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Landscape Structure and Mature Forest Biodiversity in Wet Eucalypt Forests: A Spatial Analysis of Timber Production Areas in South-Eastern Australia

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Abstract: Fire and timber harvesting can diminish the extent of older forests in the near term. The amount and configuration of mature and regenerating forest in the landscape (landscape structure) influences habitat suitability for mature-forest-associated species. We applied spatial analysis to describe the landscape structure of three wet eucalypt forest landscapes in south–eastern Australia and used the results from empirical biodiversity studies to frame interpretation of possible impacts on habitat suitability. We determined the extent of structurally mature forest, its reservation status, and the extent to which it may be edge affected. We also assessed how landscape structure potentially impacts the re-establishment of mature-forest-associated species into previously harvested areas through the proximity to (mature forest influence)—and extent of (landscape context)—mature forest in the surrounding landscape. Our analyses were designed to inform forest management initiatives that draw on these landscape-scale concepts. Central Highlands Victoria had less structurally mature eucalypt forest (4%) compared to North West Tasmania (14%) and Southern Forests Tasmania (21%). Detrimental effects of edge influence on structurally mature forest appeared relatively minor. Low levels of mature forest influence combined with low-medium surrounding mature forest cover (landscape context) indicate potential limitations on recolonisation of coupes by mature-forest-associated species. Our results vindicate the recent shift toward variable retention silviculture and landscape context planning. Our approach to landscape analysis provides a useful framework for other managed forest landscapes.

Keywords: landscape context; mature forest influence; edge effects; spatial scale; landscape ecology; biodiversity conservation; retention forestry; variable retention; clearcutting; disturbance

1. Introduction

Forest managers seeking to achieve sustainable forest management must carefully balance the social, economic, and environmental values of forest ecosystems [1,2]. According to ecologically sustainable forest management principles, timber harvesting should be conducted in a way that does not compromise biodiversity within the ecosystem [3,4]. The fragmentation of harvested forest landscapes can have detrimental effects on biodiversity that manifest at a range of spatial scales from the harvested coupe to the wider forest landscape. Understanding how forest landscape structure (defined here as the spatial pattern of patches of cover of overstory of different ages, *sensu* [5]) contributes to maintenance of biodiversity in harvested landscapes is a key challenge for modern forest managers [5], including those seeking to implement forest conservation initiatives at multiple spatial scales [6]. This paper focuses on three components of forest landscape structure with particular reference to how they inform forest management and conservation of mature forest biodiversity in timber production landscapes. These are edge effects into mature remnants ('edge influence'), proximity of harvested areas to nearest mature forest ('forest influence'), and proportion of mature forest in landscapes surrounding harvested areas ('landscape context').

Traditionally, ecologists studying forest landscapes influenced by timber harvesting have focused on the effects of timber harvesting on forest species living in remnant forest patches within or near to harvested units ('coupes') [7–10]. The magnitude and distance of 'edge influence' from coupes can have profound effects on the structure and species composition of adjacent intact forest at the local scale [10]. Edge influence from coupes has been found to affect a range of taxa worldwide [11–15]. While the resilience of biodiversity in intact forest patches is clearly important, the importance of the role of harvested areas as habitat in their own right is gaining increasing recognition because they provide habitat for young-forest-associated species of high conservation value and because mature-forest-associated species can recolonise regenerating stands over time [16,17].

The process of recolonisation of harvested areas by mature-forest-associated species involves local and landscape scale mechanisms, including: (a) the dispersal capacity of the various flora and fauna groups; (b) the composition (age, structure, floristics) and environmental characteristics (slope, aspect, microclimate) of the regenerating forest; and (c) the composition, extent, and proximity of source populations in the surrounding landscape [17]. Whilst biodiversity within harvested areas will generally progress back toward its pre-harvest state through general successional processes [18], the re-establishment of mature-forest-associated species can be facilitated by the proximity to and amount of nearby mature habitat [17,19]. Proximity to unlogged mature forest buffers environmental conditions in harvested areas [15,20,21] and provides source populations for recolonisation by individuals or propagules. The latter is particularly important for dispersal-limited species that do not survive within areas subject to harvesting and regeneration treatments [22,23]. The local-scale distance at which adjacent mature forest facilitates recolonisation of harvested areas ('mature forest influence'; *sensu* [17]) may be less than 10 m for fungi and some vascular plants, intermediate distances for bryophytes and beetles, but extends to hundreds of meters for some mammals and birds [17,21,24–26] (Figure 1). Distance relationships are affected by regenerating forest age through its effect on microclimate, forest floor composition, and canopy structure, as well as the role of time in allowing gradual dispersal [17,26] (Figure 1).

Recolonisation of harvested areas by mature-forest-associated species may also be influenced at the landscape-scale by the cover of suitable habitat in the surrounding forest matrix ('landscape context'; *sensu* [27]). Threshold values of forest cover that positively influence the persistence of these species in the landscape are rare, and tend to be described for cases where the surrounding matrix habitat has been substantially altered, for example, cleared for agriculture (e.g., [28]) or where forestry disturbances are markedly different from the natural disturbance regime (e.g., [29,30]). However, biological responses to the surrounding landscape may be stronger in post-harvest regenerating forest than in mature forest remnants. For example, Wardlaw et al. [19] found that the occurrence of 40%–50% of commonly encountered mature-forest-associated bird and plant species in regenerating wet eucalypt forest increased significantly as the intensity of disturbance in their surrounding landscape decreased and the amount of surrounding mature forest increased.

The wet eucalypt forests of south-eastern Australia are disturbance-driven ecosystems with a history of intensive timber harvesting [31]. Landscape-scale wildfires and harvesting in the last century have diminished the extent of mature forest in these landscapes, which has raised concerns for the conservation of flora and fauna that are reliant on mature forest habitat [19,32,33]. In response, the concepts of mature forest influence and landscape context are being integrated into multi-scaled forest management practices in wet eucalypt forests in south-eastern Australia. In Tasmanian and Victorian wet eucalypt forests, the recent introduction of variable retention silviculture, where patches of undisturbed forest are retained within harvested coupes, is sometimes replacing use of clearfell, burn and sow silviculture (clearcutting) [34–36]. Variable retention explicitly aims to ensure minimum levels of harvested area under mature forest influence at the coupe scale. This is facilitated by targets specifying that at least 50% of harvested areas should be within one-tree-height of long-term retention, where one tree height is a pragmatic estimate of the region under forest influence [34,37,38]. Tasmanian forest managers also recently introduced a 'Landscape Context Planning System' [39] which includes a policy of designating at least 20% forest area within a 1000 m radius around each coupe in reserve or long-term retention, giving priority to retention of mature forest where possible. Victorian forest managers have implemented long-term retention of 30% of native forest in landscape-scale forest management units occupied by the endangered Leadbeater's Possum (*Gymnobelideus leadbeater*i McCoy; [40]). These initiatives complement an existing network of formal and informal reserves in the landscape. It is important to understand how effectively this reserve network delivers conservation outcomes at multiple spatial scales [6].

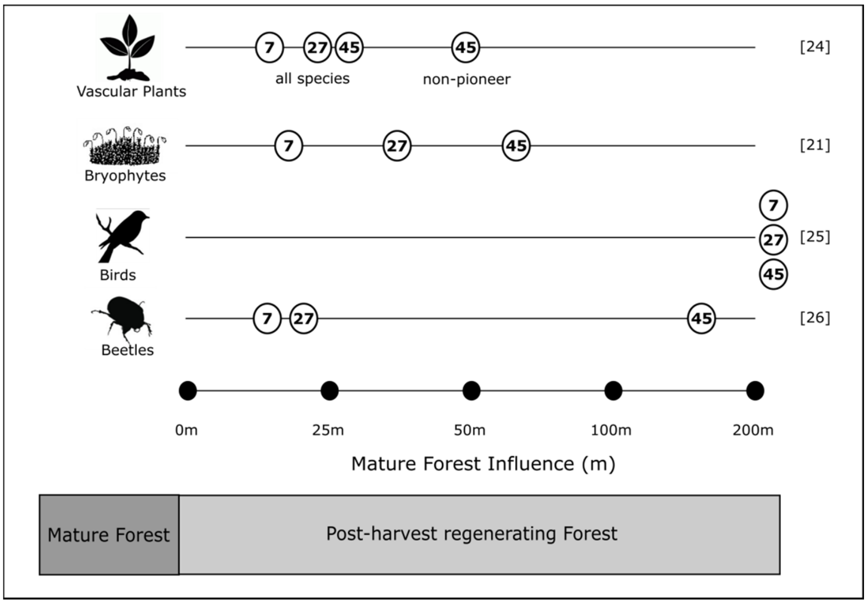


Figure 1. Mature Forest Influence for a suite of mature-forest-associated species in the wet eucalypt forests of Tasmania based on a series of concurrent studies in Southern Forests Tasmania [21,24–26]. Mature Forest Influence refers to the predicted distance from an edge into harvested forest (represented by circles) up to which community composition differs from the regeneration forest interior. There were five replicate sites of three age classes of clearcutting; ~7 year old, ~25 year old, and ~45 year old coupes. At each site, three transects of plots extended from 35 m into mature forest, across edges, to 200 m in the centres of regenerating forest in the clearcuts. Bootstrapping was used to predict the distance from edge where community composition was 95% similar to that in the clearcut centres. These distances were thus the predicted extent of mature forest influence. Datasets were: 108 vascular plant species [24], 96 bryophyte species [21], 271 ground-active beetle species [26], and 38 bird species [25].

In this study of three intensively managed wet eucalypt forest landscapes, we use spatial analyses to investigate the amount of remaining structurally mature forest and the degree to which it may be edge influenced. We also assess the degree to which the proximity to mature forest (i.e., mature forest influence) and surrounding mature forest cover (i.e., landscape context) are likely to impact recolonisation of harvested areas by mature forest species, using known responses by several mature-forest-associated taxa to frame interpretation. In addition, we used tenure maps to assess the contribution of different types of formal and informal reserves to the long-term retention of mature forests at scales relevant to these biodiversity measures. We discuss implications for forest managers seeking to incorporate multi-scaled concepts into planning frameworks.

2. Materials and Methods

2.1. Forest Landscapes

Our study focused on three forest landscapes in south-eastern Australia: Southern Forests Tasmania (174,000 ha), North West Tasmania (83,000 ha), and the Central Highlands Victoria (81,000 ha) (Table 1; Figure 2). The three forest landscapes (Figure 2) are broadly defined by the following criteria: (a) dominated by wet eucalypt forest; (b) largely within timber production management zones; (c) unburned by recent landscape scale fire events (2009 in Victoria; 2016 in North West Tasmania); and (d) within a 1000 m buffer around a core set of harvested patches (extent of analysis metrics; described below). The three forest landscapes are topographically complex and characterized by relatively high and reliable rainfall with generally cool to moderate temperatures [31,41]. The focal wet eucalypt forests are dominated by *Eucalyptus regnans* F.Muell in Victoria [32] and *E. obliqua* L'Hér. and *E. regnans* in Tasmania [41,42], but also include some areas of dry eucalypt forests, *Nothofagus*-dominated rainforest, non-eucalypt forests (e.g., *Acacia* spp.), and softwood and hardwood plantations. Wet eucalypt forests are the primary sources of native forest timber in south-eastern Australia and are generally taller, higher in biomass, and comprise a denser understorey compared to other eucalypt-dominated forests across Australia [41].

The eucalypt forests comprised a mosaic of structural types (regenerating saplings, regrowth poles, and mature and senescent trees) that reflected a history of timber harvesting and fire. Timber harvesting in these forests has historically created even-aged stands through a regime of clearfell, burn and sow silviculture on rotations of 45–100 years [43,44] with coupe sizes ranging from approximately five to fifty hectares. However, since ~2007 in Tasmania and ~2015 in Victoria, there was a shift to using variable retention forestry in some sites (mostly coupes containing old-growth forest in Tasmania, and coupes within the range of Leadbeater's Possum in Victoria) to increase the degree of multi-agedness of harvested forests at the coupe scale [34]. Depending on the intensity of fire events, unharvested forest stands were even-aged or multi-aged [42,45]. There are some similarities in the frequency of fire events in Victoria (e.g., 1850s; 1926; 1939, 1983; 2009) and Tasmania (e.g., 1898; 1934; 1967, 2016), however, Victorian fires tend to be higher intensity and stand-replacing [41].

Table 1. Descriptive statistics for harvested patches and structurally mature forest patches (defined as having ≥5% irregular crown cover of eucalypts) in three study areas.

	Southern Forests (Tas)	North West (Tas)	Central Highlands (Vic)
Study Area			
Total area (ha)	174,228	73,060	81,238
Harvested Patches			
Harvest year	1960–2015	1960–2015	1968–2015
No. patches	1002	348	897
Total patch area (ha)	48,128	13,836	16,251
Mean patch area (ha)	48	40	18
Harvest intensity (% area harvested)	28%	19%	20%
Structurally Mature Forest Patches			
Total patch area (ha)	36,138	10,800	3194
Proportion of study area (%)	20.7%	13.8%	3.9%
No. patches	997	721	206
Mean patch area (ha)	36	15	15
Irregular crown cover 5%–20%	46%	63%	98%
21%–40%	29%	26%	1%
41%–70%	22%	10%	1%
71%–100%	3%	1%	0%

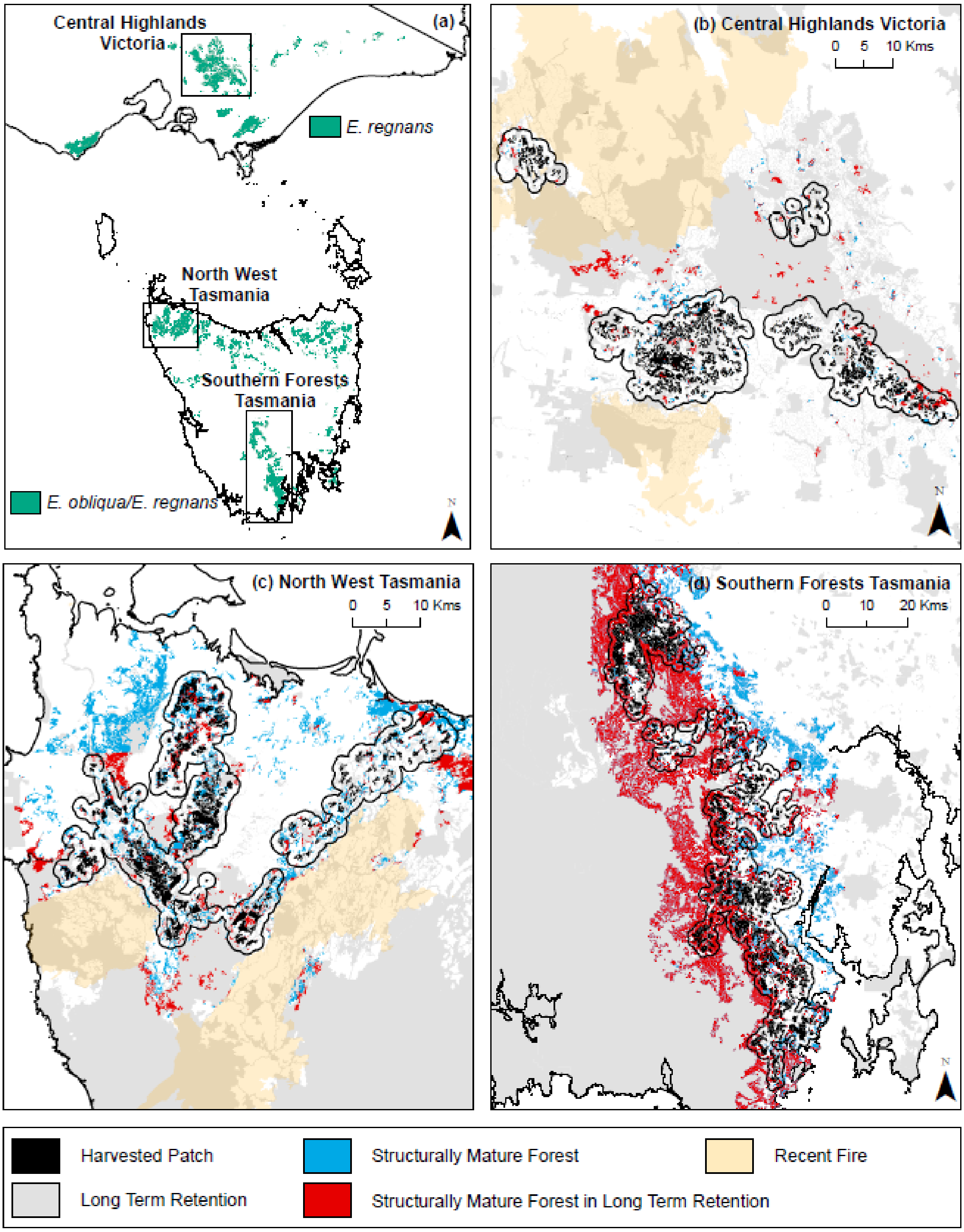


Figure 2. (**a**) Location of three study landscapes in wet eucalypt forests managed for timber production in south-eastern Australia. Central Highlands Victoria is dominated by *Eucalyptus regnans* F.Muell. Southern Forests Tasmania and North West Tasmania are dominated by *Eucalyptus regnans* F.Muell and/or *Eucalyptus obliqua* L'Hér.; (**b**–**d**) Harvested patches (1960–2015) and structurally mature forest (≥5% cover of irregular crowns) within the three study areas. Only mature forest patches within 10 km of harvested areas are shown. Areas in long-term retention and areas burned in the 2009 (Victoria) and 2016 (Tasmania) fires are shown. The solid line illustrates a 1000 m buffer within which mature forest influence and landscape context metrics were calculated.

2.2. Spatial Datasets

Forests managed for timber production in Victoria and Tasmania have been comprehensively mapped using aerial photograph interpretation as part of the Photo Interpretation typing in Tasmania (PI; [46]) and State Forest Resource Inventory in Victoria (SFRI; [47]). The PI and SFRI spatial datasets continue to underpin forest planning and management, although LIDAR and other remotely sensed products are likely to supersede this mapping. These spatial datasets are made up of derived polygons describing relatively homogenous forest attributes such as tree species, stand structure, age, disturbance type, and harvesting history. Photogrammetrists manually delineated polygons using visual interpretation of stereo images at a scale of approximately 1:20,000. Stand boundaries were interpreted from aerial photography acquired in the year 1995–1996 in Central Highlands Victoria, 2002 in Southern Forests Tasmania, and 2005–2006 in North West Tasmania. In both states, boundaries are updated and kept current to account for harvesting and fire events. We used these maps to delineate the following elements for analysis: (1) harvested patches (coupes); (2) structurally mature forest patches; and (3) patches of 1939 regrowth (Victoria only).

2.3. Harvested Patches

The SFRI and PI maps delineate harvested patches based on aerial photography, historical logging records, and field-derived measurements of coupe boundaries. Using spatial attributes describing the size, type, and date of harvested patches for the three study areas, we selected all patches ≥5 ha that were harvested by clearfell, burn and sow, or variable retention silviculture between 1960 and 2015. We excluded any harvested patches < 1000 m (extent of analysis metrics; see below) from the mapped extent of the 2009 fires in Central Highlands Victoria and the 2016 fires in North West Tasmania. This was necessary because the stand structural attributes of burnt areas have not been mapped since these fires.

2.4. Structurally Mature Forest

Information on forest age is recorded within the Victorian SFRI (e.g., 1939 or 1983 regrowth) although mapping of old-growth in this landscape is unreliable. There is no equivalent age mapping for Tasmania. As such, our spatial analysis of forest maturity is reliant on descriptions of forest structure. We refer to 'structural maturity' to distinguish from 'old-growth' or other age-based descriptors of maturity. Both states have mapped eucalypt dominated stands according to percent canopy cover of three distinct structural elements [46,48]. These structural elements broadly (but not exclusively) describe three stages of crown structure along an ecological succession from (1) young trees with narrow, conical crowns regenerating from a recent disturbance event (e.g., Victoria = 'Regrowth'; Tasmania = 'Aged Regeneration'); through (2) compact, smooth textured circular or oval shaped crowns typical of regrowth pole-stage trees (e.g., Victoria = 'Regular'; Tasmania = 'Unaged Regrowth'); to (3) older trees that have experienced significant loss of crown foliage or branches (e.g., Victoria = 'Irregular'; Tasmania = 'Mature').

We used the percentage cover of 'Irregular' or 'Mature' crowns (herein, 'irregular crowns') in the SFRI and PI maps to delineate patches of structurally mature forest in the landscape. We consider any forest stand mapped as ≥5% irregular crowns to be structurally mature. This aligns with operational and research-based definitions of mature forest (e.g., [19,39]). The two states classify polygons according to different categorical crown cover estimates and the Victorian SFRI also includes a continuous variable of irregular crown cover from 0%–100%. Given the non-conformity in crown cover categories across states, we selected polygons with ≥5% irregular crown cover using categorical crown cover estimates for Tasmania and continuous crown cover estimates for Victoria. Some selective harvesting may have occurred in these patches in the early 20th century, although the legacy effects of this harvesting are likely to be relatively minor in the context of our analysis.

We assumed that presence of irregular crowns represents forest that has intrinsic value for mature forest biodiversity—the focus of our paper. Irregular crowns are characteristic of senescent trees and indices of crown irregularity from both SFRI and PI have been found to be associated with hollow abundance in wet eucalypt forests [49–51]. Hollows provide crucial nesting habitat for hollow-dependent species [52,53]. Coarse woody debris, derived once these trees die and fall over, is likely to be of higher value for saproxylic invertebrates and fungi than logs derived from younger trees [54,55]. We relied on the best available data used by management agencies, recognizing that collapse of mature trees [56] and recruitment of mature trees may lead to discrepancies with current stand conditions.

2.5. Long-Term Retention

We used spatial maps of land tenure to delineate areas of forest in long-term retention, that is, areas in some form of reservation or zoning category that excludes harvesting for at least 100 years. Zoned tenures comprising long-term retention in Tasmania and Victoria selected for this study are detailed in Appendix A and include the following: National Parks and World Heritage Areas; Formal and Informal Reserves; Special Management Zones and Special Protection Zones; and selected exclusion zones established under the auspices of state-based codes of forest practice. Each state had different classification systems for tenure and it was not possible to ascribe consistent zones across states. As such, comparisons of long-term retention between states should be made with caution.

2.6. 1939 Regrowth in Long-Term Retention

Structurally mature forest in Victoria has been greatly diminished due to a series of stand replacing fires over the last century [33]. As a result, forest managers have been including 'future mature' forest in management decisions by reserving areas of regrowth forest [36,40]. In the absence of stand-replacing fire events, large swathes of reserved, unharvested 1939 regrowth in the landscape will eventually progress to structural maturity [56]. We included these areas of potential 'future mature' forest in our analysis framework in Victoria by delineating regrowth stands (SFRI regeneration year = 1939; SFRI regeneration cause = fire) that were in long-term retention (see below).

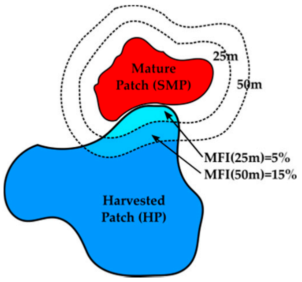
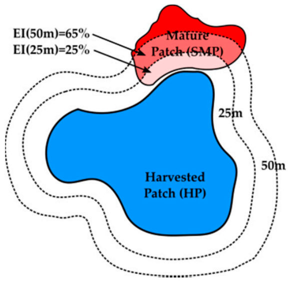
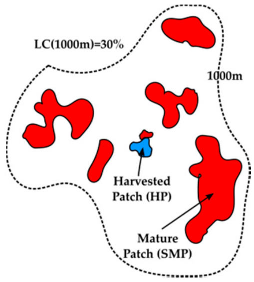
2.7. Analysis

2.7.1. Geospatial Metrics

We calculated three simple metrics to quantify (a) the proportion of each harvested patch within a particular distance of a structurally mature forest patch (mature forest influence); (b) the proportion of each structurally mature patch within a particular distance of a harvested patch or road (edge influence); and (c) percent cover of structurally mature forest around each harvested patch (landscape context). Table 2 describes and illustrates these metrics and outlines the patch types (e.g., harvested, structurally mature, 1939 regrowth) and tenure types (e.g., all tenures, long-term retention) that were used in calculations. Maps of the past extent of mature forests do not exist and therefore we could not account for mature forest patches that provided habitat historically, but were subsequently harvested and were considered in our maps as recently harvested areas with minimal mature forest habitat value.

Inverse cumulative relative frequency distributions were calculated to represent: (a) the proportion of harvested patches in each landscape that exceeded different values of mature forest influence or surrounding mature forest cover (i.e., landscape context); and (b) the proportion of mature forest patches in each landscape that exceeded different values of edge influence. These were calculated as follows (using mature forest influence as an example): (1) calculate mature forest influence for each harvested patch (see Table 2); (2) calculate the relative frequency of mature forest influence values for each study landscape, binned into one percent intervals; (3) calculate the cumulative relative frequency by successively adding relative frequencies for each interval; (4) calculate the inverse relative frequency (1-cumulative relative frequency), which represents a summary of the frequency proportion of harvested patches above a given value of mature forest influence. We examined trends in mature forest influence over time for each study area by calculating decadal averages of harvest patch area and mature forest influence.

Table 2. Geospatial metrics to quantify (a) the influence of structurally mature forest on historically harvested patches (Landscape Context and Mature Forest Influence) and (b) the influence of harvested patches and roads on structurally mature forest (Edge Influence). Mature Forest Influence and Landscape Context metrics were also calculated for all forest types in long-term retention, mature forest in long-term retention and 1939 regrowth in long-term retention (Victoria only).

	Mature Forest Influence (MFI)	**Edge Influence (EI)**	**Landscape Context (LC)**
Definition	Proportion of harvested patch within a particular distance of a structurally mature patch	Proportion of mature patch within a particular distance of harvested patch or road	Percent cover of mature forest in 1000 m buffer around harvested patch
Schematic #			
Calculations	Proportion of HP within a particular distance (25 m, 50 m, 100 m, 200 m) of (i) SMP; (ii) LTR; (iii) SMP + LTR; or (iv) 1939 + LTR.	Proportion of SMP within a particular distance (25 m, 50 m, 100 m, 200 m) of HP or RD.	Percent cover of (i) SMP; (ii) LTR; (iii) SMP + LTR; or (iv) 1939 + LTR in a 1000 m buffer around perimeter * of HP.
Units	% harvested patch area	% mature patch area	% buffer area

Abbreviations: Harvested Patch (HP), Structurally Mature Patch (SMP), Long-Term Retention (LTR), Structurally Mature Forest in Long-Term Retention (SMF + LTR), 1939 Regrowth in Long-Term Retention (1939 + LTR), Road (RD). 1939 + LTR was calculated for Victoria only. # only 25 m and 50 m distances shown for clarity.

Inverse cumulative frequency distributions enabled assessment of the effect of different levels of edge influence, mature forest influence, and landscape context for each study area. Drawing on these distributions, we calibrated our results against parameters in operational forest planning guidelines in our study area [39] and recent research on landscape context [19], mature forest influence (see Figure 1), and edge influence [15,57–59] in wet eucalypt forests. We used distance relationships presented in Figure 1 to examine how distance to adjacent mature forest effects the recolonisation of harvested patches in our landscapes by species with different dispersal abilities, for example, birds, beetles, vascular plants, and bryophyte communities benefited from nearby mature forest at predicted scales of approximately 200 m, 176 m, 60 m, and 64 m from mature forest into harvested patches ~45 years after harvest, respectively (Figure 1). We consider potential for recolonisation to be optimal when >50% of a harvested patch is under mature forest influence for a particular taxon. This is a common 'rule of thumb' for operational decisions regarding forest management and variable retention coupe planning in Tasmania [34] and more widely [37].

2.7.2. Long-Term Retention

For each study area, tenure maps were used to calculate (a) the proportion of all forest types in long-term retention and (b) the proportion of structurally mature forest in long-term retention. We then compared the relative extent of four types of long-term retention (Appendix A) for areas of structurally mature forest at three spatial scales: (1) the study area; (2) 1000 m buffers around each harvested patch; and (3) 100 m buffers around each harvested patch.

3. Results

3.1. Structural Maturity

Within our study landscapes, Southern Forests Tasmania (20.7%) and North West Tasmania (13.8%) had a substantially higher landscape cover of structurally mature forest than Central Highlands Victoria (3.9%) (Table 1). For structurally mature patches, the two Tasmanian study areas had a higher proportion of patches with ≥20% irregular crown cover (Southern Forests 54%; North West 37%) compared to the Central Highlands Victoria (2%) (Table 1).

3.2. Edge Influence

The amount of edge influence from roads and harvested patches on structurally mature forest patches was similar for each study area for distances of 25 m and 50 m (Figure 3a,b), but higher in Central Highlands Victoria for distances of 100 m and 200 m (Figure 3c,d). Across the study areas, we detected no edge influence in 27%–38% of mature forest patches at a distance of 25 m (Figure 3). Only ~11% of mature patches had more than 50% of their area within 25 m of roads or harvested patches (Figure 3).

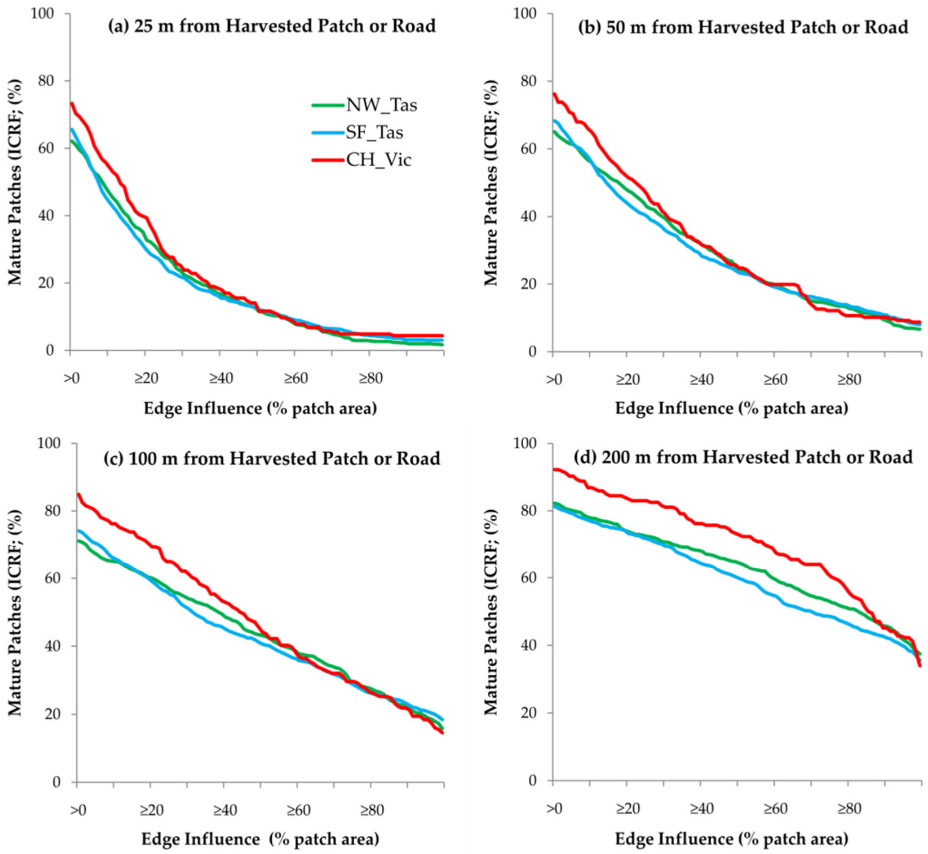


Figure 3. Inverse cumulative relative frequency (ICRF; %) of mature forest patches at different levels of *edge influence* for three study areas (Southern Forests Tasmania (SF); North West Tasmania (NW); Central Highlands Victoria (CH)). Edge influence is the proportion of a mature forest patch that is within a particular distance of harvested patches or roads: (**a**) 25 m; (**b**) 50 m; (**c**) 100 m; and (**d**) 200 m. For example: in (**a**), 11% of mature forest patches in Southern Forests Tasmania had more than 50% of their patch area within 25 m of a harvested patch or road.

3.3. Mature Forest Influence

Mature forest influence on harvested patches was highest in North West Tasmania and lowest in Central Highlands Victoria (Figure 4). The proportion of harvested patches with at least 50% of patch area within 50 m of mature forest was 3.0%, 8.0%, and 0.8% for Southern Forests Tasmania, North West Tasmania, and Central Highlands Victoria, respectively (Figure 4b). Increasing the distance factor (25 m > 50 m > 100 m > 200 m) incrementally increased the degree of mature forest influence on harvested patches (cf. Figure 4a–d). Mature forest influence on harvested patches has increased since ~1980 in North West Tasmania and Southern Forests Tasmania (Figure 5). Forest influence provided by 1939 regrowth in long-term retention in Central Highlands Victoria is equivalent to (25 m, 50 m)—or higher than (100 m, 200 m)—mature forest influence currently provided by mature forest in Tasmania (Figure 4).

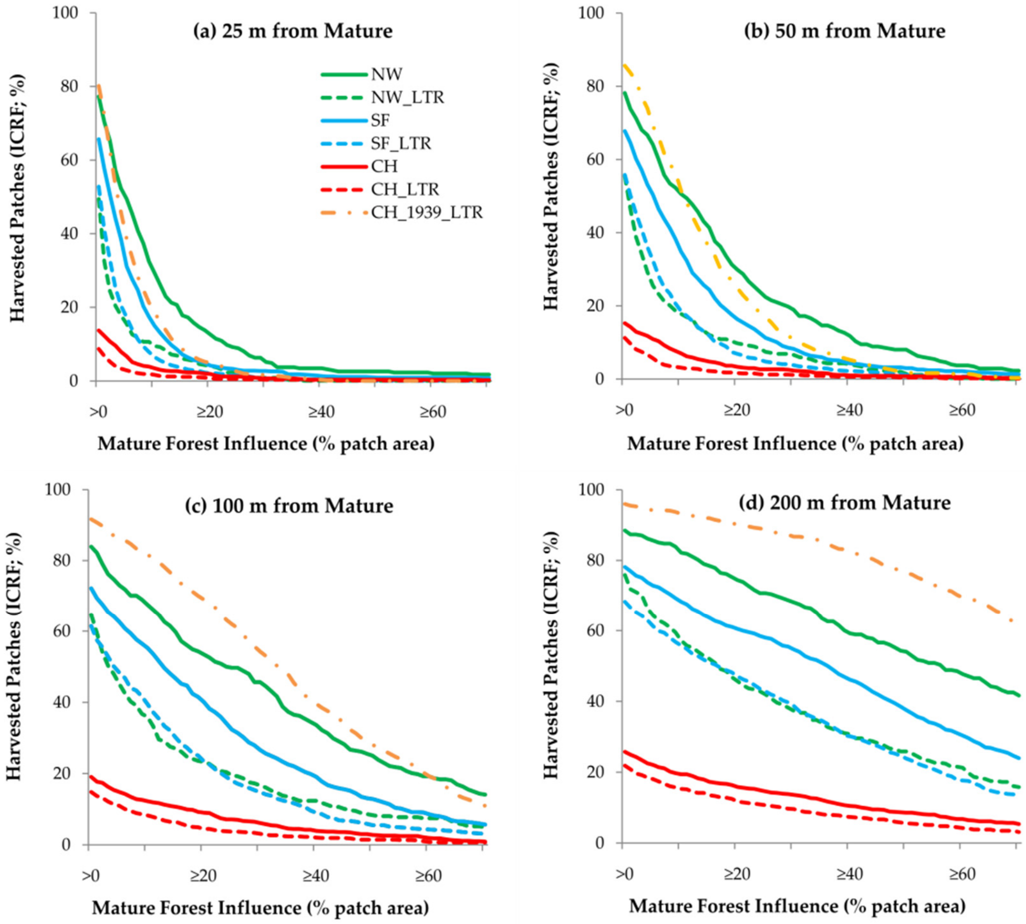


Figure 4. Inverse cumulative relative frequency (ICRF; %) of harvested patches at different levels of mature forest influence for three study areas (Southern Forests Tasmania (SF); North West Tasmania (NW); Central Highlands Victoria (CH)). Mature forest influence is the proportion of harvested patch area within a particular distance of structurally mature forest distance: (**a**) 25 m; (**b**) 50 m; (**c**) 100 m; and (**d**) 200 m. ICRF curves were calculated for all mature forest patches (no suffix) and mature forest patches in long-term retention (_LTR). In Victoria, relationships were also generated for 1939 regrowth in long-term retention (CH_1939_LTR). For example: in (**a**), 19% of harvested patches in Southern Forests Tasmania had more than 10% of their patch area within 25 m of a mature forest patch.

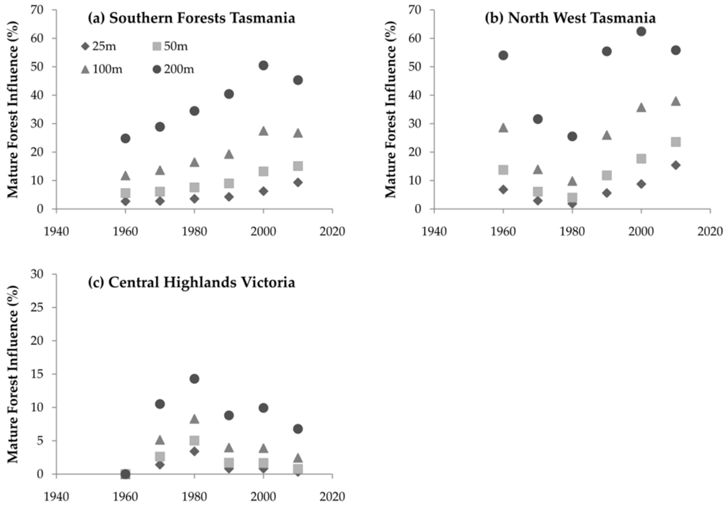


Figure 5. Average proportion of harvested patch area within 25 m, 50 m, 100 m, and 200 m of structurally mature forest (i.e., mature forest influence) over time for (**a**) Southern Forests Tasmania; (**b**) North West Tasmania; and (**c**) Central Highlands Victoria.

3.4. Landscape Context

The cover of mature forest in the surrounding landscape (i.e., landscape context) was highest in Southern Forests Tasmania, followed by North West Tasmania and Central Highlands Victoria (Figure 6a). Southern Forests Tasmania and North West Tasmania had 44.1% and 29.6% of harvested patches with at least 20% cover of structurally mature forest in the surrounding landscape, respectively (Figure 6a). In the Central Highlands Victoria, only 2.5% of harvested patches exceeded 20% cover of mature forest in the surrounding landscape (Figure 6a). The proportion of harvested patches (of any age) with ≥20% of their 1000 m buffer in long-term retention was 38%, 54%, and 71% for Southern Forests Tasmania (Figure 6b), North West Tasmania, and Central Highlands Victoria, respectively. In Central Highlands Victoria, 1939 regrowth in long-term retention provided a similar surrounding mature forest cover to the structurally mature forest in the Tasmanian study areas (34.9%; Figure 6a).

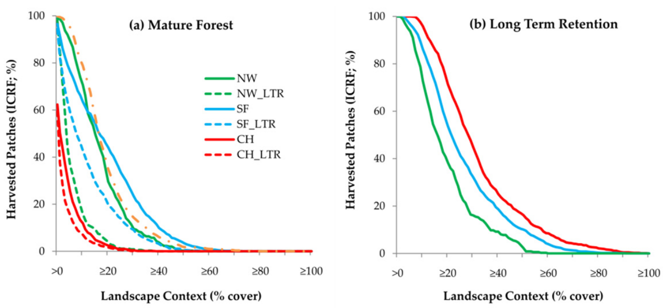


Figure 6. Inverse cumulative relative frequency (ICRF; %) of harvested patches at different levels of surrounding mature forest cover (i.e., landscape context) for three study areas (Southern Forests Tasmania (SF); North West Tasmania (NW); Central Highlands Victoria (CH)). Landscape context is the percentage cover of (**a**) structurally mature forest or (**b**) long-term retention (of any age) within a 1000 m buffer around the perimeter of a harvested patch. In (**a**) ICRF curves were calculated for (i) structurally mature forest patches (no suffix) and (ii) structurally mature forest patches in long-term retention (_LTR). In Victoria, ICRF curves were also generated for 1939 regrowth in long-term retention (CH_1939_LTR). For example: in (**a**), 44% of mature forest patches in Southern Forests Tasmania had more than 20% mature forest cover in the surrounding 1000 m buffer.

3.5. Long-Term Retention

The proportion of structurally mature forest in long-term retention (Southern Forests Tasmania (SF) = 64%; North West Tasmania (NW) = 35%; Central Highlands Victoria (CH) = 60%) was higher than long-term retention when all forest types were considered (SF = 34%; NW = 20%; CH = 37%). In the Tasmanian study areas, formal reserves such as National Parks contributed progressively less to the provision of long-term retention of mature forests around regenerating patches with decreasing spatial scale (Figure 7). Long-term retention of mature forests in Central Highlands Victoria was comparatively insensitive to spatial scale (Figure 7). Informal reserves, special protection/management zones, and exclusion zones were the primary form of long-term retention at local scales (100 m) in all three study areas (Figure 7).

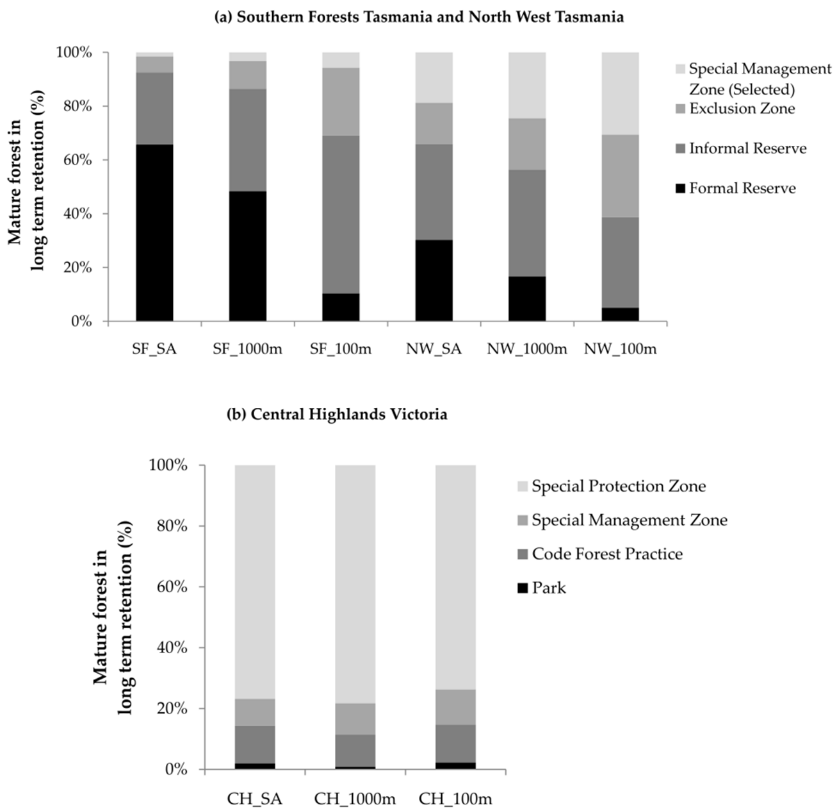


Figure 7. Relative proportion of structurally mature forest in four types of long-term retention at three spatial scales in (**a**) Tasmania and (**b**) Victoria. Statistics were calculated for (i) the study area (_SA); (ii) 1000 m buffers around each harvested patch (_1000m), i.e., landscape context scale; and (iii) 100 m buffers around each harvested patch (_100m), i.e., forest influence scale. Southern Forests Tasmania (SF); North West Tasmania (NW); Central Highlands Victoria (CH). Tenure types included in long-term retention categories are detailed in Appendix A.

4. Discussion

4.1. Structural Maturity

Structurally mature or old-growth forests are globally recognized as providing important habitats for many species of conservation significance as well as for carbon storage, social amenity, and other values [60,61]. We used maps derived from aerial photograph interpretation to compare the extent of structurally mature forest (i.e., ≥5% irregular crown cover) in three wet eucalypt forest landscapes in south eastern Australia that have been a focal point for timber production. The two Tasmanian study landscapes had substantially more structurally mature forest compared to Victoria. The proportion of mature forest patches with high densities of irregular crowns (i.e., ≥20% cover) was also markedly higher in Tasmania compared to Victoria. The intensity of harvesting over a fifty year period in the Tasmanian and Victorian landscapes (19%–28% and 20% of study area harvested respectively; Table 2 was similar. Therefore, the disparity between the extent and density of structurally mature forest is probably largely due to a series of high-severity fires in the Central Highlands Victoria study area (e.g., 1926, 1939, and 1983; [33]) that converted relatively fire-sensitive *Eucalyptus regnans* F.Muell forest to predominantly (but not exclusively; [45]) even-aged regrowth forests [32]. The 2009 fire in Victoria was excluded from our analysis, but is known to have burned large swathes of structurally mature forest outside our study area [33]. Wet forests in the Tasmanian study areas have experienced a similar frequency of fire (e.g., 1898; 1934; 1967; [62]), but structurally mature forest has persisted in the landscape due to the effects of landscape-scale fire refugia [63] and the propensity of mature forest trees in *E. obliqua* L'Hér. forests to survive fire through adaptations such as thick bark and epicormic resprouting [42].

The consequences of these fragmented distributions of small patches of mature forests for biodiversity are well documented for south-eastern Australia [31,33,64], particularly for the Central Highlands of Victoria where there is concern for the population viability of several threatened mammals following the widespread collapse of old trees with hollows [33]. The depletion of mature forests in regions such as Finland and Sweden has had devastating consequences for a broad range of taxa [61,65]. Around the world, the amount of remaining mature forest influences policies on forest reservation [60,61,66] and the strategic reservation and restoration of older age classes should remain a high priority in the wet eucalypt forest of south-eastern Australia.

4.2. Edge Influence

Edge influence from harvested areas and roads into structurally mature forest was similar for the Victorian and Tasmanian landscapes. In Tasmania, the effect of forest edges on vascular plants, bryophytes, and ground-active beetles usually dissipates by ~25 m [58,67]. This is comparable with studies of forest edges elsewhere [68–70]. A considerable proportion of structurally mature patches (27%–38%) within the three study areas had no roads or harvested areas within 25 m and the proportion of unaffected patches declined only slightly (24%–32%) when the buffer distance was extended to 50 m (relevant to ground-active beetles in streamside reserves [59]). The change in non-edge affected patches with increasing edge buffer width was comparable with two production forest landscapes with contrasting forestry histories in Sweden and Russia [71]. Very few (~11%) had more than 50% of their area within 25 m of roads or harvested patches. Our numbers may be conservative, because we treated sites harvested since 1960 as equivalent to sites harvested more recently. It is possible that older sites exert little or no edge influence [10,23], although there is some evidence for long-term persistence of edge effects [10,12]. Thus, our results show that the majority of structurally mature forest patches are unlikely to have compromised habitat conditions for vascular plants, bryophytes, and ground-active beetles in Tasmania as a result of edge influence.

4.3. Mature Forest Influence

Knowledge of the spatial scales of biodiversity responses from empirical studies can provide a framework for interpreting results of GIS-based analyses [71]. In Tasmania, the depth of mature forest influence into harvested coupes varies markedly amongst communities of birds [25], beetles [26], vascular plants [24], and bryophytes [21], and increases as the regenerating forest ages (see Figure 1). Combining our landscape analyses with this taxon-specific information provides an opportunity to estimate the proportion of harvested patches in the contemporary Tasmanian forest landscape that are likely to have the capacity to be successfully recolonised by these particular taxa within a 50–100 year harvest rotation. Birds arguably have the best dispersal ability of the studied taxa in Southern Tasmania; species have been shown to occupy harvest areas equally at distances between 0 and 200 m of mature forest edges [25] (Figure 1). In Tasmania, 37%–54% of harvested patches had at least 50% of their area within 200 m of mature forest (Figure 4d), suggesting that birds may be well established within harvested patches in our study areas. After ~45 years, bryophytes and late-successional vascular plant re-establishment only benefited from nearby mature forest ~60 m into harvested patches [21,24] (Figure 1). Very few (3%–8%) harvested patches in the Tasmanian study areas had more than 50% of their area within 50 m of mature forest (Figure 4b). Given their short dispersal distance (<25 m) into young harvesting regrowth (~7–27 years old [26]) (Figure 1), late-successional ground-dwelling beetles are likely to have colonised very few patches harvested in the last thirty years (<3%; Figure 4a). However, in older regrowth, mature forest influence extended to 176 m for ground-dwelling beetles [26] (Figure 1), thus proportionally more patches harvested from the 1960s and 1970s (~30%–45%; Figure 4c) could be successfully occupied by mature-forest-associated beetles. Ongoing monitoring in an adaptive management framework is required to test the veracity of these projected responses over time and in other landscapes.

In summary, patches harvested in the Tasmanian study areas between 1960–2015 are likely to be depauperate in mature-forest-associated beetles (in young regrowth), vascular plants, and bryophytes, both as a result of unsuitability of general habitat conditions relating to succession, but also because of dispersal limitations [22,26,72]. In contrast, mature-forest-associated beetles (in older regrowth) and birds are probably reasonably well dispersed throughout harvested areas. Traditional clearfell, burn and sow silviculture may therefore limit habitat availability for mature-forest-associated species with low dispersal ability. Encouragingly, the amount of mature forest influence on harvested patches has increased steadily in Tasmania since the ~1970s. This is probably related to a reduction in coupe size over time associated with regulatory changes and a shift to harvesting in more topographically complex areas as well as adoption of variable retention for some coupes in the last decade [24].

Both in south-east Australia and globally, forest managers tend to focus efforts on improving forest influence at the scale of individual variable retention harvest units, either directly via 'forest influence targets' [34,73] or indirectly via maximum allowable distances between retention patches [34]. Our results suggest that recent adoption of site-level approaches such as variable retention silviculture to increase habitat suitability for mature-forest-associated species is appropriate in these forests. We expect these results to translate to other forest landscapes around the world. In this regard, the aggregated retention form of structural retention where undisturbed patches are retained (protecting not only trees, but understorey, leaf litter, and soil communities) may be more likely to facilitate forest influence by providing source populations for a broader array of species than dispersed retention where only scattered trees are retained [17,72,74].

The proportion of harvested patches under mature forest influence in Victorian Central Highlands is currently low to very low across the range of distances explored in this study. In the future, 1939 regrowth forests in long-term retention across the Victorian Central Highlands landscape have the potential to provide mature forest influence on historically harvested patches to an extent similar to that currently provided by mature forests in Tasmania. However, the time frames for reserved regrowth to develop mature forest attributes are long (>50 years) and the likelihood of fire events truncating the progression from regrowth to mature forest is high [56]. As such, Victorian forest managers may benefit from research into how forest species recolonising harvested patches respond to distance from both mature *and* regrowth forest. Understanding the extent of so-called 'regrowth forest influence' will help assess biodiversity conservation benefits of harvesting coupes in the Victorian Central Highlands under 'regrowth retention silviculture'—a recently implemented (since 2014) form of variable retention where patches of regrowth forest are retained within harvested areas [36].

4.4. Landscape Context

Landscape context, or the amount of mature forest in landscapes surrounding a harvested patch, has been shown to affect the recolonisation of harvested patches by a suite of vascular plants, birds, and beetles in Tasmanian wet eucalypt forests [19] and is likely to be influential for the persistence of some arboreal marsupials and other mature-forest-associated species in the Victorian Central

Highlands [75,76]. Reviews of surrounding habitat cover required by biodiversity in forested landscapes show marked variation across species and regions, but identify 10%–30% cover as a practical guide for land managers [71,77,78]. In Tasmania, mature-forest-associated species of birds and plants reached levels of occurrence in silvicultural regeneration that were comparable with mature eucalypt forests when their 1000 m surrounding landscape contained ~20%–30% cover of mature eucalypt forest [19]. Less than half of historically harvested patches exceed 20% structurally mature forest in their surrounding 1000 m landscape in Southern Forests Tasmania and less than a third exceed this level in North West Tasmania (Figure 6). Surrounding mature forest cover is universally very low in Central Highlands Victoria (Figure 6). Thus, by this measure, recolonisation of a large proportion of historically harvested patches by mature-forest-associated birds and plants in both Victoria and Tasmania is likely to have been impeded by a lack of sufficient mature forest in the surrounding landscape, although a caveat to this conclusion is that we were unable to assess the contribution of some mature forest patches that provided habitat historically, but were subsequently harvested.

Not all structurally mature forest patches contributing to surrounding mature forest cover are in long-term retention. In recognition of this fact, and based on the findings of Wardlaw et al. [19], forest managers in Tasmania have recently implemented landscape context targets into forest planning [39]. Planning targets do not consider landscape context in terms of mature forest *per se*, but instead aim for at least 20% cover of surrounding forest in long-term retention, with guidelines to focus on retention of mature forest patches where available. In the Tasmanian landscapes, 38%–54% of historically harvested patches have ≥20% of their surrounding 1000 m buffer in long-term retention (Figure 6), suggesting additional long-term retention may be needed in parts of the landscape for future coupes. More than two-thirds (71%) of harvested patches exceeded this threshold in Central Highlands Victoria (Figure 6). If these reserved forests transition to maturity over time, they may provide important additional habitat to facilitate the recolonisation by mature-forest-associated species of both future coupes and historically harvested coupes. However, in these flammable ecosystems, fires may truncate the transition to maturity and managers should continue to develop strategic planning systems that retain mature forest in parts of the landscape representing the lowest fire risk (e.g., because of landscape position or forest type; [63,79,80]).

Our study and the empirical studies of Wardlaw et al. [19] focus specifically on how surrounding mature forest cover affects areas regenerating after harvest. Other studies have also found that landscape context is an influential factor for measures of biodiversity in post-harvest regeneration. For example, in Finland, Kouki et al [81] found that overall insect species richness was lower in restoration burns when the surrounding landscape had a much greater intensity of previous forest harvesting. In Sweden, landscape context impacted red-listed vascular and non-vascular plants and fungi in former abandoned pastures and meadows, with an apparent time delay of 120 years in some cases, suggesting a possible extinction debt [82]. Thus, new approaches to conservation and restoration that incorporate landscape-scale as well as patch-scale thinking are needed, and use of approaches such as ours for landscape-analysis complemented with a management tool akin to the Landscape Context Planning System [39] warrant consideration by managers. However, we consider a landscape context planning approach to be a useful complement to, not a replacement for, a backbone of strategic retention networks in formal and informal reserves, to highlight regions of the landscape that might be deficient in mature forest or reserved habitat.

4.5. Long-Term Retention

The relatively high retention of structurally mature forest compared to other forest types in our study areas reflects a history of policy initiatives directed toward reserving forests in older age classes [83,84]. This is appropriate in disturbance-driven eucalypt forests where harvesting combined with wildfires interact to reduce the average age of the forest. Informal reserves are designed to complement formal reserves and can contribute to conservation of mature-forest-associated species in managed forest landscapes [64,85]. Informal reserves were an important component of forest reservation in our study areas and landscapes elsewhere in Australia (43% of NSW State Forests are in informal reserves; [85]), North America [86] Sweden [6], and Russia [71]. South-east Australia has a higher proportion of both formal and informal reserves than certain other regions; for example, in a forest stewardship council (FSC) certified landscape in Sweden, only 3% of forest is formally reserved while 9% is in voluntary set aside [71]. Informal reserves, special management/protection zones, and exclusions zones provide for long-term retention of mature forests at local scales within close proximity to regenerating harvested areas. As such, these informal reserve types have the potential to complement larger formal reserves elsewhere in the landscape [4,71] and are likely to be important for facilitating the re-establishment of species into regenerating areas through provision of mature forest influence through time.

5. Conclusions

Aspects of mature forest influence and landscape context are being incorporated into contemporary forest management in Victoria and Tasmania under the auspices of variable retention silviculture and landscape context planning. The low cover of structurally mature forest in the Central Highlands Victoria will make achieving mature forest influence and landscape context targets like those applied in Tasmania challenging. As such, developing planning systems that retain regrowth forest in the landscape to progress to mature forest should remain a management priority. While Tasmania has a comparatively large area of structurally mature forest in the landscape, our results suggest that successful recolonisation of the majority of historically harvested patches by mature–forest-associated species may be limited by low mature forest cover in the surrounding landscape (i.e., landscape context). Further field-based research, however, is warranted to test this hypothesis at different spatial scales. Given that our study categorized structurally mature forest from aerial photograph derived GIS layers, the extent to which such patches represent habitat for different mature-forest-associated taxa also needs to be determined. Planners looking to incorporate additional reserves in the landscape to reach landscape context targets for future coupes under the Landscape Context Planning System should also consider their contribution to the recolonisation of historically harvested patches. The degree of mature forest influence on historically harvested patches was low in both Tasmanian study areas and very low in Victoria. This highlights a key deficiency of traditional clearcut silviculture and vindicates the recent shift to variable retention silviculture which explicitly seeks to increase mature forest influence at the coupe scale. Because of predicted increased future fires [87] managers in Tasmania may wish to adopt aspects of regrowth retention currently being developed for regrowth dominated landscapes in Central Highlands Victoria.

Applied biodiversity research has provided a basis for understanding how mature forest influence and landscape context are important for facilitating re-establishment of mature forest associated species into post-harvest regenerating forests as well as the extent to which edge influence might compromise habitat conditions in patches of remaining mature forest. Our landscape analysis draws on this research to show the extent to which forest influence and landscape context functionally achieve biodiversity conservation outcomes for previously harvested areas and highlights the importance of informal reserve types in the long-term retention of mature forest habitat at scales relevant to these mechanisms. Our analytical approach is readily applicable to any managed forest landscape with high quality maps of forest structure and composition. We encourage land managers in other forested regions to consider these important ecological concepts within strategic planning frameworks.

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Appendix

Categorisation of tenure types into various forms of long-term retention in Tasmania and Victoria are outlined in Tables A1 and A2, respectively. In Victoria, the inclusion/exclusion of particular codes of forest practice and special management zones for long-term retention (as in Tasmania) was not possible due to insufficient spatial resolution for those forest tenures. Each state had different classification systems for tenure, and it was not possible to ascribe consistent zones across states. As such, comparisons of long-term retention between states should be made with caution.

Table A1. Tenure types in public native forest in Tasmania. Categories included in long-term retention are highlighted in italics. Adapted from Landscape Conservation Planning System [39] and based on spatial data from the Management Decision Classification [88] and other spatial layers of tenure (i.e., Tenplus and Provcoupe exclusion codes).

Tasmania	Description	Long-Term Retention (Y/N)
Public Formal	*Formal Reserves on Public Land*	Y
Public Informal	*Informal Reserves on Public Land including those established through Forest Practices Code*	Y
Special Management Zones	*Masked Owl* *Swift Parrot* *Long-Term Retention* *Stag Beetle* *Variable Retention;* Other Special Management Zones #	Y Y Y Y Y N
Provisional Coupe Exclusion Zones	*Streamside Reserves* *Wildlife Habitat Clumps* Other Exclusion Zones ^	Y Y N
Private Informal	Informal Private Reserves	N
Future Potential Production	(not previously reserved)	N
Plantations	Forestry Tasmania Plantations	N
Wood Production Zones	Forestry Tasmania Wood Production	N
Other Public and Private Land	Other Public and Private Land	N

e.g., Wildlife Habitat Strips; Threatened Flora/Fauna Reserves; Cultural Heritage, Geomorphological or Visual Landscape Value; ^ e.g., Inaccessible, Non-commercial, Regeneration Problems, Rainforest, Steep, Unloggable.

Table A2. Tenure types in public native forest in public native forests in Victoria. Categories included in long-term retention are highlighted in italics. Based on the Forest Management Zone spatial layer described in [89].

Victoria	Description	Long-Term Retention (Y/N)
Park	National Parks, State Parks, Regional Parks, Flora and Fauna Reserves	Y
Special Management Zone	Managed to conserve specific features, while catering for timber harvesting operations under special conditions	Y
Special Protection Zone	Managed for particular conservation values # to complement formal conservation reserve system. Timber harvesting operations generally excluded	Y
Code Forest Practice	Exclusion areas where timber harvesting cannot occur due to streamside protection buffers, steep slopes, etc.)	Y
General Management Zone	Managed for a range of uses and values, but timber harvesting operations will have a high priority.	N
Other Public Land	Other Public Land	N
Plantation	Plantation	N

e.g., Aboriginal, Historic, Recreation, Spotted Tree Frog, Rainforest, Landscape, Old-Growth, Leadbeater's Possum, Sooty Owl, Powerful Owl, BawBaw Frog, Riverside, Endemic/Edge Species.

References

1. Lindenmayer, D.B.; Margules, C.R.; Botkin, D.B. Indicators of biodiversity for ecologically sustainable forest management. *Conserv. Biol.* **2000**, *14*, 941–950. [CrossRef]
2. Howell, C.; Wilson, A.; Davey, S.; Eddington, M. Sustainable forest management reporting in Australia. *Ecol. Indic.* **2008**, *8*, 123–130. [CrossRef]
3. Hunter, M.L. *Maintaining Biodiversity in Forest Ecosystems*; Cambridge University Press: Cambridge, UK, 1999.
4. Lindenmayer, D.B.; Franklin, J.F. *Conserving Forest Biodiversity: A Comprehensive Multiscaled Approach*; Island Press: Washington, DC, USA, 2002.
5. Lindenmayer, D. Interactions between forest resource management and landscape structure. *Curr. Landsc. Ecol. Rep.* **2016**, *1*, 10–18. [CrossRef]
6. Gustafsson, L.; Perhans, K. Biodiversity conservation in Swedish forests: Ways forward for a 30-year-old multi-scaled approach. *Ambio* **2010**, *39*, 546–554. [CrossRef] [PubMed]
7. McGarigal, K.; McComb, W.C. Relationships between landscape structure and breeding birds in the Oregon Coast Range. *Ecol. Monogr.* **1995**, *65*, 235–260. [CrossRef]
8. Jokimäki, J.; Huhta, E. Effects of landscape matrix and habitat structure on a bird community in northern Finland: A multi-scale approach. *Ornis Fenn.* **1996**, *73*, 97–113.
9. Drapeau, P.; Leduc, A.; Giroux, J.-F.; Savard, J.-P.L.; Bergeron, Y.; Vickery, W.L. Landscape-scale disturbances and changes in bird communities of boreal mixed-wood forests. *Ecol. Monogr.* **2000**, *70*, 423–444. [CrossRef]
10. Harper, K.A.; Macdonald, S.E.; Burton, P.J.; Chen, J.; Brosofske, K.D.; Saunders, S.C.; Euskirchen, E.S.; Roberts, D.; Jaiteh, M.S.; Esseen, P.A. Edge influence on forest structure and composition in fragmented landscapes. *Conserv. Biol.* **2005**, *19*, 768–782. [CrossRef]
11. Larrivée, M.; Drapeau, P.; Fahrig, L. Edge effects created by wildfire and clear-cutting on boreal forest ground-dwelling spiders. *For. Ecol. Manag.* **2008**, *255*, 1434–1445. [CrossRef]
12. Dupuch, A.; Fortin, D. The extent of edge effects increases during post-harvesting forest succession. *Biol. Conserv.* **2013**, *162*, 9–16. [CrossRef]
13. Chen, J.; Franklin, J.F.; Spies, T.A. Vegetation responses to edge environments in old-growth Douglas-fir forests. *Ecol. Appl.* **1992**, *2*, 387–396. [CrossRef] [PubMed]
14. Mascarúa López, L.E.; Harper, K.A.; Drapeau, P. Edge influence on forest structure in large forest remnants, cutblock separators, and riparian buffers in managed black spruce forests. *Ecoscience* **2006**, *13*, 226–233. [CrossRef]
15. Baker, T.P.; Jordan, G.J.; Dalton, P.J.; Baker, S.C. Impact of distance to mature forest on the recolonisation of bryophytes in a regenerating Tasmanian wet eucalypt forest. *Aust. J. Bot.* **2014**, *61*, 633–642. [CrossRef]
16. Chazdon, R.L.; Peres, C.A.; Dent, D.; Sheil, D.; Lugo, A.E.; Lamb, D.; Stork, N.E.; Miller, S.E. The potential for species conservation in tropical secondary forests. *Conserv. Biol.* **2009**, *23*, 1406–1417. [CrossRef] [PubMed]
17. Baker, S.C.; Spies, T.A.; Wardlaw, T.J.; Balmer, J.; Franklin, J.F.; Jordan, G.J. The harvested side of edges: Effect of retained forests on the re-establishment of biodiversity in adjacent harvested areas. *For. Ecol. Manag.* **2013**, *302*, 107–121. [CrossRef]
18. Pulsford, S.A.; Lindenmayer, D.B.; Driscoll, D.A. A succession of theories: Purging redundancy from disturbance theory. *Biol. Rev.* **2014**, *91*, 148–167. [CrossRef] [PubMed]
19. Wardlaw, T.; Grove, S.; Balmer, J.; Hingston, A.; Forster, L.; Schmuki, C.; Read, S. *Persistence of Mature Forest Biodiversity in a Production Forest Landscape Managed under a Regional Forest Agreement*; Forest and Wood Products Australia: Hobart, Tasmania, Australia, 2012.
20. Heithecker, T.D.; Halpern, C.B. Edge-related gradients in microclimate in forest aggregates following structural retention harvests in western Washington. *For. Ecol. Manag.* **2007**, *248*, 163–173. [CrossRef]
21. Baker, T.P.; Jordan, G.J.; Baker, S.C. Microclimatic edge effects in a recently harvested forest: Do remnant forest patches create the same impact as large forest areas? *For. Ecol. Manag.* **2016**, *365*, 128–136. [CrossRef]
22. Tabor, J.; McElhinny, C.; Hickey, J.; Wood, J. Colonisation of clearfelled coupes by rainforest tree species from mature mixed forest edges, Tasmania, Australia. *For. Ecol. Manag.* **2007**, *240*, 13–23. [CrossRef]
23. Matlack, G.R. Vegetation dynamics of the forest edge–trends in space and successional time. *J. Ecol.* **1994**, *82*, 113–123. [CrossRef]

24. Balmer, J. Floristic Response to Landscape Context in Vascular Plant Communities in *Eucalyptus obliqua* and *Eucalyptus regnans* Wet Forest, Southern Tasmania. Ph.D. Thesis, University of Tasmania, Hobart, Australia, 2015.
25. Hingston, A.B.; Jordan, G.J.; Wardlaw, T.J.; Baker, S.C. Bird assemblages in Tasmanian clearcuts are influenced by the age of eucalypt regeneration but not by distance from mature forest. *Glob. Ecol. Conserv.* **2014**, *2*, 138–147. [CrossRef]
26. Fountain-Jones, N.M.; Jordan, G.J.; Baker, T.P.; Balmer, J.M.; Wardlaw, T.; Baker, S.C. Living near the edge: Being close to mature forest increases the rate of succession in beetle communities. *Ecol. Appl.* **2015**, *25*, 800–811. [CrossRef] [PubMed]
27. Mazerolle, M.J.; Villard, M.-A. Patch characteristics and landscape context as predictors of species presence and abundance: A review. *Ecoscience* **1999**, *6*, 117–124.
28. Radford, J.Q.; Bennett, A.F.; Cheers, G.J. Landscape-level thresholds of habitat cover for woodland-dependent birds. *Biol. Conserv.* **2005**, *124*, 317–337. [CrossRef]
29. Betts, M.G.; Forbes, G.J.; Diamond, A.W. Thresholds in songbird occurrence in relation to landscape structure. *Conserv. Biol.* **2007**, *21*, 1046–1058. [CrossRef] [PubMed]
30. Drapeau, P.; Villard, M.A.; Leduc, A.; Hannon, S.J. Natural disturbance regimes as templates for the response of bird species assemblages to contemporary forest management. *Divers. Distrib.* **2016**, *22*, 385–399. [CrossRef]
31. Wood, S.; Bowman, D.; Prior, L.; Lindenmayer, D.; Wardlaw, T.; Robinson, R. Tall eucalypt forests. In *Biodiversity and Environmental Change*; Lindenmayer, D., Burns, E., Thurgate, N., Lowe, A., Eds.; CSIRO Publishing: Canberra, ACT, Australia, 2014; pp. 531–581.
32. Lindenmayer, D. *Forest Pattern and Ecological Process: A Synthesis of 25 Years of Research*; CSIRO Publishing: Melbourne, Australia, 2009.
33. Lindenmayer, D.; Blair, D.; McBurney, L.; Banks, S. *Mountain Ash: Fire, Logging and the Future of Victoria's Giant Forests*; CSIRO Publishing: Melbourne, Australia, 2015.
34. Baker, S.C.; Read, S.M. Variable retention silviculture in Tasmania's wet forests: Ecological rationale, adaptive management and synthesis of biodiversity benefits. *Aust. For.* **2011**, *74*, 218–232. [CrossRef]
35. Gustafsson, L.; Baker, S.C.; Bauhus, J.; Beese, W.J.; Brodie, A.; Kouki, J.; Lindenmayer, D.B.; Lõhmus, A.; Pastur, G.M.; Messier, C. Retention forestry to maintain multifunctional forests: A world perspective. *Bioscience* **2012**, *62*, 633–645.
36. VicForests. *Regrowth Retention Harvesting Instruction. Version 2.0.*; VicForests: Melbourne, Victoria, Australia, 2016.
37. Keenan, R.J.; Kimmins, J. The ecological effects of clear-cutting. *Environ. Rev.* **1993**, *1*, 121–144. [CrossRef]
38. Scott, R.E.; Neyland, M.G.; McElwee, D.J.; Baker, S.C. Burning outcomes following aggregated retention harvesting in old-growth wet eucalypt forests. *For. Ecol. Manag.* **2012**, *276*, 165–173. [CrossRef]
39. Forestry Tasmania. *Landscape Context Planning System Manual*; Forestry Tasmania: Hobart, Tasmania, Australia, 2014.
40. Department of Environment and Primary Industries (DEPI). *Planning Standards for Timber Havesting Operations in Victoria's State Forests 2014: Appendix 5 to the Management Standards and Procedures for Timber Harvesting Operations in Victoria's State Forests 2014*; Department of Environment and Primary Industries: Melbourne, Victoria, Australia, 2014.
41. Wood, S.W.; Prior, L.D.; Stephens, H.C.; Bowman, D.M. Macroecology of Australian tall eucalypt forests: Baseline data from a continental-scale permanent plot network. *PLoS ONE* **2015**, *10*, e0137811. [CrossRef] [PubMed]
42. Turner, P.A.; Balmer, J.; Kirkpatrick, J. Stand-replacing wildfires: The incidence of multi-cohort and single-cohort *Eucalyptus regnans* and *E. obliqua* forests in southern Tasmania. *For. Ecol. Manag.* **2009**, *258*, 366–375. [CrossRef]
43. Attiwill, P.M. The disturbance of forest ecosystems: The ecological basis for conservative management. *For. Ecol. Manag.* **1994**, *63*, 247–300. [CrossRef]
44. Hickey, J.; Wilkinson, G. The development and current implementation of silvicultural pratices in native forests in Tasmania. *Aust. For.* **1999**, *62*, 245–254. [CrossRef]
45. McCarthy, M.A.; Lindenmayer, D.B. Multi-aged mountain ash forest, wildlife conservation and timber harvesting. *For. Ecol. Manag.* **1998**, *104*, 43–56. [CrossRef]

46. Stone, M. Forest-type mapping by photo-interpretation: A multi-purpose base for Tasmania's forest management. *Tasforests* **1998**, *10*, 15–32.
47. Hamilton, F.; Penny, R.; Black, P.; Cumming, F.; Irvine, M. Victoria's Statewide Forest Resource Industry—an outline of methods. *Aust. For.* **1999**, *62*, 353–359. [CrossRef]
48. Brookhouse, M.; Brack, C.; McElhinny, C. The distance to structural complement (DiSCo) approach for expressing forest structure described by Aerial Photograph Interpretation data sets. *For. Ecol. Manag.* **2010**, *260*, 1230–1240. [CrossRef]
49. Fox, J.C.; Hamilton, F.; Ades, P.K. Models of tree-level hollow incidence in Victorian State forests. *For. Ecol. Manag.* **2008**, *255*, 2846–2857. [CrossRef]
50. Fox, J.C.; Hamilton, F.; Occhipinti, S. Tree hollow incidence in Victorian state forests. *Aust. For.* **2009**, *72*, 39–48. [CrossRef]
51. Koch, A.; Baker, S. Remotely assessing hollow availability using aerial photographs. *Biodivers. Conserv.* **2011**, *20*, 1089–1101. [CrossRef]
52. Gibbons, P.; Lindenmayer, D. *Tree Hollows and Wildlife Conservation in Australia*; CSIRO Publishing: Melbourne, Australia, 2002.
53. Koch, A.J.; Munks, S.A.; Driscoll, D.; Kirkpatrick, J. Does hollow occurrence vary with forest type? A case study in wet and dry *Eucalyptus obliqua* forest. *For. Ecol. Manag.* **2008**, *255*, 3938–3951. [CrossRef]
54. Yee, M.; Grove, S.; Richardson, A.M.; Mohammed, C. Brown rot in inner heartwood: Why large logs support characteristic saproxylic beetle assemblages of conservation concern. In *Insect Biodiversity and Dead Wood: Proceedings of a Symposium for the 22nd International Congress of Entomology*; Gen. Tech. Rep. SRS-93; Grove, S.J., Hanula, J.L., Eds.; U.S. Department of Agriculture Forest Service, Southern Research Station: Asheville, NC, USA, 2006; pp. 42–56.
55. Wardlaw, T.; Grove, S.; Hopkins, A.; Yee, M.; Harrison, K.; Mohammed, C. The uniqueness of habitats in old eucalypts: Contrasting wood-decay fungi and saproxylic beetles of young and old eucalypts. *Tasforests* **2009**, *18*, 17–32.
56. Lindenmayer, D.B.; Blanchard, W.; McBurney, L.; Blair, D.; Banks, S.; Likens, G.E.; Franklin, J.F.; Laurance, W.F.; Stein, J.A.; Gibbons, P. Interacting factors driving a major loss of large trees with cavities in a forest ecosystem. *PLoS ONE* **2012**, *7*, e41864. [CrossRef] [PubMed]
57. Westphalen, G. The Ecology of Edges in Tasmanian Wet Forests Managed for Timber Production. Ph.D. Thesis, University of Tasmania, Hobart, Tasmania, Australia, 2003.
58. Baker, S.C.; Barmuta, L.A.; McQuillan, P.B.; Richardson, A.M. Estimating edge effects on ground-dwelling beetles at clearfelled non-riparian stand edges in Tasmanian wet eucalypt forest. *For. Ecol. Manag.* **2007**, *239*, 92–101. [CrossRef]
59. Baker, S.C.; Barmuta, L.A.; Richardson, A.M. Response of ground-dwelling beetles across logging coupe edges into streamside reserves. *Aust. J. Entomol.* **2009**, *48*, 194–203. [CrossRef]
60. Spies, T.A.; Duncan, S.L. *Old Growth in a New World: A Pacific Northwest Icon Reexamined*; Island Press: Washington, DC, USA, 2012.
61. Bauhus, J.; Puettmann, K.; Messier, C. Silviculture for old-growth attributes. *For. Ecol. Manag.* **2009**, *258*, 525–537. [CrossRef]
62. Hickey, J.; Su, W.; Rowe, P.; Brown, M.; Edwards, L. Fire history of the tall wet eucalypt forests of the Warra ecological research site, Tamania. *Aust. For.* **1999**, *62*, 66–71. [CrossRef]
63. Wood, S.W.; Murphy, B.P.; Bowman, D.M. Firescape ecology: How topography determines the contrasting distribution of fire and rainforest in the south-west of the Tasmanian Wilderness World Heritage Area. *J. Biogeogr.* **2011**, *38*, 1807–1820. [CrossRef]
64. Koch, A.; Chuter, A.; Munks, S.A. *A Review of Forestry Impacts on Biodiversity and the Effectiveness of "Off-Reserve" Management Actions in Areas Covered by the Tasmanian Forest Practices System*; Forest Practices Authority: Hobart, Tasmania, Australia, 2012.
65. Berg, Å.; Ehnström, B.; Gustafsson, L.; Hallingbäck, T.; Jonsell, M.; Weslien, J. Threatened plant, animal, and fungus species in Swedish forests: Distribution and habitat associations. *Conserv. Biol.* **1994**, *8*, 718–731. [CrossRef]
66. Bunnell, F.L.; Dunsworth, G.B. *Forestry and Biodiversity: Learning How to Sustain Biodiversity in Managed Forests*; UBC Press: Vancouver, BC, Canada, 2010.

67. Neyland, M.G.; Jarman, S.J. Early impacts of harvesting and burning disturbances on vegetation communities in the Warra silvicultural systems trial, Tasmania, Australia. *Aust. J. Bot.* **2012**, *59*, 701–712. [CrossRef]
68. Kowal, V.A.; Cartar, R.V. Edge effects of three anthropogenic disturbances on spider communities in Alberta's boreal forest. *J. Insect Conserv.* **2012**, *16*, 613–627. [CrossRef]
69. Harper, K.A.; Macdonald, S.E.; Mayerhofer, M.S.; Biswas, S.R.; Esseen, P.A.; Hylander, K.; Stewart, K.J.; Mallik, A.U.; Drapeau, P.; Jonsson, B.G. Edge influence on vegetation at natural and anthropogenic edges of boreal forests in Canada and Fennoscandia. *J. Ecol.* **2015**, *103*, 550–562. [CrossRef]
70. Lacasella, F.; Gratton, C.; de Felici, S.; Isaia, M.; Zapparoli, M.; Marta, S.; Sbordoni, V. Asymmetrical responses of forest and "beyond edge" arthropod communities across a forest–grassland ecotone. *Biodivers. Conserv.* **2015**, *24*, 447–465. [CrossRef]
71. Elbakidze, M.; Angelstam, P.; Andersson, K.; Nordberg, M.; Pautov, Y. How does forest certification contribute to boreal biodiversity conservation? Standards and outcomes in Sweden and NW Russia. *For. Ecol. Manag.* **2011**, *262*, 1983–1995. [CrossRef]
72. Baker, S.C.; Halpern, C.B.; Wardlaw, T.J.; Kern, C.; Edgar, G.J.; Thomson, R.J.; Bigley, R.E.; Franklin, J.F.; Gandhi, K.J.; Gustafsson, L.; et al. A cross-continental comparison of plant and beetle responses to retention of forest patches during timber harvest. *Ecol. Appl.* **2016**, *26*, 2493–2504. [CrossRef] [PubMed]
73. Mitchell, S.; Beese, W. The retention system: Reconciling variable retention with the principles of silvicultural systems. *For. Chron.* **2002**, *78*, 397–403. [CrossRef]
74. Franklin, J.F.; Berg, D.R.; Thornburgh, D.A.; Tappeiner, J.C. Alternative silvicultural approaches to timber harvesting: Variable retention harvest systems. In *Creating a Forestry for the 21st Century: The Science of Ecosystem Management*; Kohm, K.A., Franklin, J.F., Eds.; Island Press: Washington, DC, USA, 1997; pp. 111–139.
75. Lindenmayer, D.; Blanchard, W.; McBurney, L.; Blair, D.; Banks, S.; Driscoll, D.; Smith, A.; Gill, A.M. Fire severity and landscape context effects on arboreal marsupials. *Biol. Conserv.* **2013**, *167*, 137–148. [CrossRef]
76. Todd, C.R.; Lindenmayer, D.B.; Stamation, K.; Acevedo-Cattaneo, S.; Smith, S.; Lumsden, L.F. Assessing reserve effectiveness: Application to a threatened species in a dynamic fire prone forest landscape. *Ecol. Model.* **2016**, *338*, 90–100. [CrossRef]
77. Andren, H. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: A review. *Oikos* **1994**, *71*, 355–366. [CrossRef]
78. Angelstam, P.; Dönz-Breuss, M.; Roberge, J.-M. Targets and tools for the maintenance of forest biodiversity: An introduction. *Ecol. Bull.* **2004**, *51*, 11–24.
79. Leonard, S.W.; Bennett, A.F.; Clarke, M.F. Determinants of the occurrence of unburnt forest patches: Potential biotic refuges within a large, intense wildfire in south-eastern Australia. *For. Ecol. Manag.* **2014**, *314*, 85–93. [CrossRef]
80. Mok, H.F.; Arndt, S.K.; Nitschke, C.R. Modelling the potential impact of climate variability and change on species regeneration potential in the temperate forests of south-eastern Australia. *Glob. Chang. Biol.* **2012**, *18*, 1053–1072. [CrossRef]
81. Kouki, J.; Hyvärinen, E.; Lappalainen, H.; Martikainen, P.; Similä, M. Landscape context affects the success of habitat restoration: Large-scale colonization patterns of saproxylic and fire-associated species in boreal forests. *Divers. Distrib.* **2012**, *18*, 348–355. [CrossRef]
82. Tilman, D.; May, R.M.; Lehman, C.L.; Nowak, M.A. Habitat destruction and the extinction debt. *Nature* **1994**, *371*, 65–66. [CrossRef]
83. Commonwealth of Australia. *Tasmanian Regional Forest Agreement between the Commonwealth of Australia and the State of Tasmania*; Department of Agriculture, Fisheries and Forestry: Canberra, Australia, 1997.
84. Commonwealth of Australia. *The Central Highlands Regional Forest Agreement between the Commonwealth of Australia and the State of Victoria*; Department of Agriculture, Fisheries and Forestry: Canberra, Australia, 1998.
85. Slade, C.; Law, B. The other half of the coastal State Forest estate in New South Wales; the value of informal forest reserves for conservation. *Aust. Zool.* **2016**. [CrossRef]
86. Patry, C.; Kneeshaw, D.; Wyatt, S.; Grenon, F.; Messier, C. Forest ecosystem management in North America: From theory to practice. *For. Chron.* **2013**, *89*, 525–537. [CrossRef]

87. Fox-Hughes, P.; Harris, R.; Lee, G.; Grose, M.; Bindoff, N. Future fire danger climatology for Tasmania, Australia, using a dynamically downscaled regional climate model. *Int. J. Wildland Fire* **2014**, *23*, 309–321. [CrossRef]
88. Orr, S.; Gerrand, A. Management Decision Classification: A system for zoning land managed by Forestry Tasmania. *Tasforests* **1998**, *10*, 1–14.
89. Department Natural Resources and Environment (DNRE). *Forest Management Plan for the Central Highlands*; DNRE: Melbourne, Victoria, Australia, 1998.