 2019). For example, warming and drying conditions increased levels of regeneration failure among Lodgepole Pine (*Pinus contorta*) and Douglas-Fir seedlings following fire (Hansen and Turner 2019). Major disturbances like large, severe wildfires that remove extensive areas of canopy can open up forests to greater wind speeds (Gratkowski 1956; Schwartz et al., 2017), altering microclimatic conditions in early successional forests (Rosenberg et al., 1983), and influencing the persistence and survival of legacies (McKenzie et al., 2011; Lindenmayer et al., 2018a).

The effects of post-disturbance environmental conditions have been observed in Mountain Ash forests. For example, following the 2009 wildfire, seedling density in early successional forests increased with annual precipitation and with decreasing temperature. It also increased with increasing soil moisture availability, particularly when plants began to exceed 50 cm in height (Smith et al., 2016). We have documented other effects of post-disturbance environmental conditions in Mountain Ash and Alpine Ash forests. For example, recent work has shown there are important interactions between long-term climate and short-term weather on the post-fire recovery of key groups of biota such as birds). Post-fire, bird recovery is impaired on sites characterized by long-term cool and wet conditions (Lindenmayer et al., unpublished data).

3.5 Impacts of post-disturbance management on habitat suitability and ecosystem processes

The habitat value of early successional forest can be affected not only by stand conditions prior to disturbance and the severity and type of disturbance, but also management practices following disturbance (Fig. 2). For example, post-disturbance salvage logging operations can remove key legacies such as large old fire-killed trees, insect-damaged trees and fallen deadwood, thereby impairing the habitat value of recovering stands for a wide range of biotic groups (Hutto 2006; Leverkus et al., 2018; Thorn et al., 2018). Finally, post-fire salvage logging can increase the risk of further fire in young forests (Donato et al., 2006). The patches of unburned vegetation remaining after wildfires are another key type of biological legacy that has significant values but which can be undermined by post-disturbance management activities such as “black-out burning”. This is where patches of unburned vegetation in otherwise burned landscapes are subsequently targeted for burning by fire managers (Backer et al., 2004). The loss of unburned “green areas” can have major negative effects on biota dependent on post-fire refugia (Mackey et al., 2012).

The effects of post-disturbance management have been well documented in Mountain Ash forests including those on large old trees, understorey and midstorey vascular plants and ferns (Blair et al., 2016; Bowd et al., 2018) and birds (Lindenmayer et al., 2018c). Some of these impacts can be long lasting. For example, in Mountain Ash forests, the negative effects of salvage logging on the structure and nutrient status of soils may persist for at least 80 years (Bowd et al., 2019). Similarly, if large old trees are removed in salvage logging operations, the recruitment of new cohorts of such trees may require almost two centuries because of the prolonged time required for such trees to develop (Lindenmayer et al., 2017a).

3.6 The importance of spatial context and maintaining different forest ages at landscape and regional scales

The spatial extent of early successional forest can have profound impacts on entire forest ecosystems. Early successional forests in some ecosystems can be prone to high-severity wildfire (Thompson et al., 2007; Lindenmayer et al., 2009; Taylor et al., 2014; Zylstra 2018). If early successional forests occupy a high proportion of the landscape, then the whole ecosystems, including surrounding areas of older forest, can be prone to repeated fire at short time intervals due to high fuel densities in young forests (Taylor et al., 2014; Zylstra 2018). This comes with corresponding risks of developing into a "landscape trap" in which forests become trapped at a young age because repeated fire prevents stands from becoming old (Lindenmayer et al., 2011). If fire becomes too frequent, then a regime shift may occur (*sensu* Carpenter et al., 2011) in which the original ecosystem is lost and replaced by a different kind of forest ecosystem (Lindenmayer and Sato 2018).

There can be other spatial effects associated with extensive areas of early successional forest. These include significantly reduced water yields and levels of carbon storage from watersheds dominated by large areas of early successional forest (Vertessy et al., 2001; Keith et al., 2017; Taylor et al., 2019). Other effects of early successional forest occurring across a high proportion of total forest cover include declines in species associated with older or intact forest (Gibson et al., 2011, reviewed by Watson et al., 2018). In the case of Mountain Ash and Alpine Ash forests, rates of mortality and collapse of large trees are significantly elevated in landscapes characterized by large amounts of early successional logged or burned forest (Lindenmayer et al., 2016; Lindenmayer et al., 2018a; Lindenmayer et al., 2018b). Species such as the Yellow-bellied Glider (*Petaurus australis*) are uncommon or absent from Mountain Ash and Alpine Ash landscapes dominated by large areas of early successional forest (Lindenmayer et al., 1999a). Also in Mountain Ash and Alpine Ash forests, bird species richness and the occurrence of almost all individual species of birds is significantly depressed in landscapes dominated by large areas of burned and/or logged forest (Lindenmayer et al., 2019b). Moreover, bird species richness and the occurrence of individual species is substantially lower relative to late successional forest (Lindenmayer et al., 2019b). This result suggests that the spatial extent of early versus late successional forest may influence the size and location of source populations of particular species able to recolonize areas after disturbance (Lindenmayer et al., 2019b).

The above examples indicate a need to consider the relative amounts and spatial patterns of early successional and late successional forest across broader landscapes and even entire ecosystems. This is especially true when: **(1)** There are risks that a spatial imbalance of one age cohort might dramatically alter key ecological processes fundamental to the persistence of an ecosystem (and the biota it supports). And, **(2)** The age of a forest influences the type, number and extent of biological legacies in a newly disturbed stand. In the Mountain Ash forests of the Central Highlands of Victoria, the presence of large areas of late successional forest will be critical to ensuring that where forests are disturbed, they will subsequently become early successional stands with high values for biodiversity and ecosystem function.

4. Recommendations for management

We suggest there are four key strategies to enhance the management and conservation of early successional forests. Some of these will be short-term actions such as limiting the extent and intensity of post-disturbance (salvage) logging, whereas others will be long-term strategies like ensuring the development of late successional forest to produce greater pulses of key biological legacies in the event of a major perturbation.

4.1 Identify species typically associated with early successional forests

The number and diversity of species associated with early successional environments can vary markedly between different forest ecosystems (Hutto et al., 2015). For example, the wet ash-type eucalypt forests of Victoria, Australia that we have described in this paper differ in some respects from the Douglas-Fir forests of the Pacific Northwest of the USA (Franklin et al., 2002; Swanson et al., 2011; Swanson et al., 2014). Therefore, a key part of managing early successional forests is to identify the suite of species that are confined to, or closely associated with, early successional forests (Hutto et al., 2015). Part of such assessments would involve determining whether early successional specialists are obligate users of early successional forest or are facultative taxa that can make use of other age cohorts (albeit potentially at lower abundance) (Hutto 1995). Notably, some species that are strongly associated with early successional environments can experience severe negative impacts from post-disturbance management practices such as salvage logging (Hutto 2006). There also is value in determining how well patterns of early successional response conform to different ecological theories about the trajectory of post-disturbance response (Donato et al., 2012) (e.g. Initial Floristic Composition versus Relay Succession; reviewed by Pulsford et al., 2016).

Different approaches to management may well be required where communities of early successional specialists are species-rich in comparison to ecosystems with few such species. For example, where species are rare, targeted species-specific management strategies may well be effective. More complex sets of multi-faceted approaches and/or more general habitat-based approaches might be needed where species-rich assemblages are confined to early successional forests.

4.2 Document the types, distribution and roles of biological legacies in early successional forests

It is important to document and study the types, numbers and distribution patterns of biological legacies in early successional forests given the range of key roles they play such as in stand regeneration, biodiversity recovery, and the maintenance of key ecological processes. Moreover, biological legacies provide for a continuum of habitat suitability over time as, for example, the structures remaining after late successional forests are disturbed strongly affect habitat suitability in subsequent early successional forest (Franklin et al., 2000). Such information is also important for determining the types, numbers and patterns of biological legacies that need to retained in forests subject to logging operations such Variable Retention harvesting (Fedrowitz et al., 2014). That is, prescriptions for Variable Retention harvesting that govern what structures and patches to leave behind during logging should be informed by what biological legacies characterize early successional stands following natural disturbance. These include prescriptions for the amount of deadwood left in a forest (Müller and Bütler 2010; Thorn et al., 2016; Thorn et al., 2017), as well as those for the number of retained overstorey trees and patches of understorey and ground cover.

As the value of early successional forests is influenced by biological legacies and these are, in turn, a function of the state of a pre-disturbance stand, many ecosystems will need to be managed in ways to ensure the occurrence of large areas of late successional forest across landscapes and regions. This is critical to ensure better ecological functionality of post-disturbance environments. Indeed, extensive areas of late successional forest is needed because when they do burn, they may be the only places that support suitable early successional conditions for particular disturbance-associated species. However, extensive areas of intact late successional forest are now rare in many forest ecosystems globally

(Mackey et al., 2015; Watson et al., 2018), and special protection strategies may be required to expand their coverage. This may be particularly important in ecosystems where the amount of late successional forest has been significantly depleted relative to historical levels. The Mountain Ash ecosystem in Victoria is a good example, with late successional stands covering $1/30^{th}$-$1/60^{th}$ of what they did ~150 years earlier (Burns et al., 2015, Lindenmayer et al., 2019a). Strategies to significantly expand the extent of late successional forest in the future through enhanced protection policies have been recommended as part of forest landscape restoration in the Mountain Ash ecosystem (Lindenmayer 2018). The amount of forest set aside may need to be substantial. For example, if an objective is to reach a pre-determined target of 30% of the ecosystem being late successional forest (Leadbeater's Possum Advisory Group 2014); then up to 50% or more may need protection from human disturbance as some forest will inevitably be lost in the interim as a result of wildfire (Lindenmayer et al., 2013a).

4.3 Limit management practices that can negatively affect biological legacies

How early successional forests are managed in the recovery phase following natural disturbance can have profound effects on their ecological values. Post-disturbance activities like salvage logging can have long-term negative impacts on biological legacies such as large old trees, long-lived understorey plants, soil conditions, and key groups of biota (Lindenmayer et al., 2017b; Leverkus et al., 2018; Thorn et al., 2018). Salvage logging operations should be excluded wherever possible to limit undermining the values of early successional environments (Lindenmayer et al., 2017b; Leverkus et al., 2018; Thorn et al., 2018) . In the case of the Mountain Ash and Alpine Ash forests of Victoria, past work has shown that places that supported high levels of bird species richness prior to fire also were likely to be comparatively more species-rich after fire, even where a high-severity conflagration has occurred (Lindenmayer et al., 2014b). To maintain their ecological values, post-fire salvage logging operations should not occur in such places.

Where salvage logging operations do take place, their intensity should be limited to ensure adequate retention of biological legacies and to minimise disturbance of soils and plants regenerating after fire. Prescriptions for salvage logging should be guided by the type and spatial and temporal abundance of biological legacies typically found in naturally disturbed early successional forest. Critically, as is common practice for harvesting of unburnt forest, unharvested blocks of forest should be retained within areas otherwise targeted for harvesting following natural disturbances.

4.4 Consider how extensive areas of early successional forest may alter key ecosystem processes

There can be marked differences in key ecosystem processes between early successional forests and late successional forests. These can include differences in disturbance dynamics such as fire regimes (Zylstra 2018), plant responses to disturbance, tree germination, and tree mortality. Such differences in processes can, in some cases, threaten the long-term integrity of ecosystems and even whether such environments continue to persist (Lindenmayer and Sato 2018). These changes in ecosystem processes would, in turn, have major effects on ecosystem service provision such as water production, timber production, and carbon storage (Lindenmayer and Sato 2018). The risk of regime shifts may be particularly acute where early successional forests are widespread, late successional forests are rare (but were once extensive), and problems like landscape traps may manifest (Lindenmayer et al., 2011). The spatial extent of early versus late successional forest can therefore become a key consideration for managers, including ensuring there is not too little or too much of a given age cohort across a landscape. We note, however, that in some regions, naturally characterized by infrequent but very large fires, huge pulses of early-seral (composing >30% of a large regional landscape) may be the norm under historical conditions at certain points in time. The Pacific Northwest of the USA is one example; another is part of the Greater Yellowstone Ecosystem (Turner et al., 2003).

Considerations of the spatial extent of different age cohorts of forest highlight the need not only for site-level, but also landscape-scale perspectives on early successional forest. They also underscore an apparent paradox that the maintenance of functional, early successional forests, may be dependent on ensuring that landscapes support extensive areas of late successional forest prior to the occurrence of natural disturbance. This key point has critical temporal dimensions, as it can take a prolonged period for late successional forest to develop, but only a very short period to be converted to early successional stands.

5. Conclusions

Early successional forest is an important stage in forest ecosystems in many parts of the world, especially those where the natural disturbance regime can include stand-replacing disturbance events. Early successional forests can support a range of species not found in, or which are rare in, other age cohorts of forest. Habitat values and key ecosystem functions (e.g. carbon storage) in early successional forests can be profoundly affected by the age of a forest at the time it is disturbed. Disturbances in late successional forests will often produce more biological legacies (that persist for longer) relative to when young forests are perturbed. The presence of biological legacies can facilitate the persistence of species in a disturbed stand, even ones subject to extreme perturbation. Biological legacies also can accelerate the rate at which disturbed areas can be recolonized by organisms that are initially lost from disturbed forests. The key roles and functions of biological legacies can be undermined by post-disturbance management practices such as salvage logging and black-out burning.

Understanding the types, abundances, and spatial patterns of biological legacies that remain after natural disturbance can provide a template for the biological legacies that should be retained within cutblocks targeted for timber harvesting.

Key actions to enhance the management of early successional forests include: **(1)** Identify species typically associated with early successional forests. **(2)** Avoid or limit post-disturbance activities like salvage logging that undermine the ecological values of, and ecosystem processes in, early successional forests. And, **(3)** Balance the relative amounts of early successional versus late successional forest in a given landscape or region. Paradoxically, in some forest ecosystems, the development of an ecologically functional early successional forest will be dependent on ensuring there are large areas of late successional forest in the landscape that will support large numbers of biological legacies in the event of a major natural disturbance (such as a wildfire).

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Figures and captions

Figure 1. Conceptual model showing the six interacting factors (each of which are numbered) influencing biodiversity, habitat suitability and ecosystem processes in early successional forests where stand-replacing natural disturbances are a predominant component of the natural disturbance regime. The model shows the broad environmental domain for early successional species. Within that domain, ecological processes and biodiversity can be affected by interactions between the type and severity of disturbance, pre- disturbance (starting) conditions, the type of disturbance, post-disturbance conditions, post-disturbance management practices, and the spatial extent of early versus late successional forest. Biological legacies are a critical element through which many of these factors influence the ecological values of early successional forest.

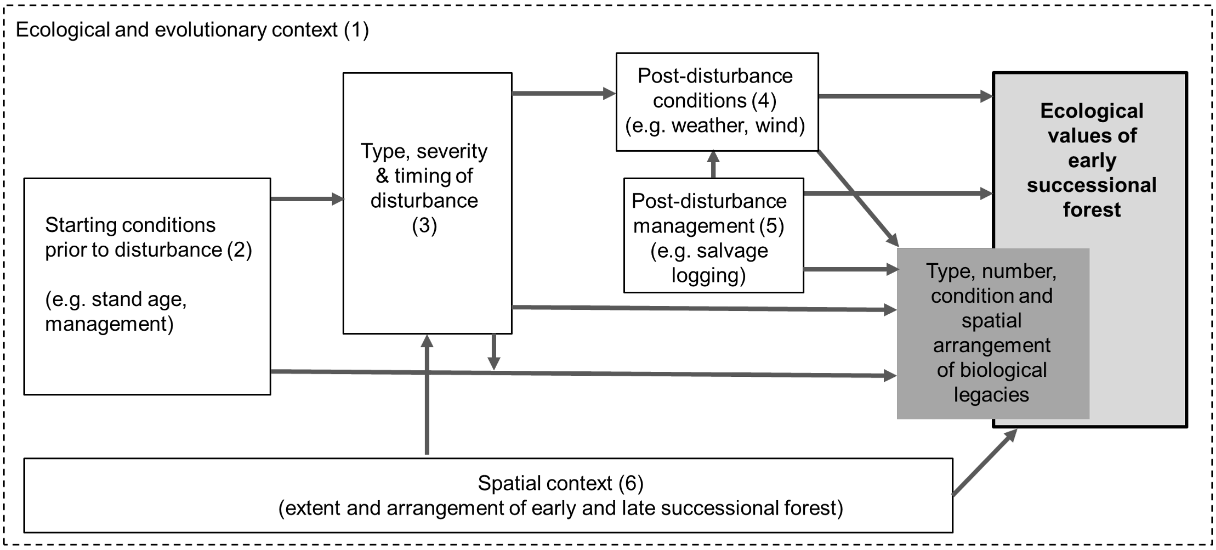

Figure 2. Simplified schematic showing differences in biological legacies between burned old versus young forest.