RESEARCH PAPER

Spurious thresholds in the relationship between species richness and vegetation cover

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ABSTRACT

Aim Thresholds often exist in the relationship between species richness and the area of remaining habitat in human-modified landscapes, prompting debate about the mechanisms responsible. We hypothesize that if species–area relationships differ with underlying factors such as landscape productivity, and such factors correlate with patterns of habitat clearance, then spurious thresholds can arise where the separate species–area relationships intersect. We assessed whether this phenomenon could explain landscape-level species–area relationships for birds occupying 31 landscapes of 100 km² in eastern Australia.

Location Eastern Australia.

Methods Landscape-level species richness estimates were modelled as a function of the percentage of native vegetation remaining in the study landscapes. The performance of traditional species–area curves and continuous and discontinuous piecewise models was compared using an information theoretic approach. Separate models for high- and low-productivity and high- and low-fragmentation landscapes were examined to determine whether they implied different species–area relationships.

Results The species–area relationship exhibited a rapid change-point at approximately 40% vegetation cover, but this was most parsimoniously explained by two disjunct slopes rather than a continuous threshold model or a classic species–area curve. Exploration of models fitted separately to high- and low-productivity landscapes suggested that such landscapes may differ in their characteristic species–area relationships.

Main conclusions The observed pattern is consistent with the spurious threshold hypothesis, and opens a new avenue of enquiry into the processes behind apparent ecological thresholds. This hypothesis may be valid in other regions where clearing history is confounded by underlying factors such as landscape productivity, and demands further research. In such systems, real thresholds for different landscape types may occur at different levels of cover, or might not exist at all. If so, a simple space-for-time substitution may not be valid, and management prescriptions based on threshold values (e.g. 40%) will be flawed.

Keywords

Australia, bird richness, habitat fragmentation, landscape modification, landscape productivity, species–area relationship, species richness estimators, thresholds, vegetation cover.

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INTRODUCTION

The existence, nature and cause of thresholds in the relationship between habitat extent and species richness have long been debated (Andrén, 1994, 1997; Lindenmayer & Luck, 2005; Swift & Hannon, 2010). Species–area relationships in oceanic archipelagos and habitat islands commonly exhibit one or more rapid change-points (Lomolino, 2000; Santos *et al.*, 2010), yet examples relating to habitat extent at the landscape level were, until recently, rare. There is now growing evidence that such thresholds are common, though not ubiquitous, in landscape ecological studies (Swift & Hannon, 2010). In particular, recent work examining patterns of landscape-level species richness in faunal assemblages has found sudden change-points when native vegetation cover is about 10–20%, often with a limited effect of vegetation cover on species richness above this level (Radford *et al.*, 2005: Schmidt & Roland, 2006). However, both the mechanisms behind such threshold relationships and their spatial generality remain unclear (Swift & Hannon, 2010).

The simplest explanation for relationships between species richness and habitat extent is that of random or passive sampling (Connor & McCoy, 1979) – more habitat contains more individuals, which will include more species through chance alone. This hypothesis cannot, however, explain the existence of sudden thresholds. The rapid decrease in richness below a certain (generally low) percentage of habitat cover in a given landscape suggests different processes operating or emerging to dominate in low-cover landscapes.

Three main classes of explanation have been advanced for the existence of such thresholds. Firstly, disproportionately greater fragmentation at low levels of habitat cover may compound species loss, as decreases in mean patch area and increases in isolation accelerate in landscapes once habitat cover drops below about 10–30% (Andrén, 1994). Secondly, thresholds might reflect nonlinearities in the relationship between population size and extinction risk. Reduction to a certain amount of habitat could mean population sizes fall below the 'extinction threshold', triggering Allee effects (Fahrig, 2003). Thirdly, if the response of species to habitat loss is lagged in time, then as clearing continues, payment of the extinction debt will start to occur as population decline 'catches up' (Tilman *et al.*, 1994; Swift & Hannon, 2010).

We propose an alternative mechanism that may explain the existence of apparent thresholds in the species–area relationship. Multiple factors correlate with decreasing native vegetation cover across different landscapes (Radford *et al.*, 2005). For example, the amount of habitat loss in a landscape is commonly confounded by productivity gradients and, consequently, land use (McAlpine *et al.*, 2002). Among anthropogenic landscapes, those with low levels of remaining habitat cover are those with more fertile (and thus productive) soils, while more intact landscapes tend to be those on poorer, rockier soils and/or steeper topography (Scott *et al.*, 2001; Pressey *et al.*, 2002). Such biases in anthropogenic modification could result in an artefactual threshold at the point in the species–area relationship where landscapes with more vegetation cover are those dominated by lower underlying productivity and less-intensive matrix land uses.

If the shift in system dynamics below the threshold level of vegetation cover is due to different species–area relationships associated with different underlying productivity in low-cover and high-cover landscapes, this could mean that thresholds in those different relationships may be masked, or indeed, may not exist at all (Fig. 1). In this situation, the space-for-time substitution assumption inherent in many studies of patterns of species richness in modified landscapes may not be valid, and management prescriptions based on thresholds will be flawed.

In this paper, we examined whether different underlying species–area relationships could generate spurious thresholds in the relationship between landscape-level species richness of woodland-dependent birds and native vegetation extent using data from eastern Australia. Firstly, we asked: do rapid change points exist in the relationship between vegetation cover and species richness, and are these best characterized by classic species–area curves, single threshold models or two or more separate underlying relationships? And secondly, do differences among landscapes in underlying productivity or habitat fragmentation better explain nonlinearities in the species–area relationship? We show that the species–area relationship in this system is poorly characterized by classic species–area models and continuous threshold models. While rapid change-points exist, they may arise in this case from the intersection of separate species–area relationships, possibly associated with underlying productivity gradients. Spurious thresholds which emerge through this mechanism may mask genuine thresholds in separate, system-specific species–area relationships, with important consequences for our understanding of landscape dynamics.

MATERIALS AND METHODS

Study area

The study was conducted in the *c.* 27 million ha Brigalow Belt South Bioregion (BBS) located in the eastern Australian states of Queensland and New South Wales (Fig. 2). Broadscale land clearing commenced in the 1960s, and during the 1990s and early 2000s clearing rates in this region were amongst the highest in the world, before broadscale clearing was significantly controlled through legislation (Lepers *et al.*, 2005; Seabrook *et al.*, 2006; McAlpine *et al.*, 2009). Approximately 40% of the original vegetation of the BBS remains. The original vegetation on the more productive soils of the BBS was forest and woodland dominated by *Acacia harpophylla* (brigalow), *Casuarina cristata* (belah) and *Eucalyptus populnea* (poplar box), while that of the sandier and rockier soils at slightly higher elevations was mainly *Callitris glaucophylla* (white cypress pine), *Eucalyptus* spp. (eucalypt) and *Corymbia citriodora* ssp. *variegata* (spotted gum) forest (Sattler & Williams, 1999). Although large blocks of forest remain on the poorer soils, most of the productive landscapes have been heavily cleared for agriculture, with vegetation often occurring in small patches and linear strips along roadsides and edges of cultivation. The climate is subtropical, with summer-
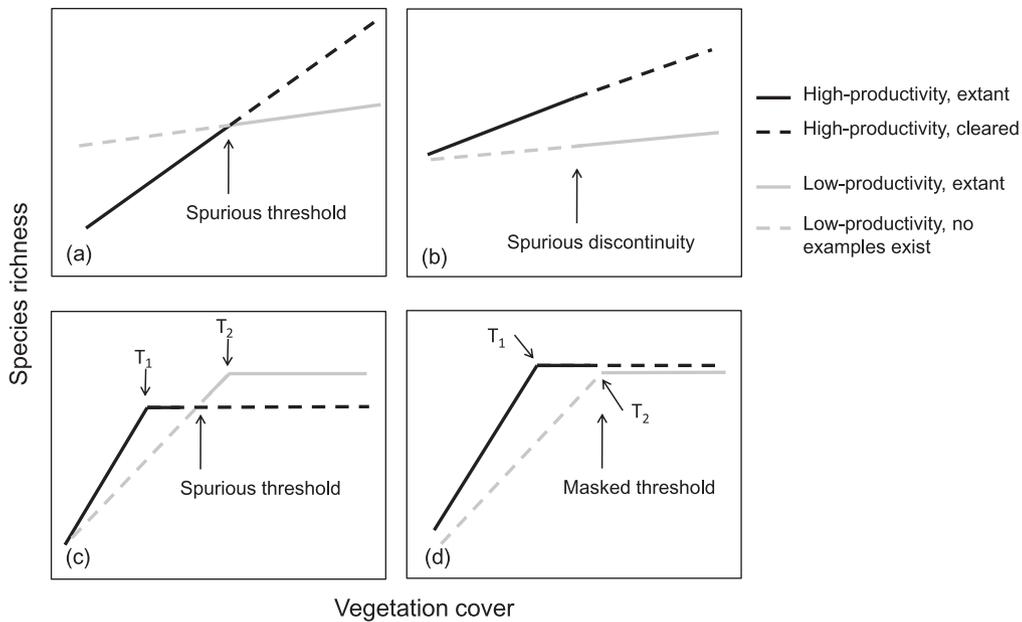
Figure 1 Examples of how spurious thresholds could emerge from separate species–area relationships when non-random clearing patterns result in combinations of landscape productivity and remnant vegetation cover which no longer exist (i.e. high productivity and high cover) or never existed (i.e. low productivity but low cover). Genuine thresholds are marked T$_i$. A threshold could appear where linear relationships intersect (a) and even identical intercepts but different slopes (or vice versa) could produce a discontinuity (b). Separate but intersecting threshold relationships could produce a spurious threshold in a third location (c), and one of two thresholds in non-intersecting threshold relationships could be masked (d).

dominant rainfall (mean annual rainfall at Goondiwindi, 28°52′S 150°33′E, 614 mm) and temperature ranges of 20–34 °C in the austral summer and 5–19 °C in winter.

Estimation of landscape-level species richness

Bird survey data from standard 20-min, 2-ha surveys (Loyn, 1986) across the BBS were collated from several sources including the Birds Australia Atlas database, the Queensland Department of Environment and Resource Management database, and data collected by the authors as part of other research projects across the region (Bowen *et al.*, 2009; Eyre *et al.*, 2009). Only surveys conducted since 2000 were used for this analysis. Bird species were classified as either 'woodland-dependent' or 'non woodland-dependent' following the classification of Radford *et al.* (2005) or, for species not occurring in their region, applying their criteria. Only woodland-dependent bird species were used for this analysis (see Appendix S1 in Supporting Information).

Locations of surveys were projected onto a map of native vegetation in the BBS over which a 10 × 10 km grid was laid. Each 100 km^2 landscape which was located fully within the BBS boundary and for which data from at least 10 separate surveys were available was considered for inclusion in the analysis (a total of 53 landscapes). To be retained for further analysis, landscapes must have had surveys conducted in at least three of their four quadrants, and in each category of woodland element present in the landscape (large, small and linear patches).

We calculated the estimated species richness for each landscape using the sample-based species richness estimator Chao2 in the program EstimateS 8.2 (Colwell, 2009). Chao2 is a non-parametric approach for estimating the true number of species based on multiple repeated samples (Colwell & Coddington, 1994; Chao, 2005). Where the estimated coefficient of variation for Chao2 using the bias-corrected formula was > 0.5, estimations were re-computed using the classic formula and the greater estimate from Chao2 and the incidence-based coverage species richness estimator (ICE) was used (Colwell, 2009). As the completeness of the species inventories for the landscapes varied widely, we discarded those landscapes for which the estimates of Chao2/ICE with the last five surveys differed by more than two species.

Vegetation cover data

For each of the 31 study landscapes with robust bird richness estimates (Fig. 2), we quantified the percentage cover of all woody vegetation (including regrowth) and remnant woody vegetation only. The datasets available for calculating vegetation cover differed between Queensland and New South Wales, but both were derived from Landsat Thematic Mapper imagery (25-m resolution) using similar methods to define vegetation cover. In Queensland, we defined 'all woody vegetation' according to the Statewide Landcover and Trees Study dataset, where woody vegetation is classified as any vegetation with a minimum foliage projective cover of 8% (Department
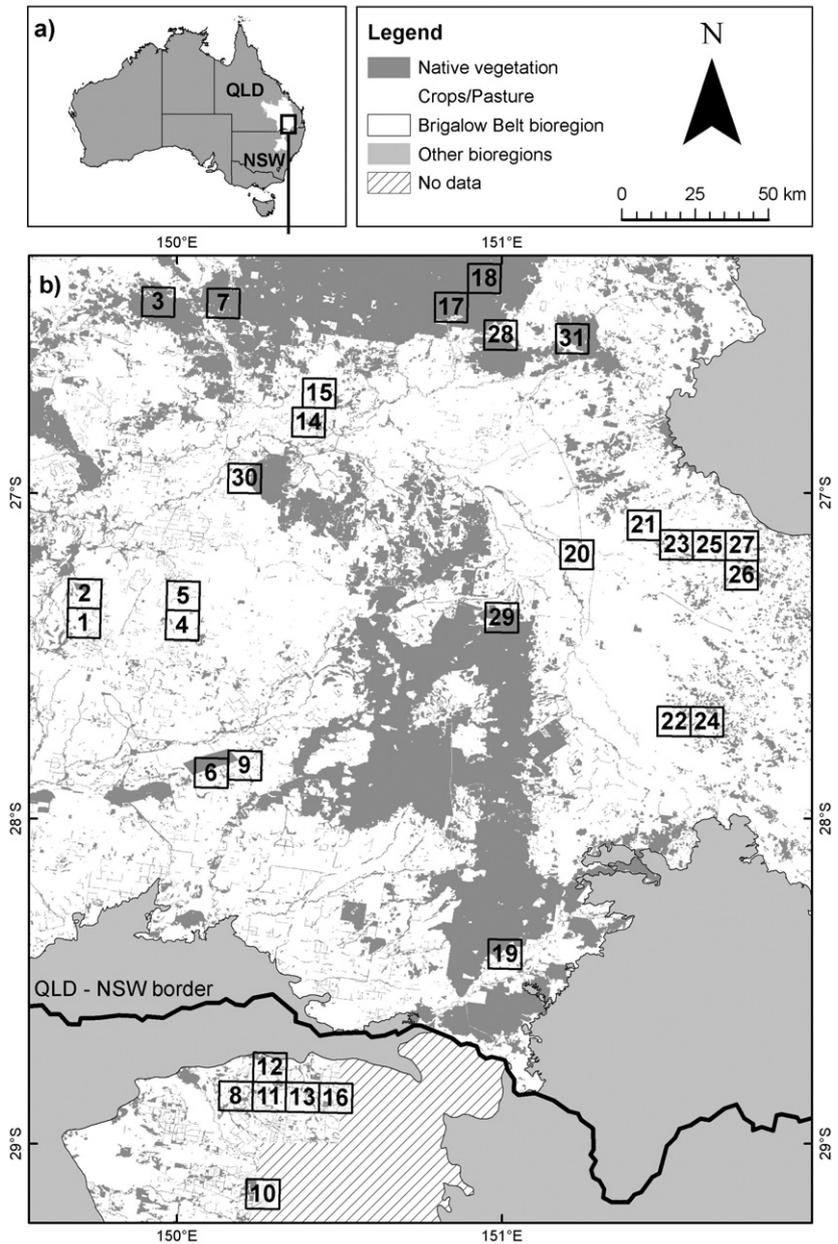
Figure 2 Location of study landscapes in the Brigalow Belt South Bioregion, eastern Australia.

of Environment and Resource Management, 2009). To distinguish remnant vegetation (i.e. not previously cleared) from regrowth vegetation, we calculated the area of vegetation defined as remnant according to the Queensland Regional Ecosystems dataset (Queensland Herbarium, 2003). Woody vegetation cover for landscapes in New South Wales was calculated using the New South Wales North West Vegetation Mapping dataset for Moree Shire (NSW Department of Land and Water Conservation, 2001). We examined a series of historical aerial photographs (1958–2004) to distinguish areas of remnant and regrowth vegetation, where we defined remnant as woody vegetation that had no evidence of prior clearing and regrowth as vegetation for which there was evidence of past clearing. The summed area of all woody vegetation and

remnant vegetation were calculated for each landscape and converted to percentage cover.

Landscape classification

We used the pre-clearing extent of vegetation types typical of fertile systems as a proxy for landscape productivity. Data sources included the Regional Ecosystem Classification in Queensland (Sattler & Williams, 1999; Queensland Herbarium, 2003; Neldner *et al.*, 2005) and in New South Wales the Australian Soil Resource Information System (ASRIS) database (CSIRO, 2006) combined with site visits and local knowledge. The Regional Ecosystem Classification combines information about the floristic composition of the dominant overstorey

Model	Remnant vegetation			All woody vegetation		
	Change-point	w_i	Adj. R^2	Change-point	w_i	Adj. R^2
Linear	n.a.	0.026	0.04	n.a.	0.047	0.04
Exponential	n.a.	0.098	0.12	n.a.	0.113	0.09
Piecewise						
Fixed threshold	35%	0.015	0.05	40%	0.058	0.09
Best threshold	11.5 ± 5.4%	0.038	0.13	28 ± 10.1%	0.059	0.12
Discontinuous	35%	0.823	0.30	40%	0.723	0.27

Table 1 Akaike weights (w_i) calculated from the Akaike information criterion corrected for finite sample size (AIC_c) and adjusted R^2 values for alternative regression models of estimated bird species richness as a function of the percentage of remnant and all woody vegetation cover in 100-km^2 landscapes.

'Best threshold' change-point estimates are shown ± 1 SE. Akaike weight values > 0.80 indicate strong support for a model being the best candidate model.

species with geology, landform and soil. Using this information, landscapes were categorized as 'high-productivity' if the pre-clearing extent of ecosystems classified as *A. harpophylla* and *E. populnea* vegetation on fertile landzones (alluvial plains, clay deposits on undulating plains, basalt plains, or fine-grained sediments on undulating plains) was > 50%, and 'low productivity' if the pre-clearing extent of these regional ecosystems was < 50%. We used the number of patches of remnant vegetation (> 1 ha) per landscape as our indicator of fragmentation, with landscapes with more than 15 patches (the median value) being 'high fragmentation' and 15 or fewer patches 'low fragmentation'. Although both the pre-clearing extent of productive vegetation types and the number of patches in a landscape are continuous variables, such categorization was necessary in order to compare species–area relationships between landscape types.

Data analysis

To identify the presence and nature of nonlinearities in the relationship between species richness and vegetation cover, we fitted a series of models to the Chao2/ICE estimated species richness values, separately using the percentage of remnant vegetation cover and of all woody vegetation cover as independent variables. Firstly, we compared the performance of the models most commonly used to characterize the species–area relationship. The problem of how landscape-level habitat extent affects landscape-level species richness is more akin to that of increasingly large samples from within an unbounded space, rather than samples representing isolates such as islands or patches. As such, the commonly used convex models (the power model $S = cA^z$ and the exponential or semi-log model $S = c + z\log(A)$, where S = species richness and A = area) were evaluated as they are more appropriate for samples from continuous areas (Tjorve, 2003). The exponential model ($R^2 = 0.15$) marginally outperformed the power model ($R^2 = 0.14$), and so we included the exponential model in subsequent analyses. We fitted exponential models of estimated species richness as a function of vegetation cover including, separately, productivity and fragmentation category as covariates to examine interaction effects.

Secondly, we compared the performance of linear, exponential, threshold (continuous piecewise) and discontinuous piece-wise regressions using the Akaike information criterion corrected for finite sample size (AIC_c) and calculated their Akaike weights (w_i). Akaike weights show the 'weight of evidence' in favour of model being the actual Kullback–Leibler best model in the set (Burnham & Anderson, 2002). For threshold models, we used the *segmented* package in R (Muggeo, 2008) to fit a model with a fixed threshold point based on visual inspection of the data, and also to search for the most parsimonious change-point. The discontinuous piecewise models reflected visual estimates of discontinuity points.

Finally, we explored whether differences in adjacent segments of piecewise models corresponded to differences in underlying landscape productivity or fragmentation by examining models fitted separately to high- and low-fragmentation and high- and low-productivity landscapes. Curves that intersected near an apparent change-point were considered candidates for separate species–area relationships underlying apparent thresholds.

RESULTS

An average of 44 surveys per landscape yielded recorded species richness values for woodland-dependent birds ranging between 23 and 59 (mean 40) (see Appendix S2). There was no relationship between the number of surveys per landscape (n) and the Chao2/ICE estimated richness (richness = $45.223 + 0.080n$; $F_{1,29}$ = 0.939; $P = 0.341$; $R^2 = 0.031$). The extent of both remnant and all woody vegetation within each landscape was negatively correlated with the pre-clearing extent of brigalow/poplar box communities on productive landzones ($r = -0.844$ and $r = -0.884$, respectively) and the number of patches in the landscape ($r = -0.742$; $r = -0.725$).

The relationship between estimated species richness and vegetation cover appeared discontinuous, with a steep increase in richness up to about 35% of remnant vegetation cover and 40% all woody vegetation cover, followed by a sharp decline and then a more gradual increase above this level of cover (Fig. 3). The exponential models were a better fit to the data than the linear models, but by far the best-performing models for both vegetation classes were the discontinuous piecewise models (Table 1, Fig. 3g,h), suggesting two separate groupings of data either side of *c.* 35% remnant or *c.* 40% all woody vegetation cover. There
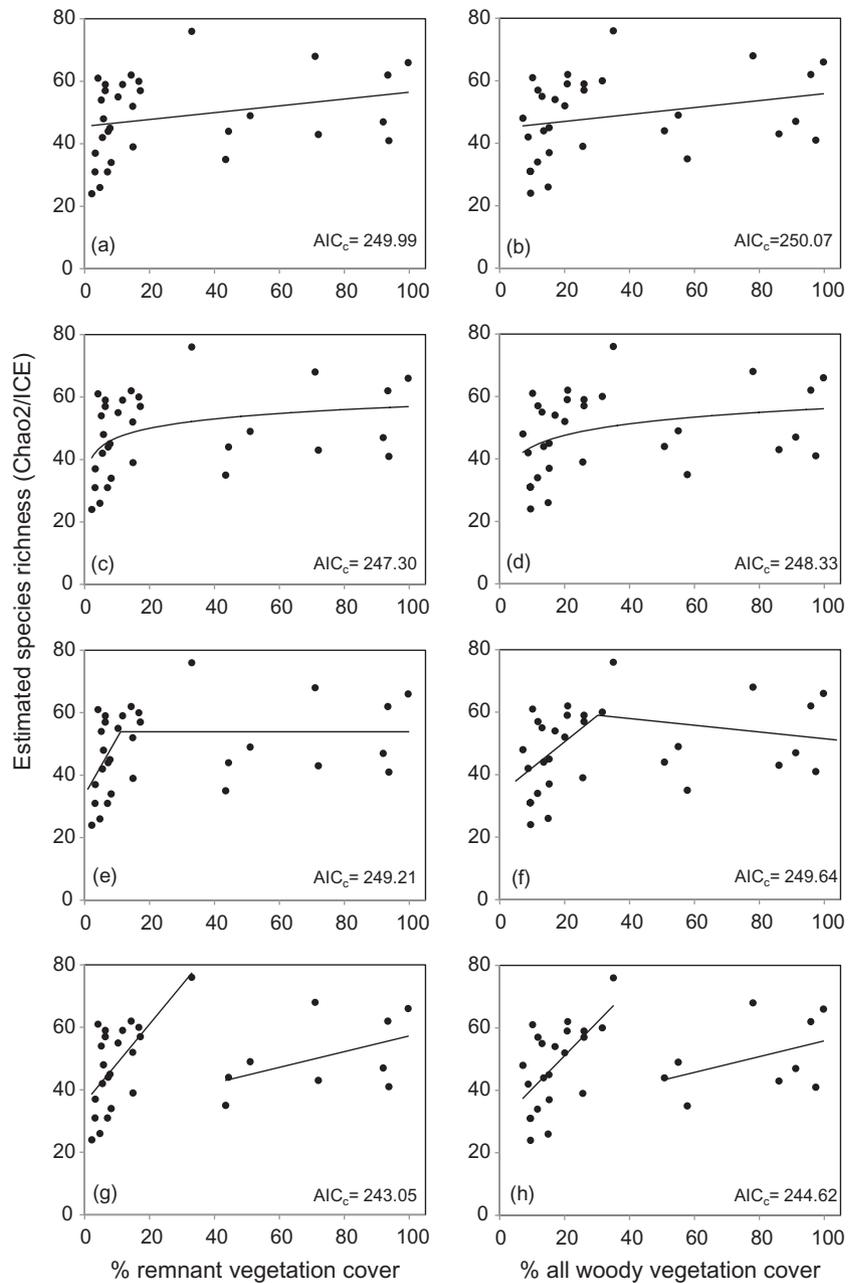
Figure 3 Linear (a, b), exponential (c, d), best threshold (e, f) and discontinuous piecewise (g, h) models of the relationship between bird species richness and vegetation cover (remnant vegetation, a, c, e, f; all woody vegetation, b, d, f, g). AIC$_c$: Akaike information criterion corrected for finite sample size.

was a significant interaction between log remnant vegetation cover and productivity category (model $F_{3,27} = 4.29$, $P < 0.014$; interaction $\beta = 12.02 \pm 4.98$, $t = 2.42$, $P = 0.023$). Interactions between log all woody vegetation cover and productivity, and between both log remnant and log all woody vegetation cover and fragmentation category, were not significant.

Landscapes in the 'high vegetation cover' group of the discontinuous piecewise model were typically low-productivity and low-fragmentation landscapes, and while all but two in the 'low vegetation cover' group were high-productivity, several were also classed as low-fragmentation. Exploration of separate species–area relationships for high- and low-productivity landscapes revealed a steep increase in species richness with habitat area in high-productivity landscapes, but only a weak relation-

ship emerged in low-productivity relationships (Table 2, Fig. 4). However, the curves for high- and low-productivity landscapes appeared markedly different. For all woody vegetation, the point at which the two productivity-specific species–area curves intersected corresponded approximately with the location of the rapid change-point (Fig. 4). Linear regressions fitted separately to data from high- and low-fragmentation landscapes showed non-intersecting curves of similar slope (Table 2, Fig. 4).

DISCUSSION

Our study contributes to the debate about the nature and cause of thresholds in the relationship between species richness and habitat extent (Andrén, 1994; Lindenmayer & Luck, 2005; Swift

Factor	Segment	Remnant vegetation			All woody vegetation		
		Intercept	Coefficient	R^2	Intercept	Coefficient	R^2
Dominant pre-clearing vegetation type	High productivity	26.0	9.9	0.37	14.0	12.0	0.26
	Low productivity	61.2	−2.6	0.05	68.3	−4.1	0.04
Fragmentation (number of patches)	High	45.9	1.9	0.01	25.4	9.0	0.17
	Low	24.7	6.9	0.37	11.8	9.6	0.28

Table 2 Summary of exponential models of estimated bird species richness as a function of remnant and all woody vegetation cover within the separate productivity and fragmentation categories.
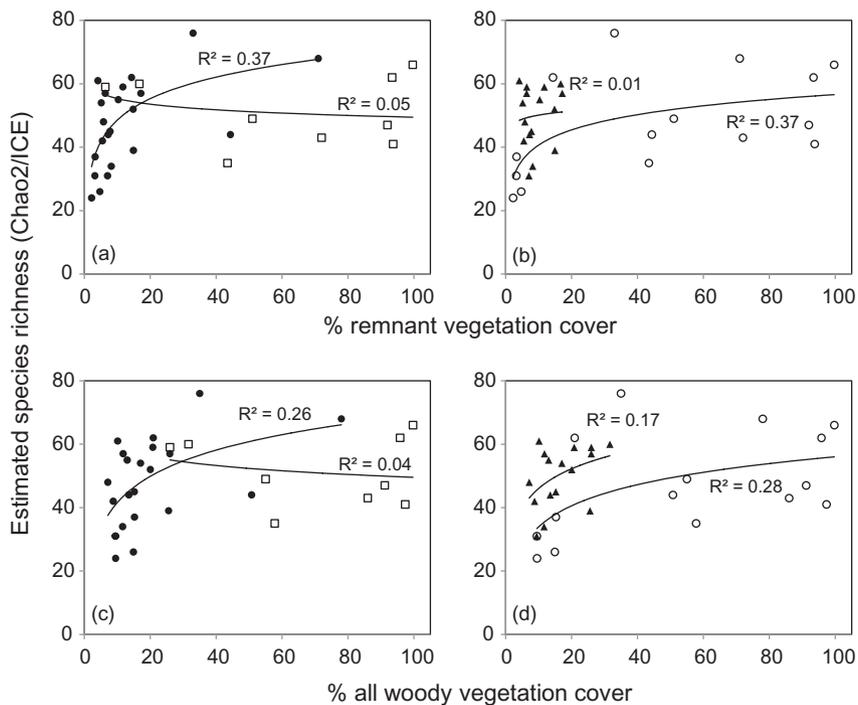

Figure 4 Relationship between bird species richness and remnant (a, b) and all woody vegetation cover (c, d) in low-productivity (open squares) and high-productivity (filled circles) landscapes (a, c), and low-fragmentation (open circles) and high-fragmentation (filled triangles) landscapes (b, d).

& Hannon, 2010). We proposed an alternative mechanism linked to landscape productivity that may give rise to artificial thresholds in the species–area relationship. Spurious thresholds which emerge due to underlying landscape differences such as productivity may mask genuine thresholds in separate, system-specific species–area relationships, with important consequences for biodiversity conservation.

Our analysis revealed evidence of a sharp discontinuity in the relationship between species richness and vegetation cover. The species richness of woodland birds increased steeply with vegetation cover, but only in landscapes with less than *c.* 40% vegetation cover. The relationship beyond this point did not approach an asymptote, but rather dipped sharply before increasing approximately linearly again. Thus, the point at which rapid change was evident represents a discontinuity in the relationship between species richness and vegetation cover, suggesting a composite pattern emerging from the presence of at least two underlying species–area relationships.

Causes of thresholds in species–area relationships

A threshold in the relationship between species richness and habitat extent represents a point at which there is a shift in underlying processes determining species richness (Andrén, 1994). Most previous explanations for this shift have related to rapid changes in species responses to habitat area *per se* at low levels of remaining habitat, or factors inescapably linked to habitat area, such as fragmentation. However, we propose that thresholds can also arise as artefacts of two or more separate underlying species–area relationships, of which only part are evident because of bias in patterns of habitat removal. Our results supported the spurious threshold hypothesis, as the rapid change-point in the relationship between species richness and habitat extent manifested as a sharp discontinuity. The effect of remnant vegetation extent on species richness differed significantly between landscapes classified as being of high and low productivity (using the extent of fertile landzones as a proxy), and

the location of the discontinuity corresponded with the intersection of species–area curves for landscapes differing in underlying productivity. However, the slopes of these separate curves differed from those of the discontinuous piecewise models, and so our productivity-based categorization of the landscapes is unlikely to explain fully the pattern we observed. Nevertheless, there do appear to be underlying differences in the species–area relationships of landscapes which vary in productivity.

The slope of the species–area relationship changes with multiple factors, including productivity (Pastor *et al.*, 1996; Weiher, 1999), type of matrix habitat (Watson *et al.*, 2005), habitat heterogeneity and topographic diversity (Kallimanis *et al.*, 2008) and latitude (Drakare *et al.*, 2006). Soil fertility and productivity are closely linked to historical patterns of landscape transformation, a correlation evident in agricultural landscapes world-wide (Taverna *et al.*, 2004; Lunt & Spooner, 2005). Weiher (1999) found that the slope of the species–area relationship was positively correlated with productivity, and the constant was negatively related to productivity. Such a pattern would yield a family of intersecting curves along a productivity gradient (Weiher, 1999). Thus, if productivity is closely linked to the amount of habitat in a landscape, spurious thresholds may appear at the points of intersection.

Possible interactions between habitat quality and quantity in species–area relationships, and multiple thresholds, were suggested by Lindenmayer & Luck (2005), although the possibility that these factors might yield spurious thresholds has not previously been explored. Our eastern Australian woodland bird data support the hypothesis that the species–area relationship varies with indicators of productivity in such a way as to present a spurious threshold. The 'hump' evident in the species–area relationship is a section of the curve which contained the few examples of landscapes with both relatively high levels of vegetation cover and high productivity. Few landscapes remain which have a high underlying productivity but still retains higher levels of vegetation, so immediately beyond the hump, the shallower slope characteristic of less-fertile landscapes dominates. It is possible that such a mechanism may underlie other examples of rapid change-points in the vegetation cover species richness relationship. For example, Radford *et al.* (2005) compared the performance of several different models and concluded that a piecewise regression with a change-point at 10% vegetation cover was best supported. However, support for their loess model, which revealed a slight hump at *c.* 10%, was not dissimilar to that for their piecewise model. They also reported a steeper slope of the species–area relationship for more dispersed landscapes, which in their study correlated with intensity of agriculture and therefore probably underlying productivity.

Underlying productivity, linked to patterns in soil and vegetation types, is but one factor likely to covary with landscape-level habitat cover. Increased fragmentation is also characteristic of lower-cover landscapes, and thus disproportionate fragmentation effects at low levels of vegetation cover is perhaps the mechanism most commonly proposed for nonlinearities in species–area relationships (Andrén, 1994, 1997; Bascompte & Solé, 1996; Betts *et al.*, 2007). We found no significant interac-

tion between vegetation cover and fragmentation, and the species–area curves for high- and low-fragmentation landscapes appeared similar. However, the number of patches is one of many possible fragmentation metrics, and the lack of examples of high-cover, high-fragmentation landscapes limited our ability to conclude whether differences in underlying species–area curves with fragmentation may partially explain the pattern we observed.

Another factor likely to covary with landscape-level habitat cover is the type and intensity of land-use, which has important consequences for matrix quality (Dauber *et al.*, 2003). Highly cleared and productive landscapes tend to be those favoured for high-intensity land uses like irrigated cropping, while low-productivity landscapes tend to be used for lower-impact land uses, such as grazing of native pastures. High-intensity land uses that rely on large and heavy machinery often require a highly transformed matrix to minimize obstacles to movement (Maron & Fitzsimons, 2007). Simulations of species responses to habitat loss suggest that the location of a threshold can shift considerably when matrix quality is altered, such that greater amounts of habitat are needed when matrix quality is poor (Fahrig, 2001; Watson *et al.*, 2005). Thus, the nature of the species–area relationship may vary in high- and low-productivity landscapes as a consequence of the intensity of land use (Whittaker *et al.*, 2005).

Time since clearing

Contrary to expectations, the rapid change-point evident in our dataset was at 35–40% vegetation cover – at the higher end of observed threshold values (Swift & Hannon, 2010). Although the rapid change-point could not be estimated with high precision due to limited data points in the region, the minimum likely change-point (*c.* 20%) is still much higher than the 10% identified for bird species richness in landscapes of southern Australia (Radford *et al.*, 2005). Radford *et al.* (2005) proposed that during faunal relaxation, the position of the threshold should shift to the right – that is, rapid decreases in species richness should become evident below a point representing a higher level of vegetation cover. As most clearing ceased relatively recently in much of our study region, the higher value of our rapid change-point suggests that our dataset is unlikely to reflect this process. However, if the spurious threshold hypothesis we introduce in this paper is true, then variation in threshold positions may have little to do with temporal shifts linked to faunal relaxation.

Implications for conservation and management

There are important differences in the implications of the competing hypotheses relating to changes in species richness dynamics below threshold levels of habitat cover. In particular, our hypothesis of separate, system-specific species–area relationships contrasts with the hypothesis that shifts in dynamics are linked to disproportionately greater fragmentation effects below the threshold. This is because highly fragmented, high-cover landscapes cannot exist, and low-cover landscapes are nec-

essarily subject to at least some aspects of fragmentation such as small patch size. However, both low-productivity, low-cover landscapes and high-productivity, high-cover landscapes are possible. Therefore, care must be taken in extrapolating from apparent thresholds. If non-random clearing histories linked to underlying factors such as productivity gradients are even partly responsible for the thresholds or discontinuities we observe, then we cannot know how these observed relationships would translate to novel combinations of these factors. For example, a target to restore vegetation in productive landscapes to 40% cover may not be justified if the species–area relationship in such landscapes would continue linearly beyond this point. Similarly, to restrict removal of vegetation to 60% cleared land in low-productivity landscapes may result in a real threshold for such landscapes being crossed. As food security concerns and the push for biofuels increase pressure to clear land which was not previously considered productive (Fargione *et al.*, 2008; Godfray *et al.*, 2010), the importance of understanding how species loss relates to habitat extent becomes ever more urgent.

ACKNOWLEDGEMENTS

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SUPPORTING INFORMATION

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

Appendix S1 Woodland-dependent species recorded during the surveys.
Appendix S2 Number of surveys, observed and estimated species richness, and vegetation cover for each landscape.

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BIOSKETCH

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