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Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco



From clearfell coupe to old-growth forest: Succession of bird assemblages in Tasmanian lowland wet eucalypt forests

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ARTICLE INFO

Article history:
Received 4 August 2009
Received in revised form 30 October 2009
Accepted 2 November 2009

Keywords:
Bird communities
Clearcutting
Forest management
Silviculture
Stand-age
Wildfire

ABSTRACT

As forests undergo succession after major disturbance events their assemblages of birds also change. Thus the frequency and extent of wildfire or clearfelling in the landscape can potentially affect the species-richness and abundance of forest birds. We used a chronosequence approach to investigate succession of bird communities in Tasmanian lowland wet eucalypt forest, from shortly after disturbance through to old-growth forest aged approximately 200-250 years. The number of native bird species recorded per survey per site increased as a linear function of stand-age. However, succession did not involve a unidirectional transition in assemblage-composition because of differences in successional responses among individual species and also among guilds of birds that mostly inhabited different strata of the forest. This was exemplified by the crescent honeyeater, which was observed most frequently in the youngest (6-8 years) and oldest (200-250 years) forests that we surveyed, and by the superb lyrebird (introduced to Tasmania from mainland south-eastern Australia) which favoured mid-aged regrowth (42-43 years) after clearfelling. Forests aged 200-250 years had the greatest richness-per-survey of those native species that were observed mostly in the lower layer or mid-layer. However, the greatest richness-per-survey of canopy-dwelling species and the highest native species-richness across the survey period were found in forests aged around 150 years. Younger regrowth was generally less rich in birds, although regrowth in the first decade after clearfelling was the only seral stage inhabited by superb fairy-wrens. These results suggest that, in the Tasmanian lowland wet eucalypt forest landscape, species-richness of birds may be greatest when old-growth forest is interspersed with young regrowth forests. Hence for bird conservation, a challenge is to ensure that old-growth forest continues to prevail in the production forest landscape.

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1. Introduction

As forests undergo successional changes following disturbance, their bird assemblages also change as species that inhabit newly disturbed sites are progressively replaced by those favouring older forests (Loyn, 1980, 1985a; Helle, 1985; Imbeau et al., 1999; Williams et al., 2001; Keller et al., 2003; Knutson et al., 2005; Venier and Pearce, 2005; Schieck and Song, 2006; Summers, 2007; Haney et al., 2008). Thus, by altering the relative proportions of the forest landscape at various seral stages, the frequency and extent of wildfire or logging can influence the composition of forest bird assemblages. In most situations, species-richness and abundance increase as forests age after wildfire or clearfelling (Helle, 1985; Loyn, 1985a; Hobson and Bayne, 2000; Williams et al., 2001; Knutson et al., 2005; Venier and Pearce, 2005; Schieck and Song,

2006; Summers, 2007; Moning and Müller, 2009). However, this increase is sometimes preceded, or followed, by a decline (Loyn, 1980; Helle, 1985; Keller et al., 2003), and species-richness and abundance are occasionally greatest during the first decade after disturbance (Imbeau et al., 1999; Keller et al., 2003). Changes in species-richness and abundance during succession can also vary among birds that inhabit different strata of a forest (Loyn, 1980, 1985a; Helle, 1985; Hobson and Bayne, 2000; Keller et al., 2003; Venier and Pearce, 2005; Nikolov, 2009).

In Tasmania, vegetation succession in areas suited to lowland wet eucalypt forests can continue for several centuries after a major disturbance event. The eucalypt trees that dominate the canopy during early succession have a maximum life-span of some 400 years (Alcorn et al., 2001) and are dependent on fire within this period for regeneration. Wildfire can result in forests of one or more cohorts of eucalypts, depending on whether or not all of the existing eucalypts are killed by the fire (Turner et al., 2009). In the absence of fire, the eucalypts progressively die out and succession proceeds to cool temperate rainforest that has been infiltrating beneath the ageing eucalypt canopy (Gilbert, 1959; Jackson, 1968;

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Noble and Slatyer, 1980). Harvesting of these forests in the past 50 years has chiefly involved clearfelling, followed by burning of logging residue to encourage eucalypt regeneration (Hickey, 1994). This is expected to continue on rotations of 80–100 years (Hickey, 1994), or around 65 years if the eucalypts are thinned after 25–35 years (Whiteley, 1999). However, many areas of oldgrowth within production forests are excluded from harvesting for conservation or operational reasons (Hickey, 1994). Thus the production forest landscape typically consists of a mosaic of oldgrowth and regrowth forests, with the relative proportion of the various seral stages depending on the history of wildfire and harvesting.

Although it is known that the bird assemblages in Tasmanian lowland wet eucalypt forests shift towards those of old-growth eucalypt forests during the first 30 years after clearfelling and burning (Hingston, 2000), the pattern of later successional change has not been documented. It is not known how long it takes for bird assemblages to return to the compositions present in old-growth eucalypt forests (Hingston, 2000). We also do not know whether bird assemblages after clearfelling change directly into those that are characteristic of old-growth eucalypt forests as the regrowth ages, or whether there are assemblages uniquely characteristic of older regrowth (Lefort and Grove, 2009).

In this study we use a chronosequence, or space-for-time, approach to examine the succession of bird assemblages in Tasmanian lowland wet eucalypt forests. We test the hypotheses that (a) turnover in bird assemblage-composition is unidirectional and continuous from shortly after disturbance through to the development of old-growth forest, and that (b) this turnover is consistent among guilds of species that inhabit different strata of the forest. Because clearfelling has been the major form of disturbance in these forests during the past 40 years (in the absence of major wildfires during this period), our chronosequence entails younger forests derived from clearfelling and older forests regenerated after wildfire. To assess whether bird assemblages are similar after these two forms of disturbance, we compare assemblages in the oldest available regrowth following clearfelling with those in even-aged stands that regenerated concurrently after wildfire.

2. Methods

2.1. Study-sites

Eleven study-sites were selected within 10 km of each other, at 120–380 m a.s.l. (Table 1), approximately 60 km west-southwest of Hobart in southern Tasmania (Fig. 1). All sites were dominated by *Eucalyptus obliqua* L'Herit, and surrounded by a matrix of production forest of various ages. Each site comprised a plot, at a particular stage of succession, of 6.25 ha (250 m × 250 m) in

extent, with the exception of site 66S which was only 3.5 ha. Nine sites carried relatively even-aged regrowth with few old living or dead trees, because they had been subjected to either intense wildfire within the past 110 years or to clearfelling and burning within the past 43 years, while the other two sites supported oldgrowth forest (Table 1). One of the old-growth sites (OGS) had oldgrowth trees and scattered younger regrowth. Characteristics of fire-scars on older trees, and the size of younger regrowth, were comparable to those in nearby regrowth aged 75 and 111 years (sites 34S and 98S). No fire-scars or young eucalypt regrowth were observed at the other old-growth site (OGN), suggesting that it had not been burned in the past 111 years. One age-class (42-43 years) had sites with two forms of disturbance (clearfelling and wildfire, Table 1). Hence, there were six treatment-age combinations (Table 1). All combinations, except 1934 wildfire, had two replicates encompassing both northerly and southerly aspects (Table 1).

2.2. Survey procedures

Birds were surveyed at each of the 11 sites on 17 occasions from 23 October 2008 to 29 March 2009. Sites were surveyed sequentially to ensure that the seasonal distribution of surveys was similar for each site. Surveys were done in fine weather with little wind (<Beaufort scale 3), between sunrise and sunset. Each site was surveyed four times before 10:00 h, four between 10:00 h and 13:00 h, five between 13:00 h and 16:00 h, and four after 16:00 h. As far as possible each site was surveyed sequentially in these four time-periods. No site was surveyed more than once per day.

Point-surveys were chosen for this study in preference to areasearches, because the latter were impractical in several of the sites with dense undergrowth (see also Wardell-Johnson and Williams, 2000), and because point-surveys have previously been used successfully locally (Hingston, 2000; Lefort and Grove, 2009). Point-surveys of 5 min each were carried out at each corner of a 50 m \times 50 m square at the centre of each 250 m \times 250 m plot. Hence each survey comprised 20 min of observations, spread over 30–40 min because of the time taken to walk between the four points. Tracks were cut around the perimeter of the squares with thick undergrowth so that the observer (ABH) could approach each point quietly.

The identities of all birds seen or heard were recorded within 25 m horizontally of each point. The stratum of the forest in which each bird was observed was also noted so that species could be allocated to guilds according to whether they mostly inhabited the canopy, the mid-layer, or the lower layer. If a bird was flushed from within 25 m of a survey-point as the observer approached the point, the bird was included in the data-set and the 5-min survey commenced immediately. Species that were flying more than 20 m

Table 1 Characteristics of the 11 study-sites.

Study-site	Latitude (S)	Longitude (E)	Treatment	Year of disturbance	Age-class (years)	Aspect	Slope (°)	Altitude (m)
OGN	43°12′52″	146°42′32″	Old-growth mixed forest	Circa 1759?	>200	N	30-40	380
OGS	43°05′31″	146°38′39″	Old-growth mixed forest	Circa 1809?	>200	S	30-35	120
98N	43°06′10″	146°44′50″	Wildfire regrowth	1898	111	N	10-20	240
98S	43°05′26″	146°38′51″	Wildfire regrowth	1898	111	S	10	160
34S	43°05′20″	146°38′40″	Wildfire regrowth	1934	75	S	25-40	180
67N	43°06′34″	146°50′14″	Wildfire regrowth	1967	42-43	NNE	15-25	120
66S	43°10′03″	146°48′26″	Wildfire regrowth	1966	42-43	SE	10-20	280
66CN	43°09′29″	146°46′15″	Regrowth from clearfell, burn and sow	1966	42-43	NW	10-30	260
66CS	43°06′56″	146°47′01″	Regrowth from clearfell, burn and sow	1966	42-43	SSW	10-20	200
03CN	43°03′13″	146°43′21″	Regrowth from clearfell, burn and sow	2003	6-8	NW	15-30	160
01CS	43°05′52″	146°41′00″	Regrowth from clearfell, burn and sow	2001	6–8	S	10–15	120

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