Chapter 5
Forest Stand Dynamics Drive a Conservation Conundrum for the Critically Endangered Leadbeater's Possum

Patrick J. Baker, Craig R. Nitschke, Raphael Trouvé, and Andrew P. Robinson

Abstract Leadbeater's possum (*Gymnobelideus leadbeateri*) is a critically endangered arboreal marsupial found primarily in the mountain ash forests of Victoria's Central Highlands in southeastern Australia. It has two very specific and well-known habitat requirements: a dense, connected lower stratum of *Acacia* spp. for foraging and movement within the forest and hollow-bearing trees for nesting. Early habitat suitability models for Leadbeater's possum focused primarily on the dynamics of the hollow-bearing tree component, assuming that sufficient *Acacia* persisted throughout the development of the stand. Recent research has highlighted the transient nature of the *Acacia* component in these forests and shown that old-growth forests are relatively poor habitat for Leadbeater's possum. The stand dynamics of mountain ash forests mean that the presence and abundance of *Acacia* and hollow-bearing trees are largely independent of one another. This presents a fundamental conundrum for the conservation of Leadbeater's possum – the *Acacia* component is associated with young, post-disturbance forests, whereas hollow-bearing trees are associated

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with older forests. Conservation-oriented silviculture needs to accommodate these dynamics and focus on the provision of both habitat elements in close proximity to each other in time and space. A landscape-scale approach that focuses on long-term habitat restoration and management will be critical to the long-term viability of Leadbeater's possum, particularly in a warming climate.

Keywords *Acacia dealbata* · *Eucalyptus regnans* · Habitat suitability · Conservation-oriented silviculture

5.1 Introduction

Forests are complex, dynamic systems; yet they often develop in relatively predictable ways. The emergent patterns of forest stand development and the factors that drive these patterns are similar in forests around the world (Oliver and Larson, 1996). The interaction between deterministic factors, such as the physiological responses of trees and other plants to available resources, and stochastic factors, such as disturbances, climate variability, and post-disturbance dispersal, lead to complex patterns in forest structure and composition at the stand and landscape scales. Many animal species depend on forests for suitable habitat. For some animal species, the presence of forest cover alone may be sufficient. For others, suitable habitat may depend on the presence of specific structural features in the forest. Where these structural features are rare or absent, the animal species that depend on them are also likely to be rare or absent.

The dynamic nature of forests means that there is an important temporal component to the relative abundance of particular structural features (Nitschke et al., 2020). That is, stand structures or specific features that are rare today may have been more common in the past or may be more common in the future. As a forest stand develops and grows, there will be periods when particular structural features may be relatively abundant and periods when they are rare (Shifley et al., 2006; Sturtevant et al., 1996). Consequently, critical structural features may also be transient, occurring for a period of time linked to the processes that generated them. This has important conservation implications for plant and animal species that depend on specific stand structures within a landscape (Marzluff et al., 2002). During periods when a particular structure is not common, populations that depend upon it may contract or disappear from that area of forest. If the requisite habitat features were abundant in the past, but have been declining, individuals or populations of the species may be in decline and vulnerable (Clare et al., 2019). In landscapes subjected to a long history of land-use change and forest fragmentation, the ability of most animals to move within or between landscapes in search of more suitable habitat is limited. In extreme cases, this may pose the existential threat of local or regional extinction for a species.

In this chapter we describe the role of forest stand dynamics on habitat suitability of a critically endangered arboreal marsupial, Leadbeater's possum (*Gymnobelideus leadbeateri* McCoy), which is found in a small area of forests in southeastern Australia (Harley, 2016; Smith and Lindenmayer, 1988). Leadbeater's possum is particularly interesting because it depends on two distinct structural features of the forests it inhabits – and the relative abundance of these structural features does not covary temporally in any meaningful way. This creates the conservation conundrum of the chapter title – managing for one of the structural features typically reduces the availability of the other and vice versa – which greatly complicates efforts to develop effective conservation and management strategies for the species. It also provides an illustrative case study for how forest stand dynamics can drive the relative abundance of an endangered species at fine scales, how knowledge of the underlying stand development patterns can help to anticipate when individual structural features are likely to occur, and how different management strategies can influence the population trajectory of a species over long periods and large spatial scales. Here we present an overview of these issues. We begin by reviewing the standard model describing the temporal dynamics of Leadbeater's possum habitat suitability that has been used for several decades. We then discuss recent advances in understanding of forest stand dynamics in the forests where Leadbeater's possum occurs and consider the implications for the conservation of the species.

5.2 Leadbeater's Possum: Habitat Requirements and Population Trajectories

Leadbeater's possum has been the subject of intensive study over the past 35 years (Harley, 2016; Smith and Lindenmayer, 1988, 1992). Originally discovered in 1867 in swamp forest near Bass River in southwest Gippsland, it was believed to have gone extinct in the early 1900s due to the broadscale conversion of the region's forests to farmland. However, in 1961 Leadbeater's possum was rediscovered in mountain ash (*Eucalyptus regnans*) forests in Victoria's Central Highlands. Its primary habitat is the montane ash forests of Victoria's Central Highlands that are dominated by mountain ash, alpine ash (*E. delegatensis*), or shining gum (*E. nitens*), although small populations have subsequently been found in high-elevation snow gum woodlands and in swamp forest in the foothills of the Central Highlands.

To assess which structural features of the forest were associated with Leadbeater's possum occurrence, Lindenmayer et al. (1991) modelled the influence of a range of variables describing various aspects of montane ash stand structure. They found that the occurrence of Leadbeater's possum was strongly associated with two specific stand structural features: (1) the number of hollow-bearing trees, which are used for nesting and (2) a dense, connected understory of *Acacia* spp., which is used for movement and foraging (Lindenmayer et al., 1991; Smith and Lindenmayer, 1988, 1992). Their final logistic model included only two variables: the number of

hollow-bearing trees per three hectares (HBT) and the basal area of *Acacia* spp. (BAA):

$$logit(p) = -2.482 + 0.093 \times BAA + 0.097 \times HBT$$

It is worth noting here that this and subsequent studies describing the habitat requirements of Leadbeater's possum have all stressed the importance of both components of forest structure for Leadbeater's possum – without hollow-bearing trees, abundant *Acacia* spp. alone are insufficient for Leadbeater's possum to occur and absent sufficient *Acacia* in the understorey, even large numbers of hollow-bearing trees will not ensure the occurrence of Leadbeater's possum.

While much is known about the biology and ecology of Leadbeater's possum, accurate estimates of population size and trajectory do not exist. Recent estimates suggest that the total population of Leadbeater's possum may be between 2000 and 20,000 individuals (Department of the Environment and Energy, 2018). There is justifiable concern that the current size of the population puts it at serious risk of extinction. However, absent accurate estimates of population size, the primary focus of conservation efforts has been on the amount of suitable habitat currently available, the rate at which it is changing, and the primary drivers of observed changes in habitat availability.

5.3 Management and Conservation of Montane Ash Forests

The montane ash forests that are the primary habitat of Leadbeater's possum are also amongst the most productive forests in the world and their timber is highly prized. This has generated a decades-long conflict between conservation groups wanting to protect the forests and timber groups wanting to harvest trees in the forest. Since the 1950s the standard silvicultural prescription for montane ash forests has been the clearfell, burn, and sow (CBS) system, in which all trees within a coupe (i.e., harvest area or cut block) are harvested, the site is burnt to prepare a suitable seed bed, and seeds are sown (Attiwill, 1994). Because stand-replacing fires are the dominant disturbance type in these forests, the CBS system attempts to emulate the microenvironmental conditions that occur after a stand-replacing fire, in particular the high light conditions and exposed, heat-baked soil. However, there are some obvious and important differences in the impacts of the CBS system and catastrophic fire. Most notably, the CBS system removes all trees, including those with hollows, in the harvesting operations. This has been the subject of profound concern amongst conservation groups because of the negative impacts on arboreal species, such as Leadbeater's possum, that require hollow-bearing trees for nesting. In contrast, stand-replacing fires leave many dead trees, which are still available for nesting as animals recolonise the site. While Leadbeater's possum require both hollow-bearing trees and a dense understorey of *Acacia*, most research on the impacts of forest management on Leadbeater's possum habitat

has focused on hollow-bearing trees due to the long time required for them to develop. Many studies have catalogued the abundance and described the dynamics of hollow-bearing trees in southeastern Australian forests, in general, and the montane ash forests of the Central Highlands, in particular, as well as the impacts of forest harvesting on hollow-bearing trees (e.g., Gibbons and Lindenmayer, 1996; Lindenmayer et al., 1993, 2012). These studies have shown that the abundance of hollow-bearing trees is declining and that timber harvesting has contributed to this decline. However, Gibbons and Lindenmayer (1996) noted the challenges facing forest managers in developing prescriptions that retained hollow-bearing trees within coupes, and highlighted the lack of data on key issues related to the development and demographics of hollow-bearing trees in native eucalypt forests in southeastern Australia.

For the montane ash forests of Victoria's Central Highlands, current understanding of the dynamics of hollow-bearing trees is largely based on a single, large network of small (3 hectare) permanent forest measurement plots established in the 1980s (Lindenmayer et al., 1990) and expanded in the 1990s (Lindenmayer et al., 2003). This plot network was established to monitor Leadbeater's possum and other arboreal marsupials and their habitat and consequently has some inherent sampling biases. First, the individual sites were initially selected because they represented high-quality habitat and, in particular, had high densities of hollow-bearing trees (Lindenmayer et al., 1990). Second, the plots are relatively close to roads (median distance from plot edge to nearest road is <1 m) for easy access by volunteers and researchers who would spend evenings watching hollow-bearing trees for various arboreal marsupials, including Leadbeater's possum, to emerge. Finally, approximately two-thirds of the plots in the network were located in forests that had established in the wake of the devastating 1939 fires. At the time of plot establishment these stands were <50 years old; they are now >80 years old. These plots have shaped discussions regarding the ecology, dynamics, and management of these forests for several decades. However, as we discuss later in this chapter, recognition of these biases provides useful context for understanding the differences between competing models describing the dynamics of Leadbeater's possum habitat dynamics.

Over the years the partial dependence of Leadbeater's possum on hollow-bearing trees, which are typically large and old, has led to an implied association between Leadbeater's possum and old-growth forests. This, in turn, has led to specific policy positions and decisions that have sought to protect old-growth montane ash forests as habitat for Leadbeater's possum. For example, the Australian Federal Government's Species Profile and Threats Database states that the "[Leadbeater's] possum's *ideal habitat* [is] the old-growth mountain ash forest in the Central Highlands of Victoria." (emphasis added). And in the early 2000s a network of remnant old-growth forest patches were specifically set aside as Leadbeater's Possum Reserves by the Victorian State Government.

5.3.1 The Standard Model of Leadbeater's Possum Habitat Dynamics

There have been several attempts to model the long-term dynamics of habitat suitability under different management and disturbance regimes to better understand their implications for Leadbeater's possum population viability. For example, Lindenmayer and Possingham (1995a) modelled the response of Leadbeater's possum in patches of old-growth montane ash forests with and without fires and then explored the metapopulation dynamics of Leadbeater's possum within several larger catchment areas. Nearly identical analyses were also published in Lindenmayer and Possingham (1995b, 1996) and more recently by Burns et al. (2015) and Todd et al. (2016). In each of these analyses, stand-level patterns of Leadbeater's possum habitat suitability were driven by its two key habitat requirements: the basal area of *Acacia* spp. in the forest understorey and the abundance of hollow-bearing trees (Fig. 5.1).

The underlying model of stand development (i.e., absent timber harvesting) that informed these analyses is based on a catastrophic bushfire that kills most of the trees within a stand and across the landscape. This model assumes that for the

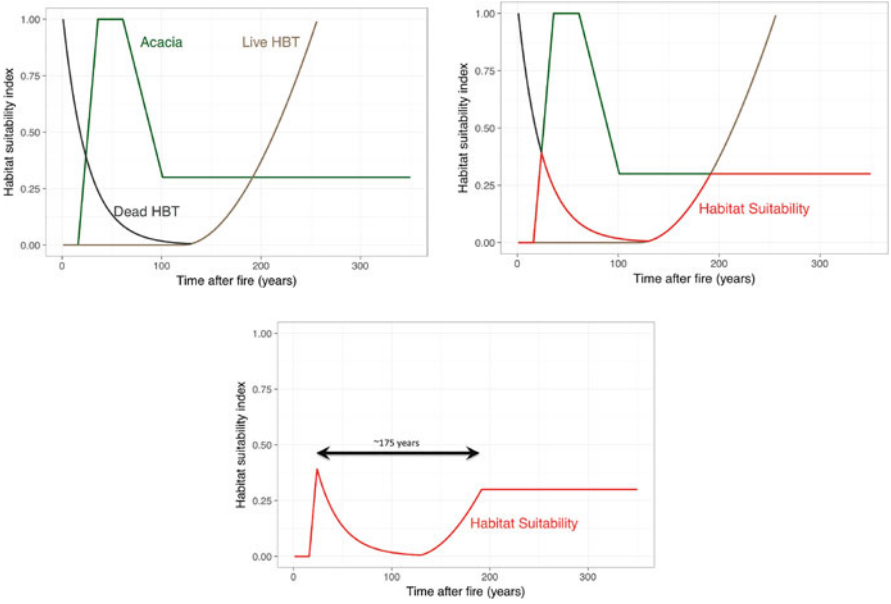

Fig. 5.1 Temporal dynamics of the two key features of Leadbeater's possum habitat – understorey *Acacia* and hollow-bearing trees – after a stand-replacing fire (upper left panel). The habitat suitability index is a relative score that is calculated as the minimum of the scores for the two habitat components (in red in the upper right and lower panels). The model is based on Lindenmayer and Possingham (1995a); see text for details

first 15 years of development after a catastrophic fire there is insufficient *Acacia* for the Leadbeater's possum, but that from years 15 to 35 the amount of *Acacia* increases and eventually becomes sufficient to support Leadbeater's possum. The *Acacia* stays at maximum levels from 35 to 60 years post-fire, declines from 60 to 100 years, and then persists at the minimum level required by the Leadbeater's possum in perpetuity (Fig. 5.1, green line).

The bushfire also impacts the abundance and dynamics of hollow-bearing trees. The model assumes that most live hollow-bearing trees are killed in the fire. The newly dead hollow-bearing trees then begin to decay and eventually collapse over time. However, new live hollow-bearing trees only begin to develop 150 years after the bushfire. As a result of the interaction between the dynamics of these two key habitat features, habitat suitability for Leadbeater's possum varies over time (Fig. 5.1, lower panel). During the first 15 years after a fire, the lack of *Acacia* means that habitat suitability is low despite the abundance of hollow-bearing trees. After ~35 years post-fire habitat suitability increases rapidly as both *Acacia* and hollow-bearing trees are abundant. However, the highest quality habitat only persists for a few decades. From about 80 to 220 years after the fire, habitat suitability is too poor to support Leadbeater's possum due to the decline of the *Acacia*, the loss of the initial cohort of fire-killed hollow-bearing trees, and the lack of recruitment of new hollow-bearing trees. Approximately 220 years after the initial fire event, the model suggests that recruitment of mature hollow-bearing trees and *Acacia* are both sufficient to be considered suitable Leadbeater's possum habitat.

This model of habitat suitability has been widely used to inform policy decisions regarding forest management and conservation of Leadbeater's possum in Victoria. For example, in the early 2000s a network of reserves was established to protect isolated patches of old-growth forest with the stated intention of providing long-term habitat for Leadbeater's possum. Similarly, in 2014 the mountain ash forest ecosystem was listed on the IUCN's Red List of Ecosystems due, in part, to analyses based on this model (i.e., Burns et al., 2015). However, recent dendroecological and modelling analyses of these forests have highlighted some critical shortcomings of the assumptions that underpin the model and, in turn, raise important questions about the temporal dynamics of habitat suitability for Leadbeater's possum (Nitschke et al., 2020; Simkin and Baker, 2008). To better understand these issues, it is worth taking a closer look at the stand development patterns of mountain ash forests to see how they influence the long-term suitability of Leadbeater's possum habitat.

5.4 The Dynamics of Mountain Ash Forests

Mountain ash forests have been closely studied in Tasmania and Victoria for more than 60 years (e.g., Ashton, 2000; Cremer, 1971; Gilbert, 1959; Trouve et al., 2019). The broad outline of their dynamics is typical of forest ecosystems subject to catastrophic, stand-replacing disturbances (e.g., Oliver, 1980). David Ashton,

a pioneering Australian forest ecologist, described the development of Victorian mountain ash forests after fire in extraordinary detail, based on survey plots that he established in the early 1950s and followed for half a century (Ashton, 1976, 2000). More recently, Simkin and Baker (2008) used tree rings to reconstruct the development of an area of montane ash forest and cool temperate rainforest impacted by the catastrophic 1939 fire and Trouve et al. (2019) showed how overstorey mountain ash influence growth and mortality of understorey *Acacia*. The basic developmental pattern of these forests is relatively simple and consistent with well-known descriptions of even-aged, mixed-species stand dynamics (Kelty et al., 1992; Oliver and Larson, 1996). Mountain ash (*Eucalyptus regnans*) are obligate seeders that regenerate after high-intensity fires, which kill a large proportion of the trees (Trouve et al., 2021), often over large areas (10s to 100s of thousands of hectares). In the wake of these fires seeds stored in the forest canopy are released to germinate in the burnt soil. Other plant and tree species that are found in the soil seed bank germinate at the same time, leading to dense regeneration of mountain ash in mixtures with other species. The tree species, including both eucalypts and non-eucalypts, such as wattles (*Acacia* spp.) and *Pomaderris aspera*, grow rapidly in these highly productive forests and quickly establish a closed canopy. However, the height growth patterns of the tree species differ and after 10–15 years the mountain ash begin to outgrow the other tree species in height. Twenty to twenty-five years after the fire, the forest canopy has begun to exhibit distinct stratification, with an upper stratum composed of mountain ash emerging above a lower stratum of *Acacia* spp. and other non-eucalypt tree species. Over subsequent decades this stratification becomes increasingly pronounced with the mountain ash often reaching heights of 80 m or more and most of the non-eucalypt tree species rarely exceeding 20 m in height (although *Acacia dealbata* and *A. melanoxylon* occasionally reach 30–40 m tall).

These dynamics have important implications for Leadbeater's possum because the two key components of Leadbeater's possum habitat – the *Acacia* understorey and hollow-bearing trees – do not develop in synchrony over time. After fire *Acacia* emerge from the soil seed bank rapidly and often establish in great numbers, forming dense thickets within five years. Their relative abundance in subsequent decades is driven by two factors: time since fire and the density of the eucalypt overstorey. The two most common *Acacia* species that establish after fires, *Acacia dealbata* (silver wattle) and *Acacia obliquinervia* (mountain hickory wattle), are relatively short-lived with maximum known ages of 94 years and ~45 years, respectively. However, the amount of eucalypts in the forest canopy has a strong negative influence on all demographic parameters of these *Acacia* species. Using a network of forest inventory plots and tree-ring analyses, Trouve et al. (2019) showed that as the basal area of overstorey eucalypts increases, the probability of *Acacia* presence and total basal area of *Acacia* decreases (Fig. 5.2).

Trouve et al. (2019) also estimated the probability of reaching specific values of *Acacia* basal area as a function of stand age and basal area of the eucalypt overstorey (Fig. 5.3). This provides a useful tool for forest managers because the Action Statement for Leadbeater's Possum (DEPI, 2014), which guides forest management

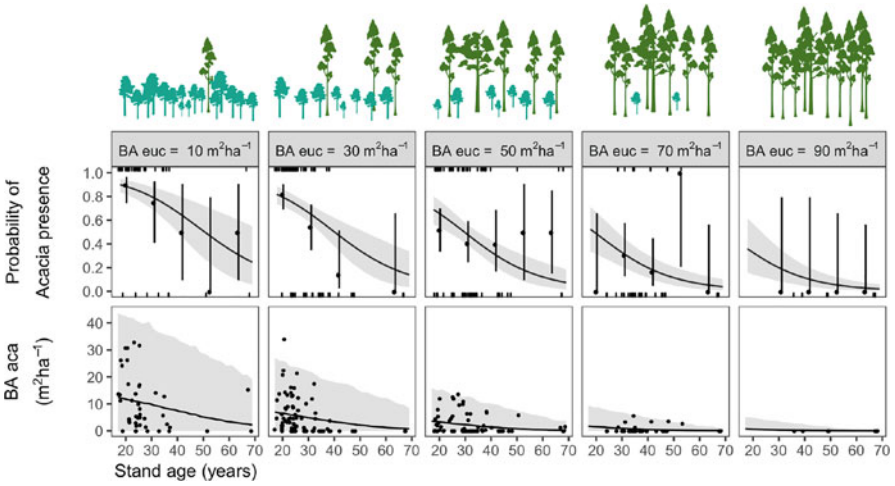

Fig. 5.2 Influence of eucalypt canopy on *Acacia* demography in the understorey. Each column represents a different level of overstorey eucalypt basal area (from low (left) to high (right) with a general indication of relative abundance shown in the figures above each column). The upper panels show the probability of *Acacia* presence as a function of stand age. The lower row shows the basal area of *Acacia* as a function of stand age. See Trouve et al. (2019) for details

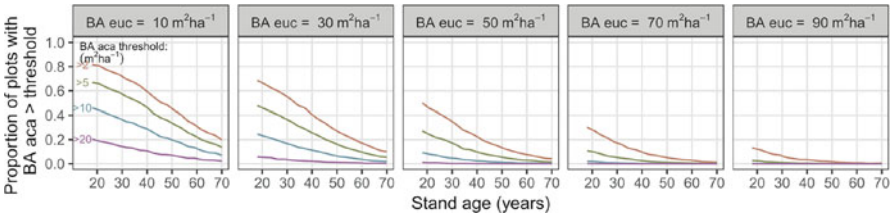

Fig. 5.3 Influence of eucalypt canopy on the probability of specific threshold values of *Acacia* basal area as a function of stand age. The regulatory definition of Leadbeater's possum habitat is areas of forest with $>5\,m^2$ per ha of *Acacia* basal area (i.e., green line in this figure) and >10 hollow-bearing trees per three ha. See Trouve et al. (2019) for details

relating to Leadbeater's possum, specifically defines suitable Leadbeater's possum habitat as montane ash forest with $>5\,m^2$ per ha of *Acacia* basal area and >12 hollow-bearing trees per three ha area in patches greater than 10 ha in total area. However, it shows that at moderate to high levels of eucalypt canopy density ($>50\,m^2$ basal area per ha), the probability of having $5\,m^2$ per ha of *Acacia* in the understorey never exceeds 30% and by 40 years post-fire is ~10%.

This pattern is primarily driven by availability of resources, particularly light. The *Acacia* species in these forests are shade intolerant and are associated with high-light environments during the stand initiation stage post-fire. As the stand begins to stratify due to species-specific differences in height growth, the *Acacia* are increasingly likely to be shaded by eucalypts, particularly when the latter is

relatively abundant. When full canopy closure by the emergent mountain ash occurs, the reduced light levels accelerate the decline of the overtopped *Acacia*.

In contrast, hollow-bearing trees may be abundant after the fire as either hollow-bearing trees that were dead prior to the fire and were not consumed in the fire or as live hollow-bearing trees that were killed by the fire. In both cases, the hollow-bearing trees will decompose and degrade in the years and decades following the fire. The rate at which hollow-bearing trees degrade and the factors that influence this process are not well documented for the eucalypts of the montane ash forests. Lindenmayer et al. (2012) monitored the fate of large (>50 cm DBH) hollow-bearing trees from 1997 to 2011, a period that included the Millennium Drought and the 2009 Black Saturday fires. They found that both fire and drought influenced the collapse rates of large hollow-bearing trees with higher rates during the Millennium Drought and a spike of losses associated with the 2009 bushfires, particularly amongst dead hollow-bearing trees in sites with severe fire impacts. However, their plots are notable for having extremely high densities of hollow-bearing trees (~7 per ha), being situated close to roads, and being dominated by 1939 regrowth forest. Recent extensive surveys that used a mix of targeted and stratified random sampling in the Central Highlands found an average of 1.1–2.5 hollow-bearing trees per ha across several hundred plots in montane ash forest (Jiang, 2020; Nelson et al., 2017). Whether rates of loss of hollow-bearing trees are as high in these sites as those observed by Lindenmayer et al. (2012) is unclear. However, forests adjacent to edges, such as those in the Lindenmayer et al. (2012) study, have been shown to have higher rates of turnover due to increased light availability, temperature, and exposure to wind (e.g., Laurance et al., 1998; Oberle et al., 2018). In addition, the majority of hollow-bearing trees in their study would have originated in the 1939 fire and would have been dead for 60–70 years. While it is unknown how long it takes for mountain ash trees to lose their structural integrity due to internal rot, it is reasonable to expect that after that many decades the likelihood of decay and collapse would be increasing.

5.4.1 The Acacia Understorey Component

The model parameterisation of Lindenmayer and Possingham (1995a) and the empirical data of Trouve et al. (2019) treat the dynamics of the *Acacia* understorey component differently in three important ways. First, Lindenmayer and Possingham (1995a) suggest that stands do not develop sufficient *Acacia* for Leadbeater's possum for the first 15–20 years after a fire. A recent survey of Leadbeater's possum habitat occupancy in the Central Highlands found Leadbeater's possum using dense thickets of regenerating forest within 10 years of disturbance (Nelson et al., 2017). There is also anecdotal evidence of Leadbeater's possum being found in the 2009 Black Saturday fire regrowth less than a decade post-fire. Second, in the Lindenmayer and Possingham (1995a) model *Acacia* only begins to decline after 60 years. Trouve et al. (2019) showed that *Acacia* is uncommon in these forests by

60 years. In particular, they highlighted that the amount of *Acacia* in the stand was heavily dependent on the density of eucalypts in the overstorey. Where the eucalypt overstorey was dense, the *Acacia* had often disappeared decades earlier or was at such low levels that it was not suitable habitat for Leadbeater's possum. Both of these differences are ones of timing and illustrate how additional data from different sources (e.g., dendroecology, which is rarely used in these ecosystems due to the lack of annual growth rings in most eucalypts) can refine understanding of stand development patterns.

The third difference is more consequential, however. In the Lindenmayer and Possingham (1995a) model *Acacia* declines from maximum suitability between 35–60 years to a lower level of suitability at 100 years. After that it stabilises at the minimum amount required by Leadbeater's possum and persists at that level in perpetuity. This is neither consistent with the known biology of the *Acacia* species (i.e., shade tolerance, short life-span) nor with the empirical evidence of *Acacia* abundance in montane ash forests (e.g., Ashton, 2000; Trouve et al., 2019). Because most *Acacia* will have died within 50–75 years of the original stand-initiating fire, maintaining sufficient (i.e., $>5\,m^2$ basal area per ha) *Acacia* for Leadbeater's possum would require additional disturbance. It has been suggested that this can occur as stand development progresses through the understorey reinitiation stage. Self-thinning amongst the canopy eucalypts would create gaps in the forest canopy that would allow *Acacia* to establish in the understorey (David Blair, personal communication). However, it is useful to understand what $5\,m^2$ basal area per ha represents in terms of crown area, as this gives an indication of the severity of the required disturbance.

Based on data from a network of plots established to measure *Acacia* dynamics in montane ash forests, the relationship between crown radius (CR, in metres) and diameter at breast height (DBH, in centimetres) can be expressed as:

$$CR = e^{-1.348+0.749\times ln(DBH)}$$

Because the basal area of a tree that is 20 cm DBH is $0.031\,m^2$, it would require approximately 160 trees that are 20 cm DBH to meet the threshold value of $5\,m^2$ of basal area per hectare that defines suitable Leadbeater's possum habitat. Using the equation above, an *Acacia* that is 20 cm DBH will have a crown radius of 2.45 m and therefore a crown area (assuming a circular crown) of approximately $18.8\,m^2$. This means that, on average, $2992\,m^2$ of total crown area (i.e., 160 trees $\times$ $18.8\,m^2$/tree) of *Acacia* is required to meet the threshold basal area value when the average tree size is 20 cm DBH. In other words, to have sufficient basal area of *Acacia* in a montane ash stand to meet the threshold value for suitable Leadbeater's possum habitat, nearly one-third of the stand would have to have *Acacia* crown cover. If, as Lindenmayer and Possingham (1995a) implicitly assume, subsequent disturbances are required to maintain sufficient *Acacia* resources for Leadbeater's possum after 100 years, then they are clearly more substantial disturbances than the gap dynamics that result from density-dependent self-thinning (Fedrigo et al., 2019; Trouve et al., 2017). A more realistic scenario is that the forest experiences a fire of intermediate

intensity that kills a significant proportion, but not all, of the overstorey eucalypts. There is a growing body of research that supports this view for montane ash forests (Lindenmayer, 2009). For example, Fedrigo et al. (2019) who found two to four cohorts of overstorey eucalypts within stands resulting from different fires that had occurred over the past 350 years. Remote-sensing and field-based analyses of fire severity after the 2009 bushfires showed that the majority of forest within the fire footprint experienced non-catastrophic canopy fire. This spanned a gradient of fire severity from areas in which overstorey mortality was <80% through to areas in which the fire never reached the forest canopy. Stands that have experienced partial, but substantial, overstorey mortality are well suited for *Acacia* regeneration and subsequent growth (Fedrigo et al., 2019).

5.4.2 The Hollow-Bearing Tree Component

Forests in Australia lack bird species such as woodpeckers that actively excavate hollows in trees and can accelerate the formation of hollows (Cockle et al., 2011). Consequently, the formation of hollows in trees has largely been viewed as a time-dependent process, albeit with recognition that there are a range of factors (e.g., species, topography, fire history) that contribute to variability in the abundance of hollows in trees (Lindenmayer et al., 1993). Several studies (e.g., Lindenmayer and Sato, 2018; Lindenmayer et al., 1993, 2012, 2017; Smith and Lindenmayer, 1988) have argued that montane ash forests may require as much as 190 years before individual trees are large enough (~210 cm DBH) to form the types of hollows that Leadbeater's possum prefer to use. However, this estimate is based on the simple log-linear model described by (Ashton, 1976):

$$log(DBH) = 1.02 \times log(age)$$

which did not explicitly provide estimates of the variability in the underlying DBH-age data.

This relationship highlights the two key components of the hollow-bearing tree component of Leadbeater's possum habitat: the size of trees required for suitable hollows and the time required for trees to reach such sizes. While the mean size threshold of 210 cm DBH for suitable hollow-bearing trees is commonly cited, it overshadows the wide variability in the size of hollow-bearing trees that Leadbeater's possum actually uses. In one of the landmark studies on the nesting habits of Leadbeater's possum, Smith and Lindenmayer (1988) found Leadbeater's possum were using hollows in trees as small as 110 cm DBH. They also found a marked difference in the size of living and dead hollow-bearing trees that were being used by Leadbeater's possum. The modal size class for dead trees being used was 110–150 cm DBH, whereas the modal size class for the living trees was >250 cm, although individual animals were also observed using live trees 110–150 cm DBH. Indeed, the majority of observations of Leadbeater's possum nesting described in

Smith and Lindenmayer (1988) were in dead trees <200 cm DBH. A comprehensive assessment of hollow occurrence in several Victorian eucalypt species by Fox et al. (2008) showed that mountain ash start forming hollows by 80 cm DBH and that hollows occurred in ~40% of trees that were 120 cm DBH.

In terms of the time required to reach a suitable size for Leadbeater's possum, the relationship described by Ashton above shows that the *mean* age of trees that are 210 cm DBH is ~190 years. However, Ashton was very clear in showing (e.g., Figure 5 in Ashton, 1976) and stating that there is considerable variability in this relationship – that is, trees of a given size may come from a broad range of ages. This level of variability in age-size relationships is a well-known feature of forests and trees (Baker, 2003; Harper, 1977; Oliver and Larson, 1996). The data in Ashton (1976) show that *Eucalyptus regnans* can reach 210 cm DBH within 120–130 years of a stand-initiating fire. Observations of such exceptional growth in mountain ash are not uncommon. For example, a recent resurvey of the Silvicultural Systems Project trial at Tanjil Bren in the Central Highland recorded several 80-year old *Eucalyptus regnans* trees that were ~130 cm DBH (Hammond, K. *in prep.*). As noted above, Leadbeater's possum have been found using hollows in trees that are smaller than these. This suggests that it may well be possible for sufficient densities of suitable hollow-bearing trees to develop in considerably less than 190 years.

5.5 Rethinking the Dynamics of Habitat Suitability for Leadbeater's Possum

Advances in our knowledge of stand development patterns in mountain ash forests over the past 25 years merit revisiting and updating the model proposed by Lindenmayer and Possingham (1995a) to describe the temporal dynamics of Leadbeater's possum habitat suitability. In particular, recent work on the dynamics of *Acacia*, a critical but generally overlooked component of suitable habitat for Leadbeater's possum, suggests a different model of habitat suitability over time. Figure 5.4 provides a graphical summary of the differences in habitat suitability between the original model and new empirical data for *Acacia* described by Trouve et al. (2019). The key differences are the earlier increase in habitat suitability after a stand-replacing fire and the lack of suitable Leadbeater's possum habitat as the forest becomes older absent subsequent disturbances. It is important to note that the density of hollow-bearing trees is effectively irrelevant in older forests if they have no *Acacia* in or near them.

We can treat these two models of habitat suitability dynamics as competing hypotheses that can be tested against empirical data (Hilborn and Mangel, 1997). For example, both models predict that Leadbeater's possum should currently be declining in forests dominated by regrowth from the 1939 fire, although the mechanisms driving this decline differ. Recent observations support this prediction and have shown that Leadbeater's possum are becoming less abundant in 1939

regrowth forest (e.g., Lindenmayer and Sato, 2018; Lindenmayer et al., 2017). The models differ, though, in their predictions of Leadbeater's possum habitat suitability in young and old forests. Our model suggests that Leadbeater's possum should be found in forests <15 years old, whereas the model proposed by Lindenmayer and Possingham (1995a) only has Leadbeater's possum habitat becoming suitable 21 years after a fire. Smith and Lindenmayer (1992) found Leadbeater's possum in sites that had been logged 12 years previously. Recent camera-trapping observations (2015–2019) by the Arthur Rylah Institute in montane ash forests that re-established after the 2009 Black Saturday bushfire (i.e., <10 years old) have found Leadbeater's possum, often at considerable distances from identified nesting sites. These observations support the hypothesis that Leadbeater's possum are using post-disturbance forests within the first decade of stand development.

Perhaps the greatest difference in the two competing models is in their predictions of the suitability of old forests as habitat for Leadbeater's possum. Our model predicts that Leadbeater's possum should rarely be found in old-growth forest, whereas Lindenmayer and Possingham (1995a) predict that this is amongst the most suitable habitats. In a recent study, however, Lindenmayer et al. (2017) demonstrated that Leadbeater's possum is almost never found in old-growth forest. Specifically, they found that emergence rate from hollow-bearing trees in old-growth forests was 0.6%, whereas emergence rates in young (27–56 years old) stands from the same study were 22.7% – that is, Leadbeater's possum were nearly 40 times more likely to emerge from hollow-bearing trees in young forests than in old-growth forests. It is also worth noting that these align very closely with earlier work by Smith and Lindenmayer (1992), who found peak densities of Leadbeater's possum in regrowth stands 15–50 years after disturbance (including both fire and logging). Smith and Lindenmayer (1992) noted that this period coincides with the period of maximum basal area of *Acacia*. Where Leadbeater's possum were found in old-growth forests, the forests were either multi-aged, supported a well-developed *Acacia* understorey, or were adjacent to young regrowth forest. More recently, Lindenmayer et al. (2021) noted that "sites in wood production forests were more likely to support Leadbeater's possum than sites in protected areas." They found this surprising because the wood production forests had fewer hollow-bearing trees and were subject to logging. However, this outcome is consistent with the known habitat preferences of Leadbeater's possum, published observations of emergence probabilities in different forest age classes, and the underlying dynamics of the key forest elements that constitute Leadbeater's possum habitat.

These observations of emergence from hollow-bearing trees are, of course, contingent on the presence of hollow-bearing trees within the stand. Where hollow-bearing trees do not occur, both models predict that Leadbeater's possum will be much less likely to occur. However, as Nelson et al. (2017) found in their extensive plot network, Leadbeater's possum may be found foraging in young stands without hollow-bearing trees if hollow-bearing trees occur in nearby forest. In addition, as noted earlier, Leadbeater's possum also occurs in high-elevation sites that do not support large hollow-bearing trees. So, under certain circumstances it appears that

Leadbeater's possum may be able to use other nesting resources, although to date it is unclear what those are and how they are used.

It is also important to recognise that most of the research on Leadbeater's possum comes from a limited number of study plots in forests that are structural and compositionally considered to be high-quality habitat. Two recent studies suggest that Leadbeater's possum is also found in habitat that is not typically considered suitable. In a recent extensive survey, Leadbeater's possums were found in 52% of 289 surveyed sites; however, only 3.4% of these sites would be considered suitable habitat under current regulations to qualify for protection (Nelson et al., 2017). In particular, 72% of the hollow-bearing trees in the survey did not meet the standards for hollow-bearing trees defined by the Leadbeater's possum Survey Standards (Nelson et al., 2017). In a separate study McBride et al. (2020) found Leadbeater's possum in mixed-species forests – a forest type dominated by a mix of several non-montane ash eucalypt species. These studies indicate that Leadbeater's possum can occur in a wider range of forest conditions and types than previously considered.

5.6 Management Implications

Casting the dynamics of long-term habitat suitability for Leadbeater's possum in the context of forest stand dynamics highlights the titular conservation conundrum of this chapter. Leadbeater's possum require disturbed forest to have sufficient *Acacia*, but they also require older forest elements (i.e., hollow-bearing trees) that often take a century or more to develop. Any strategy to ensure the long-term viability of the Leadbeater's possum must account for the dynamic nature of these forests and the fact that these two elements of Leadbeater's possum habitat are temporally unrelated and unsynchronised. Most of the actions that have been proposed to conserve Leadbeater's possum in the past treat habitat as a static feature of the landscape that can be protected by removing direct human threats. Because the preferred habitat of Leadbeater's possum is a transient feature of stand development, this type of passive management, on its own, is doomed to fail in such a dynamic system. Strict protection of forest will lead to loss of the *Acacia* component that Leadbeater's possum requires for foraging. However, without some protections, large trees capable of supporting hollows for nesting are also unlikely to develop. Expecting suitable Leadbeater's possum habitat to just develop over the course of 200–300 years ignores this fundamental conundrum and the stand development patterns that underpin it. Ensuring long-term continuity of habitat for Leadbeater's possum will require active management that restores key habitat features. Restoration-focused forest management needs to increase the recruitment of large trees – the habitat feature that is most limiting across the Central Highlands landscape due to the history of logging and fires – and provide a connected understorey of *Acacia* for movement and foraging. While passive management – in which identifiable human threats are removed from an ecosystem – has a long

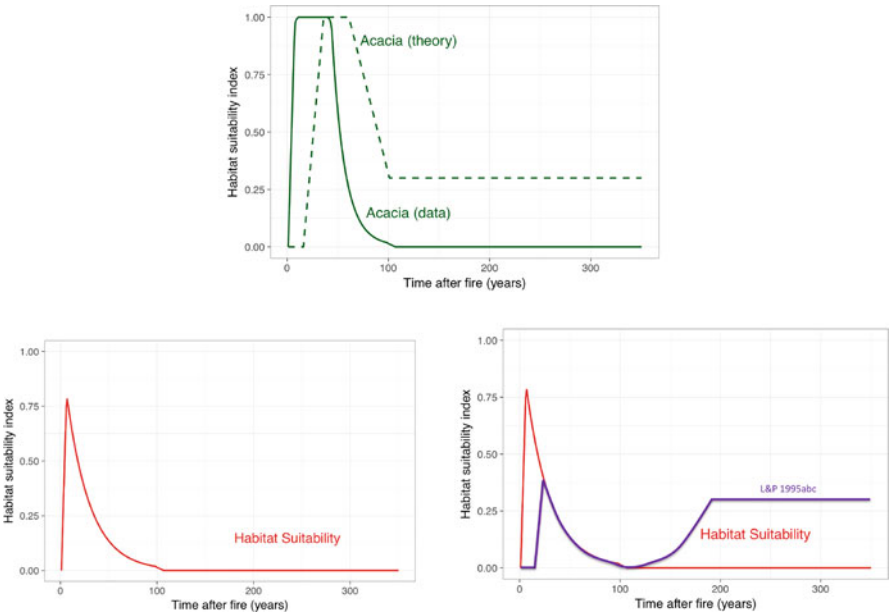

Fig. 5.4 Temporal dynamics of the *Acacia* component of Leadbeater's possum habitat as described by the model assumptions of Lindenmayer and Possingham (1995a) compared to empirical data derived from tree-ring analyses (upper panel). The lower left panel shows the habitat suitability for Leadbeater's possum based on the empirical data on *Acacia* abundance over time. The lower right panel compares this with the assumed habitat suitability from Lindenmayer and Possingham (1995a). The key differences are the earlier establishment of suitable Leadbeater's possum habitat after the stand-replacing fire and the absence of suitable habitat in older forests due to the lack of foraging habitat in the understorey. Note that this assumes no subsequent fires of low to moderate intensity that may create a pulse of *Acacia* establishment without catastrophic loss of the eucalypt canopy

history in conservation science and management, the belief that simply reducing or eliminating threats, such as logging or mining, will return ecosystems to a more "natural" state is often overly optimistic (Carey, 2003; Holl and Aide, 2010).

Knowledge of the underlying forest stand dynamics suggests two management options that would explicitly address the conservation conundrum described here for Leadbeater's possum. The first option would be to develop and apply silvicultural prescriptions that create multi-aged stands. Nelson et al. (2017) found that Leadbeater's possum was most abundant in two-aged forests. Stands that had established after the 1939 fires, but had also experienced some harvesting over the preceding 13–38 years had 69% occupancy. Silvicultural prescriptions that generate similar structures in the future would need to remove enough of the forest canopy to ensure a vigorous germination and growth response from the *Acacia* stored in the soil seed bank, but retain enough canopy eucalypts to ensure rapid growth of future potential hollow-bearing trees. Heavy crown thinnings that reduce the overstory

density by 60–70% would be one approach to achieving this. Recent surveys of the Silvicultural Systems Project at Tanjil Bren have found Leadbeater's possum in shelterwood sites in which the initial harvest removed 70% of the overstorey, but the remaining shelterwood was not removed. Alternatively, small patches of <1 ha could be cut into the forest allowing sufficient light for *Acacia* regeneration and increased growth of the eucalypts along the edge of the coupe.

The second option is to focus on the landscape-scale distribution of the two key habitat elements. This would require having a interdigitated matrix of young forest with *Acacia* and older forest with hollow-bearing trees in close proximity to each other. Unfortunately, current conservation planning for Leadbeater's possum involves establishing a 200-m radius exclusion zone around the location of any sightings. This point-based approach ignores the key habitat features that Leadbeater's possum depends on, their spatial arrangement within the landscape, and their temporal dynamics as stands develop and the various structural features increase or decrease in abundance. However, a landscape-scale approach (e.g., Nitschke et al., 2020) would require data on the relative abundance of key habitat features and forest dynamics models to predict how they will change over time. Until recently this was not possible, but recent advances in airborne LiDAR-based estimates of forest structure have the potential to provide landscape-scale maps of hollow-bearing tree density and understorey cover (Jiang, 2020). These data could then be linked to key elements of growth models described in Trouve et al. (2017, 2019) to estimate long-term changes in habitat suitability for Leadbeater's possum (Fig. 5.5). This approach would provide an empirical framework for planning forest management activities within the landscape and developing a system of dynamics conservation reserves that would maximise available and potential Leadbeater's possum habitat over the coming century.

Depending on stand- and landscape-scale mixes of age classes, stand densities, and/or species composition, individual stands may never achieve the desired state or may take a prohibitively long time to do so. Active management in the context of forested ecosystems uses silvicultural prescriptions to increase or decrease the rate at which a given stand moves along a desired developmental pathway or to shift the stand onto a different, more desirable, developmental pathway. This is particularly important where the current conditions have been heavily impacted by humans or where past disturbances have created large imbalances in age or size structures of forests within a fragmented landscape. In such a complex and dynamic forested landscape, proposals to eliminate forest management activities represent a significant leap of faith that these forests will revert to a preferred earlier state on their own in sufficient time to ensure the persistence of Leadbeater's possum. In addition, climate change will influence species ranges and fire regimes, which may reduce the habitat quality of current and proposed reserves in the future (Nitschke et al., 2020). A passive management approach would limit the possibility of adaptive actions to maintain developmental pathways or forest structures under future climatic conditions. In contrast, an active approach that identifies and manages for specific habitat targets or reintroduces specific ecosystem processes could accelerate the creation of key features of Leadbeater's possum habitat.

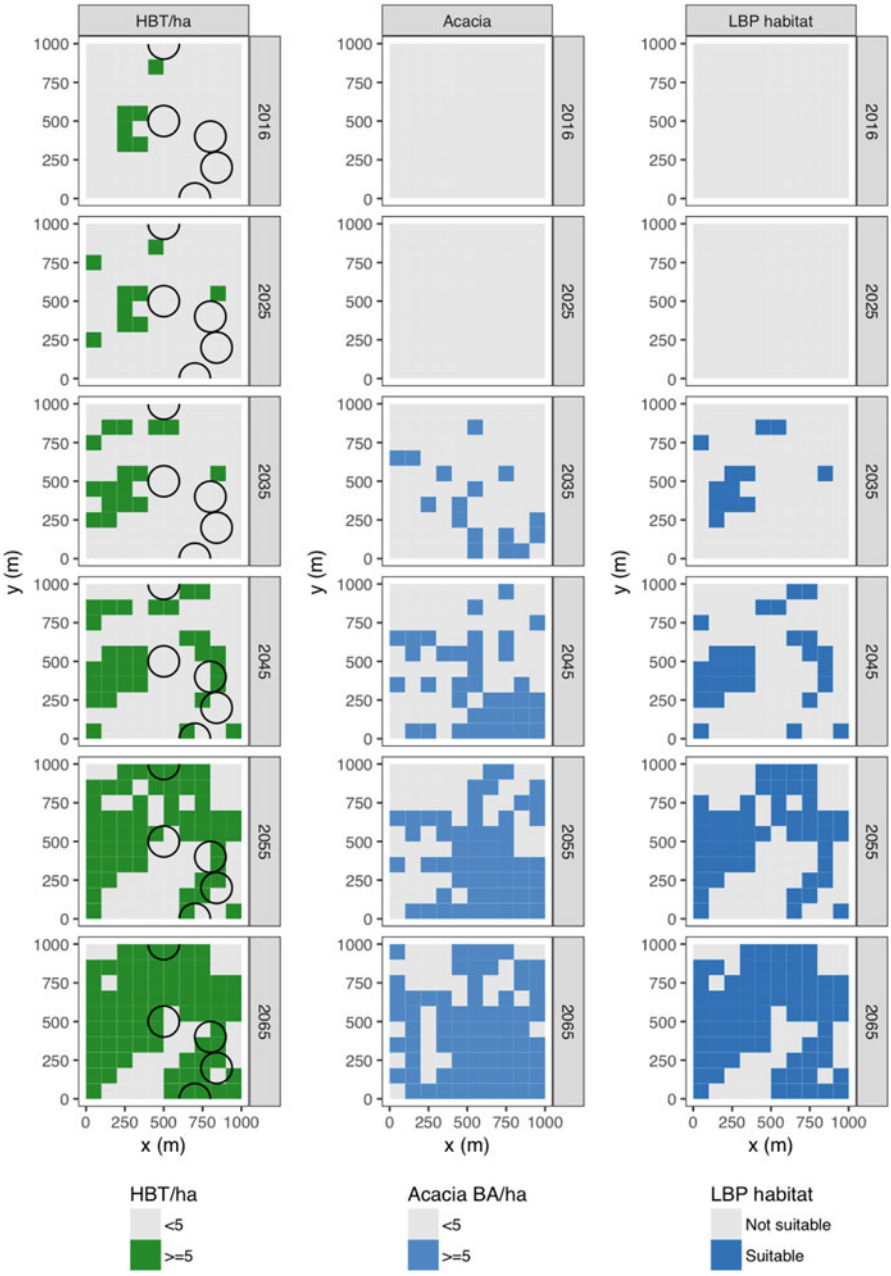

Fig. 5.5 (continued) Example of spatiotemporal dynamics of future Leadbeater's possum habitat suitability. The first column shows decadal changes in hollow-bearing tree density with 2016 in the uppermost panel and 2065 in the lowermost. The second column shows changes in *Acacia*

However, promoting active management of montane ash forests for Leadbeater's possum habitat would necessitate a fundamental shift in forest management philosophy and practice in the Central Highlands. It would involve a much greater emphasis on habitat restoration and management in the long term. Importantly, it would also require coordinating silvicultural treatments in space and time across the landscape to ensure that key habitat features were developing over the coming decades and in targeted priority areas that could act as spatial catalysts *sensu* (Pressey et al., 2007) for conservation (e.g., corridors between existing Leadbeater's possum reserve areas). The long-term viability of Leadbeater's possum populations will likely depend on such an active, landscape-scale ecological restoration effort.

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Fig. 5.5 (continued) basal area per hectare over time. Coloured pixels in each column are those that meet a specified threshold criterion. The third column shows the temporal dynamics in spatial patterns of suitable Leadbeater's possum habitat, where a pixel is considered suitable habitat in any given decade if it has met or exceeded the threshold value for *Acacia* basal area (centre column) and there is at least one nearest-neighbour pixel that has met or exceeded the hollow-bearing tree threshold (left-most column)

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