



# ‘Ecologically complex carbon’ – linking biodiversity values, carbon storage and habitat structure in some austral temperate forests

Narelle Hatanaka<sup>1,2</sup>, Wendy Wright<sup>1</sup>, Richard H. Loyn<sup>3</sup> and Ralph Mac Nally<sup>2\*</sup>

<sup>1</sup>School of Applied Sciences and Engineering, Monash University, Gippsland, Churchill, Victoria 3842, Australia, <sup>2</sup>Australian Centre for Biodiversity, School of Biological Sciences, Monash University, Melbourne, Victoria 3800, Australia, <sup>3</sup>Arthur Rylah Institute for Environmental Research, Department of Sustainability and Environment, Heidelberg, Victoria, Australia

\*Correspondence: Ralph Mac Nally, Australian Centre for Biodiversity, School of Biological Sciences, Monash University, Melbourne, Vic. 3800, Australia.  
E-mail: Ralph.MacNally@sci.monash.edu.au

## ABSTRACT

**Aim** We assessed how avian biodiversity and above-ground carbon storage were related in different forest age-classes, including mature stands (> 100 years), in a managed, mixed-species eucalypt forest.

**Location** Gippsland, south-eastern Australia.

**Methods** In 50 2-ha stands ranging in age from ≤ 5 years to mature stands > 100 years, we undertook repeated avian surveys, performed detailed habitat measurements and estimated amounts of above-ground carbon. Extensive wildfire reduced the number of sites to 28 (seven in each of four age classes) upon which analyses and inferences were made. We also analysed data on carbon storage and some bird responses from previously published studies.

**Results** Mature vegetation (> 100 years) had the greatest richness, abundance and biomass of birds. Key ecological resources, such as tree-hollows for nesting, generally occurred mostly in stands > 60 years. Avian richness per unit of above-ground carbon storage was relatively low for stands of 20–60 years. While above-ground carbon storage appeared to increase in a monotonic fashion as stands age and mature, there were quantum increases in all measures of avian biodiversity in mature stands (> 100 years).

**Main conclusions** Our results suggest that carbon is organized in a different way, with substantially greater biodiversity benefits, in very old stands. Mature vegetation simultaneously maximizes both avian biodiversity and above-ground carbon storage. These results bolster arguments for allocating highest priorities to the preservation of old-growth forest stands rather than alternative investments (e.g. reforestation for carbon sequestration).

## Keywords

**Australia, avifaunas, carbon storage, forest management, forest spatial structure, Gippsland, mixed-species managed forests, timber harvesting.**

## INTRODUCTION

There is a groundswell of interest in investments in forest-based carbon storage and its potential relationship to biodiversity values (Bekessy & Wintle, 2008; Horner *et al.*, 2010). For example, a reallocation of REDD (‘reduced emissions from deforestation and degradation’) expenditure could double the protection of forest vertebrate biodiversity at the expense of a 4–8% reduction in carbon emissions relative to an optimal

allocation of funds for the latter alone (Venter *et al.*, 2009). This connection between biodiversity and carbon management needs to be developed further, especially in relation to overall forest management rather than just forest clearance *per se* (Mackey *et al.*, 2008). That is, total clearance of extant forest is at the extreme end of carbon loss, but there is a wide range of silvicultural practices that are less severe than total clearance. There are some reports of concurrent biodiversity and carbon-storage benefits in forests managed in sustainability-oriented

ways compared with more commonly used methods (Imai *et al.*, 2009).

Our focus is on the biodiversity values (here forest-dependent birds) and above-ground carbon storage of managed forests. We focus on above-ground carbon because this is most reliably measured, but it seems likely that the total storage including roots and dead biomass may be 70% greater (Keith *et al.*, 2009a). Managed forests are significant in this regard for two reasons. First, they represent a large fraction of the extant forest in much of Australia and in many parts of the world (Keith *et al.*, 2009b). Second, owing to rotational harvesting, we could obtain chronosequences of forest-stand ages in which we could concurrently measure habitat structure, carbon storage and biodiversity values.

We also introduce the perspective of 'ecologically complex' carbon. By this, we mean that a given quantity of forest carbon can be organized in many different ways, and some of these are much more advantageous than others for species reliant on those forests. For example, across much of the inland slopes of the Great Dividing Range of eastern Australia, extant woodlands have been converted from relatively open 'parklands', with many large old trees, to dense ranks of pole-sized trees by coppicing for wood production (ECC, 2001). The idea of ecologically complex carbon harks back to the importance given to structurally complex forest by avian ecologists many decades ago (MacArthur & MacArthur, 1961). So, while debates may focus on amounts of carbon supported on a given hectare of land, all carbon is 'not the same' from the viewpoint of ecological opportunities for the native biota to exploit.

Remnant patches of ecologically mature forest are often embedded in a regrowth matrix in many commercially exploited forests. These remnant stands offer wide-branching canopies, shrubs, bare ground and large, hollow-bearing and dead standing trees (Loyn, 1985). These components provide a range of nesting and foraging opportunities that often are limited in earlier stages of regrowth forest, plantations or revegetation (Vesk *et al.*, 2008).

Although the effects of timber harvesting on biodiversity have been considered extensively (Lindenmayer & Hobbs, 2004), the impact of harvesting on carbon dynamics in forest ecosystems is less well documented (Schulze *et al.*, 2000). Timber harvesting involves removal of primary production, disturbance of the ground layer and changes in micrometeorology (Baldocchi, 2003). Carbon stocks in above-ground biomass are reduced on an on-going basis so that the forest does not support as much carbon as it might (Roxburgh *et al.*, 2006). Following timber harvesting, regenerating forests have the highest rate of carbon sequestration and may be significant carbon sinks over the shorter term (Roxburgh *et al.*, 2006), but this does not offset the losses of carbon from old-growth stands (Harmon *et al.*, 1990).

There is an extensive literature on how forest avifaunas are related to time-since-harvest (Sallabanks *et al.*, 2000). There also is much on how carbon storage is related to forest maturity (Venter *et al.*, 2009). However, there is little if anything that focuses on relating these two key issues together, and that is our

focus here. We report on Boola Boola Forest, Victoria, Australia, from which we obtained high-quality information on both (above-ground) carbon storage and biodiversity values (forest birds) at high spatial resolution. There does not appear to be anything comparable in the literature to our study. The current work, involving such resolution and a well-defined chronosequence of stand age, may be among the first to explore the issue of ecologically complex carbon storage, and the outcomes suggest that such fine-scaled knowledge is necessary to make sensible judgements regarding the relationships between biodiversity maintenance and carbon sequestration. We discuss our results in relation to measured carbon storage in dominant forest types across south-eastern Australia, and also to results from a study of avian responses to a chronosequence of replanted forest plots in central Victoria.

## METHODS

### Study area

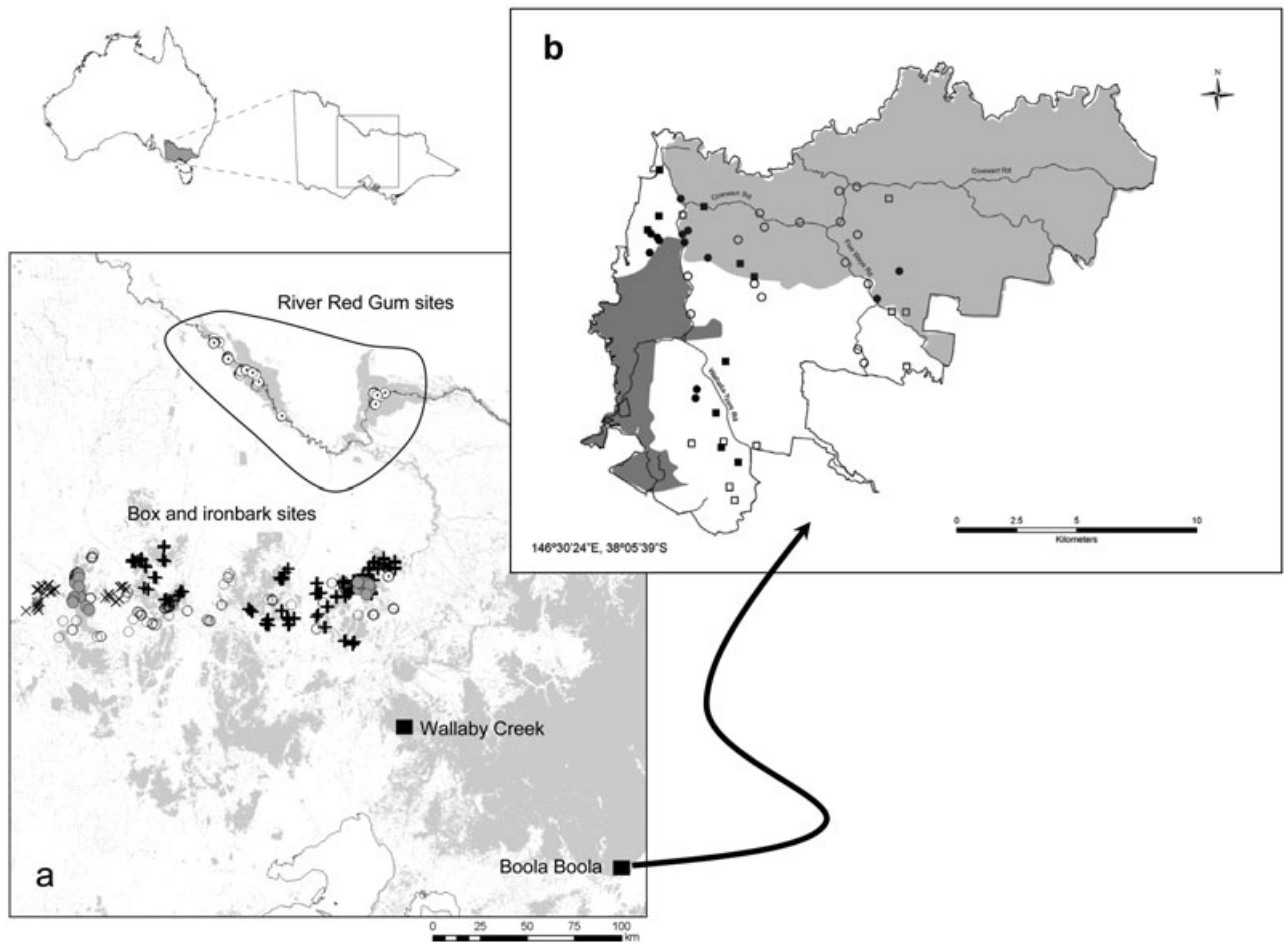
Boola Boola Forest (146°30'24" E, 38°05'39" S) is a 20,000-ha forest in eastern Victoria, Australia. The forest forms the southern part of continuous native forest that extends over most of the Great Dividing Range of eastern Australia. It is a dry sclerophyll eucalypt forest with hilly terrain (elevations of 200–425 m) and an extensive creek system. Historically (1931–2008), the average rainfall was 1101 mm, but since 1996 (Cai & Cowan, 2008), Victoria's rainfall has declined by an average of 15.3% (National Climate Centre, 2008). The mean maximum temperature was 23.2 °C in summer (min. 12.4 °C) and 10.8 °C in winter (min. 4.2 °C), but the region is warming (Bureau of Meteorology, 2008).

Vegetation types throughout Victoria are assigned to 'ecological vegetation classes' (EVCs) based on vegetation and landform (Woodgate *et al.*, 1994). The predominant EVCs at Boola Boola are 'lowland forest' in the southern part of the study area and 'shrubby foothill forest' in the north. These EVCs are dominated by silvertop ash (*Eucalyptus sieberi*) and messmate (*Eucalyptus obliqua*), often mixed with yertchuck (*Eucalyptus consideriana*) and brown stringybark (*Eucalyptus baxteri*). Riparian areas are primarily classed as 'wet forest' and 'damp forest' EVCs, where mountain grey gum (*Eucalyptus cypellocarpa*) is the dominant eucalypt with messmate and narrow-leaf peppermint (*Eucalyptus radiata*).

The region has been extensively exploited over the past 150 years for timber (Forests Commission, 1979). Since the 1940s, the forest has been systematically harvested for sawlogs and pulpwood. Most harvest is by clear-fell (S. Griffiths, 2005, personal communication), with just a few old trees retained (< 10 ha<sup>-1</sup>).

### Site selection

Fifty study sites were initially selected on ridges and upper slopes throughout the forest (Fig. 1). Each site was 2 ha (200 × 100 m) and of a known age class (i.e. time since harvest, known forestry



**Figure 1** (a) Locations of all sites referred to in the main part of the paper (Boola Boola Forest, see inset b) and in the Discussion (river red gum, *Eucalyptus camaldulensis*, box and ironbark (various eucalypts), montane (mostly *E. regnans*, Wallaby Creek) and Boola Boola Forest (various eucalypts). Symbols, many overlapping, denote the following: open circles, box–ironbark (Mac Nally *et al.*, 2000) ( $n = 149$ ); multiplication signs, box–ironbark (Harwood & Mac Nally, 2005) ( $n = 56$ ); addition signs, box–ironbark (Soderquist & Mac Nally, 2000) ( $n = 114$ ); grey circles, box–ironbark ‘large-old tree’ sites (A. F. Bennett, pers. comm.) ( $n = 24$ ); circled dots, river red gum (Lada *et al.*, 2007, 2008) ( $n = 203$ ). (b) Map of Boola Boola Forest, Victoria, Australia, and the distribution of sites categorized into one of four age classes: (1) younger regrowth (0–20 years old); (2) mid-aged regrowth (21–40 years); (3) older regrowth (41–60 years); and (4) mature sites ( $c. > 100$  years). Symbols indicate the age class of site: younger regrowth (●), mid-aged (○), older (■), mature sites (□). The dark shading shows the fire-affected area from the Moondarra fire (Jan–Feb 2006) (no sites within this area) and the light shading shows the fire-affected areas from the Cooper Creek fire (Dec 2006–Jan 2007) and which sites were affected.

records). The average distance between sites was  $6.5 (\pm 3 \text{ SD})$  km. Fifty sites were located in forest of four age classes: (1) younger regrowth aged 0–20 years, 14 sites; (2) mid-aged regrowth aged 21–40 years, 16 sites; (3) older regrowth aged 41–60 years, 10 sites; and (4) mature forest, 10 sites. Mature forest was defined as that occurring in areas that had not been harvested for  $> 100$  years and that met the criteria of old-growth forest (Woodgate *et al.*, 1996). Even these old stands have not reached their maximum carbon storing potential. Using this definition, about 30% of the forest is mature forest stands. During the course of the current study, two wildfires, both due to arson, burnt through the study area (19 January to 1 February 2006, 1760 ha; 1 December 2006 to 7 February 2007, 6100 ha).

This reduced the number of sites we could use to seven per age class (hence 28 sites).

### Environmental variables

Environmental variables were measured at two scales, in-site and landscape, and values are listed in the Supporting Information (Table S1). In-site variables characterized site-specific habitat attributes and vegetation structure. Landscape variables considered wider-scale characteristics of the area surrounding each site within a 500 m radius, and included land-use type and vegetation type. A digital map of the study area with data layers showing land use and EVC classifications was used to derive

three in-site variables and all landscape variables using a geographic information system (GIS) (ARCMAP Version 9.2, ESRI Inc.).

#### *In-site variables*

Aspect was measured in the field and described as 'northerliness' [ $\cos(\text{aspect})$ ] and 'easterliness' [ $\sin(\text{aspect})$ ] (Roberts, 1986). Habitat attributes and vegetation assessments were carried out at the 28 unburnt sites following the December 2006 fire. Numbers of hollow-bearing trees and standing dead trees  $> 1$  m were counted. Percentage covers for each vegetation component (canopy, tall shrubs  $> 5$  m, medium shrubs 1–5 m, small shrubs  $< 1$  m, ground fern and graminoids) were measured for the site. A  $50 \times 15$  m plot was laid out in each of the 28 sites. Diameter at breast height (d.b.h.) for each canopy tree in the plot was measured. These data were used to calculate total basal area  $\text{ha}^{-1}$ . The total number of stems counted in each plot was used to estimate stem density  $\text{ha}^{-1}$ .

#### *Estimation of on-site carbon storage*

About 50% of the dry weight of a tree's biomass is carbon and can be estimated from tree diameter and age (Grierson *et al.*, 1992). Carbon storage ( $\text{t C ha}^{-1}$ ) in forest stands was estimated from tree diameters measured at the 2-ha sites. Biomass equations for 13 common eucalypt species in south-eastern Australia (Bi *et al.*, 2004) were used to estimate the total above-ground tree biomass for each of our eucalypt species. The equations are based on bole, bark, branch and foliage measurements as functions of d.b.h. for individual trees up to at least 80 cm d.b.h. (all  $R^2 > 0.96$ ). There were fewer than two trees  $> 80$  cm d.b.h. at any one site, so possible extrapolation errors (Roxburgh *et al.*, 2006) were negligible. For species not listed by Bi *et al.* (2004), carbon storage was estimated using equations for similar species. For example, carbon storage of *E. baxteri* was estimated using the equation of yellow stringybark (*Eucalyptus muelleriana*). Our calculations were based on above-ground biomass of live trees alone. Fallen timber is likely to be an important component in carbon storage, but is likely to be much less than  $50 \text{ t C ha}^{-1}$  (Kilinc *et al.*, in press), especially for the non-mature sites.

#### *Landscape variables*

The digital map (20-m resolution) was used to determine stand age and elevation, and to estimate closest distance to a waterway (Strahler stream order 1 or greater). The 'buffer' tool in ARCMAP was used to create a circular area with a radius of 500 m from the site's centre, defining an area of 78 ha. This area was chosen because of known average home ranges and bird movements (Loyn *et al.*, 1980). The proportions of harvested forest and of each EVC surrounding a site within a 500-m radius were calculated. While seven EVCs were recorded, only three EVCs (i.e. dry forest, lowland forest, and wet or damp forest) were included in analyses due to low representation ( $< 5\%$ ) of the other four.

### **Bird surveys**

Sites were surveyed by N. Hatanaka in three sampling periods: (1) austral winter 2006 (June to early September 2006); (2) austral summer 2006–07 (late November 2006 to January 2007); and (3) austral winter 2007 (July to early September 2007). There were two visits to each site in each time period, amounting to six surveys per site over a full annual cycle, including the breeding season. This degree of repeat-visit surveying is consistent with studies of hundreds of sites in southern and eastern Australia (Radford & Bennett, 2007; Mac Nally *et al.*, 2009). Diurnal bird surveys were conducted using a standard 20 min–2 ha search technique in which all birds seen or heard were registered (Loyn, 1986). Detailed territory-mapping work conducted previously by R. H. Loyn showed that these standard surveys produced data that were unbiased with respect to stand age (Loyn, 1980), so that differential detectability is unlikely to be a major factor in our subsequent analyses. Visitation order to sites was randomized within survey rounds. Surveys were not conducted in high winds or temperatures or during rain.

### **Bird-response variables**

Bird data were collated for the three sampling periods. Response variables were expressed as averages per standard search at each site. 'Bird abundance' is the number of individuals of all bird species recorded per search for each site. 'Richness' is the number of bird species recorded per search at each site. Note that this is not the total number of species occupying the site at some time (i.e. asymptotic species richness), which is a measure that depends on sampling effort (Mac Nally & Horrocks, 2002; Gilmore *et al.*, 2007). 'Bird biomass' is the total mass of all species recorded per search at each site. Values were obtained from combining areal densities and mass estimates from data in the Handbook of Australian, New Zealand and Antarctic Birds (full list of volumes available at: <http://www.birdsaustralia.com.au/hanzab/handbook-of-australian-new-zealand-and-ant-arctic-birds.html>, accessed 23 November 2009). 'Guild-based abundance' are total abundances of birds in foraging and nesting guilds to which each bird species was assigned (see Table S2 based on existing classifications; Loyn & Kennedy, 2009; Mac Nally *et al.*, 2009). Foraging guilds group birds according to their feeding substrates, such as birds that feed on invertebrates (in bark, in the canopy or in shrubs); birds that feed on seeds (on the ground or in vegetation); nectarivores; and carnivores. Nesting guilds group birds with similar nesting requirements, such as nesting in vegetation (shrubs or canopy), in small or large hollows, or on the ground.

### **Statistical analyses**

We first analysed data using a Mantel test to determine whether there was evidence of spatial autocorrelation (Fortin & Payette, 2002; Fleishman & Mac Nally, 2006). We correlated data for bird-species composition based on Bray–Curtis dissimilarities and Euclidean distance among sites using the 'vegan' package in R (Oksanen, 2008).



**Table 1** Mean ( $\pm$  SE) for bird response variables in each forest age-class at Boola Boola Forest, Victoria, Australia.

Response variables	Younger	Mid-aged	Older	Mature
Bird abundance	17.6 $\pm$ 0.8	13.0 $\pm$ 1.2	13.0 $\pm$ 1.3	22.4 $\pm$ 1.3
Number of species	6.6 $\pm$ 0.2	5.2 $\pm$ 0.1	5.8 $\pm$ 0.4	10.0 $\pm$ 0.5
Bird biomass (g)	764.5 $\pm$ 114.3	852.8 $\pm$ 113.3	1297.6 $\pm$ 188.5	2285.3 $\pm$ 242.1
Feeding guilds				
Bark foragers	0.8 $\pm$ 0.6	0.9 $\pm$ 0.6	1.2 $\pm$ 0.2	1.5 $\pm$ 0.3
Insectivores that feed in canopy	5.1 $\pm$ 0.2	5.1 $\pm$ 0.2	4.6 $\pm$ 1.0	6.3 $\pm$ 0.7
Insectivores that feed on damp ground	0.6 $\pm$ 0.1	0.5 $\pm$ 0.1	0.3 $\pm$ 0.2	1.0 $\pm$ 0.2
Frugivores	0.1 $\pm$ 0.2	0.3 $\pm$ 0.1	0.3 $\pm$ 0.1	0.4 $\pm$ 0.2
Nectarivores	0.9 $\pm$ 0.6	0.9 $\pm$ 0.3	0.7 $\pm$ 0.2	3.0 $\pm$ 0.5
Open ground foragers	2.4 $\pm$ 0.1	0.9 $\pm$ 0.1	0.6 $\pm$ 0.2	2.1 $\pm$ 0.3
Ground seed eaters	0.1 $\pm$ 0.2	0.2 $\pm$ 0.2	0.2 $\pm$ 0.1	0.8 $\pm$ 0.2
Vegetation seed eaters	0.6 $\pm$ 0.9	0.7 $\pm$ 1.2	1.0 $\pm$ 0.2	1.4 $\pm$ 0.2
Insectivores that feed in shrubs	5.5 $\pm$ 0.4	2.4 $\pm$ 0.3	2.5 $\pm$ 0.7	3.9 $\pm$ 0.6
Carnivores	1.1 $\pm$ 0.5	0.9 $\pm$ 0.5	1.1 $\pm$ 0.2	1.4 $\pm$ 0.1
Nesting guilds				
Large hollow nesters	1.0 $\pm$ 0.1	1.4 $\pm$ 0.1	1.8 $\pm$ 0.3	2.8 $\pm$ 0.3
Small hollow nesters	0.7 $\pm$ 0.2	0.9 $\pm$ 0.2	1.1 $\pm$ 0.1	1.5 $\pm$ 0.3
Birds that nest in small hollow/burrow in ground	0.2 $\pm$ 0.1	0.2 $\pm$ 0.1	0.3 $\pm$ 0.1	0.7 $\pm$ 0.2
Birds that nest in branches of tree/tall shrub branches	0.9 $\pm$ 0.1	0.5 $\pm$ 0.1	0.8 $\pm$ 0.2	1.1 $\pm$ 0.2
Birds that nest in shrub vegetation	14.4 $\pm$ 0.2	9.7 $\pm$ 0.1	8.5 $\pm$ 1.3	15.3 $\pm$ 1.2

Ages classes are defined as: (1) younger regrowth < 20 years; (2) mid-aged regrowth 21–40 years; (3) older regrowth 41–60 years; and (4) mature forest > 100 years. Data were averaged over three sampling periods: winter 2006 (Jun–Sep 2006), summer 2006–07 (Nov 2006–Jan 2007) and winter 2007 (Jul–Sep 2007) and expressed as birds per standard 20-min search.  $n = 7$  for all measurements.

Differences in bird assemblages among age classes were explored using one-way analysis of similarity (ANOSIM) of Bray–Curtis similarities in PRIMER version 5 (Clarke & Gorley, 2001; Clarke & Warwick, 2001). These values were square-root transformed abundances to reduce the influence of abundant species. We used 4999 permutations.

Bird-response variables (richness, total abundance, total biomass and guild-based abundances) were compared among regrowth sites (younger, mid-aged and older) and mature forest sites using analysis of variance (ANOVA) in SPSS for Windows (SPSS Inc., Chicago, USA, version 16.0). Tukey's tests were used for post hoc comparisons.

Generalized linear modelling (GLM) with Bayesian model averaging (BMA) was used to determine environmental variables that were correlated most strongly with variation in bird-response variables (Hoeting *et al.*, 1999). BMA involves fitting multiple models, and predictor variables having the highest posterior probabilities of inclusion in good models are found. An environmental variable with a probability of inclusion  $\Pr(\text{inc}) > 75\%$  was considered a strong candidate for inclusion into the model and a 'key predictor' for the response variable (Thomson *et al.*, 2007). The posterior mean coefficient is a measure of the magnitude and direction of the relationship between the predictor and response variables. Poisson GLMs were deemed appropriate for non-negative count data (e.g. richness), while Gaussian GLMs were used for other variables, such as total biomass. The 'bic.glm' function in the 'BMA' package of R was used for the analyses (Raftery *et al.*, 2008).

Highly correlated variables ( $r > 0.7$ ) influence results of BMA analyses (Thomson *et al.*, 2007) and were identified to ensure that only weakly or uncorrelated variables were included in an analysis. Where possible, one variable in highly correlated pairs was discarded using the authors' ecological knowledge of factors more likely to affect bird assemblages in this forest as a guide to which variable to retain.

## RESULTS

### Differences in environmental variables among forest age classes

The vegetation structure of mature forest had shrubs of all size cohorts, ground cover, significantly more hollow-bearing trees and fewer, but larger, trees (Table S1). Dense stands of regenerating saplings and understorey species were characteristic of sites in younger regrowth (Table S1). Canopy cover was similar among age classes but there was less variation among sites within mid-aged and older age classes (Table S1).

### Bird assemblages among age classes

Sixty-seven bird species were recorded during the study (Table S2). There was little evidence of spatial autocorrelation in bird-assemblage composition [Mantel correlation = 0.095, not significant (n.s.)]. Mature forest stands had the highest number of bird species, abundance and biomass, and the most distinctive

**Table 2** Results of Bayesian model averaged analyses of bird variables in relation to environmental variables at Boola Boola Forest in Victoria, Australia.

Response variable	Environmental variable	Pr(inc)	Coefficient $\pm$ SD
Bird abundance	Northerliness	1	$-3.740 \pm 1.07$
	Hollow-bearing trees per site	0.84	$0.779 \pm 0.49$
Number of species	Stand age	0.92	$0.009 \pm 0.001$
	Hollow-bearing trees per site	0.99	$0.345 \pm 0.09$
Bird biomass	Wet or damp forests within 500 m	1	$-40.730 \pm 12.14$
	Stand age	1	$0.269 \pm 0.06$
	Harvested forest within 500 m	0.99	$-28.573 \pm 10.29$
	Dead standing trees > 1 m per site	0.90	$3.957 \pm 2.11$
	% Canopy cover	0.75	$0.254 \pm 0.19$
Canopy feeders	Northerliness	0.87	$-1.039 \pm 0.61$
	Total tree basal area ha <sup>-1</sup>	0.87	$0.045 \pm 0.02$
	Easterliness	0.86	$-1.302 \pm 0.80$
	Wet or damp forests within 500 m	0.77	$4.822 \pm 3.56$
Nectarivores	Hollow-bearing trees ha <sup>-1</sup>	1	$0.219 \pm 0.06$
	Stand age	1	$0.019 \pm 0.01$
	Northerliness	0.91	$-0.508 \pm 0.26$
Open ground foragers	Total tree basal area ha <sup>-1</sup>	0.95	$-0.017 \pm 0.01$
	% Cover of small shrubs < 1 m	0.77	$0.024 \pm 0.02$
Insectivores feeding in shrubs	Elevation (m)	0.97	$0.006 \pm 0.00$
	% Cover medium shrubs 1–5 m	0.88	$0.015 \pm 0.01$
Large-hollow nesters	Hollow-bearing trees per site	1	$0.222 \pm 0.07$
	Stand age	1	$0.018 \pm 0.01$
	% Cover medium shrubs 1–5 m	0.98	$-0.026 \pm 0.01$
Nests in shrubby vegetation	Northerliness	0.97	$-2.722 \pm 1.12$
	% Cover medium shrubs 1–5 m	0.86	$0.091 \pm 0.05$

'Pr(inc)' denotes the probability of inclusion of the term into 'good' models and posterior mean coefficients  $\pm$  SD are presented.

bird assemblages compared with regrowth forest sites (Table 1). On the basis of post hoc tests, the following relationships held. Richness: mature > younger > (mid-age  $\approx$  older); total abundance: mature > younger > (mid-age  $\approx$  older); total biomass: mature > older > (mid-age  $\approx$  younger) (where ' $\approx$ ' denotes not distinguishably different). There were few strong patterns in guild analyses (Table 1). Nectarivorous species were more prevalent in mature sites than elsewhere, as were granivores (both ground and on-vegetation seeds). Numbers of species requiring large hollows for nesting increased with stand age, from *c.* 1 species in young regrowth up to *c.* 2.8 in mature forest (Table 1).

There were significant differences (ANOSIM global  $R = 0.252$ ,  $P < 0.001$ ) in bird assemblages among sites of different age classes. In the six pair-wise comparisons among forest age classes, only the mid-age versus older comparison was not statistically significant. The largest difference in bird assemblages ( $R = 0.450$ ,  $P < 0.001$ ) was observed between younger and older regrowth sites.

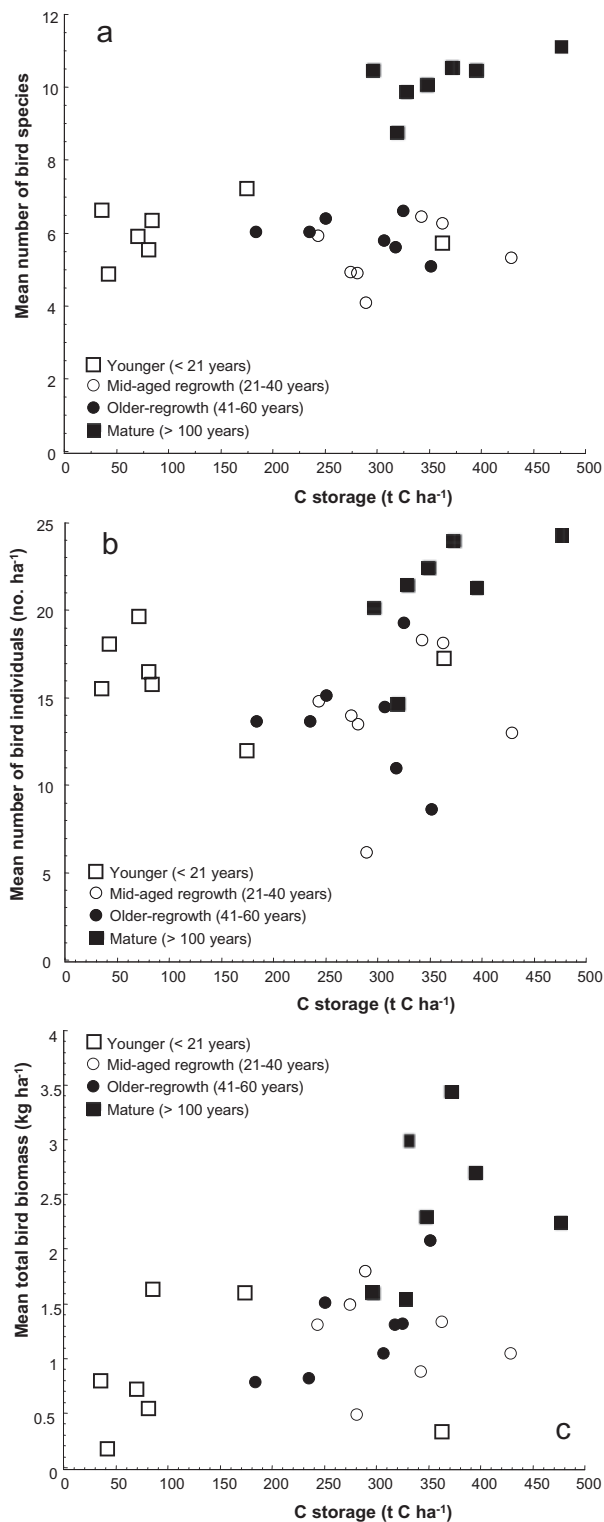
### Bird responses to environmental variables

There were significant models for 9 of the 19 bird-response variables based on Bayesian model averaging (Table 2). Nectarivores, canopy-feeders and shrub-nesting species were more likely to occur at sites with southerly aspects (Table 2). Nectari-

vores and large-hollow nesters were influenced by the number of hollow-bearing trees and stand age and occurred predominantly in mature forests (Table 2). Some environmental variables, such as basal area and medium-sized shrub cover, were key predictors for several response variables, but the direction of the relationships differed. Birds that feed in the canopy preferred sites with higher basal areas, but open-ground feeders did not (Table 2). Higher bird biomass was recorded at sites with a relatively low proportion of harvested forest surrounding the site, and with high numbers of dead standing trees and high canopy coverage. These habitat conditions were observed at sites in older regrowth forest stands and in mature forest (Table 2).

### Carbon storage and bird measures

Estimated amounts of above-ground carbon stored at sites in mature forest were > 300 t ha<sup>-1</sup> (Fig. 2). Some sites in regrowth forest > 20 years had carbon storage estimates within the range of mature forests. Regrowth forest stands  $\leq$  20 years had much lower values of stored carbon (< 180 t ha<sup>-1</sup>) (Fig. 2). An exception was one regrowth site (18 years) with carbon storage estimates similar to older forest stands due to deliberate management to retain several trees with larger diameters (> 30 cm) in one part of the site.



**Figure 2** Relationships between above-ground carbon storage ( $\text{t C ha}^{-1}$ ) and (a) mean number of bird species, (b) average total bird abundances (summed over all species of birds, numbers  $\text{ha}^{-1}$ ), and (c) mean total bird biomass (summed over all species of birds,  $\text{kg ha}^{-1}$ ) at Boola Boola Forest, Victoria, Australia, 2006–07.

Notwithstanding the steady accumulation of above-ground carbon, and its approaching the mature-forest value for older regrowth stands, there was a quantum increase in bird biodiversity measures between all regrowth classes and mature-forest stands. On average, there were 72% more species per stand in mature stands than in older regrowth (41–60 years, Fig. 2a). There also were 72% more individuals (Fig. 2b) and a huge increase in bird biomass (176%, Fig. 2c).

## DISCUSSION

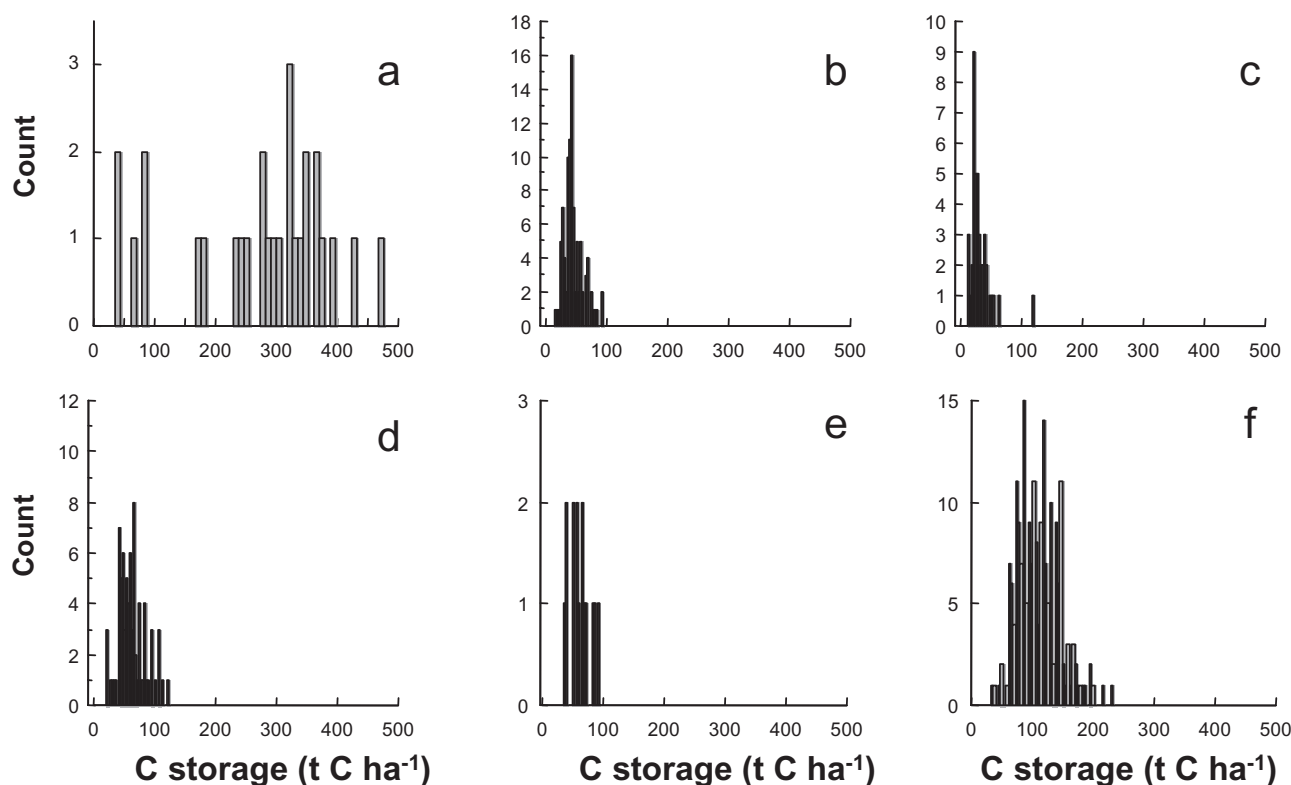
### Carbon storage and (bird) biodiversity

We preface these remarks by noting that our measures of biodiversity refer to only one taxon, forest-dependent birds, albeit a taxon upon which much thinking in terrestrial ecology and conservation has been built (Fahrig, 2003). Nevertheless, we think that results shown in Fig. 2 have an important contribution to make in our understanding of how the issues of carbon storage and biodiversity are linked. The most salient point is that the manner of carbon organization matters.

Carbon storage builds relatively steadily as regrowth stands age (Law *et al.*, 2001; Law *et al.*, 2003). There is no clear separation between stands of adjacent age classes, and, perhaps most surprising is that some mid-aged stands (21–40 years) had accrued as much above-ground carbon as had mature stands (Fig. 2). The amounts stored are commensurate with world-wide figures for cool-temperate moist forests [ $377 (\pm 182 \text{ SD}) \text{ t C ha}^{-1}$ ] (Keith *et al.*, 2009b). These values much exceed estimates for most tropical forests, upon which much of the REDD focus has been ( $\text{c. } 180 \text{ t C ha}^{-1}$ ) (Keith *et al.*, 2009b).

Our results given in Fig. 2 show that the difference between mature vegetation and even the oldest regrowth stands ( $\text{c. } 60$  years) involves a qualitatively different form of carbon organization, at least from a (bird) biodiversity perspective. Therefore, the way carbon is stored generates ecologically important outcomes that would not be represented well by a unidimensional focus on  $\text{t C ha}^{-1}$  measurements *per se*. These forms of carbon are multiple canopy layers, wide-girthed trees having large boughs (necessary for tree-hollow formation), and extensive flowering episodes. None of these observations is new from a biodiversity point of view – ecologists have long known the value of a structurally complex habitat (Bell *et al.*, 1991) – but our quantification of carbon storage supports attaching a high priority to conserving mature stands with ecologically important old-growth components.

The extent to which regrowth provided habitat for birds was largely determined by habitat complexity (i.e. the variety of distinct structural elements; Bell *et al.*, 1991), which does not necessarily increase linearly with stand age. We found that dense stands of regenerating saplings, understorey species and open ground were characteristic of regrowth forest stands  $\leq 20$  years. These stands provided nesting and foraging opportunities for some species, contributing to relatively high bird abundances (Loyn *et al.*, 1980). Extensive shrub cover supported large populations of small-bodied birds (7–10 g) that



**Figure 3** Histograms of above-ground carbon storage ( $\text{t C ha}^{-1}$ ) for a range of studies across south-eastern Australia: (a) the current study (managed, mixed-species eucalypt forest,  $n = 28$ ); (b) box-ironbark (Mac Nally *et al.*, 2000) ( $n = 149$ ); (c) box-ironbark (Harwood & Mac Nally, 2005) ( $n = 56$ ); (d) box-ironbark (Soderquist & Mac Nally, 2000) ( $n = 114$ ); (e) box-ironbark 'large-old tree' sites (A. F. Bennett, pers. comm.) ( $n = 24$ ); (f) river red gum, *Eucalyptus camaldulensis* (Lada *et al.*, 2007, 2008) ( $n = 203$ ).

nest or feed in that vegetation. Regrowth stands > 20 years lacked both the dense sub-canopy vegetation characteristics of younger regrowth sites and the structural complexity of mature forests. The transition from early stages of regrowth to full maturity appears to pass through a stage within which ecological resources are limited for many bird species (Vesk & Mac Nally, 2006). This is reflected in the low biodiversity measures of birds in the 20–60 years bracket. This result accords with earlier observations from the same forest (Loyn *et al.*, 1980), and is now based on a larger sample of stands in that age bracket.

Hollow-bearing trees widely are regarded as a critical resource for many Australian animals (Vesk *et al.*, 2008). Regrowth sites in the forest had very few hollow-bearing trees retained during harvesting operations, regardless of time since harvest. Preservation of existing hollow-bearing trees and trees that will potentially form hollows in the near future is an essential strategy for biodiversity conservation (Loyn, 1985).

The timeframe during which regrowth forest can provide conditions suitable for birds that require mature forest appears to be much longer than 60 years since timber harvest, but we cannot state how long that may actually take owing to the relative youth of even our oldest regrowth stands. The latter, which are currently 60 years, may take at least another 50 years, probably much more (Keith *et al.*, 2009a), to mature into the same

complex vegetation that is characteristic of mature forest. This may take even longer under the mooted drying conditions for the region under climate change (Kirschbaum, 2000).

### Our results in a regional perspective

R.M. and his colleagues have used a consistent, relatively time-intensive methodology to measure habitat structure in many forest and woodland stands across much of the State of Victoria (Mac Nally *et al.*, 2000). From these measurements, it was possible to develop a context for assessing the amounts of above-ground carbon storage for the values we provide here for Boola Boola. These data show that carbon storage at Boola Boola (Fig. 3a) far exceeds the vast majority of forest stands across central Victoria (box and ironbark forests; Fig. 3b–e) and northern Victoria (river red gum, floodplain forests; Fig. 3f). This is not surprising, for two reasons. First, the box and ironbark forests across the state's centre occur mainly on impoverished soils and in a low-rainfall belt (ECC, 2001). Very few stands exceeded  $100 \text{ t C ha}^{-1}$ . While the floodplain forests typically occur on better soils and with potentially greater access to water, water availability/flooding has been much curtailed by management and over-extraction since the 1930s, and by much reduced rainfall in recent years (Horner *et al.*, 2009). Only 3 of 203 stands exceeded  $200 \text{ t C ha}^{-1}$ . Second, both box

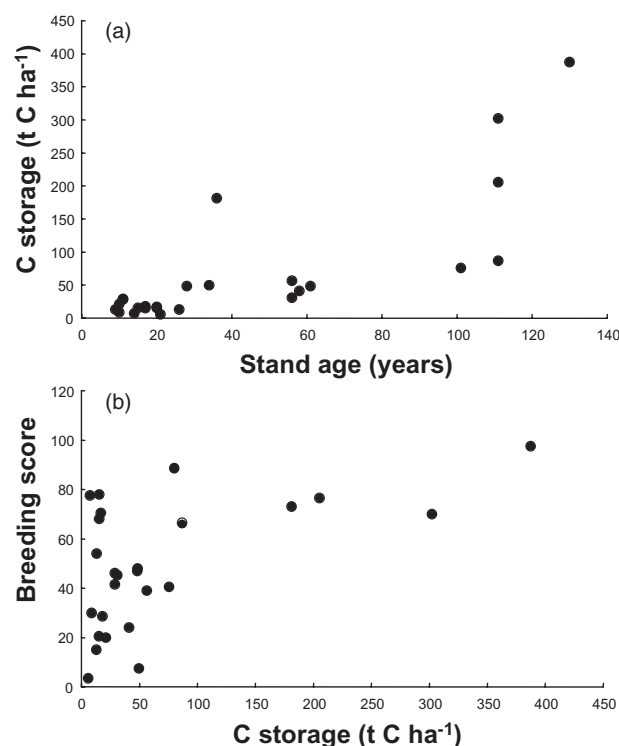


and ironbark and floodplain forests have been subjected to intense harvesting for over a century, and this is reflected in the stand structure of box and ironbark stands (typically most trees < 40 cm d.b.h.). Values much greater than any of these, and much exceeding any of those from Boola Boola, occur in higher-elevation montane sites on excellent soils in the central highlands of Victoria (e.g. 630–920 t C ha<sup>-1</sup>) (Kilinc *et al.*, in press).

The issue that is germane to our paper relates to how biodiversity and carbon storage are linked. The advantage of our work in Boola Boola is that we have a good knowledge of time since logging, and so we can relate measures of bird biodiversity not only to carbon storage but also to the way carbon is organized as a function of stand age. For the vast majority of the stands for which we present data in Fig. 3, there are few, if any, records on when harvesting activities took place. Moreover, stands generally are logged selectively or coppiced, which makes them difficult to assess in the same way as we have done for Boola Boola. However, one data set allows us to explore the bird biodiversity–carbon storage–stand age relationships directly. We have detailed information on habitat structure from which carbon storage can be computed for 25 replanted stands of box and ironbark forest from central Victoria, Australia (Selwood *et al.*, 2009). Given the increase in average girth of trees reported previously (Vesk *et al.*, 2008), carbon storage is positively associated with time since establishment (Fig. 4a). We also have reported elsewhere a means by which breeding performance at the bird-assemblage level can be tallied (Selwood *et al.*, 2009), which is a better indicator of population viability than richness, abundance or biomass *per se* (Mac Nally, 2007). The breeding score is given to each nest and is weighted according to the evidence that successful fledging has occurred. Thus, feeding young outside the nest is highly weighted (weight = 9), while males and females courting is of low weight (weight = 1). A site-based breeding score is the sum (over all species of birds) for all nests on the site (Mac Nally, 2007). There is a strong relationship between assemblage-level breeding score and carbon storage, although the increase is comparatively shallow once sites accumulate > 150 t C ha<sup>-1</sup> (Fig. 4b). This may be due to sites of that loading becoming sufficiently ‘complex’ (e.g. through provision of tree hollows) to support close to the full complement of potential species for breeding (Vesk *et al.*, 2008).

## CONCLUSIONS

There is a need to complement carbon crediting with biodiversity credits to avoid perverse investment outcomes (Bekessy & Wintle, 2008; Venter *et al.*, 2009). Our results suggest that assuming a simple linear function between carbon stored and biodiversity benefits does not represent well the potentially synergistic way in which carbon storage and biodiversity interact. ‘Carbon complexity’ from an ecological perspective adds much greater value to old stores of carbon than would be evident by sequestration measures alone. If our results are widely applicable, then the preservation of old-growth forests is about a



**Figure 4** (a) Carbon storage (t C ha<sup>-1</sup>) as a function of time since planting (Vesk *et al.*, 2008). (b) Bird breeding score, the summed reproductive performance of all nests on a site (Selwood *et al.*, 2009), as a function of carbon storage (t C ha<sup>-1</sup>) in box–ironbark forests of central Victoria.

two-fold greater (bird) biodiversity benefit compared with even the oldest regrowth stands, notwithstanding comparable above-ground carbon storage levels.

There is an urgency to conserve mature forest in the broader forest landscape, as well as elements of mature forest among regrowth (Loyn, 1985). In Victoria, a range of forest prescriptions and management plans have been developed to pursue these aims, and work continues to refine the forest planning system (DSE, 2007). Biodiversity conservation in commercially harvested forest mosaics requires a whole-of-landscape approach to management that includes an understanding of the ecosystem services provided by regrowth forest (Loyn, 2000). Protected forests contribute significantly to biodiversity conservation, but wildlife also occurs in commercially productive forests, which are a large fraction of the forest estate in many parts of the world (33% in Victoria) (DSE, 2005). Hence, those forests must also be managed to play a key large role in maintaining regional- and larger-scale biodiversity.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Table S1** Mean and standard error for all environmental variables at site and landscape scales at sites of each age class in Boola Boola Forest, 2006–07.

**Table S2** Guild classifications for bird species used in the analyses.

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## BIOSKETCHES

**Narelle Hatanaka** is a research student within the School of Applied Sciences and Engineering and the School of Biological Sciences, Monash University, and has interests in forest management for avian conservation.

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