Australian Government
Land & Water Australia

technical report

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The fourth dimension: incorporating time into landscape-level biodiversity assessments

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Published by: Land & Water Australia

Product Code: PN30222

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Land & Water Australia
Native Vegetation and Biodiversity Program
Technical Report

Project Title: The fourth dimension: incorporating time into landscape-level biodiversity assessments.

Project Reference Number: DUV11

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Introduction

A fundamental issue in ecological research is measuring spatial and temporal variation in natural systems in order to assess the effect and magnitude of anthropogenic disturbances. While spatial variation is measured routinely, most ecological studies do not measure temporal variation: sampling is usually limited to relatively short periods and rarely has temporal replication. This not only devalues the spatial comparisons because historical levels of variability are not considered but also precludes assessments of temporal trends (rates of change), or time lags between cause (e.g. vegetation loss) and consequence (e.g. species loss). To reliably compare rates of change, time must be included in the study design, yet most studies employ space-for-time substitution. In this study, we build on an existing dataset collected in 2002/03 during DUV06 'Landscape level thresholds for conservation of biodiversity in rural environments' by re-surveying birds across 24 landscapes, thus incorporating time into an existing study design. This allows us to monitor changes in landscape-level responses in real-time in multiple landscapes that sample a gradient in extent of native vegetation and contrasting configuration.

It is commonly accepted that some species will persist in landscapes but in dwindling numbers for some time following habitat loss before eventually disappearing: that is, landscapes carry an 'extinction debt' of species still present but destined for local extinction (Tilman *et al.* 1994). Accordingly, theory predicts that the rate (a function of time) of population declines will be faster in more extensively cleared landscapes. Further, for landscapes with a similar amount of native vegetation, theory suggests that population declines will be faster in landscapes with more subdivided native vegetation. However, there is scant empirical evidence documenting extinction debts, or more importantly, corroborating the influence of landscape composition and configuration on rates of population decline and species loss.

How might these theoretical expectations be realized in agricultural landscapes in Australia? We propose five possible scenarios.

1) The extinction debt may already have been fully realized in landscapes with very low (<10%) native vegetation cover and these landscapes are unlikely to experience further species loss, whereas landscapes with medium (10-30%) and high (>30%) cover will continue to lose species. In this case, the differences in species richness identified in DUV6 between landscapes with high and low cover would decrease over time (Fig. 1a). That is, rates of species loss would be negatively correlated with extent of tree cover (because species loss is negative value, larger negative values are associated with increasing tree cover).

2) Only low cover landscapes may still be carrying an extinction debt, in which case the difference between high and low cover landscapes would be expected to increase (Fig. 1b). That is, rates of species loss would be positively correlated with extent of tree cover.

3) Landscapes with medium native vegetation cover may experience the most change over time, shifting the species richness threshold identified in DUV6 to higher levels of cover (Fig. 1c). Here, rates of species loss would have a quadratic relationship with tree cover.

4. Species may be declining in all landscapes, such that the shape of the species richness response curve is unchanged but absolute values are consistently lower (Fig. 1d). In this case, there would be no correlation between rates of species loss and extent of tree cover.

5. There is little or no change in any landscape between time periods. In this scenario, extinction debt in all landscapes has been ‘paid’ and the fauna remains relatively stable over time.

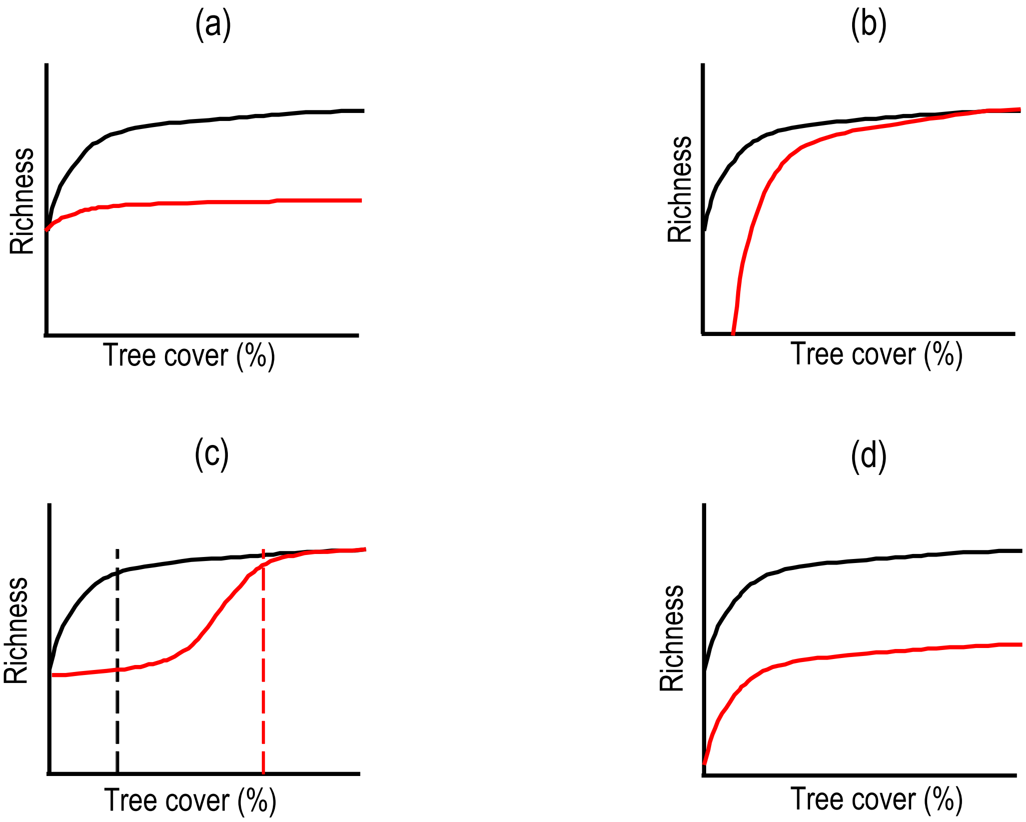


Figure 1. Four scenarios for rates of change of landscape-level species richness in relation to extent of tree cover, reflecting faster rates of change in (a) high cover, (b) low cover and (c) intermediate cover landscapes, and (d) equal rates of change in all landscapes. Black lines indicate the relationship between species richness and tree cover in 2002/03, and red lines indicate possible relationships hypothesised after temporal changes in richness.

Similar scenarios could be constructed for the response of rates of change in species richness in relation to the pattern of native vegetation in the landscape, such as the extent of aggregation. Further, we expect changes in the population size of individual species to precede any changes detected in species richness. Thus, in this study we also monitor changes in the incidence of species as an indicator of population size, in relation to landscape attributes. Key research questions to be addressed in this study therefore, are:

- In which, if any, landscapes has the extinction debt been fully realized? That is, have populations stabilized or are they still declining (or increasing)?
- What are the landscape attributes that influence trajectories of species loss (or gain), and decline (or increase) in the incidence of individual species?
- Are species more likely to be lost from high, medium or low cover landscapes in coming decades?
- Are rates of population decline and species loss negatively associated with extent (amount) and degree of aggregation of native vegetation?
- Was the spatial variability detected in the 2002/03 surveys typical of longer-term variability?

Methods

Study area

The study area covers ~20,500 km^2 of agricultural-woodland mosaic in south-eastern Australia (143° E 36° S to 147° E 37° S) (Fig. 2). This includes parts of the inland slopes of the Great Dividing Range in the south-east (altitude: ~150–700 m), and the alluvial plains of the Victorian Riverina to the north (altitude: <150 m) (Radford *et al.* 2005). The region experiences hot, dry summers with most rainfall (400–670 mm per annum) in winter and spring. In general, topographic relief and rainfall increase across the study area from west to east.

Box-ironbark forest, dominated by red ironbark *Eucalyptus tricarpa*, grey box *E. microcarpa* and yellow gum *E. leucoxylon*, is the most widespread vegetation of the inland slopes, occurring on undulating rises and low hills. Grassy and herb-rich woodlands of grey box, white box *E. albens* and yellow box *E. melliodora* occur lower on the slopes and on better-drained areas of the alluvial plain. Forests and grassy woodlands of black box *E. largiflorens* and river red gum *E. camaldulensis* are common along watercourses. Agriculture (cereal cropping, horticulture and pastoralism), forestry (native forests) and mining have profoundly changed the region, with less than 17% of the original extent of tree cover remaining (ECC 1997).

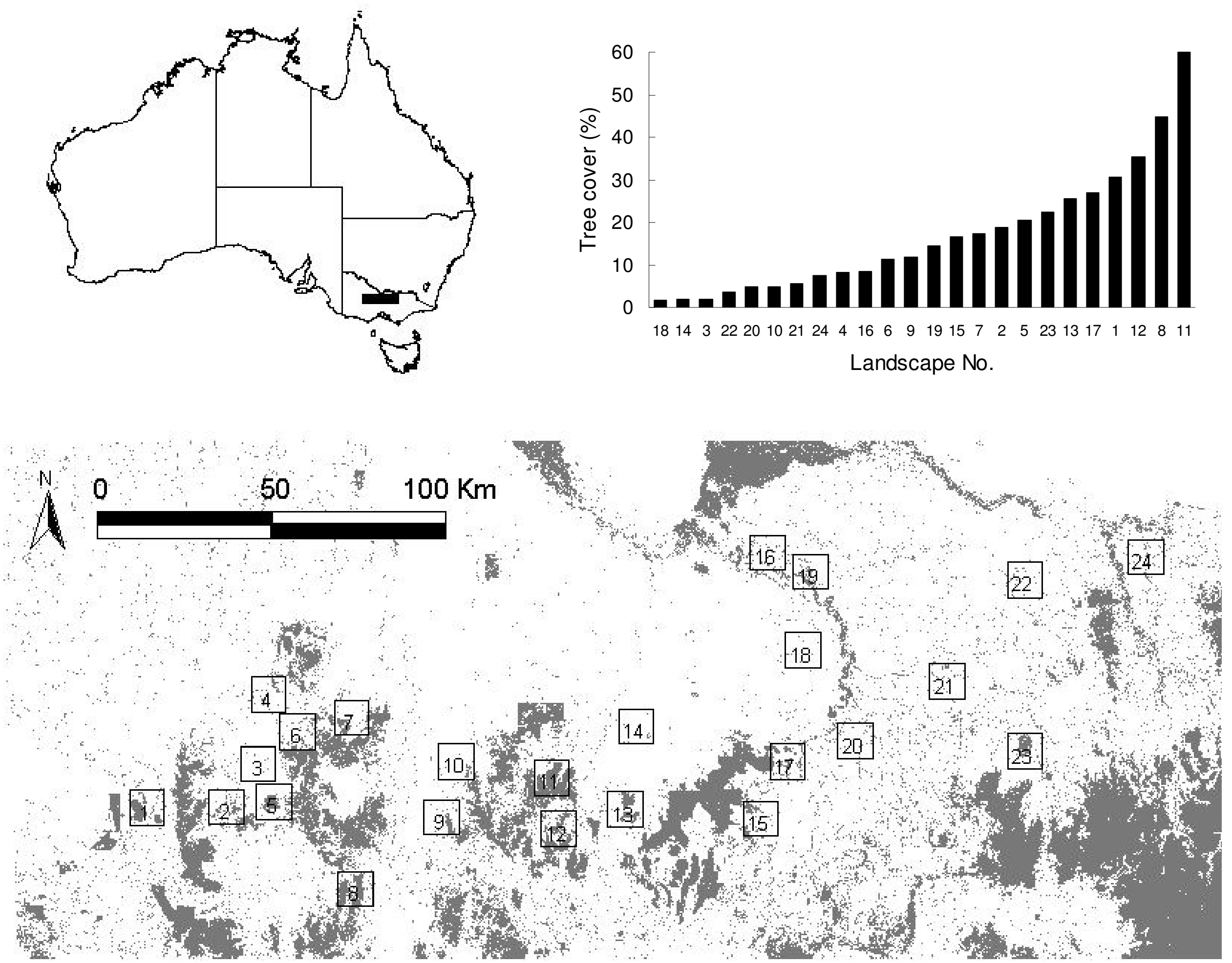


Figure 2. Location of the study region and study landscapes in northern Victoria (grey shading indicates tree cover), and histogram showing the variation in landscape-level tree cover. Landscape number on the histogram corresponds to the label on the map.

Field Methods

During DUV6 ‘Landscape level thresholds for conservation of biodiversity in rural environments’, we established a unique research infrastructure explicitly designed to examine the influence of whole-of-landscape attributes on selected faunal groups at the landscape-level (Radford *et al.* 2005, Bennett *et al.* 2006). This infrastructure comprised a set of 24 study ‘landscapes’ (each 100 km^2) with 10 survey sites in each landscape, combined with data characterizing the amount and configuration of native vegetation, and the composition of each landscape. The landscapes sampled a gradient in remnant vegetation cover from 2% through to 60%, and were strategically selected to identify pairs of landscapes with a similar amount but contrasting configuration (i.e. aggregated versus dispersed) of native vegetation (Fig. 2). Ten survey sites were established in each landscape across five landscape 'elements' – large remnants (>40 ha), small remnants (<40 ha), riparian vegetation, roadside vegetation and scattered paddock trees – approximately in proportion to their occurrence in the landscape. Four rounds of bird surveys (30-minute line-transects) were conducted at each of the 240 survey sites during 2002/03. See Radford *et al.* (2005) and Radford & Bennett (2007) for full details of landscape selection, site selection, bird survey methods and landscape variables.

In this project, we re-surveyed all 240 sites originally surveyed in 2002/03, using the same methods. This entailed four rounds of surveys at each of 240 sites, conducted in October-November 2006 (spring), March-April 2007 (autumn), June-July 2007 (winter) and September-October 2007 (spring), which mirrors the seasonal spread of the original surveys. Garry Cheers, who did half of the 2002/03 surveys, conducted all of the 2006/07 surveys.

It is important to note that this study corresponds to an extended period of below-average rainfall in the study region, beginning around 1997 and continuing to the present day (Fig. 3). Since 1997, annual rainfall has been more than 10% above the long-term average only in 2000. The 2002/03 sampling period began in the spring of an exceptionally dry year (2002: 47% below long-term average) and the entire 2006/07 sampling period occurred during years of severe rainfall deficit (2006: 44% below long-term average; 2007: 30% below long-term average). Moreover, there was an almost complete absence of eucalypt flowering in the autumn and winter of 2007.

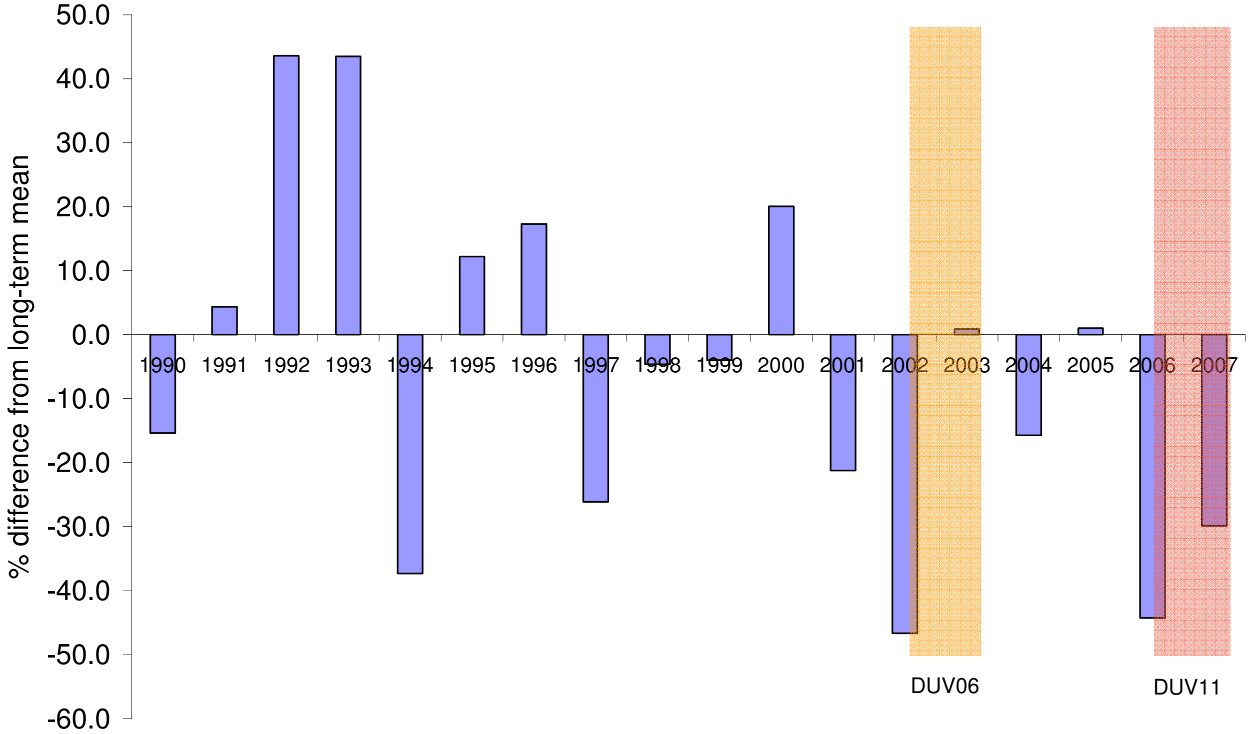


Figure 3. Deviation from long-term mean annual rainfall in the study area, 1990 – 2007. Data collated from three Bureau of Meteorology weather stations in the study area. Sampling periods for DUV06 (2002/03) and the current study (2006/07) indicated by shading.

Data Analysis

Most 'landscape-scale' studies sample the response of fauna at the *patch* level and measure attributes of the surrounding landscape to make inference about the influence of *landscape context* (Bennett *et al*. 2006). An innovative feature of our research design is that both the explanatory variables characterising landscape attributes and the faunal responses (e.g. species richness, incidence of particular species) relate to 'whole' landscapes – that is, a mosaic consisting of many patches of different character, some of which may be used as habitat by particular species. This is achieved by pooling the data from the 10 sites and 4 survey rounds per landscape to produce a single metric for the landscape as a whole. Thus, our unit of inference – entire landscape mosaics – is consistent with the spatial scale at which the processes of interest - landscape composition and heterogeneity - operate.

In this report, we present data pertaining to several measures of the avifauna:

- *species richness*: the number of different species recorded per landscape;

- *species incidence*: the number of surveys in which a particular species was recorded. Note that we report on species incidence *per landscape* and pooled across *all landscapes*;
- *mean incidence*: the average species incidence for a group of species defined *a priori*;
- *turnover*: the number of colonisations (species recorded in 06/07 but not 02/03) plus the number of extinctions (species recorded in 02/03 but not 06/07) divided by the total number of species recorded in both sampling periods per landscape.

The following analyses were conducted.

1. To assess differences in species richness and mean incidence between sampling periods, we used linear mixed models (residual maximum likelihood or REML) to account for the non-independence of sampling periods. We included survey period and tree cover (standardized) and their interaction as fixed effects and landscape unit as a random effect in the model.
2. To examine change in species richness or mean incidence in relation to landscape composition and configuration, we modeled a) absolute change (i.e. the difference between the sampling periods) and b) per cent change (i.e. the difference between the sampling periods as a percentage of the value in 2002/03) for both species richness and mean incidence from 2002/03 to 2006/07 against a suite of 10 landscape variables, using multiple linear regression. We used the all-subsets module in Genstat to compare the fit of all possible models, and chose the most parsimonious model based on AIC as the model with most support.
3. We compared the fit of a suite of univariate models (linear, logarithmic, quadratic, power and broken-stick) to examine the relationship between species richness of woodland-dependent birds and tree cover for the 2006/07 sampling period only. We used AIC corrected for small sample sizes (AIC_c) to calculate Akaike weights of the candidate models. In particular, we were interested to see whether the threshold response reported in Radford *et al.* (2005) remained the most parsimonious model.
4. To examine change between the sampling periods in species incidence per landscape, we modeled the change in incidence for each species using Bayesian logistic regression of the form:

$$r_{ij} \sim Binomial(p_{ij}, n_{ij}); \log\left(\frac{p_{ij}}{1-p_{ij}}\right) = \alpha_j + e_i$$

Here, p_{ij} is the number of surveys in which the species was recorded in landscape i in sampling period j, n_{ij} is the number of surveys conducted in landscape i in period j, α_j is the mean log-odds for period j, and e_i is the systematic (same among years) error associated with landscape i (that is, the extent that landscape *i* differs from other landscapes). We estimated the posterior probability that $\alpha_{2006\text{-}07} < \alpha_{2002\text{-}03}$ and considered a posterior probability > 0.9 very strong evidence for a decline in incidence, and a posterior probability < 0.1 very strong evidence for an increase in incidence between the survey periods.

5. To examine change in species incidence between sampling periods in relation to extent and aggregation of tree cover, we extended the model above by adding an interaction term, 'landscape by sampling period':

$$r_{ij} \sim Binomial(p_{ij}, n_{ij}); \log\left(\frac{p_{ij}}{1-p_{ij}}\right) = \alpha_j + e_i + e'_{ij}$$

Here, e'_{ij} is the change in landscape-specific error associated with landscape *i* in the 2006/07 sampling period. That is, it represents the interaction between sampling period and landscape because it is the probability that species incidence has changed at a faster or slower rate in landscape *i* relative to the mean rate of change in other landscapes. We then examined the Pearson correlation co-efficient between e'_{ij} and extent of tree cover and the aggregation index.

Results

Change in species richness between sampling periods

The number of species recorded in each landscape in each sampling period, and the per cent change for each landscape is shown in Table 1.

There was a significant decrease in mean species richness per landscape between sampling periods for all woodland-dependent species, and for woodland-dependent insectivores and nectarivores, respectively (Table 2). The effect size of sampling period for woodland-dependent species was a mean decrease of 7.96 ± 0.93 (S.E.) species per landscape; this represents a 20% decline in mean species richness between 2002/03 and 2006/07. The effect size for insectivorous species was a mean decrease of 4.00 ± 0.69 species per landscape (18% decline) and for nectarivorous species, a mean decrease of 3.38 ± 0.41 species per landscape (32% decline). There was a significant positive effect of tree cover during both sampling periods on species richness of all woodland-dependent species, insectivores and nectarivores (Table 2). There was also an indication of a significant interaction between sampling period and tree cover for richness of all woodland-dependent species, suggesting the rate of species loss was faster in high cover landscapes than in low cover landscapes (Table 2).

Table 1. Species richness of Total landbirds (i.e., all terrestrial birds 'typical' of north-central Victoria, excluding vagrants, introduced species and those associated with neighbouring bioregions), Woodland-dependent landbirds (i.e., species that require native vegetation for the majority of their daily activities), Insectivorous woodland-dependent landbirds and Nectarivorous woodland-dependent landbirds per landscape in DUV06 (2002/03) and DUV11 (2006/07), and per cent change between the sampling periods. Landscape number corresponds to Figure 2 and Tree cover is per cent native vegetation per landscape.

Landscape	**Number**	**Tree cover (%)**	**Total landbirds**			**Woodland-dependent**			**Insectivores**			**Nectarivores**		
			2002/03	2006/07	% change	2002/03	2006/07	% change	2002/03	2006/07	% change	2002/03	2006/07	% change
Gillieston	18	1.6	46	39	-15.2	12	12	0.0	9	7	-22.2	3	4	33.3
Runnymeade	14	1.9	59	46	-22.0	21	18	-14.3	9	10	11.1	8	5	-37.5
Logan	3	1.9	56	48	-14.3	28	20	-28.6	16	11	-31.3	10	4	-60.0
Tungamah	22	3.6	60	50	-16.7	27	19	-29.6	19	12	-36.8	4	3	-25.0
Miepoll	20	4.7	58	49	-15.5	23	24	4.3	11	14	27.3	9	5	-44.4
Nering	10	4.7	67	50	-25.4	36	22	-38.9	22	14	-36.4	11	7	-36.4
Cosgrove South	21	5.6	71	65	-8.5	36	33	-8.3	19	17	-10.5	10	6	-40.0
Black Dog Creek	24	7.5	73	57	-21.9	39	31	-20.5	22	19	-13.6	7	4	-42.9
Wedderburn	4	8.2	69	53	-23.2	41	27	-34.1	23	14	-39.1	12	8	-33.3
Skeleton Creek	16	8.5	69	57	-17.4	36	33	-8.3	24	21	-12.5	5	5	0.0
Wehla	6	11.4	82	62	-24.4	50	40	-20.0	26	24	-7.7	14	9	-35.7
Shelbourne	9	11.9	84	57	-32.1	46	29	-37.0	26	17	-34.6	14	8	-42.9
Undera North	19	14.4	72	67	-6.9	44	36	-18.2	27	21	-22.2	5	5	0.0
Bailieston	15	16.6	87	71	-18.4	53	39	-26.4	29	23	-20.7	15	10	-33.3
Glenalbyn	7	17.4	65	63	-3.1	36	32	-11.1	20	18	-10.0	10	8	-20.0
Stuart Mill	2	18.8	68	61	-10.3	35	31	-11.4	18	18	0.0	11	7	-36.4
Tunstalls	5	20.4	74	62	-16.2	40	32	-20.0	23	18	-21.7	12	8	-33.3
Reef Hills	23	22.4	82	71	-13.4	53	44	-17.0	33	25	-24.2	12	12	0.0
Crosbie	13	25.7	75	61	-18.7	45	37	-17.8	26	23	-11.5	13	10	-23.1
Murchison	17	27.1	80	75	-6.3	51	47	-7.8	30	27	-10.0	15	11	-26.7
Tottington	1	30.6	62	51	-17.7	33	25	-24.2	15	13	-13.3	11	7	-36.4
Axe Creek	12	35.4	83	68	-18.1	49	40	-18.4	28	26	-7.1	15	9	-40.0
Havelock	8	44.9	83	53	-36.1	45	29	-35.6	27	17	-37.0	13	8	-38.5
Wellsford	11	60.0	71	55	-22.5	43	31	-27.9	23	20	-13.0	13	8	-38.5

Table 2. Results of linear mixed models testing for the fixed effects of sampling period (YEAR), landscape-level tree cover (TREE) and their interaction (YEAR*TREE) on species richness of all woodland-dependent species, insectivores and nectarivores. Note that TREE was standardized prior to analysis.

Response variable	Model term	Variance component (± s.e.)	Wald-statistic	*d.f.*	*P*	Effect size (± s.e.)
Woodland-dependent species	Landscape (random)	34.34 ± 12.02				
	YEAR (fixed)		73.31	22	<0.001	-7.96 ± 0.93
	TREE (fixed)		28.68	22	<0.001	7.99 ± 1.39
	YEAR*TREE (fixed)		4.19	22	0.053	-1.94 ± 0.95
Insectivores	Landscape (random)	13.48 ± 5.0				
	YEAR (fixed)		34.00	22	<0.001	-4.00 ± 0.69
	TREE (fixed)		23.31	22	<0.001	4.35 ± 0.91
	YEAR*TREE (fixed)		0.67	22	0.423	-0.57 ± 0.70
Nectarivores	Landscape (random)	3.44 ± 1.27				
	YEAR (fixed)		68.19	22	<0.001	-3.38 ± 0.41
	TREE (fixed)		20.43	22	<0.001	2.27 ± 0.49
	YEAR*TREE (fixed)		1.85	22	0.187	-0.59 ± 0.42

Interpretation and practical significance: There was a systematic and dramatic decline in species richness of woodland birds in agricultural landscape of north-central Victoria between 2002/03 and 2006/07. This marked decline occurred in nearly all landscapes, irrespective of extent of tree cover. However, landscapes with more remnant tree cover still contained significantly more woodland-dependent species than landscapes with less tree cover.

Change in species richness between sampling periods in relation to landscape composition and configuration

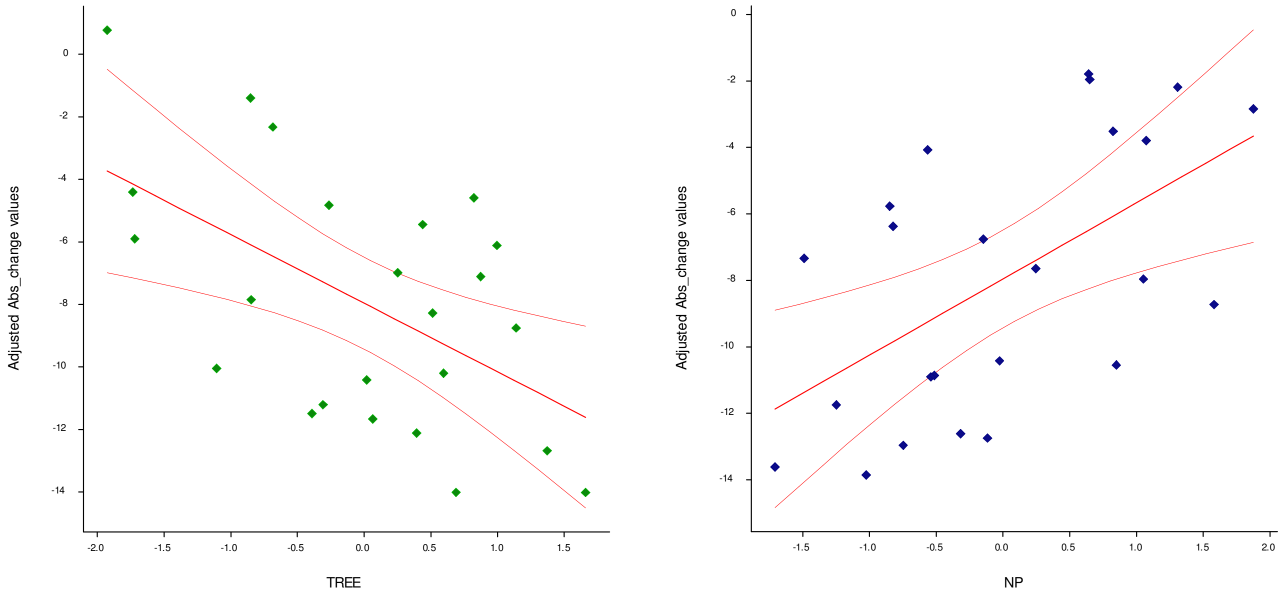
Change in absolute species richness of woodland-dependent species from 2002/03 to 2006/07 was negative in 22 landscapes, positive in one landscape and no change was detected in one landscape (Table 1). The all-subsets regression revealed that the most parsimonious model for absolute change in species richness of woodland-dependent birds included four variables: there was more change (i.e. greater loss of species) in landscapes with fewer patches, more native vegetation and more complex patch shapes, and less change (i.e. retained species) in landscapes with relatively high levels of riparian vegetation in the landscape (Table 3; Fig. 4). This model explained 43% of the variation in the change in species richness. The most parsimonious model for per cent change in total species richness included three variables: there was greater proportional change in landscapes with fewer patches that were closer to a potential source patch (> 10,000 hectares) and

Table 3. Five most parsimonious models returned from all-subsets multiple linear regression of absolute and per cent change in species richness of all woodland-dependent species between sampling periods, modelled against landscape attributes. Values in cells indicate probabilities based on F-statistics for variables included in the model.

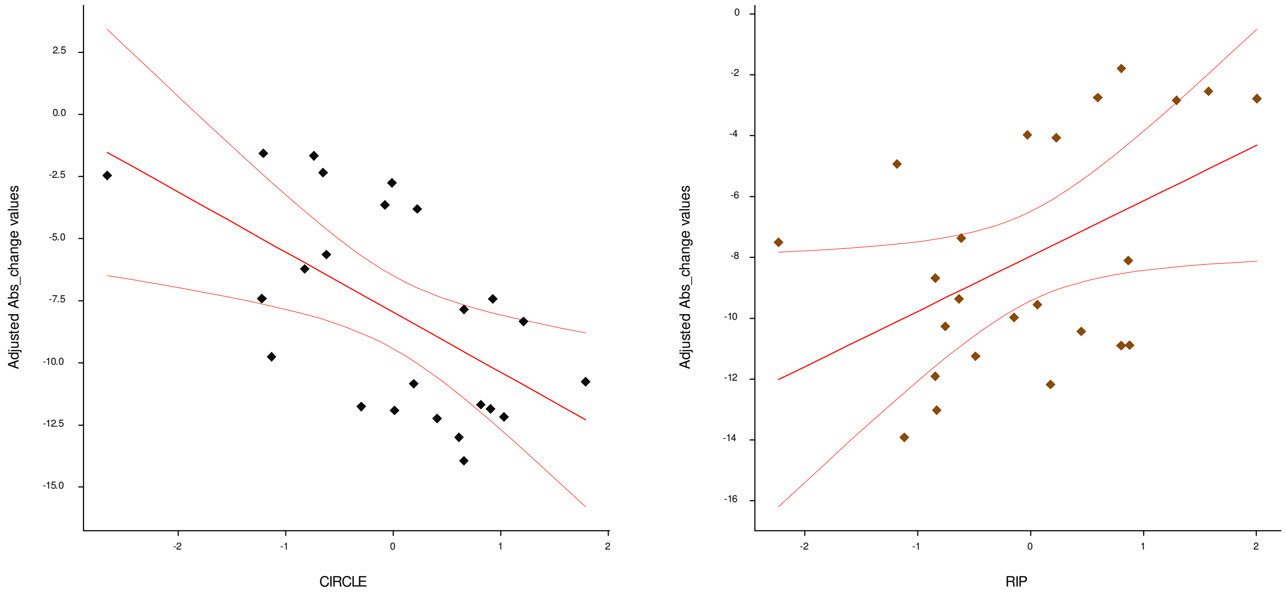
Model	Model AIC	Aggregation	Patch complexity	Habitat condition	Easting	Vegetation diversity	Predominant agricultural land-use	Number of vegetation patches	Extent of riparian vegetation	Distance to source habitat	Tree cover
Woodland-dependent species (absolute change)	26.72		0.015					0.008	0.057		0.010
	27.24		0.012					0.010	0.097	0.202	0.009
	27.81	0.322	0.021					0.082	0.058		0.011
	27.83		0.049					0.014		0.118	0.016
	28.28		0.018				0.495	0.008	0.076		0.012
Woodland-dependent species (per cent change)	25.40		0.113					0.007		0.108	
	25.48							0.010			
	25.56		0.028	0.071				0.005	0.112		
	25.79	0.203						0.117			
	25.83		0.110	0.146				0.006			

Table 4. Five most parsimonious models returned from all-subsets multiple linear regression of absolute and per cent change in species richness of insectivores and nectarivores between sampling periods, modeled against landscape attributes. Values in cells indicate probabilities are based on F-statistics for variables included in the model.

Model	Model AIC	Aggregation	Patch complexity	Habitat condition	Vegetation diversity	Predominant agricultural land-use	Number of vegetation patches	Mean annual rainfall	Extent of riparian vegetation	Distance to source habitat	Tree cover
Insectivorous species (absolute change)	27.41		0.043			0.090	0.008	0.047			
	27.72		0.019			0.035	0.007	0.019		0.182	
	27.76		0.018			0.044	0.006	0.022	0.187		
	27.87		0.155				0.022				
	28.13						0.037				
Insectivorous species (per cent change)	26.51						0.027				
	27.08		0.245				0.019				
	27.15			0.258			0.022				
	27.28				0.283		0.021				
	27.52			0.062	0.100		0.010				0.146
Nectarivorous species (absolute change)	29.39	0.044	0.089	0.001	0.030	<0.001		0.027			
	29.55		0.002	<0.001	0.016	0.001	0.045			0.025	
	29.64	0.046		0.150		<0.001		0.001			0.074
	29.86		0.001	<0.001	0.068	0.001	0.037		0.181	0.058	
	29.87	0.009				<0.001		0.001			0.003
Nectarivorous species (per cent change)	28.37		0.002	<0.001	0.026	<0.001	0.030				0.003
	30.39	0.110	0.006	<0.001	0.018	<0.001					0.009
	30.84		0.066	<0.001		<0.001	0.073	0.127			0.109
	30.90	0.076		<0.001		<0.001		0.004	0.175		
	31.00	0.082		<0.001		<0.001		0.006			

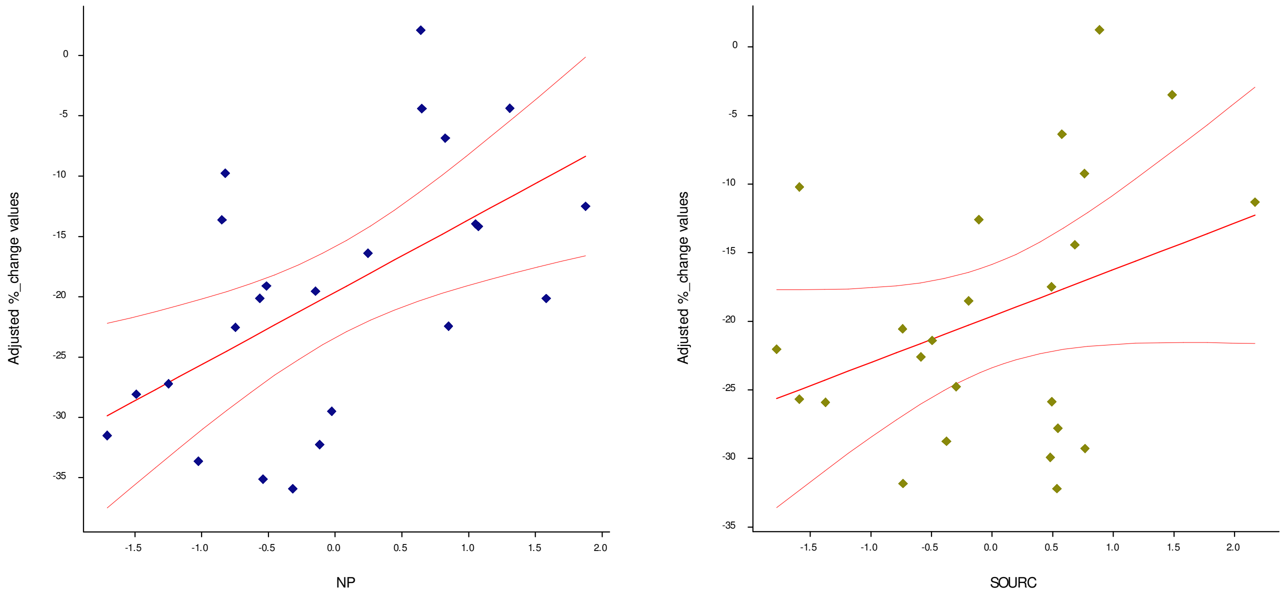

(a) Tree cover

(b) Number of patches


(c) Mean patch shape complexity

(d) Extent of riparian vegetation cover

Figure 4. Partial plots of fitted values and 95% confidence intervals (red lines) from the most parsimonious model (lowest AIC) for absolute change in woodland-dependent species richness (y-axis) versus (a) extent of tree cover; (b) number of patches of native vegetation; (c) mean patch shape complexity; and (d) extent of riparian vegetation cover. Observed values (solid diamonds) are also plotted. All explanatory variables are standardized.



(a) Number of patches

(b) Distance to source habitat

(c) Mean patch shape complexity

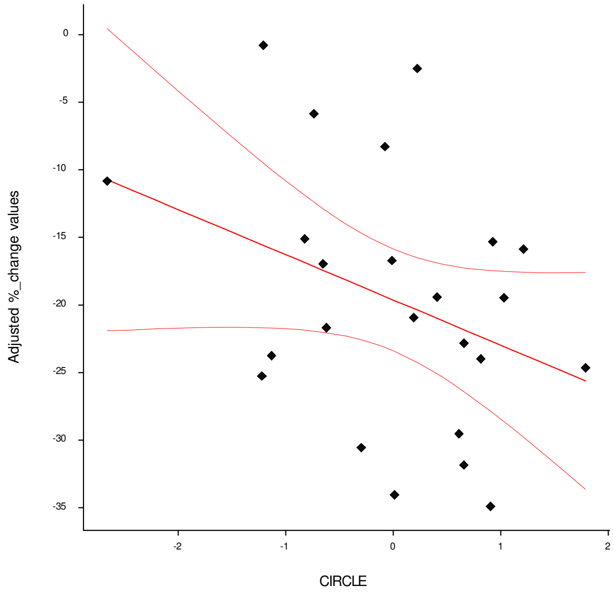


Figure 5. Partial plots of fitted values and 95% confidence intervals (red lines) from the most parsimonious model (lowest AIC) for per cent change in woodland-dependent species richness (y-axis) versus (a) number of patches of native vegetation; (b) distance to source habitat; and (c) mean patch shape complexity. Observed values (solid diamonds) are also plotted. All explanatory variables are standardized.

contained relatively complex patch shapes (Table 3; Fig. 5). This model explained 32% of the per cent change in total species richness.

The results from the all-subsets regressions for insectivores and nectarivores are presented in Table 4 but are not discussed in depth due to space constraints. Briefly, absolute change in insectivore species richness was generally greater (i.e. greater loss of species) in landscapes with fewer, more complex patches that were dominated by cropping and with higher rainfall, whereas per cent change in insectivore species richness was consistently only related to the number of patches in the landscape (Table 4). Proportional change was higher in landscapes with fewer patches of native vegetation.

Change in species richness of nectarivores was difficult to interpret, with numerous contrasting models providing similar fits to the observed data (Table 4). Indeed, each landscape variable was included in at least one of the five best models. Further, the large number of variables in the selected models risks over-fitting the model. However, in general, change in absolute species richness of nectarivores was generally greater (i.e. greater loss of species) in landscapes that were relatively aggregated with high tree cover, dominated by grazing and with higher habitat condition scores. Per cent change in nectarivore species richness was generally greater (i.e. greater loss of species) in landscapes dominated by grazing and with higher habitat condition scores but with lower habitat diversity and fewer habitat patches.

Interpretation and practical significance: An effect of landscape composition was evident for change in absolute species richness per landscape: more species were lost from landscapes with higher tree cover yet fewer species were lost as the extent of riparian vegetation increased. However, per cent change in species richness was not related to landscape composition. This indicates that the number of species lost relative to landscape-level species richness was similar in all landscapes but because higher cover landscapes support more species, they experienced greater absolute declines. Importantly, those landscapes with relatively large amounts of riparian vegetation were buffered somewhat from these declines, suggesting riparian vegetation may provide refuge for some woodland species in times of stress.

Configuration effects were evident for both absolute and per cent change in species richness of woodland-dependent birds. In general, more species and a greater proportion of species were lost from less-fragmented landscapes – those with fewer patches (relative to extent of tree cover), more complex patch shapes (reflecting greater inter-patch connectivity) and relatively close to large source blocks. Taken together, these results indicate greater species loss in higher cover and less fragmented landscapes. This may reflect the expression of an ‘extinction debt’ – a time lag effect in which the consequences of historical clearing and landscape modification are continuing to be realised as species are lost progressively from the most fragmented and modified landscapes to less fragmented landscapes. It is likely that the only species persisting in low cover landscapes in 2002/03 were relatively robust to landscape change because fragmentation sensitive species had long since disappeared from these landscapes. In contrast, high cover landscapes maintained a suite of species at low density that suffered declines during the interval between sampling periods such that they were not detected in 2006/07 (i.e. Scenario (a) in Fig. 1).

However, given the magnitude of change detected in a relatively short interval, we hypothesize that declines due to any extinction debt have been compounded and accentuated by the added environmental stress imposed by the extended dry period during which this study was conducted. We suggest that much of the observed change reflect the impacts of a drying climate on landscapes that under more favourable climatic conditions had been able to support more diverse woodland bird assemblages.

Change in species incidence between sampling periods

(i) Species incidence: pooled across landscapes

We recorded a large decline in the overall incidence (pooled across all landscapes) of most species. Of 128 terrestrial species (excluding waterbirds) that were recorded at least four times in one of the sampling periods, 48 species (38%) declined by more than 50% and a further 41 species (32%) declined by 20-50% (Table 5; Fig. 6). Thus, fully 70% of all species were **at least** one fifth less common in 2006/07 than in 2002/03. Only 11 species (9%) increased by 20% or more over the same period (Table 5).

Of the 69 woodland-dependent species recorded four times or more in one of the sampling periods, 33 species (48%) declined in overall incidence by more than 50% and a further 19 species (28%) declined by 20-50% (Fig. 6). Of the 16 nectarivorous woodland-dependent species, 12 species (75%) declined in overall incidence by >50%; 16 of 38 insectivorous woodland-dependent species (42%) declined by a similar magnitude. A further 14 insectivores (37%) declined by more than 20%.

Table 5. Overall incidence of all landbirds detected in 4 or more surveys in either sampling period in DUV06 (2002/03) and DUV11 (2006/07), and per cent change between the sampling periods. Incidence is pooled across all landscapes. Species are arranged from largest per cent decrease to largest per cent increase.

Species	DUV06 (2002 / 03)	DUV11 (2006 / 07)	% change
Swift Parrot	39	0	-100.0
Barn Owl	5	0	-100.0
Azure Kingfisher	4	0	-100.0
Brown Quail	4	0	-100.0
Yellow-faced Honeyeater	23	1	-95.7
White-naped Honeyeater	43	2	-95.3
Dollarbird	10	1	-90.0
Purple-crowned Lorikeet	109	11	-89.9
Horsfield's Bronze-Cuckoo	42	5	-88.1
Rainbow Bee-eater	88	12	-86.4
Singing Bushlark	7	1	-85.7
Fairy Martin	26	4	-84.6
Bush Stone-curlew	5	1	-80.0
White-winged Triller	39	8	-79.5
Striated Thornbill	23	5	-78.3
Noisy Friarbird	50	11	-78.0
Little Raven	306	68	-77.8
Australian Hobby	8	2	-75.0
Spotted Quail-thrush	4	1	-75.0
Speckled Warbler	4	1	-75.0
Peregrine Falcon	14	4	-71.4
Cockatiel	7	2	-71.4
Black-chinned Honeyeater	205	66	-67.8
Little Lorikeet	40	13	-67.5
White-backed Swallow	6	2	-66.7
Brown Goshawk	37	13	-64.9
Crested Bellbird	71	25	-64.8
Red Wattlebird	507	184	-63.7
Silvereye	8	3	-62.5
Yellow Thornbill	67	26	-61.2
Tree Martin	72	28	-61.1
Yellow-rumped Thornbill	99	40	-59.6
Blue-faced Honeyeater	12	5	-58.3
White-bellied Cuckoo-shrike	31	13	-58.1
Musk Lorikeet	405	172	-57.5
European Goldfinch	14	6	-57.1
Brown Thornbill	7	3	-57.1
Sacred Kingfisher	74	32	-56.8
Fuscous Honeyeater	173	76	-56.1
Rufous Songlark	89	40	-55.1
Brown-headed Honeyeater	149	67	-55.0
Varied Sittella	31	14	-54.8
Crested Shrike-tit	142	65	-54.2
Grey Fantail	83	38	-54.2
Olive-backed Oriole	54	25	-53.7
Restless Flycatcher	155	72	-53.5
Mistletoebird	57	27	-52.6
Western Gerygone	29	14	-51.7
Richard's Pipit	14	7	-50.0

Species	**DUV06 (2002 / 03)**	**DUV11 (2006 / 07)**	**% change**
Zebra Finch	8	4	-50.0
White-browed Woodswallow	82	43	-47.6
Australian Owlet-nightjar	15	8	-46.7
Grey Currawong	76	41	-46.1
Wedge-tailed Eagle	37	20	-45.9
Black-faced Cuckoo-shrike	223	122	-45.3
House Sparrow	62	34	-45.2
Little Corella	27	15	-44.4
Red-browed Finch	18	10	-44.4
Eastern Yellow Robin	73	42	-42.5
Magpie-lark	286	167	-41.6
Masked Lapwing	70	41	-41.4
Southern Whiteface	17	10	-41.2
Welcome Swallow	304	182	-40.1
Hooded Robin	21	13	-38.1
White-browed Scrubwren	16	10	-37.5
Spiny-cheeked Honeyeater	8	5	-37.5
Masked Woodswallow	19	12	-36.8
Superb Fairy-wren	185	118	-36.2
Spotted Pardalote	116	74	-36.2
Common Bronzewing	122	78	-36.1
Striated Pardalote	725	465	-35.9
Grey Butcherbird	104	68	-34.6
Rufous Whistler	117	77	-34.2
Buff-rumped Thornbill	41	27	-34.1
Brown Falcon	39	26	-33.3
Apostlebird	6	4	-33.3
Little Eagle	16	11	-31.3
Laughing Kookaburra	318	223	-29.9
Red-capped Robin	37	26	-29.7
Common Starling	101	71	-29.7
White-browed Babbler	98	69	-29.6
Golden Whistler	52	38	-26.9
White-eared Honeyeater	15	11	-26.7
Willie Wagtail	434	321	-26.0
Red-rumped Parrot	390	301	-22.8
Collared Sparrowhawk	9	7	-22.2
Grey Shrike-thrush	393	308	-21.6
Dusky Woodswallow	121	95	-21.5
Peaceful Dove	73	58	-20.5
Yellow-tufted Honeyeater	147	118	-19.7
Sulphur-crested Cockatoo	361	291	-19.4
Pied Butcherbird	32	26	-18.8
Crimson Rosella	65	53	-18.5
White-throated Treecreeper	131	108	-17.6
Brown Treecreeper	433	362	-16.4
Jacky Winter	128	108	-15.6
Pied Currawong	20	17	-15.0
Eastern Rosella	571	491	-14.0
Little Friarbird	29	26	-10.3
Australian Magpie	767	694	-9.5
Galah	705	640	-9.2
Gilbert's Whistler	12	11	-8.3
White-winged Chough	292	270	-7.5
Clamorous Reed Warbler	28	26	-7.1

Species	**DUV06 (2002 / 03)**	**DUV11 (2006 / 07)**	**% change**
Common Myna	24	23	-4.2
Crested Pigeon	194	186	-4.1
Common Blackbird	29	28	-3.4
Long-billed Corella	188	184	-2.1
Pallid Cuckoo	14	14	0.0
Whistling Kite	9	9	0.0
Emu	4	4	0.0
White-plumed Honeyeater	579	585	1.0
Noisy Miner	444	451	1.6
Australian Raven	269	283	5.2
Diamond Firetail	23	25	8.7
Weebill	146	164	12.3
Grey-crowned Babbler	16	18	12.5
Flame Robin	30	36	20.0
White-throated Gerygone	4	5	25.0
Scarlet Robin	10	15	50.0
Southern Boobook	8	12	50.0
Nankeen Kestrel	4	6	50.0
Australian King-Parrot	3	5	66.7
Tawny Frogmouth	3	5	66.7
Painted Button-quail	4	8	100.0
Black-shouldered Kite	1	4	300.0
Stubble Quail	1	4	300.0
Brown Songlark	4	29	625.0

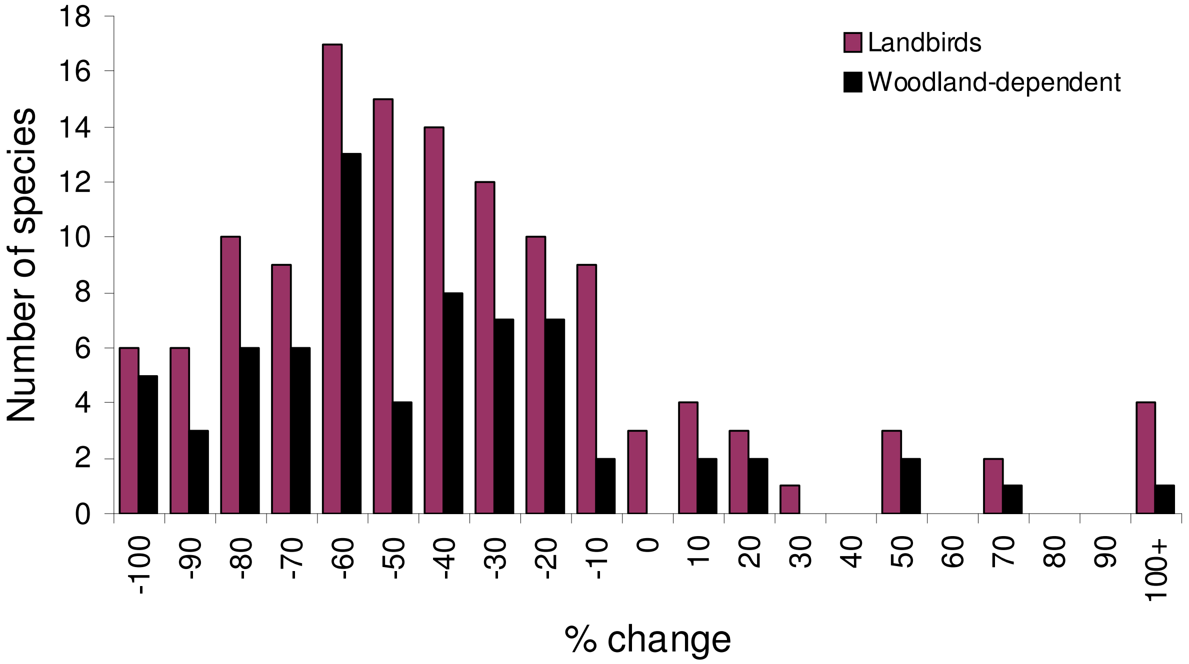


Figure 6. Histogram of change in overall incidence of all landbirds and woodland-dependent species between the 2002/03 and 2006/07 sampling periods.

(ii) Species incidence: landscape-level

We used Bayesian logistic regression to examine changes in landscape-level species incidence for 128 terrestrial species recorded at least four times in one of the sampling periods. This model tests for changes in the incidence of individual species between sampling periods while accounting for among-landscape differences.

There were 84 (66%) species with posterior probabilities > 0.9 indicating very strong evidence for a decline in incidence (Table 6). Only one species (Brown Songlark) increased, with 43 species (33%) showing no discernable change between sampling periods. The proportion of species that declined did not depend on habitat preference, mobility, foraging substrate, nesting substrate, diet, biogeographic range or conservation status (Table 6).

Interpretation and practical significance: There were systematic and dramatic declines in the incidence of an overwhelming majority of species between 2002/03 and 2006/07. Declines in incidence were evident when data was pooled across landscapes, or when interrogated at the landscape level. A key finding was that the proportion of species that declined was very similar, irrespective of foraging or nesting guilds, spatial dynamics or conservation concern. Other reports of widespread change in avifaunas have found differences attributable to these kinds of classification (e.g. Woinarski and Catterall 2004; La Sorte 2006). In our case, it seems likely that these declines are climate-driven, or at least reflect the added stresses of sharp reductions in rainfall and increases in temperatures over the past decade in southern Australia.

Table 6. Assessment of changes in incidence based on Bayesian logistic regression. Species were characterized according to several criteria relating to levels of vulnerability to habitat loss and fragmentation, foraging and nesting guilds, conservation concern (Radford and Bennett 2005), mobility (Mac Nally 1995) and distributional range (Blakers *et al*. 1984). Values are numbers of species.

Category	**Classification**	**Declining**	**No change**	**Increasing**	**Total**
Habitat association	Woodland-dependent	48	22	0	70
	Woodland-associated	22	11	0	33
	Open country	14	10	1	25
Diet	Frugivore	2	2	0	4
	Insectivore	45	18	1	64
	Nectarivore	13	6	0	19
	Raptor/vertebrate	13	10	0	23
	Granivore	11	7	0	18
Foraging substrate	Aerial	11	2	0	13
	Bark	4	0	0	4
	Canopy	25	10	0	35
	Ground	40	26	1	67
	Low shrubs	1	3	0	4
	Tall shrubs	3	2	0	5
Nesting substrate	N/A	1	0	0	1
	Burrow	5	0	0	5
	Ground	6	5	1	12
	Hollows	20	5	0	25
	Shrub/canopy	51	32	0	83
	Parasite	1	1	0	2
Conservation status	"Secure"	61	33	1	95
	Conservation concern	23	10	0	33
Biogeographic range	Dry	8	5	0	13
	Mesic	31	19	0	50
	Widespread	45	19	1	65
Mobility	Migrant	21	9	1	31
	Itinerant	11	9	0	20
	Resident	52	25	0	77
All species		84	43	1	128

(iii) Mean incidence for species groups

There was a significant decrease in mean incidence of species grouped into categories of all woodland-dependent species, insectivores and nectarivores between sampling periods (Table 7). There was an average decrease in the mean incidence of all woodland-dependent species of 1.23 ± 0.1 surveys per landscape. This represents a decrease of 37.7% in the number of surveys in which the "average" woodland-dependent species was detected in the "average" landscape (Fig. 7). Similarly, the mean incidence of insectivores decreased by 0.89 ± 0.09 or 29.7% per landscape, and by 2.09 ± 0.34 or 46.9% per landscape for nectarivores (Fig. 7). There was also a significant positive effect of extent of tree cover for all groups, and a significant interaction between sampling period and tree cover such that decreases in mean incidence in 2006/07 were greater in higher cover landscapes.

Table 7. Results of linear mixed models testing for the fixed effects of sampling period (YEAR), landscape-level tree cover (TREE) and their interaction (YEAR*TREE) on mean incidence of all woodland-dependent species, insectivores and nectarivores. Note that TREE was standardized prior to analysis.

Response variable	Model term	Variance component (± s.e.)	Wald-statistic	*d.f.*	*P*	Effect size (± s.e.)
Woodland-dependent species	Landscape (random)	0.26 ± 0.10				
	YEAR (fixed)		134.33	22	<0.001	-1.23 ± 0.11
	TREE (fixed)		37.98	22	<0.001	0.94 ± 0.13
	YEAR*TREE (fixed)		13.88	22	0.001	-0.41 ± 0.11
Insectivores	Landscape (random)	0.54 ± 0.18				
	YEAR (fixed)		99.27	22	<0.001	-0.89 ± 0.09
	TREE (fixed)		18.93	22	<0.001	0.82 ± 0.17
	YEAR*TREE (fixed)		6.95	22	0.015	-0.24 ± 0.09
Nectarivores	Landscape (random)	2.22 ± 0.90				
	YEAR (fixed)		72.79	22	<0.001	-2.90 ± 0.34
	TREE (fixed)		14.21	22	0.001	1.88 ± 0.40
	YEAR*TREE (fixed)		9.55	22	0.005	-1.07 ± 0.35

Interpretation and practical significance: Mean incidence is a surrogate measure for abundance of a group of species. These results corroborate those of the species richness analysis: that there was a dramatic decline in the abundance of a host of woodland-dependent species and that the decrease was most severe in higher cover landscapes. Nonetheless, abundance remained higher in higher cover landscapes.

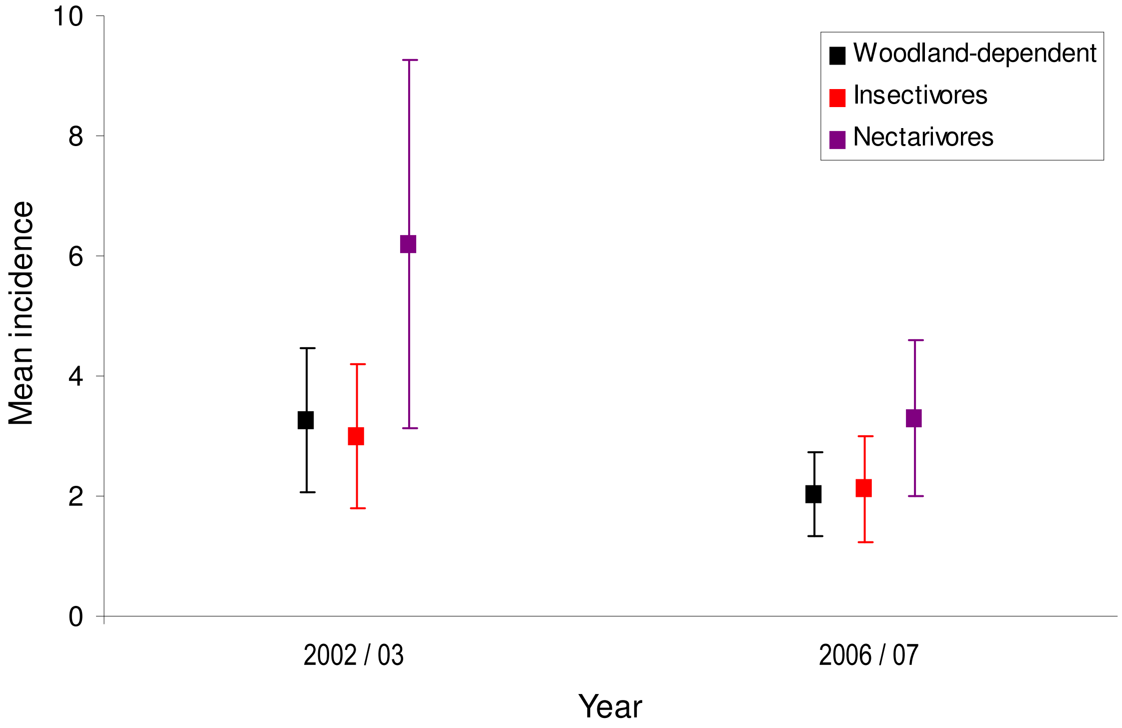


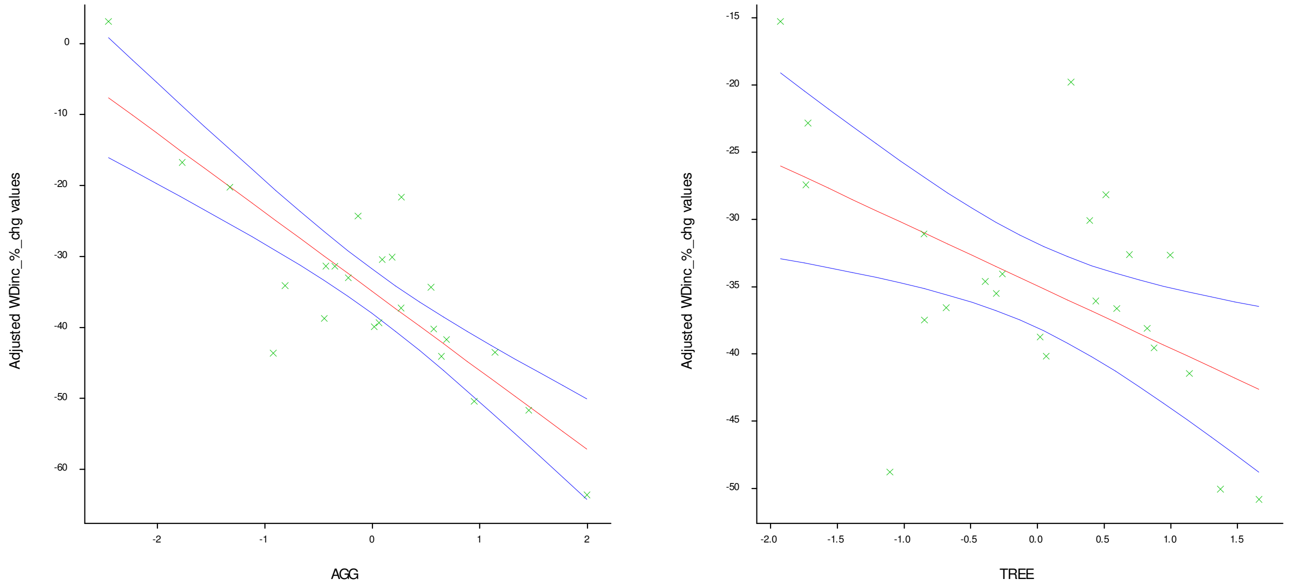
Figure 7. Mean incidence (± 1 standard deviation) of all woodland-dependent species, insectivores and nectarivores in the 2002/03 and 2006/07 sampling periods.

Change in mean incidence of woodland-dependent species between sampling periods in relation to landscape composition and configuration

Change in absolute mean incidence of woodland-dependent species from 2002/03 to 2006/07 was negative in 23 landscapes and positive in one landscape. The all-subsets regression revealed that the most parsimonious model for both absolute and per cent change in mean incidence of woodland-dependent birds included three variables: extent and the degree of aggregation of tree cover and the amount of riparian vegetation in the landscape (Table 8). Larger decreases in absolute and per cent mean incidence were observed in landscapes with more tree cover that was relatively aggregated but this was mitigated to some extent if there was relatively high cover of riparian vegetation (Fig. 8). Extent of aggregation and tree cover also exerted a strong influence on the extent of decline in mean incidence of both insectivores and nectarivores (results not discussed here).

Table 8. Five most parsimonious models returned from all-subsets multiple linear regression of absolute and per cent change in mean incidence of all woodland-dependent species between sampling periods, modelled against landscape attributes. Values in cells indicate probabilities based on F-statistics for variables included in the model.

Model	Model AIC	Aggregation	Patch complexity	Habitat condition	Vegetation diversity	Predominant agricultural land-use	Number of vegetation patches	Mean annual rainfall	Extent of riparian vegetation	Distance to source habitat	Tree cover
Woodland-dependent species (absolute change)	25.05	<0.001							0.001		<0.001
	25.61	<0.001							0.004	0.202	<0.001
	26.13	<0.001			0.310				0.001		<0.001
	26.65	<0.001	0.507						0.002		<0.001
	26.80	0.001			0.334				0.004	0.221	<0.001
Woodland-dependent species (per cent change)	24.17	<0.001							0.042		0.010
	25.49	<0.001							0.094	0.373	0.011
	25.60	<0.001					0.417		0.052		0.011
	25.61	<0.001		0.420					0.040		0.095
	25.99	<0.001									0.017



(a) Extent of aggregation

(b) Extent of tree cover

(c) Extent of riparian vegetation

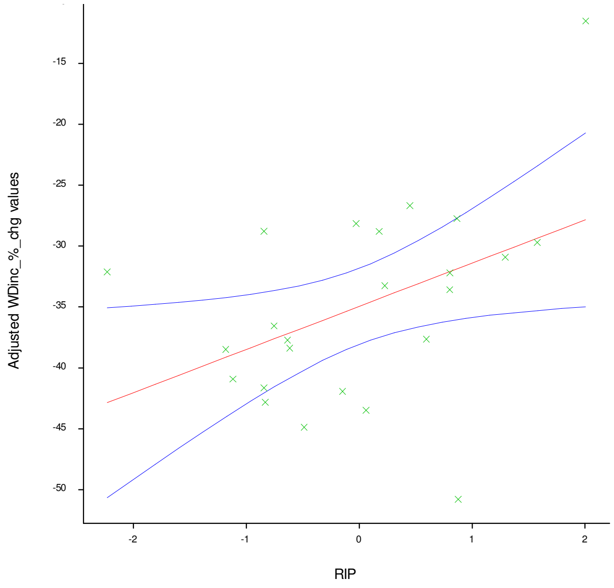


Figure 8. Partial plots of fitted values (red lines) and 95% confidence intervals (blue lines) from the most parsimonious model (lowest AIC) for per cent change in woodland-dependent mean incidence (y-axis) versus (a) extent of aggregation; (b) extent of tree cover; and (c) extent of riparian vegetation. Observed values (green crosses) are also plotted. All explanatory variables are standardized.

Interpretation and practical significance: Landscape composition had a significant effect on the degree of change in mean incidence of woodland-dependent avifauna. As with species richness, the decline in absolute mean incidence was greater in landscapes with more remnant vegetation. However, unlike species richness, proportional declines were also greater in higher cover landscapes. Thus, it appears the higher cover landscapes experienced greater decreases in mean incidence in real terms. However, the magnitude of the decline was again lower in landscapes with more riparian vegetation, suggesting riparian areas provide refugia at the landscape scale. Landscape configuration was also important, with larger declines in both absolute and proportional mean incidence detected in less fragmented landscapes.

This result is not consistent with expectations under extinction debt: that is, accelerated declines would be most expected in more fragmented and lower cover landscapes. It could be that the extinction debt has largely run its course in the low cover landscapes with only hardy species remaining. In high cover landscapes, there may be more of the sensitive species remaining that have potential to decline further as the extinction debt plays out. However, this scenario was not supported by the comparison of species declines among species groups (Table 6) which suggests a more pervasive driver is operating. It is important to note that we may expect greater *species loss* in less fragmented / higher cover landscapes under an extinction debt scenario as species occurring at low density are progressively extirpated from low to high cover landscapes, but this does not hold for changes in incidence of species. All else being equal, there is no clear reason why individual species should decline faster in more intact landscapes, and points to differential habitat quality (e.g., prevalence of predators, habitat condition) or land-use history as the driving factors rather than composition or configuration *per se*.

While the mechanism behind these declines remains unresolved (climate change, ongoing habitat degradation?), this is nonetheless an important result because it suggests population declines are as large, if not larger, in less fragmented and more intact landscapes than in more modified landscapes. Conservation strategies often assume that relatively ‘intact’ landscapes are more resistant to ongoing population declines and therefore are the foundation of most reserve systems. These results challenge that paradigm and suggest that relatively intact landscapes may not be relied upon to sustain species under current conditions and management practices.

Rates of population decline in relation to (i) extent and (ii) aggregation of native vegetation

Species incidence (i.e., the number of surveys during which the species was recorded) can be considered a surrogate for population size. Correlations between the posterior probability of an interaction between landscape-specific error and sampling period, and extent and configuration of tree cover were used to test the influence of the latter variables on population decline. Across all species (n = 159), there were only 18 species with an absolute Pearson product-moment correlation greater than 0.34 ($P < 0.1$) for extent, and 15 species with an absolute correlation greater than 0.34 ($P < 0.1$) for aggregation. Of these, 5 species were negatively correlated with each of extent and aggregation, whereas 13 and 10 species were positively correlated extent and aggregation, respectively.

Interpretation and practical significance: The rate of population decline for most species was not correlated with either extent or configuration of tree cover. However, where significant correlations did occur, they were more often positively correlated with tree cover and aggregation. That is, population declines were more likely in high cover and aggregated landscapes. As discussed above, this is counter to expectations under the extinction debt hypothesis but may reflect a 'relaxation' in less fragmented landscapes, perhaps due to the retention of more 'sensitive' species that are now undergoing substantial population declines.

Threshold response in species richness in relation to extent of tree cover

A comparison of univariate models between the species richness of woodland birds and the extent of tree cover in landscapes in 2006/07 showed that the non-linear relationship (either broken-stick or power model) that was the preferred model in 2002/03 remains prevalent in 2006/07 (Table 9; Fig. 9). The break-point for woodland-dependent richness shifted (non-significantly) slightly – from 10.2% in 2002/03 to 10.7% in 2006/07.

Table 9. Fit of univariate models of species richness of woodland-dependent birds versus tree cover in 2006/07. AIC is corrected for small sample sizes (AIC_c) to calculate Akaike weights (AIC_wt).

Model	**AICc**	**AIC_wt**	**R^2**
Linear	104.42	0.000	0.19
Logarithmic	93.05	0.123	0.50
Quadratic	94.02	0.076	0.53
Power	90.53	0.435	0.60
Broken-stick	90.87	0.366	0.64

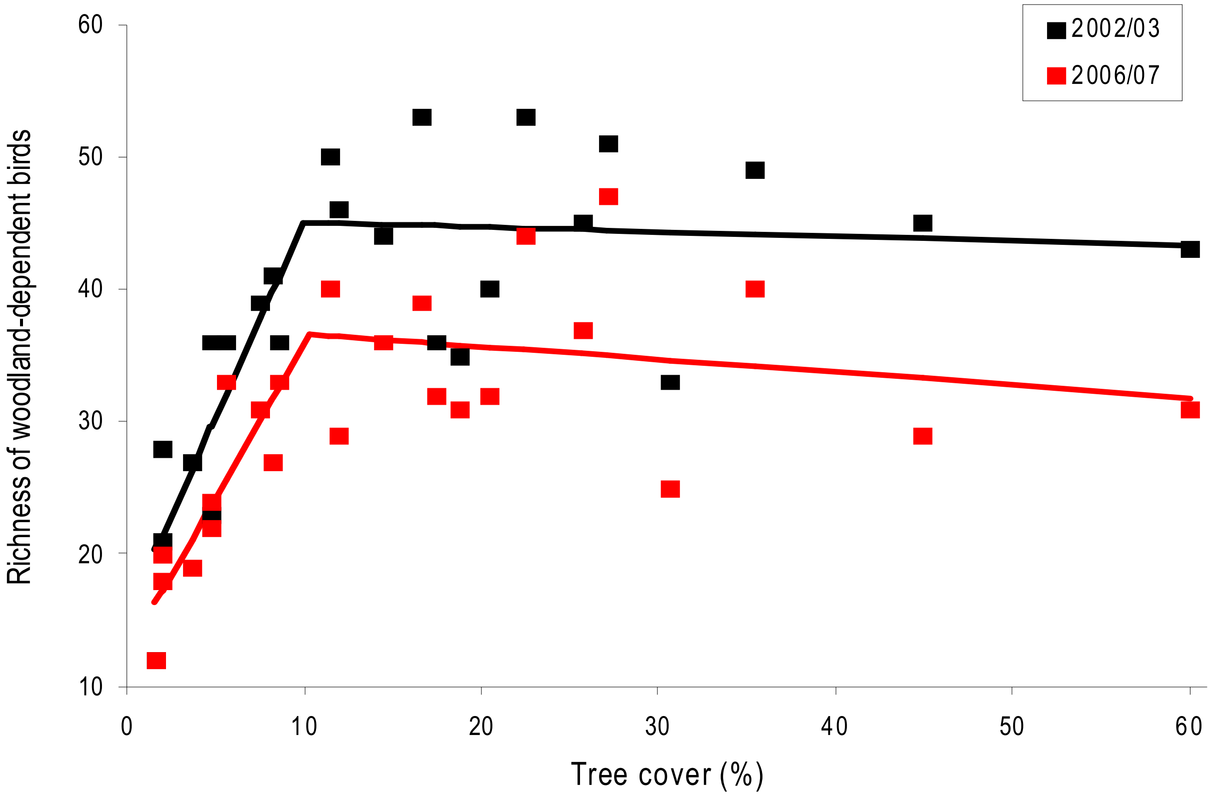


Figure 9. Threshold relationship between landscape-level species richness of woodland-dependent birds and extent of tree cover. Observed (squares) and fitted (lines) values from broken-stick regression models in 2002/03 (black) and 2006/07 (red) are shown.

Interpretation and practical significance: The threshold relationship between landscape-level tree cover and species richness of woodland-dependent birds detected in DUV6 and reported in Radford *et al*. (2005) was re-affirmed in these results. This is an important finding because it indicates the threshold response that generated so much interest when first reported is a robust and repeatable outcome. While the break-point has not moved significantly in the interval between sampling periods, the shift was in the direction predicted in Radford *et al*. (2005), and is consistent with continued loss of species in moderate cover landscapes (Scenario (c) in Fig. 1). This has significant management and policy implications because it suggests there are particular landscapes where restoration activities could achieve substantially greater benefits for similar investment (i.e. in the steepest part of the response curve) and it provides a quantitative measure for setting minimum levels of tree cover. **We re-iterate our conclusions from Radford *et al.* (2005) that the threshold value of 10% tree cover is produced by multiple species extinctions at the landscape level when tree cover falls below 15-20%.** Safe levels must be established well above the threshold. We recommend a goal of 25-35% tree cover in agricultural landscapes. Evidence that the threshold is moving to higher levels of tree cover supports this conservative approach.

Turnover of species

Species turnover (i.e., a change in the composition of the avifauna between sampling periods) was negatively related to landscape-level tree cover: that is, turnover was higher, and more variable, in low cover landscapes, for assemblages of all terrestrial birds and for woodland-dependent species (Fig. 10).

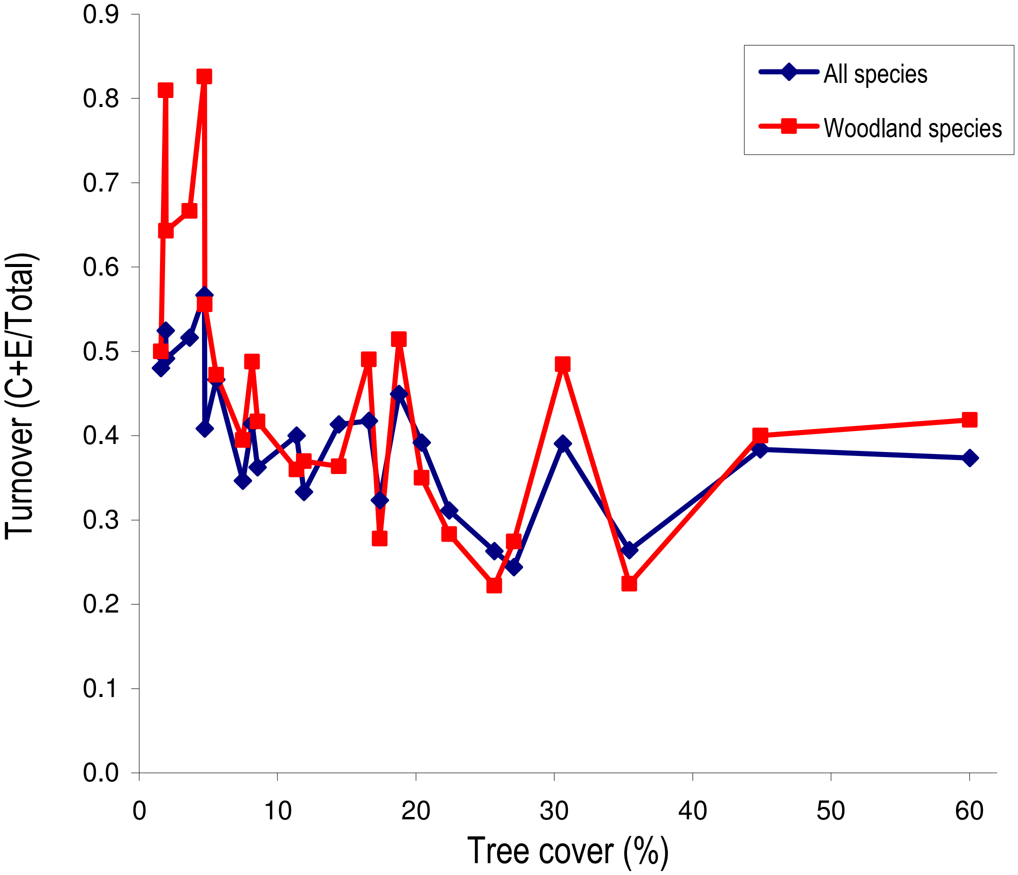


Figure 10. Species turnover [(colonisations + extinctions) / total species richness] of landbird assemblages (blue line and solid diamonds) and woodland-dependent assemblages (red line and solid squares) in relation to landscape-level tree cover.

Interpretation and practical significance: These results confirm greater volatility in assemblage-level composition in low cover landscapes: that is, not only is species richness lower but relatively more species are experiencing local (perhaps temporary) extinctions and re-colonizations in the interval between sampling periods than in high cover landscapes, where composition was relatively stable. This dynamism in community composition is not reflected in the analysis of species richness or incidence. The instability in community composition in lower cover landscapes suggests those communities are more prone to dramatic fluctuations in population size, and thus more vulnerable to local extinctions.

Conclusions

These results clearly demonstrate substantial and rapid species loss and population declines across all groups of species in all landscapes, irrespective of landscape composition and configuration (corresponding to Scenario (d) in Figure 1). However, there was also an indication that the magnitude of species loss and population decline was greater in higher cover and less fragmented landscapes. This may reflect the expression of an 'extinction debt' – a time lag effect in which the consequences of historical clearing and landscape modification are continuing to be realised as species are lost progressively from the most fragmented and modified landscapes to less fragmented landscapes. It is likely that the only species persisting in low cover landscapes in 2002/03 were relatively robust to landscape change because fragmentation sensitive species had long since disappeared from these landscapes. Thus, there was relatively little change in species richness and smaller declines in incidence in these landscapes. In contrast, high cover landscapes supported a suite of species at low density that suffered declines during the interval between sampling periods such that they were undetectable in 2006/07. This corresponds with Scenario (a) in Figure 1.

However, given the pervasive and widespread declines and the magnitude of change detected in a relatively short period, we hypothesize that declines due to any extinction debt have been compounded and accentuated by the added environmental stress imposed by the extended dry period during which this study was conducted. That is, we suggest that much of the observed change reflects the impacts of a drying climate on landscapes that under more favourable climatic conditions had been able to support more diverse and abundant woodland bird assemblages.

The mechanisms by which this marked decrease in rainfall influences the avifauna is likely to relate to on-going reduction in habitat quality and food availability. At a regional scale, there has been relatively little loss of wooded vegetation in recent decades, but habitat quality continues to decline (Department of Sustainability and Environment 2008). The collapses in species richness and incidence reported here suggest strongly that the availability of all types of food has crashed.

The mass exodus of nectarivores from central Victoria during the autumn and winter of 2007 was probably due to the complete failure of eucalypts to flower, an unusual but not unprecedented event (Mac Nally *et al.* 2009). However, if complete flowering failure becomes more frequent under climate change, as would be expected given rainfall-flowering-nectar-honey production models (Porter 1978) and as appears to be occurring (Keatley & Hudson 2007 *cf.* Mac Nally *et al.* 2009), such migrations may be required in the order of every second year rather than once every five years. Although nectarivores are generally mobile and able to track resources over large distances, few are truly migratory, and thus capable of frequent long migrations. While nectarivore abundance rebounded somewhat in 2008 (*pers. obs.*), such mass migrations must impose substantial energy and mortality costs at a population level for many species. The cumulative impost of mass migration at frequent intervals will soon become unsustainable, resulting in permanent population decreases.

The consistent and substantial declines in the sedentary (and migratory breeding) insectivores are even more alarming. These declines reflect on-going and consistent erosion of their resource base. Many insectivores, especially residents, have limited capacity to move to alternative habitats (Mac Nally 1995), so their decline signals mortality without replacement rather than movement. We suggest that the compounding effects of diminishing food resources and deteriorating nest-site quality (fewer sites with increased exposure) have severely limited recruitment over successive years, culminating in the observed population collapses (Mac Nally *et al*. 2009). Recovery of these species depends not only on improved climatic conditions but also on concerted management to alleviate the threats that continue to degrade their habitat.

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