Bird assemblages in Tasmanian clearcuts are influenced by the age of eucalypt regeneration but not by distance from mature forest

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\textbf{Abstract}
Many species of birds are adversely affected by clearcutting of Australian eucalypt forests for timber. However, recolonisation of harvested areas may be enhanced if mature forest is retained nearby (forest influence).

We test the benefits of proximity to mature Tasmanian wet eucalypt forest on birds in adjacent regenerating clearcuts. We hypothesised that bird assemblages in silvicultural regeneration would become more similar to those in adjacent mature forest with increasing proximity to the mature forest. To test this, we sampled birds in regenerating clearcuts using 25 m radius point counts centred 35, 120, and 200 m from mature forest. We also hypothesised that the magnitude of forest influence would decrease with time since harvest, across three age classes of approximately 7, 27 and 45 years-old, because the assemblages in older regeneration would be more similar to those in the mature forest.

We found that distance from mature forest had no significant effects on bird assemblage composition, native species richness per sample, or the incidences of any species. This result was apparent across all three age classes of silvicultural regeneration, despite significant changes in the assemblage composition, native species richness, and incidence of 10 species, with time since harvest.

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1. Introduction

Modern harvesting of tall wet forests for timber has generally involved clearcutting, often resulting in the replacement of mature forest with even-aged regrowth forests (Baker and Read, 2011; Bauhus et al., 2009). This silvicultural system is an efficient and safe way of harvesting and regenerating fire-dependent forests (Neyland et al., 2012), but can be detrimental to some biota (Fedrowitz et al., in press; Lindenmayer et al., 2012; Mitchell and Beese, 2002). Of course, reserves outside production forests can provide habitat for species that are more plentiful in mature forests than in regrowth forests. However, it is widely considered that such reserves are often insufficient to support viable populations at landscape scales, and that ecological sustainability of forests also requires management for biodiversity within harvested landscapes (Baker

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An example of a group that is more plentiful in mature forests than in regrowth forests is birds inhabiting Australian eucalypt forests. There are few early successional species of birds in eucalypt forests, and most species gradually recolonise regrowth forest as it matures (Atkinson, 2003; Hingston, 2000; Hingston and Grove, 2010; Loyn, 1985; Serong and Lill, 2012; Williams et al., 2001). In Tasmanian wet eucalypt forest, the composition of bird assemblages in even-aged regrowth converged towards that in old-growth forest as the regrowth matured from 6–8 to 75–111 years of age. This was mirrored by a linear increase in the mean number of native species of birds detected per survey with increasing stand age (Hingston and Grove, 2010).

In addition to the age of the forest stand in which birds are surveyed, the surrounding vegetation can also influence assemblages of birds (Bettis et al., 2007; Drolet et al., 1999; Hansson, 1983; Schlossberg and King, 2008; Thompson et al., 2012; Tubelis et al., 2004; Wardell-Johnson and Williams, 2000; Zurita et al., 2012). In Tasmanian wet eucalypt forest, assemblages of birds in 30–50-year-old silvicultural regeneration were more similar to those in mature forest when more mature forest was present in the surrounding landscape, and when mature forest was closer to the sample point (Wardlaw et al., 2012).

Because assemblages of birds in regrowth Tasmanian wet eucalypt forest become more similar to those in mature forest with both increasing age of the regrowth (Hingston and Grove, 2010) and decreasing distance from mature forest (Wardlaw et al., 2012), we hypothesise that these two factors may interact to influence birds in silvicultural regeneration. Specifically, we hypothesise that the effect of distance from mature forest on birds in regenerating stands will decrease as the stands mature because the assemblages in older stands will be more similar to those in the mature forest. In other words, we hypothesise that the positive influence of proximity to mature forest on assemblages of birds in silvicultural regeneration will be greater for the earlier stages of succession following clearcutting.

To test this hypothesis, we compare assemblages of birds in silvicultural regeneration in three age classes since clearcutting and at three distances from mature forest. We expect that:

1. birds will recolonise silvicultural regeneration in the first 50 years after harvesting such that species richness per sample will increase, and assemblage compositions will become more like those of mature forest, with increasing time since harvest;
2. for birds in silvicultural regeneration, species richness per sample will increase and assemblage compositions will become more similar to those in adjacent mature forest with increasing proximity to mature forest at the edge of the clearcut; and
3. for birds in silvicultural regeneration, the effect of proximity to mature forest on species richness per sample and assemblage composition will become less pronounced as regeneration matures.

2. Methods

2.1. Study sites

The study was carried out in lowland wet eucalypt forest, dominated by Eucalyptus obliqua L’Herit, approximately 60 km west-southwest of Hobart in southern Tasmania, Australia (Fig. 1). We selected 15 study sites at the boundaries between mature forests, which had never been subjected to clearcut harvesting, and silvicultural regeneration following a single clearcutting event. These were divided equally among sites where clearcutting occurred at an average of 45 years (harvested 1966–1970), 27 years (harvested 1983–1989), and 7 years (harvested 2002–2007) previously (Fig. 1). Average heights of the regrowth E. obliqua at these ages were 27 m, 22 m, and 7 m, respectively, while average height of the mature forest was 34 m.

At each site we established three transects, separated by at least 60 m, which ran perpendicular to the focal boundary between mature forest and silvicultural regeneration (Fig. 2). Along each transect, we surveyed at four points: one in the mature forest 35 m from the edge (−35 m), and others in the silvicultural regeneration at 35, 120, and 200 m from the edge (Fig. 2). These distances from the edge into regeneration represent distances from the closest mature forest, the maximum being limited to 200 m by the size of clearcuts.

2.2. Survey procedures

All study sites were surveyed for birds between sunrise and sunset on 10 occasions. This entailed one morning and one afternoon survey at each site in five seasonal periods: 24 Sept. 2011–11 Nov. 2011; 17 Nov. 2011–25 Dec. 2011; 27 Dec. 2011–29 Jan. 2012; 29 Jan. 2012–28 Mar. 2012; and 28 Mar. 2012–10 May 2012. Each survey round was completed before any sites were revisited, and the order in which sites were surveyed varied among rounds. At least two days elapsed between repeat surveys of any site. Days of strong winds (> Beaufort scale 4), heavy rain, and hot weather were avoided.

Each survey consisted of the observer (ABH) walking along each transect, and stopping to do a 5-min point-survey at each of the four points. The direction the three transects were walked was varied within each survey to avoid confounding
distance along transects with time of day. At each point, the species of birds seen or heard within a 25 m radius were recorded. If a bird was flushed from within 25 m of the point by the approaching observer, it was included in the data and the 5-min survey commenced immediately. Apart from raptors or aerial feeders, any birds flying more than 20 m above the vegetation were excluded from the analysis. Species nomenclature follows that of Christidis and Boles (2008).

2.3. Data analysis

To assess the effects of time since harvest (Time) and distance from mature forest (Distance), and their interaction, on bird assemblages we examined the species richness and assemblage composition of birds detected per sample. A sample comprised the pooled data from the three transects at a particular Distance during a single visit. Thus, there were 600 samples comprising 60 sample locations (15 study sites × 4 Distances) and 10 survey rounds. The one introduced species recorded (superb lyrebird (*Menura novaehollandiae*)) was excluded from analyses of species richness because we were interested in the conservation values of the various sample locations. However, superb lyrebird was included in analyses of multi-species assemblage composition.

The effects of Time and Distance, and their interaction, on bird assemblage composition in silvicultural regeneration were examined using multivariate analyses. This entailed constructing a Bray–Curtis similarity matrix for the 45 sample locations in silvicultural regeneration, based on data for the numbers of surveys (out of 10) in which each species was
recorded at each location. From this, the significance of differences among the three Times and the three Distances, and their interactions, were tested using PERMANOVA (permutational multivariate ANOVA; Anderson, 2001). PERMANOVA avoids assumptions of traditional MANOVA regarding the distributions of variables. These analyses were done in the program PRIMER V6 PERMANOVA + (Anderson et al., 2008; Clarke and Gorley, 2006).

The effects of Time and Distance, and their interaction, on native bird species richness per sample at the 45 locations in silvicultural regeneration were tested using two-way factorial analysis of variance (ANOVA) on untransformed data following checks of normality and homogeneous variance in R (R Core Team, 2014). A post-hoc test entailed the use of a Bonferroni adjustment.

The effects of Time and Distance, and their interaction, on the numbers of surveys (out of 10) in which each species was recorded at each of the 45 locations (incidence of individual species) were also tested using Poisson regression following a two-way factorial model using the GLM and anova.glm commands in R (R Core Team, 2014). Models were able to be constructed for the 20 most abundant species, and post-hoc tests entailed the use of Bonferroni adjustments.

The results of the preceding analyses prompted further investigation of the effects of Time. This entailed comparisons of the bird assemblages in the three ages of silvicultural regeneration with those in adjacent mature forest. Because of lack of independence of mature forest from adjacent silvicultural regeneration, we could not include all four age classes in a one-way PERMANOVA design. Consequently, for each of the three Times since harvest, we tested for contrasts between silvicultural regeneration and adjacent mature forest. Compositions of bird assemblages were compared between silvicultural regeneration (at 120 m from the edge) and mature forest (−35 m) using one-way PERMANOVAs based on Bray–Curtis similarity matrices derived from the numbers of surveys (out of 10) in which each species was recorded at each location. This was done separately for each of the three Times since harvest, with site included as a random factor in these models. To illustrate the variation among these bird assemblages, we constructed a canonical analysis of principal coordinates (CAP) ordination (Anderson and Willis, 2003) constrained by forest age (four age classes). This was based on the Bray–Curtis similarity matrix for the bird assemblages in silvicultural regeneration (at 120 m from the edge) and mature forest (−35 m) at each of the 15 study sites. CAP was conducted in PRIMER V6 PERMANOVA + software (Anderson et al., 2008; Clarke and Gorley, 2006).

3. Results

We found evidence supporting hypothesis 1, but not hypotheses 2 and 3. The composition of bird assemblages and the native species richness in silvicultural regeneration were significantly affected by Time since harvest (composition, Pseudo-$F_{2,36} = 2.97, P = 0.0002$; richness, $F_{2,36} = 4.55, P = 0.017$), but not by Distance from edge (composition, Pseudo-$F_{2,36} = 0.64, P = 0.89$; richness, $F_{2,36} = 0.29, P = 0.75$) or the interaction between Time and Distance (composition, Pseudo-$F_{4,36} = 0.52, P = 0.99$; richness, $F_{4,36} = 0.30, P = 0.88$).

Pairwise differences in bird assemblages were apparent between all Times since harvest. Intermediate-aged (c. 27-year-old) and the oldest (c. 45-year-old) regeneration differed significantly in both assemblage composition (t = 1.57, P = 0.0096) and species richness per sample (Fig. 3). However, the youngest regeneration (c. 7-year-old) differed from other age classes in assemblage composition (c. 45-year-old; $t = 1.94, P = 0.0001$; c. 27-year-old; $t = 1.59, P = 0.010$), but not in species richness per sample (Fig. 3).

Analyses of individual species also supported hypothesis 1, but not hypotheses 2 and 3. Of the 20 species which were encountered frequently enough to be modelled, the incidences of 10 were significantly affected by Time since harvest (Table 1, Fig. 4). However, no incidences of individual species were significantly affected by Distance, or the interaction between Time and Distance (Table 1).

Individual species responded to Time in a variety of ways (Fig. 4). The incidences of grey fantail (Fig. 4(a)) and crescent honeyeater (Fig. 4(b)) showed the same pattern with Time as that shown by native species richness, in that they were observed most often in intermediate-aged silvicultural regeneration (c. 27-years-old) and least in the oldest regeneration (c. 45-years-old). Intermediate-aged regeneration also had the highest incidences of green rosetta (Fig. 4(c)) and striated pardalote (Fig. 4(d)), although for these two species the lowest incidences were in the youngest regeneration (c. 7-years-old). The oldest regeneration also had the lowest incidences of silvereye (Fig. 4(e)), olive whistler (Fig. 4(f)) and superb

![Fig. 3. Mean (± s.e.) numbers of native bird species observed per sample in silvicultural regeneration, aged approximately 7, 27, and 45 years. Significant differences at $\alpha = 0.05$ are denoted by different letters.](image-url)
fairy-wren (Fig. 4(g)). However, these three species showed slightly different responses to Time, in that silvereye was observed significantly less in the oldest regeneration than either of the other age-classes (Fig. 4(e)), while olive whistler and superb fairy-wren were observed less frequently as regeneration aged across the range of ages that we sampled (Fig. 4(f), (g)).

Yet another response to Time was exhibited by superb lyrebird (Fig. 4(h)) and golden whistler (Fig. 4(i)), both of which were observed significantly less in the oldest regeneration than either of the other age-classes (Fig. 4(e)), while olive whistler and fairy-wren showed slightly different responses to Time, in that silvereye was inversely related to native species richness, being highest in the oldest regeneration and lowest in intermediate-aged regeneration (Fig. 4(j)).

Although the composition of bird assemblages, native species richness, and the incidences of 10 species in silvicultural regeneration were significantly affected by Time, the effect of Time only partially supported our first hypothesis of assemblages progressively becoming more like those of mature forest with increasing Time since harvest. In accordance with this hypothesis, the composition of bird assemblages in adjacent mature forest was significantly different from that in the youngest silvicultural regeneration (c. 7-years-old) (Pseudo-F1,4 = 1.92. P = 0.044), but not from that in intermediate-aged regeneration (c. 27-years-old) (Pseudo-F1,4 = 1.00, P = 0.45) (Fig. 5). However, contrary to this hypothesis, the contrast in bird assemblages between silvicultural regeneration and adjacent mature forest was least pronounced for intermediate-aged regeneration rather than the oldest regeneration. Indeed, the differences in assemblages between the oldest regeneration (c. 45-years-old) and adjacent mature forest approached significance (Pseudo-F1,4 = 1.79, P = 0.075) (Fig. 5).

4. Discussion

We found that assemblages of birds in silvicultural regeneration were influenced by the Time since clearcutting, but not by the Distance from mature forest immediately adjacent to the clearcut. This absence of an effect of proximity to nearby mature forest was consistent across all ages of silvicultural regeneration that we investigated, and all species of birds that we encountered.

4.1. Changes in bird assemblages as silvicultural regeneration matures

Our expectation that birds would recolonise silvicultural regeneration in the first 50 years after harvesting, such that assemblages would progressively become more like those of mature forest with increasing Time since harvest, was partially supported. As expected, assemblage composition in the youngest regeneration (c. 7-years-old) showed the greatest difference from that in adjacent mature forest, consistent with previous studies in wet eucalypt forests in Tasmania (Hingston, 2000; Hingston and Grove, 2010) and Western Australia (Atkinson, 2003; Williams et al., 2001). This was at least partly driven by the youngest regeneration having the highest incidence of superb fairy-wren, a species that favours young regrowth in our study area while being scarce in mature forests (Hingston, 2000; Hingston and Grove, 2010; Lefort

Table 1

<table>
<thead>
<tr>
<th>Species</th>
<th>Time</th>
<th>Distance</th>
<th>Time × Distance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Canopy birds</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Black currawong Strepera fuliginosa</td>
<td>X2 = 4.51, P = 0.10</td>
<td>X2 = 0.15, P = 0.93</td>
<td>X2 = 7.28, P = 0.12</td>
</tr>
<tr>
<td>Black-headed honeyeater Melithreptus affinis</td>
<td>X2 = 6.89, P = 0.032*</td>
<td>X2 = 2.00, P = 0.37</td>
<td>X2 = 3.77, P = 0.44</td>
</tr>
<tr>
<td>Grey-shrike-thrush Colluricinclia harmonica</td>
<td>X2 = 4.19, P = 0.12</td>
<td>X2 = 1.01, P = 0.60</td>
<td>X2 = 2.63, P = 0.62</td>
</tr>
<tr>
<td>Silvereye Zosterops lateralis</td>
<td>X2 = 10.53, P = 0.0052**</td>
<td>X2 = 3.85, P = 0.15</td>
<td>X2 = 2.82, P = 0.59</td>
</tr>
<tr>
<td>Spotted pardalote Pardalotus punctatus</td>
<td>X2 = 4.50, P = 0.11</td>
<td>X2 = 0.68, P = 0.71</td>
<td>X2 = 4.19, P = 0.38</td>
</tr>
<tr>
<td>Striated pardalote Pardalotus striatus</td>
<td>X2 = 6.99, P = 0.030*</td>
<td>X2 = 1.99, P = 0.37</td>
<td>X2 = 2.27, P = 0.69</td>
</tr>
<tr>
<td>Strong-billed honeyeater Melithreptus validirostris</td>
<td>X2 = 5.34, P = 0.069</td>
<td>X2 = 2.53, P = 0.28</td>
<td>X2 = 5.80, P = 0.21</td>
</tr>
<tr>
<td>Mid-layer birds</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Crescent honeyeater Phylidonyris pyrrhopterus</td>
<td>X2 = 9.70, P = 0.0078**</td>
<td>X2 = 4.60, P = 0.10</td>
<td>X2 = 4.81, P = 0.31</td>
</tr>
<tr>
<td>Golden whistler Pachycephala pectoralis</td>
<td>X2 = 9.73, P = 0.0077**</td>
<td>X2 = 4.32, P = 0.12</td>
<td>X2 = 2.27, P = 0.69</td>
</tr>
<tr>
<td>Green rosella Platycercus caledonicus</td>
<td>X2 = 6.24, P = 0.044*</td>
<td>X2 = 3.06, P = 0.22</td>
<td>X2 = 4.19, P = 0.38</td>
</tr>
<tr>
<td>Grey fantail Rhipidura abiscapa</td>
<td>X2 = 7.31, P = 0.026*</td>
<td>X2 = 2.92, P = 0.23</td>
<td>X2 = 2.90, P = 0.58</td>
</tr>
<tr>
<td>Yellow-throated honeyeater Lichenostomus flavicolis</td>
<td>X2 = 5.55, P = 0.062</td>
<td>X2 = 1.05, P = 0.59</td>
<td>X2 = 4.87, P = 0.30</td>
</tr>
<tr>
<td>Lower-layer birds</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bassian thrush Zoothera lunulata</td>
<td>X2 = 1.86, P = 0.29</td>
<td>X2 = 0.00, P = 1.00</td>
<td>X2 = 3.68, P = 0.45</td>
</tr>
<tr>
<td>Olive whistler Pachycephala olivacea</td>
<td>X2 = 5.93, P = 0.052*</td>
<td>X2 = 1.46, P = 0.48</td>
<td>X2 = 5.27, P = 0.26</td>
</tr>
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<td>Pink robin Petroica rodinogaster</td>
<td>X2 = 0.84, P = 0.66</td>
<td>X2 = 0.054, P = 0.97</td>
<td>X2 = 1.74, P = 0.78</td>
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<tr>
<td>Scrubtit Acanthornis magna</td>
<td>X2 = 3.75, P = 0.15</td>
<td>X2 = 0.49, P = 0.78</td>
<td>X2 = 1.33, P = 0.86</td>
</tr>
<tr>
<td>Superb fairy-wren Malurus cyaneus</td>
<td>X2 = 40.24, P &lt; 0.0001***</td>
<td>X2 = 0.72, P = 0.70</td>
<td>X2 = 1.75, P = 0.78</td>
</tr>
<tr>
<td>Superb lyrebird Menura novaehollandiae</td>
<td>X2 = 10.58, P = 0.0051**</td>
<td>X2 = 2.66, P = 0.26</td>
<td>X2 = 2.78, P = 0.60</td>
</tr>
<tr>
<td>Tasmanian scrubwren Sericornis humilis</td>
<td>X2 = 3.43, P = 0.18</td>
<td>X2 = 0.10, P = 0.95</td>
<td>X2 = 4.47, P = 0.35</td>
</tr>
<tr>
<td>Tasmanian thornbill Acathiza ewingi</td>
<td>X2 = 1.47, P = 0.48</td>
<td>X2 = 0.089, P = 0.96</td>
<td>X2 = 3.26, P = 0.52</td>
</tr>
</tbody>
</table>

*** P < 0.001, ** P < 0.01, * P < 0.05 or where significant pairwise differences were detected between treatments.
Fig. 4. Mean (± s.e.) incidence of individual bird species with significant differences among stands of different-aged silvicultural regeneration. Significant differences at α = 0.05 are denoted by different letters.
Fig. 5. CAP ordination, constrained by forest age, of samples based on assemblage composition of birds in three ages of silvicultural regeneration and adjacent stands of mature forest. Locations in silvicultural regeneration are open symbols while those in mature forest are presented as solid shapes corresponding to the age of the adjacent regeneration.

and Grove, 2009). However, of the three ages of regeneration that we sampled, the youngest also had the highest incidence of olive whistler which favours mature forest over silvicultural regeneration in these forests (Lefort and Grove, 2009). The strong contrast between assemblage composition in the youngest silvicultural regeneration and adjacent mature forest can also be attributed to the former having the lowest incidences of green roSELLa, striated pardalote, superb lyrebird and golden whistler, all of which are usually more abundant in mature forests than in regrowth in our study area (Hingston, 2000; Hingston and Grove, 2010; Lefort and Grove, 2009; but see superb lyrebird in Hingston and Grove, 2010). Indeed, we did not detect striated pardalote or golden whistler in the youngest regeneration, in accordance with Hingston and Grove (2010). However, small numbers of these two species were observed in silvicultural regeneration aged less than eight years in another study in these forests (Lefort and Grove, 2009).

In contrast to our first hypothesis, however, species richness per sample was highest in intermediate-aged (c. 27-years-old) rather than in older (c. 45-years-old) regeneration. This decline as regeneration aged is inconsistent with the previously observed linear increase in the numbers of native species as these forests mature from young silvicultural regeneration to old-growth (Hingston and Grove, 2010). This discrepancy can be attributed to the fact that the previous study did not sample regrowth aged between eight and 42 years, and was strongly influenced by the greater numbers of birds in forests more than 45-years-old (Hingston and Grove, 2010).

The relatively high species richness per sample in intermediate-aged regeneration (c. 27-years-old) appeared to be largely driven by the presence of species typically associated with mature forest, because the assemblage composition in intermediate-aged regeneration did not differ significantly from that in adjacent mature forest. Indeed, of the nine species with significantly higher incidences in intermediate-aged regeneration than in one of the other age classes, eight (grey fantail, crescent honeyeater, green roSELLa, striated pardalote, silvereye, olive whistler, superb lyrebird, golden whistler) are more common in mature forests than in silvicultural regeneration in our study area (Hingston, 2000; Lefort and Grove, 2009). However, the higher species richness in intermediate-aged, than in older, regeneration can also be attributed to the additional presence of superb fairy-wren that favours younger regrowth (Hingston, 2000; Hingston and Grove, 2010; Lefort and Grove, 2009; this study).

The decline in species richness per sample as regeneration aged from c. 27- to c. 45-years-old was driven, at least partly, by significant concurrent declines in the incidences of species associated with both younger regeneration (superb fairy-wren: Hingston, 2000; Hingston and Grove, 2010; Lefort and Grove, 2009; this study) and mature forest (grey fantail, crescent honeyeater and silvereye: Hingston, 2000; Lefort and Grove, 2009; but see Hingston and Grove, 2010). A previous study in these forests also found superb fairy-wren was absent, and crescent honeyeater was relatively scarce, in 42–43-year-old regrowth (Hingston and Grove, 2010). As a result of the declining incidences of some species typically associated with mature forests, the difference in assemblage composition between silvicultural regeneration and adjacent mature forest was greater for older than for intermediate-aged regeneration. This overall change as regeneration aged from c. 27 to c. 45 years occurred despite a significant increase in the incidence of black-headed honeyeater, another species that favours mature forest over silvicultural regeneration in our study area (Hingston, 2000; Hingston and Grove, 2010; Lefort and Grove, 2009).

Together with the findings of Hingston and Grove (2010), our study suggests that the composition of bird assemblages changes as Tasmanian wet eucalypt forests mature such that species richness per sample peaks at c. 27 years, then declines to a trough at c. 45 years, before peaking again in mature forest. Similar non-linear changes in abundance or species richness of birds associated with forest succession have been found in some studies in temperate forests elsewhere. In dry eucalypt forest in Victoria, Australia (Loyn, 1980), and boreal forest in Alberta, Canada (Schiek et al., 1995), abundance and species richness also peaked in 20–30-year-old regrowth, declined in 40–100-year-old regrowth and peaked again in mature forest. In north-eastern USA, however, the first peak in abundance or species richness occurred only 3–12 years after clearcutting and the subsequent trough occurred after only 25–30 years (Conner and Adkisson, 1975; Keller et al., 2003; Titterington et al.,
This broad shared pattern of more birds in young regrowth than in older regrowth has been attributed to structural changes in the vegetation. In all of these previous studies, the early peak in abundance was associated with dense regrowth near ground-level and the subsequent decline occurred when the understorey became sparser following canopy closure (Conner and Adkisson, 1975; Keller et al., 2003; Loyn, 1980; Schieck et al., 1995; Titterington et al., 1979). Wet eucalypt forest shows similar vegetation structural changes (Ashton, 1975), and this was apparent in our study sites (ABH pers. obs., see also Hingston and Grove, 2010). Consistent with this successional change in vegetation structure, Keller et al. (2003) observed lower- and mid-layer guilds decline in abundance after canopy closure, while Hingston and Grove (2010) found these guilds were relatively scarce in older regrowth. Accordingly, species in our study with significantly lower incidences in c. 45-year-old, than in c. 27-year-old, regeneration comprised one lower-layer species (superb fairy-wren), two mid-layer species (grey fantail and crescent honeyeater) and one canopy species (silveryeye), while another canopy species (black-headed honeyeater) exhibited the opposite pattern of incidences (guild allocations based on Hingston and Grove, 2010).

4.2. Mature forest influence on birds in silvicultural regeneration

Contrary to our expectations, we found no evidence for bird assemblages in silvicultural regeneration becoming more similar to those in adjacent mature forest with increasing proximity to the edge of the clearcut. There were no significant differences in bird assemblage composition, native species richness per sample, or the incidences of any individual species among sample locations at 35, 120 and 200 m from mature forest. Similar lack of change with distance up to 80–120 m into regrowth was found for birds in some studies from Western Australia (Atkinson, 2003; Norwood et al., 1996) and the Northern Hemisphere (DeGraaf, 1992; Hansson, 1983). However, other studies did observe relationships with distance within the range studied here. Despite consistent total bird abundance in Swedish regrowth to at least 200 m from mature forest, assemblage composition changed greatly at around 100 m from the forest edge due to species replacement (Hansson, 1983). Similarly, a meta-analysis of 17 bird species that favour early successional woody vegetation in the eastern USA found these species were less abundant within 30 m of mature forest than at over 60 m from mature forest (Schlossberg and King, 2008). Such a change in assemblage composition was not observed in our study, perhaps because of the paucity of species with strong preferences for young regrowth in these forests (Hingston, 2000; Hingston and Grove, 2010; Lefort and Grove, 2009).

It is possible that mature forest has no influence on birds in nearby regrowth in our study area. However, we argue that mature forest is likely to be affecting bird assemblages and species richness, but that it does so equally across the range of distances we sampled. In support of this, Wardlaw et al. (2012) found clear evidence that the amount of mature forest in the 500 m–2 km radius landscapes in the same forests as our study affects bird assemblages in silvicultural regeneration.

Assuming that mature Tasmanian wet eucalypt forest does influence birds in silvicultural regeneration, our findings suggest that it extends at least 200 m into regrowth. This is much further than the pragmatic threshold for forest influence of one tree height from a forest edge that is sometimes used by forest managers (Baker and Read, 2011; Baker et al., 2013a; Keenan and Kimmins, 1993; Mitchell and Beese, 2002), but is not unexpected for taxa with good dispersal abilities such as birds (Baker et al., 2013a). Consistent with this, the decline in the number of bird species per search effort in young Western Australian silvicultural regeneration after clearcutting was greater at 100–300 m from the wet eucalypt forest edge than within 100 m of the edge (Wardell-Johnson and Williams, 2000). However, the possibility should be considered that greater forest influence occurred over a very short distance from edge that could not be detected with the 25 m radius plots used in our study.

The uniform forest influence on birds in silvicultural regeneration within 200 m of mature forest was consistent across all species that we encountered. This is at odds with the observation by Wardlaw et al. (2012) of a rapid decline in species richness per sample of dense forest birds in regeneration as distance from mature forest increased up to 400 m in these forests. This anomaly cannot be attributed to rapid declines in species richness at 200–400 m from mature forest, because the data of Wardlaw et al. (2012) show a continuous decline at 0–400 m from mature forest. It may be that their observations were driven by the confounding effect of less mature forest in the landscape surrounding sites that were more distant from mature forest (Wardlaw et al., 2012), as assemblages of forest birds are often influenced by the composition of the vegetation in areas surrounding sample sites (Bett et al., 2007; Drolet et al., 1999; Hansson, 1983; Schlossberg and King, 2008; Thompson et al., 2012; Tubelis et al., 2004; Wardell-Johnson and Williams, 2000; Zurita et al., 2012).

Contrary to our main hypothesis, the effect of proximity to mature forest on bird assemblages in silvicultural regeneration did not become less pronounced as regeneration matured. This occurred despite differences in assemblage composition, native species richness, and incidences of 10 species among the three ages of regeneration: a result comparable to those of Atkinson (2003) in two regrowth ages in Western Australia and DeGraaf (1992) in three forest ages in eastern USA. Like us, these authors found non-significant variation among distances from edge in regrowth forest. In contrast, bird species richness declined more rapidly with increasing distance from native eucalypt forest in adjacent 4–15-year-old exotic pine plantations than in those 20–30 years of age (Tubelis et al., 2004), and from native South American forest into recent clearcuts and agricultural areas than into plantations (Zurita et al., 2012). Collectively, these studies suggest that mature forest influence may extend further into young native silvicultural regeneration forest than into young exotic tree plantations and agricultural areas. We postulate that this relates to the greater habitat suitability of regenerating native forests than in more highly modified landscapes where the replacing vegetation has a strong contrast with the original forest.
4.3. Implications for sustainable forest harvesting

Our findings highlight the benefits to birds of maintaining a range of stand ages in harvested Tasmanian wet eucalypt forests, with the three age classes supporting different assemblages of birds. Intermediate-aged stands (c. 27-years-old) provided habitat for a range of species typically associated with mature forest, as well as one early successional species, thereby supporting the greatest species richness per survey in regeneration and higher incidences of nine species than in one of the other ages of regeneration. However, the youngest stands (c. 7-years-old) supported a higher incidence of superb fairy-wren than did either of the other ages of silvicultural regeneration, while the oldest stands (c. 45-years-old) supported a higher incidence of black-headed honeyeater than did intermediate-aged regeneration.

Previous research in our study area indicates that the spatial integration of harvesting and mature forest retention is generally advantageous to birds (Wardlaw et al., 2012). Such approaches include variable retention forestry (Baker and Read, 2011; Baker et al., 2013a; Fedrowitz et al., in press; Lefort and Grove, 2009) and long-term retention of mature forest within the production matrix but outside of harvest unit boundaries, such as riparian buffers and wildlife habitat strips (MacDonald et al., 2005; Machtans et al., 1996). One of the major factors influencing decisions surrounding the size of retained patches of mature forest in aggregated retention forestry is that, for a given total area of retention, smaller patches will have more of the surrounding harvested area within a short distance (Baker et al., 2013a). However, our data suggest that increasing the proximity of silvicultural regeneration to mature forest within the local scale of individual variation in retention harvest units need not be a priority for management of birds in Tasmanian wet eucalypt forests, although the amount of mature forest present is important at the broader landscape scale (Wardlaw et al., 2012).

Of course, other taxa and ecosystems may require different management. For example, spatial integration of harvesting and retention of mature forest is detrimental to certain early-successional bird species in other ecosystems because they avoid areas near retained mature forest (Hansson, 1983; Schlossberg and King, 2008). In contrast, maintaining mature forest in close proximity is potentially beneficial for other taxa with poor dispersal abilities that recolonise harvested areas from retained mature forest (Baker et al., 2013b; Jones et al., 2008; Tabor et al., 2007).

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Appendix A. Supplementary data

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References


