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Landscape-level thresholds of habitat cover for woodland-dependent birds

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Abstract

Theory suggests that a disproportionate loss of species occurs when total habitat cover decreases to 10–30% of the landscape. To date, little empirical evidence has been collected to test for such thresholds in habitat cover, especially at the landscape scale. Here, we present empirical data on the species richness of woodland-dependent birds collected systematically from 24 landscapes (each 100 km^2) that sample a gradient in habitat cover from <2% to 60%. To compare the relative effects of habitat cover and habitat configuration, landscapes with similar amounts of habitat but contrasting configuration (i.e., aggregated versus dispersed) were surveyed and the richness of woodland-dependent birds collated for each landscape. The relationship between species richness, habitat cover and habitat configuration was examined using analysis of co-variance (ANCOVA), multiple linear regression and univariate non-linear modelling. There was a significant effect of habitat cover (co-variate) in the ANCOVA, but the main treatment effect of configuration was not significant. However, comparison of non-linear models indicated that the shape of the response curve of species loss with decreasing habitat cover differed between aggregated and dispersed landscapes. Species richness was significantly related to habitat cover in all analyses, explaining between 55% and 60% of the variance in regression models. Mean patch shape complexity and the extent of habitat aggregation were also significant explanatory variables, but explained less than 10% of the variance in richness of woodland birds. Biogeographic variables (range in elevation and geographic location) explained up to 14% of the variance in species richness. There was strong evidence for a threshold response in species richness: non-linear models (broken-stick, exponential, inverse) exhibiting a sharp decline in species richness in landscapes with less than 10% habitat cover provided a better fit to the observed data than linear models. To our knowledge, this is the first empirical demonstration of landscape-level thresholds in species richness. We emphasise that thresholds in species richness denote multiple species' extinction events, the *end point* of the process of species decline. For viable populations, habitat cover must be maintained well above the threshold level. Finally, thresholds of assemblage measures, such as species richness, potentially mask compositional changes in the avifauna community and may also conceal the loss of species with greater sensitivity to landscape change.
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1. Introduction

Throughout the world, concern about the effects of habitat loss and degradation has stimulated much research into the status of faunal species and assemblages in fragmented landscapes. Much of this work has been carried out at the 'patch-level'; that is, the units of study are spatially discrete remnants of habitat and their use by the fauna. This has provided new understanding of factors that influence the occurrence and status of species in remnant habitats (Bright et al., 1994; Margules et al., 1994; Redpath, 1995), and of the way in which the richness and composition of assemblages are related to attributes such as size and isolation of remnants, vegetation type, and land management practices (Klein, 1989; Hinsley et al., 1995; Bolger et al., 1997; Mac Nally et al., 2000a).

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A recurring theme from many of these studies is that effective conservation of the biota requires a broader 'landscape' or 'regional' perspective on the dynamics of populations and the function of ecological processes. First, single patches of habitat are rarely large enough to support long-term, self-sustaining populations of most species of concern. Rather, persistence depends upon multiple populations and the capacity for interaction between them (Opdam, 1991; Fahrig and Merriam, 1994). Second, some species need to have access to different types of landscape elements to obtain required resources (Law and Dickman, 1998; Dunning et al., 1992; Manning et al., 2004) This may require regular movement for concurrent use of different parts of the landscape (e.g., for foraging and breeding) or sequential use of different habitats to track temporally varying resources (Mac Nally and Horrocks, 2000; Pope et al., 2000). Third, there is considerable evidence that landscape context has an important influence on species composition and on ecological processes within habitat patches (Hobbs, 1993; Lindenmayer et al., 2002; Bennett et al., 2004). Thus, land uses within the mosaic surrounding a habitat patch warrant consideration.

There also is wide recognition among land managers that planning for conservation must occur at broad spatial scales (Saunders et al., 1996). However, knowledge of landscape-level requirements for effective conservation of biodiversity in land mosaics is limited. Key issues include the *amount* (or percent cover) of habitat needed to achieve conservation goals, and the relative importance of habitat *configuration* (Fahrig, 2002). To date, these issues have been addressed mainly through computer simulation modelling (With and Crist, 1995; Fahrig, 1997; With and King, 1999), in which the conclusions are largely dependent on the modelling approach (Fahrig, 2002). The few studies in which empirical data have been collected at the landscape level concur on the importance of amount of habitat but differ in their assessment of configuration effects (Trzcinski et al., 1999; Villard et al., 1999; Cooper and Walters, 2002; Krauss et al., 2004).

An important outcome from modelling has been the recognition that the relationship between species occurrence and landscape pattern is often non-linear. Rather, there appear to be critical thresholds at which a small change in spatial pattern can produce an abrupt shift in ecological response (Andrén, 1994; With and Crist, 1995; Huggett, this issue). The effect of habitat spatial pattern on landscape connectivity appears to be particularly influential (With and Crist, 1995), a view supported by empirical studies that have demonstrated threshold responses to spatial isolation at the patch level (Jansson and Angelstam, 1999; Cooper and Walters, 2002; Radford and Bennett, 2004). Andrén's (1994) review of modelling simulations and patch-level studies concluded that a major ecological change occurs when habitat cover declines to approximately 10–30% of the landscape. Above this level, population decline or species loss is likely to be linearly related to habitat loss, but below a critical threshold the effect of habitat loss is exacerbated by fragmentation effects and rapid population decline or species loss occurs.

These issues are significant for land management and conservation planning because they have implications for setting goals for habitat protection, and for the cost-effectiveness of restoration actions. Andrén's (1994) 'fragmentation threshold' of between 10% and 30% of habitat cover has been embraced by land managers (Barrett, 2000; McIntyre et al., 2000; North Central Catchment Management Authority, 2003) despite a lack of empirical data that test the relationship between habitat extent, habitat configuration and critical thresholds at the landscape level (Harrison and Bruna, 1999; Fahrig, 2002). In this paper, we address this gap in knowledge by reporting on an empirical study of the response of woodland-dependent birds to the pattern of woodland habitat in landscapes in south-eastern Australia. We used landscapes of 100 km^2 as the unit of investigation, selected to represent a contrast in habitat configuration at different levels of habitat cover. Two key questions underpin this study: (i) what is the relative importance of habitat amount and habitat configuration in determining species richness of woodland-dependent birds at the landscape level; and, (ii) is there evidence for a critical threshold in amount of habitat for species richness of woodland-dependent birds?

2. Study region

The study region encloses a large portion (~20,500 km^2) of north-central Victoria, Australia: from the River Murray in the north to the slopes of the Great Dividing Range in the south and east (Fig. 1). The region has a Mediterranean climate, with hot, dry summers (average daily maximum in January is ~30 °C) and most rainfall in winter and spring. Although the climate is relatively uniform across the region, rainfall increases from the north-west to the south-east (range: 400–670 mm per annum).

The two major landforms in the region are the inland slopes of the Great Dividing Range and the riverine plain of the Murray Basin (Environment Conservation Council, 1997). The inland slopes extend across the southern part of the region, ranging in elevation from ~150 to 700 m. They are characterized by Palaeozoic sedimentary rocks that form gently sloping hills and ridges, with granitic outcrops of steeper relief and slope. Box-ironbark forest (overstorey of red ironbark *Eucalyptus tricarpa*, grey box *E. microcarpa*, yellow gum *E. leucoxylon* and red box *E. polyanthemos*) occupies the poor quality soils on the undulating rises and low

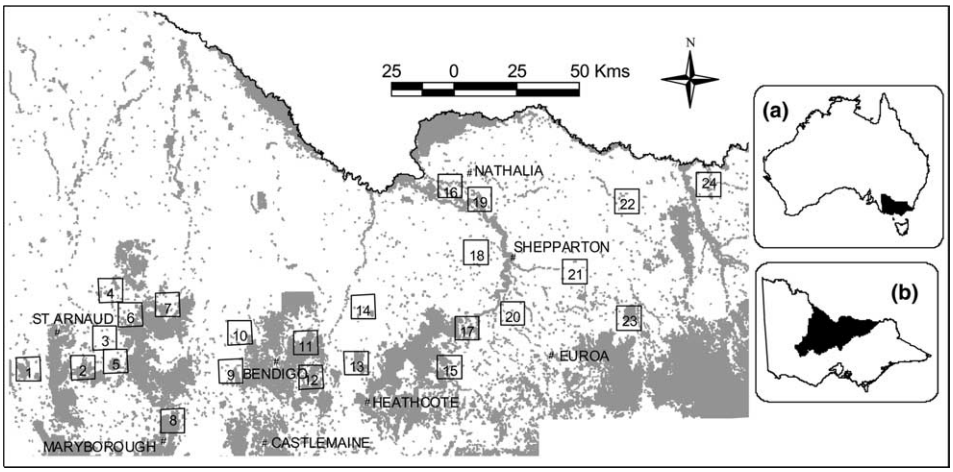

Fig. 1. Location of study landscapes in north-central Victoria (main map). Grey shading represents tree cover. Location of Victoria shown in inset (a); location of study region (inland slopes and northern plains) in Victoria shown in inset (b). Study landscapes are numbered: 1 – Tottington (30.6% tree cover); 2 – Stuart Mill (18.8%); 3 – Logan (1.9%); 4 – Wedderburn (8.2%); 5 – Tunstalls (20.4%); 6 – Wehla (11.4%); 7 – Glenalbyn (17.4%); 8 – Havelock (44.9%); 9 – Shelbourne (11.9%); 10 – Nering (4.7%); 11 – Wellsford (60.0%); 12 – Axe Creek (35.4%); 13 – Crosbie (25.7%); 14 – Runnymeade (1.9%); 15 – Bailieston (16.6%); 16 – Skeleton Creek (8.5%); 17 – Murchison (27.1%); 18 – Gillieston (1.6%); 19 – Undera North (14.4%); 20 – Miepoll (4.7%); 21 – Cosgrove South (5.6%); 22 – Tungamah (3.6%); 23 – Reef Hills (22.4%); 24 – Black Dog Creek (7.5%).

hills. Higher elevations support dry forests dominated by red stringybark *E. macrorhyncha*, red box and long-leaf box *E. goniocalyx*. Grassy woodlands of grey box, white box *E. albens*, yellow box *E. melliodora* and river red gum *E. camaldulensis* occur on the more-fertile soils lower on the slope. To the north, where elevation falls below ~150 m, the inland slopes subside into the alluvial riverine plain. This consists of Pleistocene sediments laid down as ancient floodplain and river deposits, as well as the floodplains of modern rivers and streams. Native vegetation on the riverine plain includes a range of forest, woodland, wetland and grassland communities (Land Conservation Council, 1983). Along rivers, streams and flood-prone areas, grassy woodlands and forests of river red gum and black box *E. largiflorens* are typical. Better-drained soils away from watercourses support grassy or herb-rich woodlands dominated by grey box.

Pastoralism, cropping, mining and forestry have caused profound changes to the native vegetation of the study region since European settlement. Pastoral runs were first established in 1836 and the discovery of gold in 1851 triggered rushes throughout north-central Victoria. Forests were cut extensively such that by 1870 they were severely depleted (Environment Conservation Council, 1997). Following the gold rush, much of the region was opened for farming, with incentives to clear, fence and cultivate the land. The construction of irrigation infrastructure in the 1960s resulted in establishment of horticulture and dairy enterprises in parts of the region. Today, less than 17% of the original area of tree cover remains – even less on the fertile plains and valleys – and is highly fragmented and degraded. The several large tracts of box-ironbark forest that exist are re-growth from the gold rush era and have been subjected to many years of forestry production. A recent review of land-use resulted in substantial additions to the conservation reserve system, such that 45% of public land (~190,000 ha) comprising 6.5% of the original tree cover is now included in the reserve system (Environment Conservation Council, 2001).

3. Methods

3.1. Study design and landscape selection

The study was based on avifaunal surveys in 24 'landscapes', defined as fixed areas of 10 km by 10 km (100 km^2). This size is large relative to the daily movements of most animals, includes several land-uses and vegetation types and is relevant to land management practices, but small enough to be replicated across the region. Note that in this study, the landscape was both the area of interest and unit of replication. Landscapes that satisfied pre-defined criteria were identified first, and a fixed survey effort was then applied in each landscape. This contrasts with most studies of habitat fragmentation in which survey sites or remnant patches are identified first, and landscape characteristics are then inferred from information relating to the surrounding area (i.e., "ripple-out" approach).

Study landscapes were carefully chosen to achieve two design outcomes: first, to represent a gradient in habitat loss, and second, to discriminate between landscapes on the basis of habitat configuration, independent of

habitat cover. This was achieved by selecting 'matched pairs' of landscapes in which amount of habitat was similar but was *aggregated* in one or two relatively large remnants in one landscape and *dispersed* among many smaller remnants and roadside or riparian linear networks in the other. Thus, the study design was conceptually analogous to a single-factor analysis of co-variance (ANCOVA), in which the main treatment effect was habitat configuration, habitat cover was the co-variate and landscapes were the unit of replication.

Tree cover in candidate landscapes was quantified using a geographic information system (GIS) with a grid-cell resolution of 10 m by 10 m. Accordingly, tree cover was used as a surrogate for habitat cover throughout this study. Within the design described above, landscapes were chosen to minimize variation in vegetation composition and structure, topographic relief, urbanisation and wetland areas by selecting landscapes comprised of 'box-dominated' woodlands and forests, where possible. Study landscapes were also stratified by geographic domain (study region was divided into eastern, central and western domains) in relation to amount (low: <10%, moderate: 10–20% and high: >20%) and configuration (aggregated versus dispersed) of tree cover, where possible. Fig. 1 shows the location of study landscapes in the study region.

3.2. Site selection

A pilot analysis was conducted to estimate survey effort per landscape by adapting data from a previous study on the riverine plain (Bennett et al., 1998). Between 13 and 15 survey sites were distributed among different landscape elements within five different landscapes of 100 km^2. Graphs of cumulative species richness from the 1-ha, 20-min surveys were then collated. On average, 92% of species were recorded in the first 10 surveys per landscape with only an additional 2–4 species (4%) recorded with two more surveys. Thus, survey effort in this study was fixed at ten sites per landscape (but 2-ha surveys were used to increase survey coverage).

Native vegetation was recognized as belonging to one of five landscape 'elements' : large remnants (>40 ha), small remnants (<40 ha), riparian vegetation, roadside vegetation and scattered trees. To describe and quantify the avifauna at a landscape scale, it was necessary to sample each of the landscape elements present in a representative way. However, because riparian areas harbour a different suite of birds to 'upland' vegetation (Mac Nally et al., 2000b; Tzaros, 2001), three survey sites were allocated a priori to riparian vegetation in each landscape. The remaining seven sites were stratified in relation to the proportional cover of each landscape element (i.e., 0.1–15% = 1 site; 15–30% = 2 sites; 30–60% = 3 sites; 60–90% = 4 sites; >90% = 5 sites).

Potential site locations were identified on vegetation maps, visited in random order to check suitability (e.g., access, vegetation type, continuity of canopy for roadside and riparian sites) and if appropriate, included as survey sites. Note that habitat condition per se was not a criterion for site selection. A protocol was established to ensure sites were dispersed across the landscape. Each landscape was divided into quarters and at least two sites were located in each quarter. In addition, where possible, sites in the same landscape element were located at least 1 km apart, preferably in different quarters.

3.3. Bird surveys

Fixed-width line-transects (400 m by 50 m, or 500 m by 40 m in some linear sites) were used to survey the avifauna in 2 ha plots at all 240 survey sites (24 landscapes × 10 sites). Surveys were composed of two parts. First, a 'core' survey consisted of a 20-min pass along the transect mid-line during which all species detected (aurally or visually) were recorded as either 'on' or 'off' the transect. Only birds in the hemisphere ahead of the observer were recorded as on-transect. Birds that flew across or along the transect were recorded as 'flying', either below or above the canopy. Individuals foraging above the canopy (e.g., raptors, swallows, woodswallows) were noted separately. This 20-min, 2-ha 'core' survey is consistent with many other studies conducted in south-east Australia (Mac Nally et al., 2000a; Barrett et al., 2003). The second part of the survey comprised a 10-min 'supplementary' period, during which the observer returned along the transect recording any species not detected during the core survey. Supplementary records were regarded as off-transect.

Four survey rounds were completed with every site surveyed twice in spring (October–November 2002 and 2003), once in autumn (March–April 2003) and once in winter (June–July 2003). During spring and autumn, surveys were conducted before midday and in the late afternoon (last three hours before sunset) but throughout the day in winter. The sequence of site visitation was rotated between survey rounds such that no site was surveyed more than twice in the afternoon and every site was surveyed before 10 am on at least two occasions. No more than five sites from the same landscape were surveyed on the same day. Surveys were conducted by two observers (GJC and JQR), who each surveyed each site twice during the course of the study.

3.4. Landscape attributes

Eleven landscape variables were quantified for each landscape (Table 1). Areal extent of tree cover (TREE)

Table 1
Variables used to describe landscape characteristics

Landscape variable		Description (unit)
Tree cover	TREE[a]	Extent of total tree cover per landscape (ha, %)[b]
Riparian tree cover	RIPAR[a]	Extent of riparian tree cover per landscape (ha, %)[b]
Easting	EAST	Australian Map Grid co-ordinate at the centre of each landscape (m)
Range in altitude	ALTRANGE	Difference between highest and lowest contour in landscape (m)
Rainfall	RAIN[c]	Mean annual rainfall (mm)
Landscape habitat condition	CONDITION	Mean site condition score from the 10 survey sites (max: 0.75)
Number of patches	NP_{adj}	Measure of *sub-division* of habitat: the residuals from a quadratic polynomial regression of number of patches against total tree cover
Large patch index	LPI	Index of habitat *aggregation*: area of single largest contiguous patch/total tree cover × 100 (%)
Area-weighted mean of 'related circumscribing circle'	CIRCLE	Measure of *patch shape complexity* calculated as the area-weighted mean of CIRCLE for all patches in the landscape. CIRCLE = 1 – (patch area/area of smallest circumscribing circle). For intact circular patches, CIRCLE = 0; for irregular and elongated patches, CIRCLE approaches 1.
Land use Component 1	LUSEPC1	Positively correlated with dryland grazing in unmodified pasture (loading = 0.88) and irrigated farmland (loading = 0.53); negatively correlated with grazing in modified pastures (loading = −0.95).
Land use Component 2	LUSEPC2	Positively correlated with forestry (loading = 0.70); negatively correlated with dryland cropping (loading = −0.82).

[a] Log_{10} transformed prior to modelling.
[b] Areal extent (ha) divided by 100 is equivalent to % cover because all landscapes were 10,000 ha.
[c] Categorised as two-level factor (<500, >500 mm).

was derived from 1:25,000 scale GIS mapping of tree cover. Riparian tree cover (RIPAR) was calculated by intersecting tree cover with a second GIS layer describing vegetation type and summing the area of riparian vegetation communities. Abiotic conditions were captured in three variables: easting, range in altitude (i.e., topographic relief) and mean annual rainfall (Table 1).

Habitat condition was assessed at each site using the site condition score from the 'habitat hectares' approach (Parkes et al., 2003). Briefly, this approach attempts to assess the 'naturalness', or extent of disturbance, at a site. It compares current conditions against benchmarks for seven key habitat components (number of large trees, tree canopy cover, diversity and modification of the understorey strata, weediness, natural recruitment, organic litter and logs). The benchmarks represent the average characteristics of mature stands of the same vegetation type in an undisturbed state (Parkes et al., 2003). Habitat components are weighted according to their value as indicators of disturbance and contribution to habitat complexity and site condition. The final output is a site condition score out of 0.75. Note that this score is not an index of habitat suitability for fauna, nor a measure of the rarity or conservation significance of the vegetation. This approach produces a single, quantitative estimate of habitat condition relative to an undisturbed ideal that is not confounded by variation in vegetation type. All assessments were conducted by GJC to minimize observer bias. Site condition scores from the 10 survey sites were averaged to estimate 'landscape habitat condition' (Table 1).

Spatial configuration of habitat has three primary components: (1) *sub-division* of contiguous habitat into two or more discrete patches; (2) *aggregation*, which describes the proportion of habitat in relatively large and contiguous remnants, and (3) *patch shape complexity*, which reflects the regularity of patch shape and the perimeter to area ratio. FRAGSTATS v.3.3 (McGarigal et al., 2002) was used to calculate the number of discrete patches per landscape (i.e., sub-division), size of each patch (minimum resolution of 0.01 ha) and hence extent of aggregation, and 'related circumscribing circle', an index of patch shape complexity (Table 1). Tree cover was mapped as 100 m^2 grid cells: contiguous cells, including diagonal neighbours, were defined as a single patch. Thus, discrete patches were defined by a discontinuity in the canopy cover of at least 10 m (in practice, usually much greater).

The proportional cover of seven land-use categories, which together accounted for 97% of the area of the study landscapes (i.e., dryland grazing in unmodified pasture, dryland grazing in modified pasture, irrigated grazing and cropping, dryland cropping, irrigated and dryland horticulture, forestry and nature conservation) were entered into a principal components analysis. The first two 'land-use components' explained 53% and 22% of the variance in the original variables, respectively (Table 1).

3.5. Data analyses

This paper reports only on 'woodland-dependent' species that are 'typical' of north-central Victoria. A 'typical' species is one for which north-central Victoria

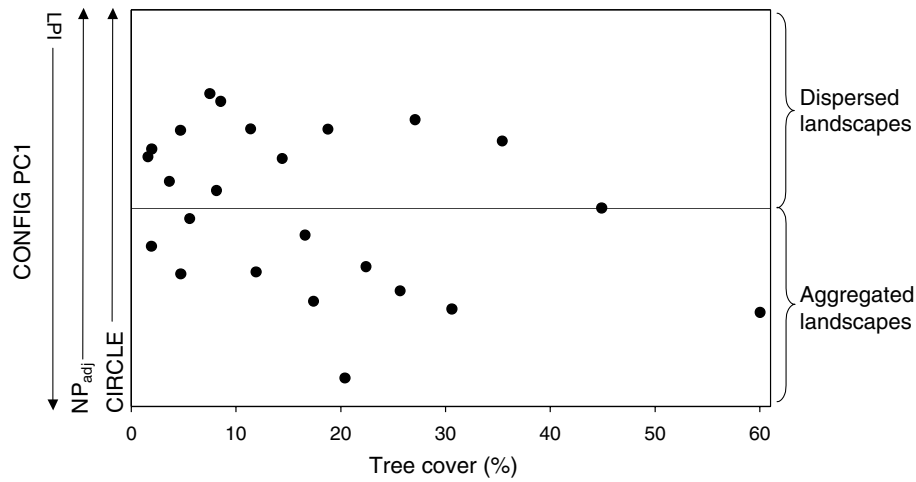

Fig. 2. Habitat configuration (represented by principal component CONFIG PC1) as a function of tree cover for the 24 study landscapes. CONFIG = 0 is indicated by a horizontal line. Landscapes with positive values for CONFIG [low large patch index (LPI), high subdivision (NP_{adj}), highly irregular patches (CIRCLE)] were classified as 'dispersed'; landscapes with negative values for CONFIG (high large patch index, low subdivision, regular patches) were classified as 'aggregated'.

represents a significant part of its biogeographic range (including seasonal migrants) or the species is widespread, though not necessarily abundant, throughout the study region. 'Woodland-dependent' species are primarily associated with woodland or forest habitat for regular daily activities (i.e., foraging, roosting and nesting) and seldom observed in modified environments. Woodland-dependent species were identified a priori and vetted by six ornithologists with extensive field experience in north-central Victoria.

Both on and off-transect records were relevant to avifaunal composition at the landscape level. Thus, all records (including 'flying through' and 'hunting above' the canopy) of woodland-dependent species were collated and three measures of species richness of woodland-dependent birds were generated for each landscape:

1. Richness (RICH) – total number of species recorded.
2. Richness, multiple surveys (RICH2SURV) – number of species recorded in two or more surveys at any particular site.
3. Richness, multiple sites (RICH2SITE) – number of species recorded at two or more sites.

Variables that did not have a normal distribution were transformed to approximate normality and stabilise the variance (Table 1). Further, all species richness variables were tested for spatial autocorrelation using Moran's C test statistic in SPLUS Spatial Stats (Mathsoft, 2000). No evidence of spatial autocorrelation was evident over test neighbourhoods of 15, 20, 30 or 50 km. Thus, it was assumed that the species richness variables were spatially independent.

A test of the a priori study design was conducted using ANCOVA. Variation in species richness (i.e., RICH, RICH2SURV and RICH2SITE) was compared between habitat configuration groups, with total tree cover ($\log_{10}$ transformed) as the co-variate. Habitat configuration groups were defined by the first component of a principal components analysis (CONFIG) that captured 58.5% of the variance of the three habitat configuration variables (i.e., LPI, NP_{adj} and CIRCLE). CONFIG was not significantly correlated with total tree cover ($r = -0.32$; Fig. 2). CONFIG represents a gradient from landscapes in which tree cover is highly aggregated (LPI loading = −0.88) in regular shaped patches (CIRCLE loading = 0.64) with low sub-division (NP_{adj} loading = 0.75) to landscapes with dispersed, highly sub-divided and irregular shaped habitat patches. Landscapes with negative values of CONFIG were designated as 'aggregated' ($n = 12$), whereas 'dispersed' landscapes ($n = 12$) have positive values (Fig. 2). There was no significant difference in tree cover between aggregated and dispersed landscapes ($t_{22} = 1.59$, $p = 0.13$). Thus, the single-factor ANCOVA is expressed as:

$$\text{Richness} = \text{CONFIG(treatment group)} + \text{TREE(co-variate)} + \text{CONFIG} \times \text{TREE}.$$

Standardized residuals and leverage values were checked to identify influential points and verify adherence to assumptions of ANCOVA. Analysis of co-variance was conducted in SPSS v.10 (SPSS Inc., 2000).

One limitation of ANCOVA is that it assumes a linear relationship between the response variable (i.e., richness variables) and the co-variate (i.e., TREE) across all treatment groups. To examine whether the shape of the relationship between tree cover and species richness differed with habitat configuration, a suite of different models (e.g., linear, logarithm, quadratic, cubic, inverse,

exponential, S-curve and power) was fitted separately for aggregated and dispersed landscapes using SPSS v.10 (SPSS Inc., 2000). Models were fitted using untransformed values of tree cover (units in ha). As recommended by Quinn and Keough (2002), the $MS_{residual}$ was used to evaluate model fit when comparing non-linear and linear models.

Multiple linear regression was used to identify relationships between species richness and landscape attributes (Table 1). The richness variables were normally distributed, so a normal error distribution with an identity link function was modelled. All sub-sets regression (GenStat v.6: VSN International, 2002) was used to select the most parsimonious model, based on the Akaike Information Criterion (AIC). In addition to checking residual diagnostics (e.g., standardized residuals, leverage), multi-collinearity diagnostics (e.g., tolerance, variance inflation factor) were also examined for selected models. Surface plots were constructed in SPLUS (Mathsoft, 2000) to examine the inter-dependence of parameters in the selected regression models. These plots are not derived from the model parameter estimates but are three-dimensional scatterplots of the observed data that have been smoothed using a spline function.

Finally, evidence for a threshold in the relationship between tree cover and species richness was examined by comparing linear regression models (tree cover untransformed and $\log_{10}$ transformed) with models fitted to the data by locally weighted non-parametric regression (loess), an exponential curve [$y = a + b\exp(-k \times \text{TREE})$, where $k = -\ln(r)$], an inverse curve [$y = a + (b/\text{TREE})$] and broken-stick regression models (sensu Yan et al., 2000) of the form:

$$\text{Richness} = a + b \times \text{TREE}, \text{ if TREE} < D; \quad \text{and} \quad a + b \times D, \text{ if TREE} > D,$$

where D is the % tree cover at the designated discontinuity. Three broken-stick models were fitted with the discontinuity at 8.5%, 10% and 12%, respectively. To assess the suitability of each model, the AIC was calculated as follows (sensu Quinn and Keough, 2002):

$$\text{AIC} = n[\ln(\text{SS}_{\text{res}})] + 2(p+1) - n\ln(n),$$

where n is the number of data points, p is the number of parameters in the model and SS_{res} is the residual sum of squares. Landscapes were not distinguished by habitat configuration in this comparison. The loess regression will highlight non-linearity in the relationship between species richness and tree cover, should it exist. However, sound evidence for a threshold response (i.e., a discontinuity) necessitates that one of the broken-stick models provides the best fit (i.e., lowest residual error) to the data, followed by the inverse, exponential, $\log_{10}$ transformed and untransformed linear models.

4. Results

4.1. Landscape characteristics

Summary statistics of landscape attribute variables are presented in Table 2. Ten landscapes contained less than 10% tree cover, seven were between 10% and 20% and seven retained more than 20% tree cover. Variation in the landscape habitat condition score was relatively low (co-efficient of variation = 13.8%), implying that, on average, site-level habitat condition was similar in most landscapes. The extent of variation in the number of patches per landscape and large patch index suggests that the landscape selection procedures succeeded in identifying landscapes with contrasting habitat configuration (Table 2; Fig. 2). However, it appears that in most

Table 2
Mean, standard deviation, minimum and maximum values of variables used to describe landscapes characteristics

Variable	Mean ± s.d.	Min–Max
Tree cover (%)	16.9 ± 14.7	1.6–60.0
Riparian tree cover (%)	1.67 ± 2.33	0.03–10.4
Easting	$282_{345} \pm 83_{542}$	152_{930}–438_{170}
Range in altitude	63.5 ± 36.0	10–140
Landscape habitat condition	0.34 ± 0.05	0.18–0.41
Number of patches (raw value)	2980 ± 1164	1255–5127
Large Patch Index	40.9 ± 28.5	2.2–89.8
Mean circumscribing circle	0.68 ± 0.08	0.47–0.82
Grazing: modified pasture (%)	46.7 ± 21.2	0.1–71.9
Grazing: unmodified pasture (%)	14.8 ± 20.4	0.2–70.4
Irrigated grazing and crops (%)	3.1 ± 12.9	0–63.2
Dryland cropping (%)	16.8 ± 14.4	0–50.2
Forestry (%)	8.9 ± 14.0	0–55.8
Nature conservation (%)	6.3 ± 6.9	0–22.7
Horticulture: irrigated and dry (%)	0.3 ± 1.2	0–5.6

Table 3
Results from analysis of co-variance for the relationship between species richness of woodland-dependent birds, habitat configuration and tree cover (co-variate) for 24 landscapes in northern Victoria

Response variable	Source[a]	d.f.	Mean square	F	p
RICH	CONFIG	1	3.1	0.059	0.811
	TREE	1	1359.4	25.818	<0.001
	CONFIG × TREE	1	137.7	2.844	0.107
	Residual	21	52.7		
RICH2SURV	CONFIG	1	0.4	0.015	0.903
	TREE	1	852.1	40.460	<0.001
	CONFIG × TREE	1	91.8	3.705	0.069
	Residual	21	28.0		
RICH2SITE	CONFIG	1	1.8	0.046	0.833
	TREE	1	1063.5	26.961	<0.001
	CONFIG × TREE	1	121.9	3.452	0.078
	Residual	21	39.5		

[a] Note that the non-significant interaction term (CONFIG × TREE) was removed and the mean square of the main effect (CONFIG) and co-variate (TREE) re-estimated.

landscapes, 'average' patch shape tended to be irregular and elongated rather than regular and solid. In general, isohyets of mean annual rainfall ranged from 400–450 to 575–600 mm per landscape, with Reef Hills notable as an outlier (675–700 mm). Eleven landscapes were classified as low rainfall (<500 mm) and 13 as high rainfall (>500 mm). The most widespread land use in the study landscapes was grazing in modified pastures, with dryland cropping and grazing in unmodified pasture moderately common. Irrigated agriculture accounted for 63% of the Gillieston landscape but was generally of lesser importance, and horticultural enterprises occurred in nine landscapes but occupied only a small proportion of land (<5%). Forestry was a significant (>15% cover) land-use in six landscapes, and nature conservation accounted for >10% of a further six landscapes.

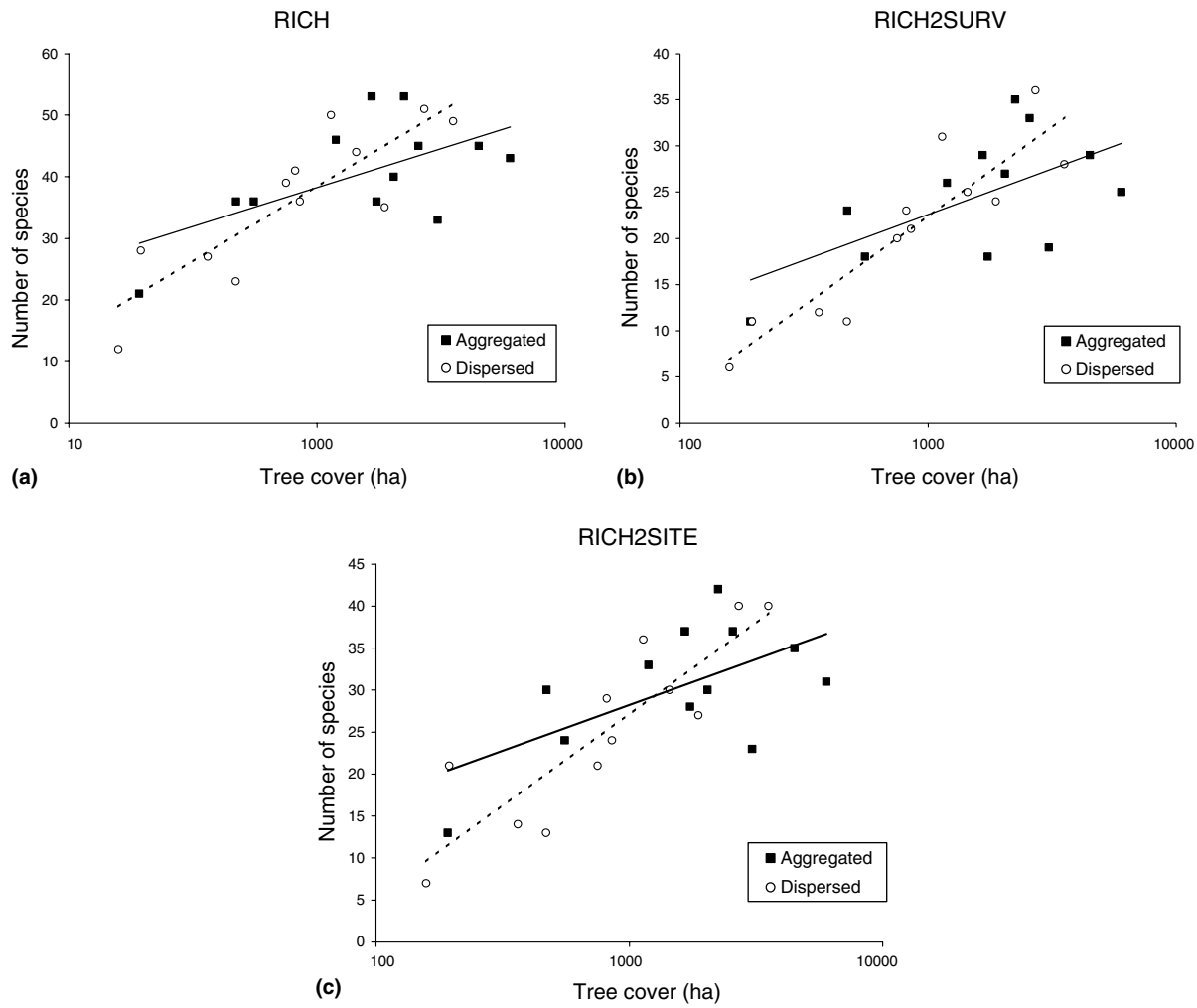

Fig. 3. Graphical representation of analysis of co-variance for the relationship between species richness, tree cover (co-variate) and habitat configuration: (a) RICH, (b) RICH2SURV and (c) RICH2SITE. Filled squares and solid lines represent aggregated landscapes; open circles and broken lines are dispersed landscapes.

Table 4
Univariate model of best-fit[a] for each of the species richness variables in landscapes with aggregated and dispersed habitat cover, respectively. Models were fitted using untransformed values of tree cover (units in ha)

Response variable	Landscape configuration	Best model	Model	$MS_{residual}$
RICH	Aggregated	Inverse	$y = 45.7 - 4645.1/\text{TREE}$	40.07
	Dispersed	Logarithm	$y = 10.6 \times \ln \text{TREE} - 34.7$	40.8
RICH2SURV	Aggregated	Inverse	$y = 28.1 - 3343.0/\text{TREE}$	27.9
	Dispersed	Logarithm	$y = 8.5 \times \ln \text{TREE} - 36.0$	16.4
RICH2SITE	Aggregated	Inverse	$y = 34.6 - 3992.5/\text{TREE}$	29.5
	Dispersed	Logarithm	$y = 9.5 \times \ln \text{TREE} - 38.6$	29.3

[a] Best-fit model selected from linear, logarithm, inverse, quadratic, cubic, power, S-curve and exponential models.

Tree cover was positively correlated with landscape habitat condition ($r = 0.496$, $p = 0.014$) but removal of the Gillieston landscape (low outlier for landscape habitat condition) rendered the correlation not significant ($r = 0.316$, $p = 0.142$). Tree cover was positively correlated with large patch index ($r = 0.550$, $p = 0.005$) and there was a similar trend with riparian tree cover ($r = 0.398$, $p = 0.054$). However, tree cover was not significantly associated with easting ($r = -0.244$, $p = 0.250$), range in altitude ($r = 0.286$, $p = 0.175$), absolute number of patches ($r = -0.025$, $p = 0.906$) or CIRCLE ($r = -0.106$, $p = 0.622$). Tree cover was similar in landscapes in low and high rainfall categories ($t_{22} = -0.561$, $p = 0.581$). Tree cover was negatively correlated with dryland cropping ($r = -0.466$, $p = 0.022$) and positively with forestry ($r_S = 0.774$, $p < 0.001$) and nature conservation ($r = 0.432$, $p = 0.035$), and hence was strongly associated with LUSEPC2 ($r = 0.636$, $p = 0.001$). None of the other land-use categories were significantly correlated with tree cover, nor was LUSEPC1 ($r = -0.098$, $p = 0.65$).

4.2. Summary of the woodland avifauna

A total of 156 species of land-birds was recorded from the 24 study landscapes. However, this analysis is

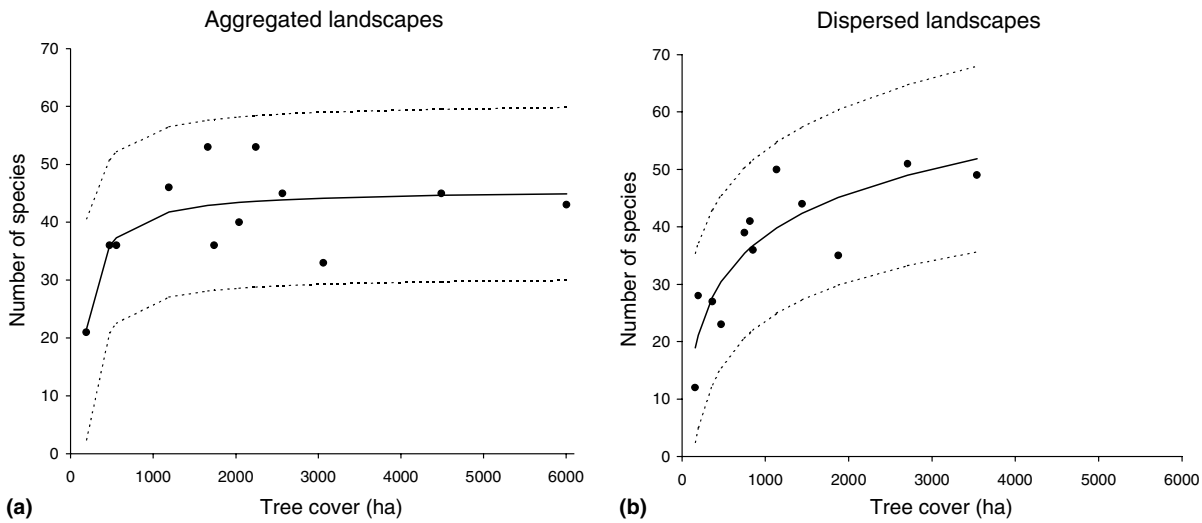

Fig. 4. Univariate model of best-fit (solid line) and 95% confidence intervals (broken line) for species richness of woodland-dependent birds versus tree cover (ha) in landscapes with (a) aggregated (inverse model) and (b) dispersed (logarithmic model) habitat configuration. Solid circles are observed values. Models were not extrapolated beyond the range of the data.

Table 5
Multiple linear regression models of species richness of woodland-dependent birds in study landscapes

Response variable	Parameter	Estimate	s.e.	β[a]	t	p	Change in adj. R^2	Tolerance[b]
RICH	Constant	−73.23	15.15		−4.835	<0.001		
	TREE	17.80	2.61	0.741	6.816	<0.001	0.550	0.910
	CIRCLE	51.97	14.94	0.386	3.478	0.003	0.065	0.871
	ALTRANGE	0.146	0.04	0.497	3.596	0.002	0.058	0.562
	EAST	4.5×10^{-5}	1.6×10^{-5}	0.357	2.739	0.013	0.080	0.633
RICH2SURV	Constant	−53.74	12.82		−4.191	<0.001		
	TREE	14.10	2.21	0.763	6.375	<0.001	0.597	0.910
	CIRCLE	28.21	12.65	0.273	2.230	0.038	0.016	0.871
	ALTRANGE	0.096	0.03	0.424	2.785	0.012	0.040	0.562
	EAST	2.9×10^{-5}	1.4×10^{-5}	0.293	2.041	0.055	0.047	0.633
RICH2SITE	Constant	−53.82	12.62		−4.266	<0.001		
	TREE	12.56	2.90	0.587	4.336	<0.001	0.576	0.653
	CIRCLE	50.60	15.30	0.422	3.306	0.004	0.034	0.734
	ALTRANGE	0.087	0.03	0.333	2.732	0.013	0.124	0.807
	LPI	0.081	0.05	0.244	1.675	0.110	0.025	0.565

[a] Standardized parameter estimates.
[b] Tolerance: the proportion of variable's variance not accounted for by the other independent variables. Calculated as 1 minus R^2 for an independent variable when it is predicted by the other independent variables in the equation. Typically, tolerance values less than 0.1 indicate multicollinearity.

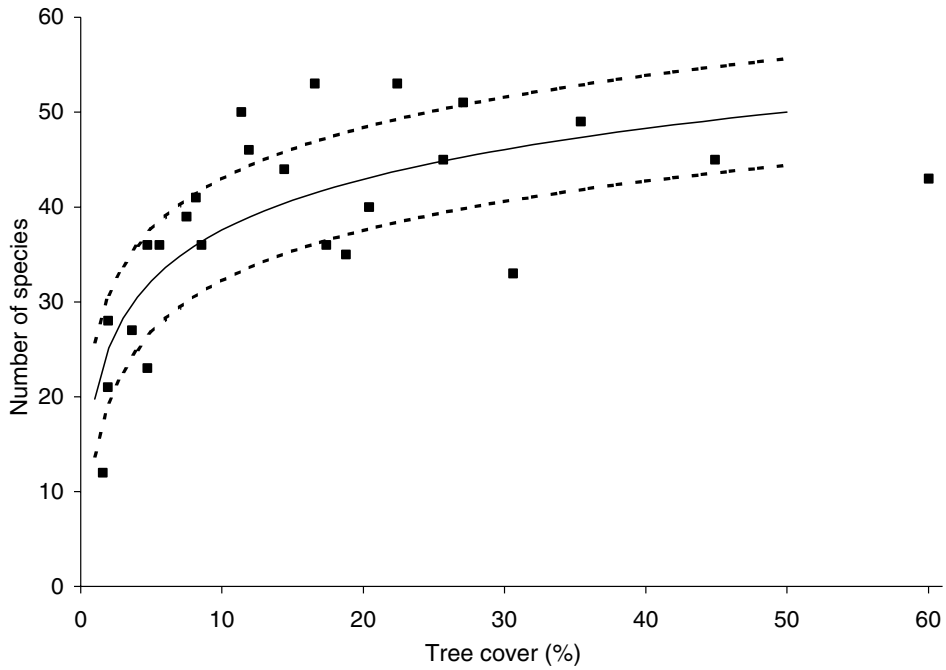

Fig. 5. Richness of woodland-dependent birds (RICH) versus percent tree cover in 100 km^2 landscapes. Filled squares are observed values; predicted values are represented by solid line ±1 standard error (broken lines). CIRCLE, ALTRANGE and EAST were held constant at mean values for predictions of species richness.

concerned only with 80 species considered both typical of the study region and woodland-dependent (see Appendix A for species list and scientific names). Of these, the most commonly recorded species were the white-plumed honeyeater (579 out of 960 surveys), red wattlebird (507 surveys), brown treecreeper (433 surveys), musk lorikeet (405 surveys) and grey shrike-thrush (393 surveys). In contrast, the painted honeyeater, superb parrot, barking owl and black-eared cuckoo were each recorded in only one survey, and a further 16 species were recorded in fewer than 10 surveys (e.g., chestnut-rumped heathwren, speckled warbler, spotted quail-thrush, bush stone-curlew). Half of all woodland-dependent species were recorded in 10–100 surveys.

The total number of woodland-dependent species (RICH) recorded from each landscape ranged from 12 to 53, with a mean of 38.4 species (±10.6 s.d.). For RICH2SURV, the number of species recorded at least twice at any site in a landscape, the mean value was 22.5 ± 8.1 species per landscape with a range from 6 to 36 species. The mean number of species recorded from at least two sites per landscape (RICH2SITE) was 27.7 ± 9.4, ranging from 7 to 42 species. Thus, RICH2SURV and RICH2SITE are more conservative estimates of species richness that exclude woodland birds that are rare or vagrant in a given landscape.

4.3. Relationship between species richness, tree cover and habitat configuration

Results from the ANCOVA were similar for each of the richness variables, RICH, RICH2SURV and RICH2SITE (Table 3; Fig. 3). In each case, the assumption of homogeneity of slopes was met; that is, the interaction between CONFIG and TREE was not significant at $\alpha = 0.05$. After removing the non-significant interaction term, the main treatment effect of CONFIG was not significant. In contrast, the co-variate TREE was significant in each analysis. This suggests that amount of tree cover is the primary factor determining species richness of woodland-dependent birds at the landscape scale. Note that the proportional difference between RICH and RICH2SURV [i.e. (RICH − RICH2SURV)/RICH] was negatively correlated with tree cover ($\log_{10}$ transformed) ($r = -0.650$, $p = 0.001$). A similar correlation exists for the proportional difference between RICH and RICH2SITE ($r = -0.574$, $p = 0.003$).

Although residual diagnostics indicated that the assumptions of ANCOVA were satisfied, non-linear univariate models were examined for aggregated and dispersed landscapes, respectively, to determine whether an improved model fit could be achieved. Furthermore, there was a (non-significant) trend for an interaction between CONFIG and TREE (Table 3, Fig. 3). The results of the curve estimation comparison were qualitatively

similar for each of the richness variables (Table 4). The inverse model achieved the best fit in aggregated landscapes; the logarithmic model was more suitable in dispersed landscapes. Differences between these curves suggest that the decline in species richness is more gradual, and commences at higher levels of tree cover, in dispersed landscapes (Fig. 4).

4.4. Multiple linear regression models of species richness

The same set of factors influencing species richness of woodland-dependent birds was selected in the models for RICH and RICH2SURV: namely, TREE + CIRCLE + ALTRANGE + EAST (Table 5). This model predicts that the richness of woodland-dependent birds

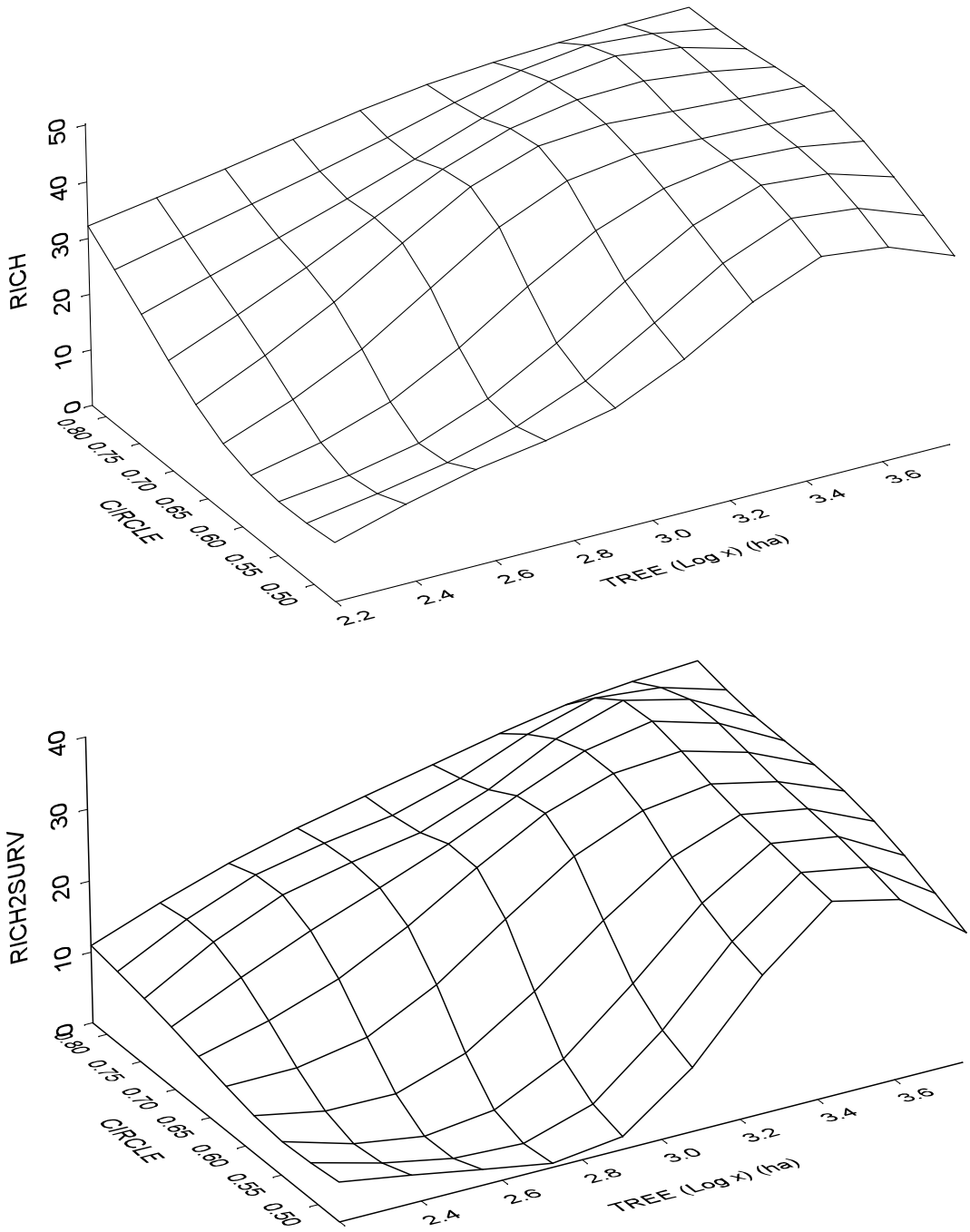

Fig. 6. Three-dimensional surface plots of observed species richness of woodland-dependent birds (z-axis) as a function of $\log_{10}$ tree cover (TREE) (x-axis) and CIRCLE (y-axis). Species richness is depicted by RICH (above) and RICH2SURV (below).

will increase with (i) increasing tree cover, (ii) decreasing regularity in patch shape, (iii) increasing range in altitude and (iv) along an eastward geographic gradient. The model accounted for 75.3% of the variance in total richness of woodland birds (RICH), and 70% of the variance in RICH2SURV. For RICH2SITE, the only difference was that the large patch index replaced easting in the chosen model, which explained 72.5% of the observed variance (Table 5). Thus, when considering only species recorded at two or more sites per landscape, species richness also increases with increasing aggregation of habitat cover.

Examination of the standardized co-efficients reveals that TREE is the most influential parameter in each of the models (Table 5). Predicted species richness declines gradually and linearly as tree cover decreases from 50% to ~15% (Fig. 5; plots for RICH2SURV and RICH2SITE were qualitatively similar with lower predicted values). Tree cover was $\log_{10}$ transformed during model selection; thus, after back-transformation the predicted rate of species loss increases as tree cover falls below 15%, and then increases precipitously in landscapes with less than ~8% tree cover (Fig. 5). However, linear models produce continuous functions, which smooth out discontinuities in the response and hence preclude identification of true threshold relationships.

The multiple linear regressions indicated that patch shape complexity (CIRCLE) was a significant factor in describing species richness at the landscape scale, after accounting for tree cover (Table 5). Surface plots of species richness, tree cover and CIRCLE demonstrate this more clearly (Fig. 6). The rate of increase in species richness attributable to an increase in patch shape complexity (i.e., along the *y*-axis) is greatest in the middle part of the tree cover axis (i.e., along the *x*-axis) (Fig. 6). Thus, it appears that variation in mean patch shape complexity (i.e., CIRCLE) has its greatest impact on species richness at low to moderate levels of tree cover (e.g., between 5% and 15%).

A surface plot was also constructed for the relationship between RICH2SITE, tree cover and large patch index (Fig. 7). The influence of habitat aggregation (i.e., LPI) varies with tree cover. At very low tree cover (<6%), landscapes with highly aggregated habitat (LPI > 60%) have greater species richness. However, as tree cover increases above ~10%, modest increases in LPI (up to ~40%) are accompanied by substantial gains in species richness (Fig. 7). That is, as amount of habitat increases, landscapes with dispersed habitat (i.e., lower LPI) are able to support a comparable number of woodland-dependent species as highly aggregated landscapes.

4.5. Test for thresholds in habitat cover

A scatterplot of the raw data fitted with a locally weighted, non-parametric regression (loess) model indicates that a non-linear relationship exists between tree cover and species richness (Fig. 8). Of the three bro-

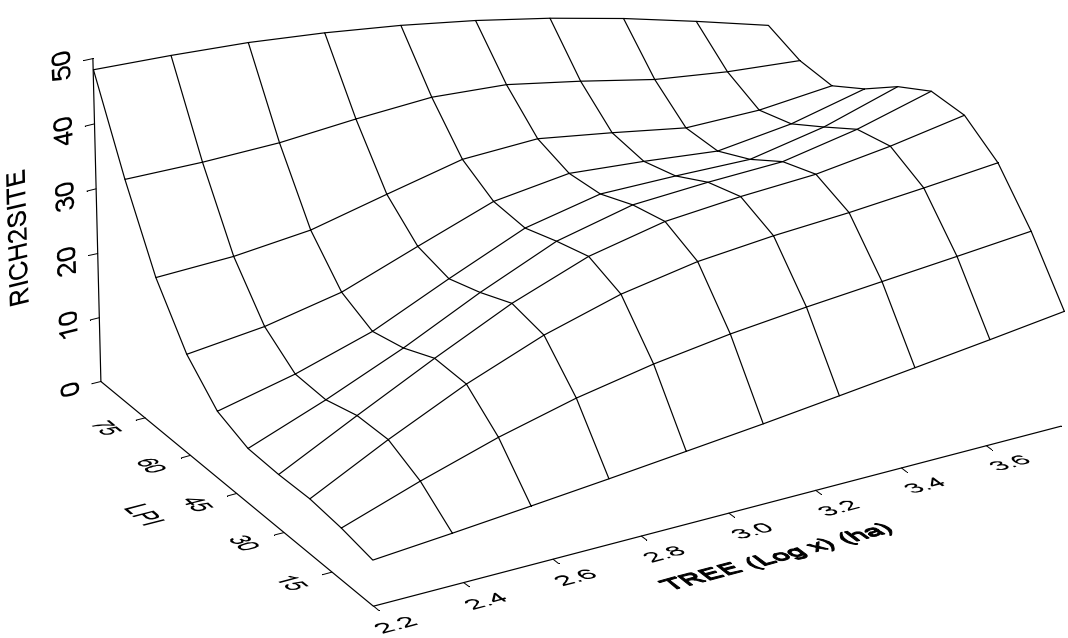

Fig. 7. Three-dimensional surface plot of observed species richness of woodland-dependent birds (RICH2SITE; *z*-axis) as a function of $\log_{10}$ tree cover (TREE) (*x*-axis) and large patch index (LPI) (*y*-axis).

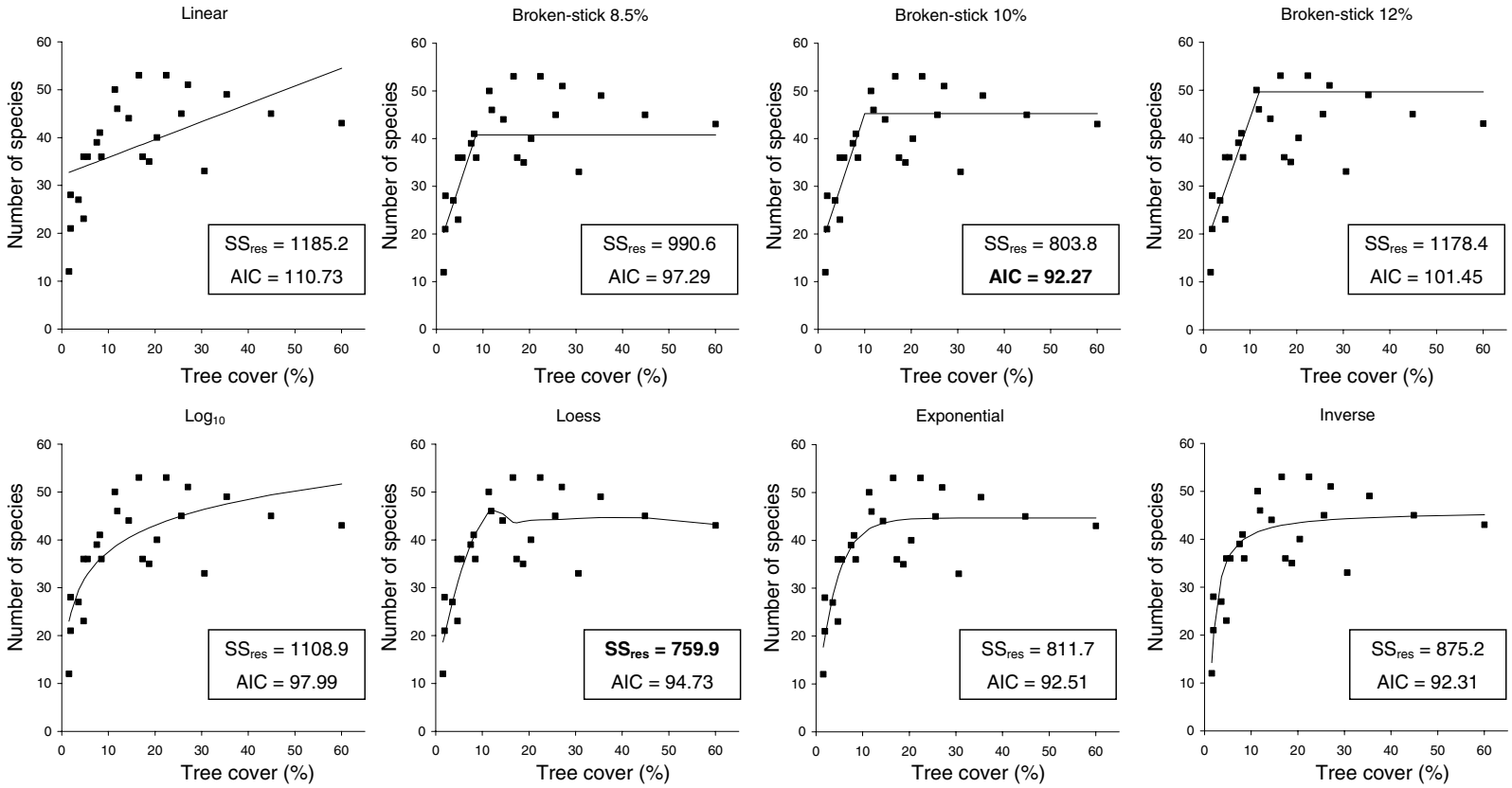

Fig. 8. Models of species richness of woodland-dependent birds (RICH) versus tree cover. The residual error (SS_{res}) and Akaike Information Criterion (AIC) for each model are presented; bold text indicates model with the best fit.

ken-stick regressions, a discontinuity at 10% tree cover was most suitable (Fig. 8). The loess model returned the closest fit to the data in terms of residual error (SS_{res}) but the broken-stick model had the smallest AIC (Fig. 8). Both models were more suitable than the linear regression ($\log_{10}$ transformed or untransformed) and both highlight the discontinuity in the relationship between tree cover and species richness around 10% tree cover. The broken-stick model ($r^2 = 0.69$) consists of a simple linear regression fitted to landscapes with less than 10% cover ($y = 15.59 + 0.029 \times \text{TREE}$), and then a constant value equivalent to the regression estimate at 10% tree cover (45.23) for landscapes with more than 10% tree cover. Note that the exponential model [$y = 44.67 - 40.26 \exp(-\ln(0.997) \times \text{TREE})$] and inverse model [$y = 45.93 - (5012/\text{TREE})$] are very similar to the broken-stick model in shape and fit to the data, and superior to the linear models, as expected for a threshold response.

5. Discussion

5.1. Relationship between woodland birds and tree cover

This study provides strong evidence of a positive relationship between species richness of woodland-dependent birds and the extent of habitat cover at a landscape scale. This concurs with current understanding of avian responses to landscape change. Hitherto, such landscape-scale responses have been demonstrated by research that relies on atlas data collected in an ad-hoc manner by volunteers with varying aptitude (Bennett and Ford, 1997; Trzcinski et al., 1999; Olff and Ritchie, 2002), was conducted at smaller spatial scales (McGarigal and McComb, 1995; Villard et al., 1999), or has implied landscape effects from patch-orientated sampling (Newmark, 1991; Hinsley et al., 1995; Seddon et al., 2003). To our knowledge, this study is unique in demonstrating an effect of habitat cover on species richness at the landscape scale based on empirical data collected systematically in landscapes selected to sample a gradient in habitat availability.

The extent of tree cover explained 55–60% of the variance in the richness variables (Table 5), and the number of species present declined markedly in landscapes with less than 10% tree cover. This implies that many woodland-dependent species have already been lost throughout much of north-central Victoria, especially the northern plains where tree cover has been greatly reduced (~6% cover). Further, the values of RICH2SURV and RICH2SITE were consistently lower than total richness, RICH. Thus, when more stringent rules for species presence in a landscape were applied, fewer species were recorded. The fraction of this difference that was common to all landscapes can be attributed to seasonal movements of some species (e.g., lower temporal occupancy) or species that naturally occur at low densities or in particular vegetation types (e.g., lower spatial occupancy). However, the difference between total richness and the more conservative richness measures was negatively correlated with tree cover. That is, in low cover landscapes, disproportionately more species occurred at low reporting rates, in terms of both number of sites per landscape and surveys per site. Assuming that reporting rate is correlated with population size (Robertson et al., 1995), many species therefore, have smaller populations in low cover landscapes, compromising their long-term persistence, or viability. This provides circumstantial evidence of an extinction debt (sensu Tilman et al., 1994) in low to moderate cover study landscapes. Thus, we agree with predictions that the full extent of species loss associated with habitat loss has yet to be fully realized in north-central Victoria (Robinson and Traill, 1996; Bennett and Ford, 1997; Recher, 1999).

Multiple linear regression identified several other landscape factors that influenced species richness, after accounting for tree cover. Range in altitude (ALTRANGE) was positively related with species richness, accounting for 4–12% of the variance in the richness variables. Higher species richness in landscapes with greater topographic variation probably reflects an increased diversity of vegetation types. A geographic gradient in species richness was also evident (i.e., EAST), with the number of woodland-dependent species higher in eastern than western landscapes, all other factors being equal. This may reflect a gradual increase in annual rainfall, and hence productivity, from west to east that was not captured by the rainfall factor. However, it may also incorporate the influence of several biogeographic features. First, the Goulburn River and its extensive corridor of floodplain woodland is located in the eastern third of the study region. Several landscapes located on the Goulburn River had higher richness than landscapes with equivalent tree cover in other parts of the region [e.g., Murchison (51 spp.) cf. Crosbie (45 spp.), Bailieston (53 spp.) cf. Glenalbyn (36 spp.)]. Second, it may reflect a gradual depletion, in a westerly direction, of species typical of the Bassian biogeographic region in south-eastern Australia.

5.2. Importance of habitat configuration

The analysis of covariance and the multiple linear regression present contrasting messages about the importance of habitat configuration in determining landscape-scale richness of woodland birds. Neither the main treatment effect of configuration, nor the interaction

between configuration and tree cover, was statistically significant at $\alpha = 0.05$ in the ANCOVA, yet two configuration variables – CIRCLE and LPI – were selected in the regression models. Further, there were differences between aggregated and dispersed landscapes in the shape of the curve of best-fit for species richness versus tree cover.

How can such contradictory conclusions be drawn? It may be that information contained in the three separate configuration variables was eroded during the dichotomous classification of landscapes as either aggregated or dispersed. When coupled with the relatively small sample of 24 landscapes (including only three landscapes in excess of 30% tree cover) and small effect size (as indicated by the curve estimation procedure), the failure to reject the null hypothesis of no significant interaction at p values between 0.07 and 0.11 (Table 3) risks Type II errors; that is, not rejecting the null hypothesis when differences are true (Quinn and Keough, 2002). Further, the within-treatment regression lines do not appear to be parallel (Fig. 3), suggesting that the failure to reject the null hypothesis may not be biologically astute. Thus, although clearly secondary to the extent of habitat cover, components of habitat configuration do appear to influence the number of woodland-dependent species in a landscape.

Mean patch-shape complexity (CIRCLE) was consistently included in the multi-variate models, explaining between 1.6% and 6.5% of the variance in species richness. However, the positive coefficient, indicating higher species richness in landscapes with complex, irregular and elongated patches, was counter to expectations that more species occur in regular-shaped habitat with low perimeter to area ratios (Murcia, 1995; Bennett, 1999; Major et al., 2001). It may be that functional connectivity is higher in landscapes with a linear network of riparian and roadside vegetation (i.e., high values of CIRCLE) compared with landscapes with regular but discrete patches (i.e., low values of CIRCLE). Increases in patch shape irregularity influenced species richness most acutely in landscapes with low to moderate tree cover (Fig. 6), environments in which functional connectivity is most likely to be compromised. These results support the contention that, all else being equal, landscapes with greater functional connectivity support more secure populations and correspondingly, a higher diversity of bird species (Taylor et al., 1993; Lynch et al., 1995). It is also relevant that CIRCLE was correlated with the extent of riparian vegetation in the landscape ($r = 0.432$, $p = 0.035$). Therefore, the inclusion of CIRCLE probably reflects the importance of riparian habitat for maintaining beta-level avian richness (Catterall, 1993; Woinarski et al., 2000).

The positive association of large patch index with richness of species present at two or more sites suggests that habitat aggregation is desirable to maintain larger populations of woodland-dependent species, which have a greater chance of persistence through time. The rationale for this lies in the well-documented relationship between patch size, species diversity and population size (Connor and McCoy, 1979; Bolger et al., 1991; Bender et al., 1998). However, landscapes with low (<10%) tree cover appear most receptive to the positive effect of aggregation of habitat (Fig. 7). Aggregated landscapes were usually based around a State Forest, most of which are severely modified by decades of silvicultural management. Thus, landscapes with aggregated habitat tended to be relatively homogenous in terms of vegetation type, habitat complexity and landscape structure. In contrast, landscapes with dispersed habitat encompass multiple patches across the landscape, which increases landscape heterogeneity and in turn provides habitat for a wider variety of species (McGarigal and McComb, 1995; Saab, 1999).

In landscapes with less than 10% tree cover, the benefits afforded by an increase in patch size (i.e., aggregation of habitat) outweigh the constraints of landscape homogeneity, resulting in increased species richness in aggregated landscapes. As habitat cover increases, richness may be enhanced when habitat is dispersed across several relatively large patches, thereby optimising the benefits of both larger patch size and landscape heterogeneity. Many woodland-dependent species (e.g., jacky winter, diamond firetail, southern whiteface) actually prefer open woodland or edge habitat that is prevalent in landscapes with moderate tree cover, and particularly those with a dispersed configuration. However, richness of woodland birds appears to plateau in high cover, aggregated landscapes; the influence of homogeneity of vegetation type and landscape structure in this response needs closer scrutiny.

The relative importance of habitat loss and habitat configuration in the process of species extinction has recently received considerable attention (Andrén, 1994; Fahrig, 1997; Mac Nally, 1999; Trzcinski et al., 1999; Villard et al., 1999; Parker and Mac Nally, 2002). This study is particularly relevant because it is based on empirical data sourced from 'whole' landscapes that directly contrast habitat configuration at different levels of habitat loss across a biogeographic region spanning more than 300 km. A common theme from our results was that tree cover (i.e., habitat loss) was the principal determinant of species richness, and correspondingly species extinction in landscapes with depleted bird communities. The amount of variance explained (adjusted R^2) by tree cover in the regression models was in the order of ten times that explained by the configuration variables (Table 5). Thus, the importance of retaining habitat for the maintenance of woodland-dependent bird diversity is paramount. Further examination of

the relative emphasis placed on habitat loss and habitat configuration based on data from regions with a greater diversity of vegetation types and landscape heterogeneity is desirable.

However, the inclusion of configuration variables in the regression models and the curve estimation procedure (Fig. 4) provides evidence that habitat configuration does influence species richness, particularly in landscapes with low habitat cover. It is possible that the small sample of landscapes with greater than 30% tree cover masked additional configuration effects at higher levels of habitat cover. Nonetheless, incremental loss of habitat is likely to have more immediate consequences in dispersed landscapes with low connectivity because the point at which patch size is compromised is reached sooner, leading to depletion of species richness. In contrast, species richness in aggregated landscapes may be more resistant to habitat loss because the single large patch, which supports the majority of woodland-dependent species, provides a buffer from the impacts of habitat loss. Major decreases in species richness appear to occur only after habitat loss reduces the size of the large patch to such an extent that it can no longer support many woodland-dependent species.

5.3. Landscape-level thresholds

This study provides strong evidence for the existence of a threshold in habitat cover below which there is a rapid decline in species richness of woodland-dependent birds. The broken-stick, loess, exponential and inverse models all exhibit a discontinuity in the tree cover-species richness relationship at close to 10% tree cover (Fig. 8). Below 10% cover there was a rapid loss of woodland-dependent birds as tree cover decreased. Above 10% cover, there was no clear trend in the relationship between tree cover and species richness. Thresholds are often interpreted as the point, or zone, at which there is a shift in underlying processes; where fragmentation effects (e.g., isolation of habitat, disrupted dispersal) exacerbate the impacts of habitat loss alone, resulting in a rapid decline in the probability of persistence of individual species or the number of species present (Andrén, 1994). The recognition that 'real' thresholds exist in 'real' landscapes is a major step forward in understanding of community level responses to landscape change.

It is important to distinguish the current study, examining thresholds in species richness, from other studies that have focused on the probability of extinction of individual species, using either simulation models (Fahrig, 1997, 2001; Hill and Caswell, 1999; With and King, 1999) or field data (McGarigal and McComb, 1995; Henein et al., 1998; Ferrier et al., 2002). A threshold response in species richness implies the simultaneous loss of many species from study landscapes, and thus, heralds *multiple* single-species extinction events. An important difference is that thresholds in species richness signify the *end-point* of the extinction process (population size = 0), whereas extinction thresholds for individual species represent the point at which the extinction process *commences* (probability of survival <1) (Fahrig, 2002). This may partly explain why studies of species richness, including the current one, identify thresholds in habitat cover at the lower end of Andrén's (1994) range (Bennett and Ford, 1997; Reid, 2000; Drinnan, this issue).

Simple richness measures are unitary and additive; a species recorded as 'present' adds a single unit of value to the measure, irrespective of the spatial or temporal extent of occupancy. However, it is imperative not to confuse occupancy with viability (i.e., probability of persistence = 1). Thus, while all species recorded as present contribute to species richness, for some species the amount of habitat in the landscape may be below their extinction threshold (i.e., probability of persistence <1). If this is common (i.e., landscapes are 'carrying' an extinction debt), it will shift the threshold for species richness towards lower levels of habitat cover compared with extinction thresholds for individual species. However, as the extinction debt is expressed over time, species that currently occur in landscapes below their extinction threshold are likely to disappear, shifting the threshold in species richness to higher values of habitat cover.

A second reason why the observed threshold in species richness was at the lower end of expectations relates to the grain of investigation (i.e., landscapes of 100 km^2), which is larger than most other 'whole-of-landscape' studies, or the scope of landscape indices used in most patch-orientated studies. The grain of our investigation may be such that configuration effects at smaller spatial scales are masked by landscape measures, particularly at moderate levels of habitat cover. That is, measures of species richness for entire landscapes are likely to be more robust to localised configuration effects (i.e., patch isolation) than patch-based richness because much of the between-site variation related to local configuration is absorbed, or dampened, in the landscape-scale richness measure. For example, a patch that is locally isolated (e.g., no habitat within 2 km) may have low species richness but other sites in the landscape compensate for this, resulting in no overall decrease in species richness at the landscape level. It is only when isolation effects become widespread or habitat loss retards ecosystem function that configuration effects are evident in landscape scale parameters.

Finally, sampling effort was biased towards low cover landscapes, in terms of proportion of woodland habitat surveyed. For example, in landscapes with 5% cover, we surveyed approximately 4% (10×2 ha/500 ha) of

available habitat compared with only 0.4% (10 × 2 ha/5000 ha) in landscapes with 50% cover. Although this sampling strategy precludes survey effort from confounding species richness (in contrast to proportional sampling) and increases the confidence placed in detected impacts of habitat loss, it may delay the point at which threshold responses become apparent, effectively shifting the detected threshold to a lower value of habitat cover.

5.4. Implications and limitations of thresholds for conservation management

Threshold responses are potentially a valuable tool for conservation planning because they can assist managers to identify quantitative goals that correspond with ecological outcomes. It is crucial to recognise that thresholds represent points of instability at which natural systems collapse and therefore must be avoided completely rather than used a minimum goal or level for management. In this instance, a goal well in excess of 10% tree cover is required to prevent the collapse of the woodland-dependent avifauna in landscapes in northern Victoria. As noted above, the rapid decline in species richness corresponds with the end point of extinction processes for multiple species. Thus, the management goal should be well on the 'safe' side of the critical threshold at which abrupt ecological changes occur. Threshold responses can also be used to achieve more efficient use of conservation resources. For example, habitat restoration of sufficient magnitude to shift a landscape across the threshold is likely to have much greater conservation benefits than actions that fall below the threshold.

There is a risk that identifying a single richness threshold for a diverse group such as 'woodland birds' may mask other important responses, because species respond to the environment in different ways (Lindenmayer et al., this issue). Some species will have extinction thresholds at higher levels of tree cover than for the overall assemblage, and may be lost from landscapes before the richness threshold is crossed. Species with specialised habitat requirements are especially vulnerable to disproportional loss of key vegetation types (e.g., on fertile soils, wetlands), such that small levels of clearing can have dramatic consequences for their survival. Other species may not show a threshold response at all. Setting management targets based on an assemblage-level response (such as species richness) may result in inadequate protection for the most sensitive species. Consequently, it is important to understand the form and shape of the response to landscape pattern for species that represent different foraging types, migratory strategies and body sizes. It is not possible to manage the landscape for every individual species, however, and so we believe it is useful to understand the response of assemblages such as woodland-dependent birds, known to be of conservation concern.

Non-linear ecological relationships do not necessarily represent threshold responses, and conversely, different types of ecological thresholds (e.g., state-transition models, degradation thresholds) are not necessarily identified by non-linear modelling (Whisenant, 1999). Further work is required to clarify what is, and what is not, usefully described as a critical threshold (Huggett, this issue). Sharp thresholds, corresponding with abrupt changes in ecological responses, will more readily translate to management guidelines than broad zones of change. From a conservation perspective, it is also imperative that the habitat measure with which a threshold is associated represents a causal relationship. Here, there is a sound basis for believing that tree cover has a causal relationship with richness of woodland birds. In addition, tree cover was clearly the most influential variable explaining the richness of woodland birds.

Long-term persistence of woodland birds in landscapes depends on maintaining breeding populations. As noted previously, analyses presented here are based on presence of species, not on occurrence of breeding populations. A major limitation in conservation planning for rural environments is an almost complete lack of knowledge of the demographic status of woodland birds in heterogeneous landscapes. We need to understand better how the extent, configuration and quality of habitats at the landscape level are associated with parameters such as population age structure, breeding success and trends in population size.

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Appendix A. Woodland-dependent species recorded in study landscapes, north-central Victoria, 2002/2003. Percentage of surveys, sites and landscapes in which each species was detected are presented

Common name	Scientific name	No. of surveys (n = 960)	No. of sites (n = 240)	No. of landscapes (n = 24)
Brown quail	*Coturnix australis*	0.42	1.67	16.67
Painted button-quail	*Turnix varia*	0.42	1.67	16.67
Peaceful dove	*Geopelia striata*	7.60	20.42	66.67
Common bronzewing	*Phaps chalcoptera*	12.71	37.08	91.67
Bush stone-curlew	*Burhinus grallarius*	0.52	1.25	12.50
Southern boobook	*Ninox novaeseelandiae*	0.83	2.50	16.67
Barking owl	*Ninox connivens*	0.10	0.42	4.17
Musk lorikeet	*Glossopsitta concinna*	42.19	65.83	75.00
Purple-crowned lorikeet	*Glossopsitta porphyrocephala*	11.35	36.25	79.17
Little lorikeet	*Glossopsitta pusilla*	4.17	13.75	58.33
Superb parrot	*Polytelis swainsonii*	0.10	0.42	4.17
Crimson rosella	*Platycercus elegans*	5.73	15.42	50.00
Yellow rosella	*Platycercus elegans flaveolus*	1.04	2.92	12.50
Swift parrot	*Lathamus discolor*	4.06	14.58	50.00
Tawny frogmouth	*Podargus strigoides*	0.31	1.25	12.50
Australian owlet-nightjar	*Aegotheles cristatus*	1.56	5.42	45.83
Dollarbird	*Eurystomus orientalis*	1.04	4.17	29.17
Azure kingfisher	*Alcedo azurea*	0.42	1.25	8.33
Sacred kingfisher	*Todiramphus sanctus*	7.71	21.25	75.00
Fan-tailed cuckoo	*Cacomantis flabelliformis*	0.21	0.83	8.33
Black-eared cuckoo	*Chrysococcyx osculans*	0.10	0.42	4.17
Horsfield's bronze-cuckoo	*Chrysococcyx basalis*	4.38	16.67	83.33
Shining bronze-cuckoo	*Chrysococcyx lucidus*	0.21	0.83	8.33
Tree martin	*Hirundo nigricans*	7.50	20.42	70.83
Grey fantail	*Rhipidura fuliginosa*	8.65	19.58	66.67
Leaden flycatcher	*Myiagra rubecula*	0.21	0.83	8.33
Jacky winter	*Microeca fascinans*	13.33	27.50	87.50
Scarlet robin	*Petroica multicolor*	1.04	3.75	20.83
Red-capped robin	*Petroica goodenovii*	3.85	10.00	54.17
Hooded robin	*Melanodryas cucullata*	2.19	5.00	29.17
Eastern yellow robin	*Eopsaltria australis*	7.60	15.42	58.33
Golden whistler	*Pachycephala pectoralis*	5.42	19.17	83.33
Rufous whistler	*Pachycephala rufiventris*	12.19	32.50	87.50
Gilbert's whistler	*Pachycephala inornata*	1.25	3.75	25.00
Grey shrike-thrush	*Colluricincla harmonica*	40.94	65.42	95.83
Crested shrike-tit	*Falcunculus frontatus*	14.79	36.25	95.83
Crested bellbird	*Oreoica gutturalis*	7.40	14.58	50.00
White-bellied cuckoo-shrike	*Coracina papuensis*	3.23	10.83	54.17
White-winged triller	*Lalage sueurii*	4.06	14.17	58.33
Spotted quail-thrush	*Cinclosoma punctatum*	0.42	1.67	16.67
Grey-crowned babbler	*Pomatostomus temporalis*	1.67	3.33	16.67
White-browed babbler	*Pomatostomus superciliosus*	10.21	18.33	58.33
Western gerygone	*Gerygone fusca*	3.02	8.33	41.67
Weebill	*Smicrornis brevirostris*	15.21	28.75	79.17
Southern whiteface	*Aphelocephala leucopsis*	1.77	4.17	33.33
Striated thornbill	*Acanthiza lineata*	2.40	6.25	37.50
Yellow thornbill	*Acanthiza nana*	6.98	15.42	66.67
Brown thornbill	*Acanthiza pusilla*	0.73	2.50	16.67
Chestnut-rumped thornbill	*Acanthiza uropygialis*	0.31	1.25	12.50
Buff-rumped thornbill	*Acanthiza reguloides*	4.27	7.92	37.50
White-browed scrubwren	*Sericornis frontalis*	1.67	2.92	20.83
Chestnut-rumped heathwren	*Hylacola pyrrhopygia*	0.21	0.83	8.33
Speckled warbler	*Chthonicola sagittata*	0.42	1.67	12.50
Superb fairy-wren	*Malurus cyaneus*	19.27	30.00	87.50
Dusky woodswallow	*Artamus cyanopterus*	12.60	31.25	83.33
Varied sittella	*Daphoenositta chrysoptera*	3.23	10.00	62.50
Brown treecreeper	*Climacteris picumnus*	45.10	55.83	95.83
White-throated treecreeper	*Cormobates leucophaeus*	13.65	21.67	75.00
Mistletoebird	*Dicaeum hirundinaceum*	5.94	19.17	75.00
Spotted pardalote	*Pardalotus punctatus*	12.08	30.42	79.17
White-naped honeyeater	*Melithreptus lunatus*	4.48	17.50	70.83
Black-chinned honeyeater	*Melithreptus gularis*	21.35	41.25	87.50

Appendix A (*continued*)

Common name	Scientific name	No. of surveys (n = 960)	No. of sites (n = 240)	No. of landscapes (n = 24)
Brown-headed honeyeater	*Melithreptus brevirostris*	15.52	33.75	91.67
Eastern spinebill	*Acanthorhynchus tenuirostris*	0.21	0.83	8.33
Painted honeyeater	*Grantiella picta*	0.10	0.42	4.17
Fuscous honeyeater	*Lichenostomus fuscus*	18.02	27.08	62.50
Yellow-faced honeyeater	*Lichenostomus chrysops*	2.40	8.33	45.83
White-eared honeyeater	*Lichenostomus leucotis*	1.56	5.42	37.50
Yellow-tufted honeyeater	*Lichenostomus melanops*	15.31	21.67	58.33
White-plumed honeyeater	*Lichenostomus penicillatus*	60.31	75.42	100.00
Red wattlebird	*Anthochaera carunculata*	52.81	73.75	91.67
Blue-faced honeyeater	*Entomyzon cyanotis*	1.25	5.00	33.33
Noisy friarbird	*Philemon corniculatus*	5.21	17.92	66.67
Little friarbird	*Philemon citreogularis*	3.02	7.92	33.33
Diamond firetail	*Stagonopleura guttata*	2.40	7.08	29.17
Red-browed finch	*Neochmia temporalis*	1.88	5.00	29.17
Olive-backed oriole	*Oriolus sagittatus*	5.63	18.75	66.67
Apostlebird	*Struthidea cinerea*	0.63	1.67	4.17
White-winged chough	*Corcorax melanorhamphos*	30.42	57.92	95.83
Pied currawong	*Strepera graculina*	2.08	7.08	33.33

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