RESEARCH ARTICLE

Landscape-specific thresholds in the relationship between species richness and natural land cover

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Abstract

1. Thresholds in the relationship between species richness and natural land cover can inform landscape-level vegetation protection and restoration targets. However, landscapes differ considerably in composition and other environmental attributes. If the effect of natural land cover on species richness depends on (i.e., interacts with) these attributes, and this affects the value of thresholds in this relationship, such dependencies must be considered when using thresholds to guide landscape management.

2. We hypothesized that the amount of natural land cover at which a threshold occurs would differ in predictable ways with particular anthropogenic, abiotic, and biotic attributes of landscapes. To test this, we related woodland bird species richness in 251 landscapes, each 100 km^2, to natural land cover in south-east Australia. We compared the fit of exponential and threshold models of the richness–natural land cover relationship, focussing on the extent of natural land cover at which thresholds presented among landscapes that differed in matrix land use intensity, heterogeneity, productivity, and the prevalence of strong biotic interactors. We used linear mixed modelling to examine how interactions between natural land cover and the various landscape attributes affected the fit of models of species richness.

3. Threshold models of the richness–natural land cover relationship were always a better fit than exponential models. Threshold values did not vary consistently with specific landscape attributes, with the exception of landscapes that were classified by the prevalence of strong biotic interactors (hypercompetitive native birds of the genus *Manorina*).

4. Natural land cover had a more positive effect on species richness in landscapes when *Manorina* prevalence was higher. This positive interaction provided the biggest improvement in explanatory power of models of species richness.

5. *Synthesis and applications*. While we detected an interaction between *Manorina* prevalence and the area of natural land cover, generalities relating to the

underlying nature of thresholds in the richness–natural land cover relationship remain elusive. Complex interactions, relating to various landscape attributes and associated ecological processes, likely underpin variation in threshold values. Until these complexities are better understood, the use of thresholds for informing landscape management and conservation target setting should be approached with caution.

1 | INTRODUCTION

Numerous applied conservation and land management actions focus on natural land cover and changes thereto (Desmet & Cowling, 2004; Possingham, Bode, & Klein, 2015; Tulloch, Mortelliti, Kay, Florance, & Lindenmayer, 2016). Where the objective is to maintain or enhance species richness at the landscape level, the richness–natural land cover relationship can guide decisions about how much native vegetation should be protected or restored (Cunningham et al., 2014; Radford, Bennett, & Cheers, 2005). However, while the area of natural land cover is a fundamental determinant of landscape-level species richness (Fahrig, 2013), the shape and functional form of this relationship have been observed to vary considerably, and is often better represented at the landscape level by models other than "traditional" monotonically increasing species–area curves (Desrochers, Kerr, & Currie, 2011; Maron et al., 2012; Radford et al., 2005).

While a topic of considerable debate (Fahrig, 2017), a key factor that is considered to act on the richness–natural land cover relationship is the configuration of remaining habitat (Haddad et al., 2017; Hanski, 2015). Andrén (1994) hypothesized that the adverse impacts of habitat fragmentation exacerbate those of habitat loss when natural vegetation cover in a landscape declines below 30%. This presents as a threshold in the richness–natural land cover relationship, whereby the number of species in a landscape falls sharply once the amount of natural land cover declines below this threshold value. Reduced fitness of individuals, impaired population processes (i.e., dispersal), increased exposure to threats, and payment of extinction debt potentially explain why richness declines rapidly below a threshold value in low cover landscapes (Swift & Hannon, 2010).

Numerous studies have detected thresholds in the richness–natural land cover relationship (Lima & Mariano-Neto, 2014; Martensen, Ribeiro, Banks-Leite, Prado, & Metzger, 2012; Morante-Filho, Faria, Mariano-Neto, & Rhodes, 2015; Muylaert, Stevens, & Ribeiro, 2016; Ochoa-Quintero, Gardner, Rosa, de Barros Ferraz, & Sutherland, 2015; Radford et al., 2005; Richmond, Jenkins, Couturier, & Cadman, 2015). Yet, the extent of natural land cover at which thresholds have been observed is inconsistent, and ranges widely around Andrén's (1994) 30% "fragmentation threshold." Understanding the factors underpinning this observed variation is important from a management perspective, since thresholds are often proposed as targets upon which to base landscape-level conservation decisions (Ficetola & Denoël, 2009; Huggett, 2005; Luck, 2005).

In addition to the amount and configuration of natural land cover, the composition of landscape mosaics and other forms of environmental variation among landscapes drive species occurrence patterns (Bennett, Radford, & Haslem, 2006). Despite this, variation in underlying attributes of landscapes is rarely considered when examining thresholds in the richness–natural land cover relationship (but see Maron et al. 2012; Richmond et al. 2015). We hypothesize that compositional and environmental attributes of landscapes interact with the area of natural land cover to affect the value of a threshold in the richness–natural land cover relationship in several ways (Figure 1).

First, intensive land use in the matrix may act on thresholds. Landscapes with more intensive matrix land use are characterized by harsher edges, reduced permeability, greater exposure to threats, and provide fewer supplemental resources to those provided by matrices characterized by lower intensity land use (Deikumah, McAlpine, & Maron, 2014; Koh & Ghazoul, 2010; Prevedello & Vieira, 2010; Resasco, Bruna, Haddad, Banks-Leite, & Margules, 2017; Swift & Hannon, 2010; Watson, Whittaker, & Freudenberger, 2005). As these factors could compound the adverse effect of fragmentation (e.g., edge effects), we hypothesize that landscapes with more intensive land use will have a higher threshold value. In other words, rapid loss of species will commence at a higher level of natural land cover in these landscapes.

Second, species richness typically increases with environmental heterogeneity (Allouche, Kalyuzhny, Moreno-Rueda, Pizarro, & Kadmon, 2012; Chocron, Flather, & Kadmon, 2015; Stein, Gerstner, & Kreft, 2014; Van Rensburg, Chown, & Gaston, 2002). Environmental heterogeneity (e.g., topographic diversity) is positively correlated with habitat differentiation and niche availability, resulting in high beta diversity (Astorga et al., 2014; Burgess & Maron, 2015; Veech & Crist, 2007). High beta diversity in heterogeneous landscapes may mean that landscape-level richness (gamma diversity) remains relatively stable as natural vegetation is lost (Tscharntke et al., 2012). Thus, we hypothesize that (naturally) heterogeneous landscapes will
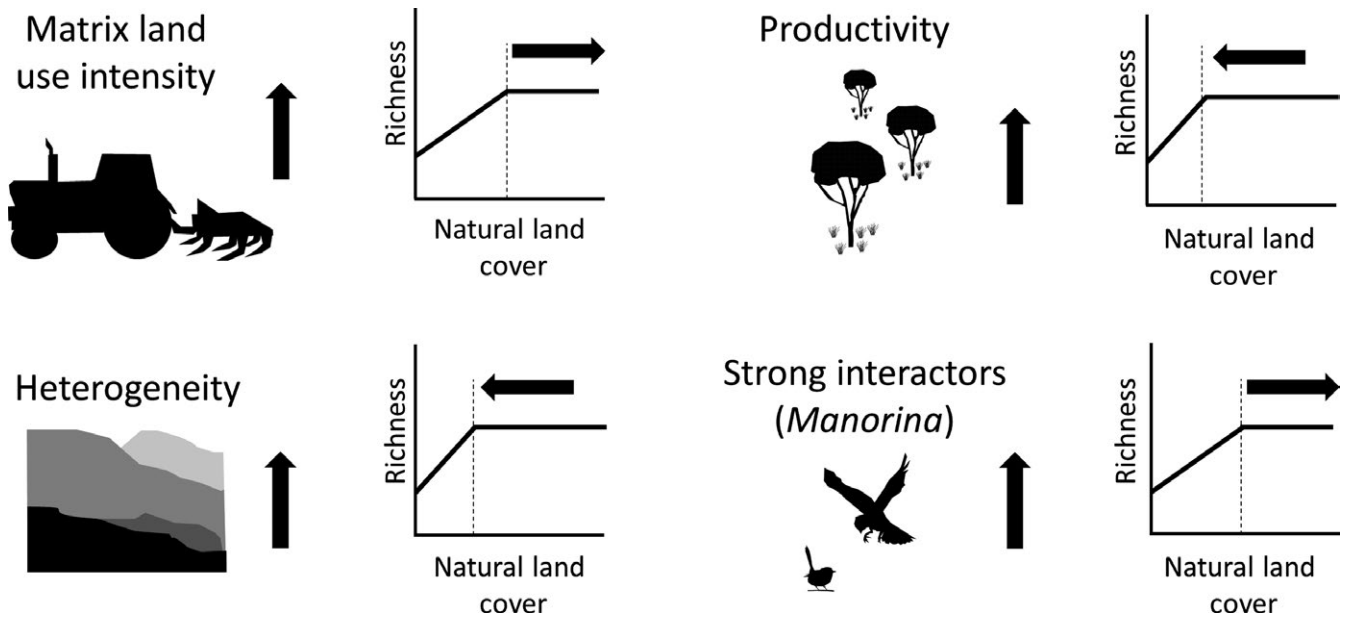
FIGURE 1 Hypothesized effect of four different landscape attributes on the richness–natural land cover relationship for Australian woodland birds. As the value of each landscape attribute increases, we hypothesize associated changes in the position of a threshold of natural land cover at which species richness suddenly changes

have a lower threshold value in the richness–natural land cover relationship because habitat heterogeneity buffers against the loss of landscape-level richness.

Third, richness tends to be positively correlated with productivity (Luck, Smallbone, McDonald, & Duffy, 2010; Storch, Evans, & Gaston, 2005). Per unit area of natural land cover, more fertile, productive habitat might be expected to support more individuals, due to greater resource availability (Lindenmayer & Fischer, 2006; Maron, 2008). Enhanced availability of resources may ameliorate adverse fragmentation effects such as reduced individual fitness (Cosgrove, McWhorter, & Maron, 2017). Because of this, we hypothesize that a threshold in the richness–natural land cover relationship in productive landscapes will occur at a lower level of cover.

Fourth, biotic interactions shape patterns of species occurrence in landscapes (Araújo & Rozenfeld, 2014; Belmaker et al., 2015). In the case of Australian birds, hypercompetitive native species of the genus *Manorina* (noisy miner [*M. melanocephala*] and yellow-throated miner [*M. flavigula*]) exclude other birds from native vegetation to the extent that they have a profound effect on the composition of assemblages (Mac Nally, Kutt, et al., 2014; Thomson et al., 2015). As these "ecological despots" have such a strong mediating effect on forest and woodland bird communities in Australia, and exacerbate adverse fragmentation effects (Kutt, Vanderduys, Perry, Mathieson, & Eyre, 2015; Maron et al., 2013), we hypothesize that the threshold in the richness–natural land cover relationship will occur at a higher level of natural vegetation cover in landscapes where these birds are more prevalent.

Here, we use a case study of Australian woodland birds to examine these four hypotheses. Our objective in this paper is to postulate and test generalities about the underlying nature of variability in the form of the richness–natural land cover relationship at the landscape

level, and particularly, the circumstances under which thresholds present.

2 | MATERIALS AND METHODS

2.1 | Study region and bird data

We analysed the relationship between bird species richness and natural land cover in 10 × 10 km landscapes of south-east Australia. This region, characterized by temperate woodlands, has been substantially modified by agriculture and urbanization (Lunt & Spooner, 2005). We used a grain size of 100 km^2 to represent landscape-level patterns in bird species richness as this quadrat size has been widely investigated in previous studies (De Camargo & Currie, 2015; Maron et al., 2012; Radford et al., 2005).

As we were interested in the effect of natural land cover on species richness, we focussed on native birds for which broad vegetation types including shrubland, woodland, and/or forest represent a key habitat component. We refer to these species as "woodland birds," noting though that the members of this broad assemblage utilize a range of structurally varied woody vegetation types, typified by *Eucalyptus* spp. and other associated genera. We included species that can also utilize cleared/transformed areas in addition to woody habitats (i.e., for foraging), but for which the presence of woody vegetation is critical for their occurrence and persistence. Species characteristic of open environments, and waterbirds, were excluded. Species habitat requirements—namely, an association with habitats characterized by woody vegetation—were confirmed using the Handbook of Australian, New Zealand, and Antarctic Birds (as summarized by Garnett et al. 2015). Occurrence data for the focal suite of species for the period
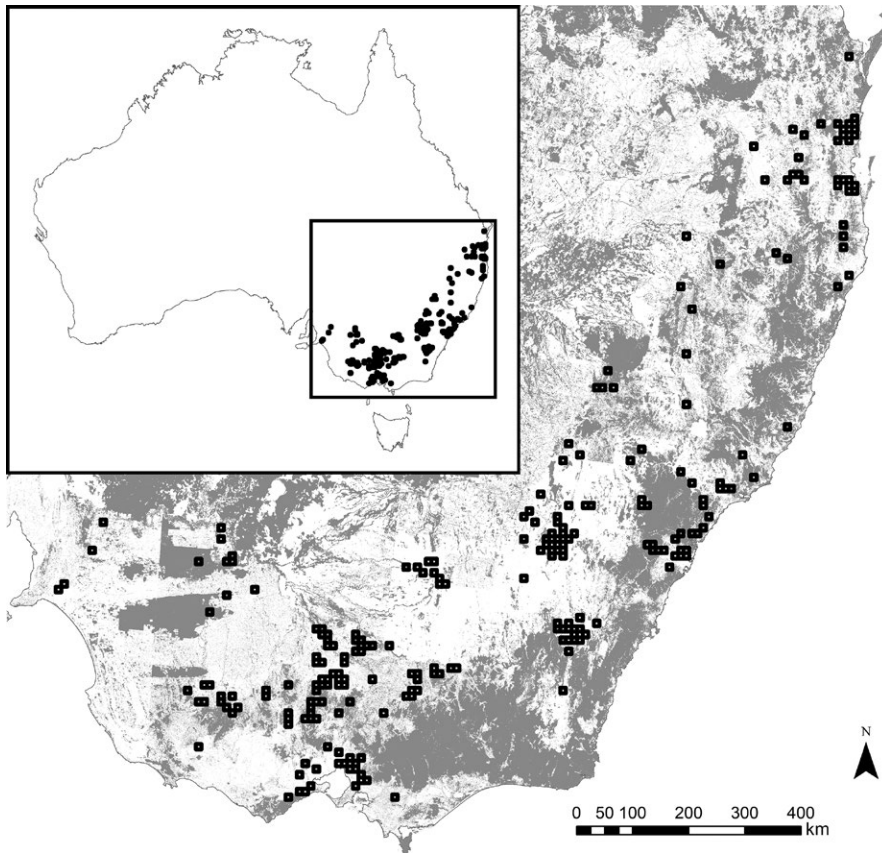
FIGURE 2 South-east Australian landscapes units (*n* = 251) with native remnant woody vegetation shown as dark grey layer

1998–2014 were extracted from BirdLife Australia's New Atlas of Australian Birds (Barrett, Silcocks, Barry, Cunningham, & Poulter, 2003) database. A detailed description of the approach we took to derive species richness estimates that were not biased by survey methodology and sampling effort is presented in Supporting Information Appendix S1.

On selecting a final set of landscape units, we applied a number of criteria to account for within-landscape spatial and temporal variability in bird sampling, and temporal changes in natural land cover over the period for which bird data were collected. To be included in this analysis, landscape units needed to satisfy all of the following criteria: (a) must have bird surveys from at least five unique locations in at least two different quadrants of a landscape; (b) must have at least five surveys from each half of the Atlas data collection period (1998–2014); (c) must have at least five surveys in each half of the year (April–September, October–March); and (d) must have less than a 5% change in total "forest" cover for the period 2000–2012 (Hansen et al. (2013) forest cover change dataset—an indication of landscape-level change in woody vegetation cover that approximately coincides with the bird data collection period). A total of 251 landscape units for which we had species richness estimates that were not biased by sampling effort met these criteria and were used in subsequent analyses (Figure 2). This final set of landscape units comprised estimates of species richness derived from 32,160 individual bird surveys and incorporated records of 232 unique species (see Supporting Information Table S1 for list of species).

2.2 | Landscape data

We used the Australian Government's National Vegetation Information System (NVIS) version 4.1 (Department of the Environment, 2012) to map the contemporary distribution of remnant native vegetation and determine the area of natural land cover in our landscape units. From this 100 m pixel resolution dataset of 33 major vegetation groups (MVGs), we identified MVGs that were characterized by remnant woody vegetation (i.e., woodland and forest) and aggregated these to calculate the percentage cover of natural land cover for each landscape unit.

Additionally, for each landscape unit, we extracted information on four attributes (Table 1). These data were used to categorize landscapes to examine our hypotheses regarding interactions between vegetation area and other attributes of landscapes, and how these may affect the position of thresholds in the richness–natural land cover relationship. Geospatial data processing and extraction were done using ArcMap10.1 (ESRI, 2016) and Geospatial Modelling Environment (Beyer, 2012). Maps of landscapes categorized by the four attributes under examination are provided in Supporting Information Figures S1–S4.

2.3 | Data analysis

We split our 251 landscapes into three subsets (terciles) for each landscape attribute, allowing us to categorize landscapes as having

TABLE 1 Landscape attribute data used to categorize landscapes

Attribute	Description	Source	Range
Matrix land use intensity	Area of the matrix that is characterized by intensive land use (i.e., irrigated production agriculture, irrigated plantations, urban, industrial, extraction)	Catchment Scale Land Use of Australia (Australian Bureau of Agricultural and Resource Economics and Sciences (ABARES), 2015)	0–9,867 ha
Heterogeneity	Range in elevation calculated as difference between highest and lowest point in landscape unit	90 m resolution digital elevation model (Jarvis, Reuter, Nelson, & Guevara, 2008)	18–1,000 m
Productivity	Mean annual rainfall	WorldClim database (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005)	269–1,801 mm
Strong biotic interactors	Reporting rate of noisy and yellow-throated miners—number of surveys in which one or both species recorded, as proportion of total number of surveys in landscape unit	20 min/2 ha bird surveys for landscape units	0%–100%

"low," "intermediate," or "high" values for each of matrix land use intensity, heterogeneity, productivity, and strong biotic interactors. Thus, we created terciles of the data for each of the four landscape attributes. While subsetting landscapes into terciles is arbitrary, it allowed for the exploration of our hypotheses about how threshold values of natural land cover change with increasing or decreasing values of particular landscape attributes.

We fitted threshold models to the terciles for each of the four landscape attributes, to explore variation in the extent of natural land cover at which thresholds occurred in the relationship between species richness (dependent variable) and natural land cover (independent variable). These models were built using the R package SEGMENTED (Muggeo, 2008). To examine the distribution of observed thresholds of natural land cover compared to thresholds expected by chance, we ran a null model (repeated 100 times on the data split into three random subsets, that is, not subset according to landscape attributes). We also fitted an exponential model to the terciles for each of the four landscape attributes, to approximate a "traditional" convex upward species–area curve (Turner & Tjørve, 2005). The level of support for threshold and exponential models was compared using Akaike's information criterion (AIC).

We also built linear mixed models using the R package LME4 (Bates, Maechler, Bolker, & Walker, 2014) to explore interactions between natural land cover and landscape attributes. Specifically, we considered how interactions between landscape attributes and the area of natural land cover affected species richness. We built four separate models that included all landscape attributes (area, matrix land use intensity, heterogeneity, productivity, and strong biotic interactors) as independent terms and individual interactions between area and each one of these four predictors. Each separate interaction term aligned with one of our four hypotheses about how interactions act on thresholds in the richness–natural land cover relationship. We compared these models to a model in which area of natural land cover was the only predictor. We included the random effect of bioregion in all models, to account

for regional differences in the response of birds to landscape structure.

3 | RESULTS

In all but two instances, threshold models were better supported, and threshold models always explained more variation than exponential models (Table 2). Landscapes that were subset by the prevalence of strong biotic interactors exhibited a trend whereby the position of the threshold (with respect to the area of natural land cover [x-axis]) increased with increasing *Manorina* reporting rate (Figure 3). We hypothesized that the threshold would be higher in landscapes where these strong biotic interactors were more frequently recorded. However, for landscapes with high *Manorina* reporting rates (and indeed, several other landscape categories), species richness actually declined with increasing natural land cover above the observed threshold.

For our other landscape types—those categorized by different levels of land use intensity, heterogeneity, and productivity—the position of the threshold did not vary consistently as hypothesized (Figure 3). Furthermore, observed threshold values ranged widely from a low of 17% natural land cover (landscapes with high heterogeneity) to a high of 50% natural land cover (landscapes with high productivity). The null modelling exercise we undertook, where threshold models were fitted to random subsets of our data, also revealed a wide distribution of threshold values (Supporting Information Figure S5). In all instances, observed thresholds from our analysis were within two standard deviations of the mean of the randomly derived thresholds from the null model. This indicates that, with the possible exception of landscapes categorized by *Manorina* prevalence, the position of thresholds that we observed was random and cannot be systematically associated with the landscape attributes that we hypothesized would predictably act on the position of the threshold.

	Exponential		Threshold			
	AIC	R^2	AIC	R^2	ΔAIC	Threshold value[a]
Matrix land use intensity						
Low	662.78	0.22	659.08	0.29	3.70	43.7 (±8.6)
Intermediate	630.04	0.05	628.19	0.11	1.85	27.8 (±7.6)
High	679.89	0.15	665.57	0.31	14.32	27.4 (±9.3)
Heterogeneity						
Low	631.16	0.05	624.69	0.16	6.47	21.8 (±7.6)
Intermediate	642.86	0.32	637.36	0.40	5.50	30.2 (±5.4)
High	657.42	0.09	660.96	0.10	−3.54	17.1 (±8.4)
Productivity						
Low	630.86	0.17	616.67	0.33	14.19	21.5 (±5.0)
Intermediate	658.61	0.28	658.77	0.31	−0.16	20.8 (±5.6)
High	658.37	0.08	654.21	0.17	4.16	50.3 (±9.0)
Strong biotic interactors						
Low	629.00	0.21	622.75	0.30	6.25	26.9 (±6.2)
Intermediate	651.32	0.15	646.71	0.23	4.61	30.0 (±7.5)
High	668.65	0.20	664.51	0.28	4.14	48.1 (±8.6)

TABLE 2 Summary of modelled relationship between area of natural land cover (independent variable) and species richness (dependent variable) for landscapes categorized into subsets (terciles) based on landscape attributes

[a]Percentage landscape natural land cover area at which threshold occurs (±error around threshold estimate).

The inclusion of interaction terms in our linear mixed models improved the explained variation in species richness, compared to a model that only included the effect of natural land cover area (Table 3). The model with the lowest AIC (and highest explained variation) included an interaction between area of natural land cover and strong biotic interactors. Area had a more positive effect on species richness when *Manorina* occurrence was higher.

4 | DISCUSSION

4.1 | Threshold values and landscape attributes

Observed thresholds in the richness–natural land cover relationship varied widely, but not in accordance with our hypotheses. Landscapes categorized by the prevalence of strong biotic interactors—two species of the genus *Manorina*—were the exception. A sudden change in species richness occurred at a progressively higher level of natural land cover in landscapes where these hypercompetitive birds were more prevalent. We hypothesized that this would occur because adverse fragmentation effects would be exacerbated by these edge specialists (Maron et al., 2013) at higher levels of (remaining) natural land cover. While we cannot attribute the observed relationships to these specific causes, this result does indicate a potential association between the occurrence of these strong biotic interactors and landscape-level thresholds.

Manorina spp. affected the patterns of richness through an interaction with natural land cover, resulting in increasing effects of cover on richness with increasing prevalence of miners. At sites where noisy miners occur at densities above 2.5 per ha, species abundance distributions of woodland bird communities have been observed to be significantly altered, with large declines in richness (Mac Nally, McAlpine, Possingham, & Maron, 2014). As these hypercompetitive birds profoundly shape Australian woodland bird communities, it is unsurprising that the positive effect of natural land cover on species richness depends on (i.e., increases with) the prevalence of these birds.

Although our results agree to an extent with previous studies showing the negative impacts of *Manorina* spp. on species richness, our findings also show that *Manorina* spp. impacts need to be examined in the context of natural land cover and additional factors in the landscape. Landscapes with the highest prevalence of *Manorina* spp. needed to have almost double the natural land cover of landscapes with intermediate *Manorina* spp. prevalence to achieve similar maximum species richness (Figure 3). A contrasting result to previous studies was the lower species richness in landscapes where *Manorina* spp. were least prevalent. One explanation for this is that *Manorina* spp. are more likely to be found in more productive landscapes that have been impacted by agriculture (Maron et al., 2013), and these landscapes naturally have higher bird species richness and biomass. Also, the measure we used to categorize landscapes and model interactions—percentage of surveys that recorded noisy and/or yellow-throated miners (reporting rate)—does not reveal the density of these birds, which is a key parameter driving their adverse effects at the site and patch level (Mac Nally, McAlpine, et al., 2014; Maron et al., 2013). Landscape-level effects of these strong biotic interactors warrant further detailed examination, particularly regarding how they mediate the effect of remaining habitat area on species richness.
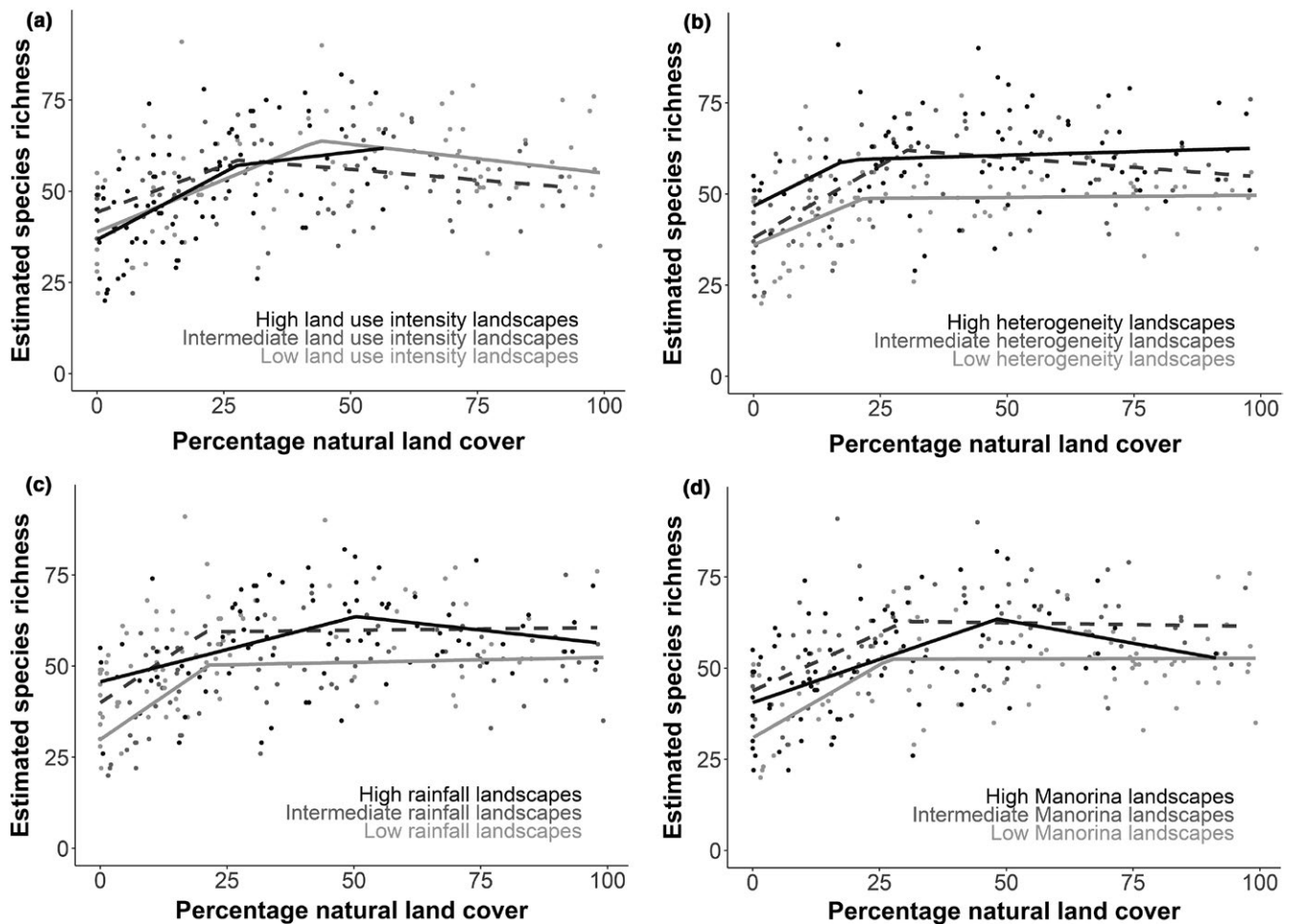
FIGURE 3 Threshold models of the richness–natural land cover relationship applied to landscape-specific subsets of data—(a) landscapes classified by matrix land use intensity; (b) landscapes classified by natural heterogeneity (range in elevation); (c) landscapes classified by productivity (mean annual rainfall); (d) landscapes classified by the prevalence of strong biotic interactors (*Manorina* spp.). Landscapes with intermediate values for each attribute are represented by the dashed line

The threshold values we recorded (17%–50%) tended to be within the range of those observed in other landscape-level studies (i.e., from low of 10% recorded by Radford et al. 2005 to high of 50% recorded by Morante-Filho et al. 2015). Indeed, this range of threshold values falls within the range returned by our null model (Supporting Information Figure S5), where thresholds were identified for random subsets of our dataset. The range of thresholds we recorded was therefore consistent with what would be expected

TABLE 3 Summary of linear mixed effects models of species richness that includes interaction term between area of natural land cover and other landscape attributes

Model fixed effects	Interaction term included	AIC	R^2
Area	NA	1,934.85	0.14
Area + Matrix + Heterogeneity + Productivity + *Manorina*	NA	1,917.52	0.22
Area + Matrix + Heterogeneity + Productivity + *Manorina*	Area × Matrix	1,912.57	0.23
Area + Matrix + Heterogeneity + Productivity + *Manorina*	Area × Heterogeneity	1,910.37	0.24
Area + Matrix + Heterogeneity + Productivity + *Manorina*	Area × Productivity	1,913.28	0.23
Area + Matrix + Heterogeneity + Productivity + *Manorina*	Area × *Manorina*	1,897.46	0.29

Area: area of natural land cover; Matrix: matrix land use intensity; Heterogeneity: range in elevation; Productivity: mean annual rainfall; *Manorina*: reporting rate (strong biotic interactors).

in random subsets of our dataset. As such, predictable trends in threshold positions related to landscape attributes (with the possible exception of strong biotic interactors) cannot be inferred from this study. Even though threshold models tended to be better supported and explained more variation than an alternative functional form (exponential model) in our study, when considered alongside the results of our null modelling exercise, we urge caution in the interpretation and applied use of observed thresholds.

Several landscape types in our study, including landscapes with high *Manorina* spp. prevalence and landscapes with low matrix land use intensity, had a peak in richness at the threshold, with declines on either side. The shape of these relationships resembles the "peaked" relationship recorded by De Camargo and Currie (2015). This peak, where bird species richness was highest in landscapes with intermediate levels of cover (approximately 50%), was attributed to the occurrence of both forest birds and birds that can use matrix habitats (De Camargo & Currie, 2015). Our study dealt only with birds that are associated with woodland/forest, and thus, the peaks we observed are unlikely to reflect richness that is enhanced by the presence of birds associated with open or transformed land. A decline in richness above a threshold indicates that other factors are acting on richness beyond intermediate levels of cover in these landscapes.

4.2 | Implications—landscape analysis and management

Thresholds in the richness–natural land cover relationship have been observed to vary widely. Our results reiterate this recorded lack of consistency in the value of thresholds. We considered whether the effect of area of natural land cover on species richness depends on other attributes of landscapes (i.e., interactions), and how this may affect the position of thresholds. Yet, generalities underpinning threshold values remain elusive. An interaction between the prevalence of birds of the genus *Manorina* and natural land cover provides more evidence for the pervasive impact that noisy and yellow-throated miners have on Australian bird communities, and highlights the need for a more detailed understanding of the effects of these ecological depots at the landscape level. Such information is important given that the noisy miner is recognized under Australian environmental law as a key threatening process for woodland and forest birds (Department of the Environment and Energy, 2014), and management actions such as the removal of these birds are being recommended over large scales (Mortelliti et al., 2016). A better understanding of the interaction between landscape-level natural land cover (inclusive of thresholds) and *Manorina* spp. densities could, for example, guide decisions about which landscapes should be targeted for *Manorina* spp. management/removal.

From a management perspective, the richness–natural land cover relationship alone may not be sufficient to guide landscape planning and interventions, because of interacting factors that likely modify the expected relationship. These interactions are complex and potentially defy the simplistic landscape classifications we have examined here. For example, applying a threshold as a management target for 'high productivity' landscapes may be fraught if there is substantial variation among such landscapes in other attributes that also interact with area to affect richness (Maron et al., 2012). Our landscape classifications did not account for these potentially confounding factors, and notwithstanding landscapes classified by *Manorina* spp. prevalence, this may explain the lack of consistency in threshold values among landscape types, and wide range of threshold values between landscape types. Generalizing the occurrence and values of thresholds and incorporating these thresholds into landscape management require that (a) these interactions are identified and understood and (b) the confounding effect of such interactions is controlled for in analyses of richness–natural land cover relationships.

5 | CONCLUSIONS

Thresholds are an attractive option for landscape management. They provide a discrete target and are simple to interpret and translate to on-the-ground action such as guiding restoration projects, or prioritizing landscapes for protection (e.g., protected areas, covenants). Our results indicate that the factors underpinning thresholds are not likely to be simple nor are thresholds in observed sample data likely to be robust. Despite substantial research effort, generalities about the causes of thresholds are lacking, and substantial variation in landscape-level threshold values continues to be observed. We add our voices to those urging caution in the applied use of thresholds (Johnson, 2013; Lindenmayer & Luck, 2005; Van der Hoek, Zuckerberg, & Manne, 2015), and particularly implementing management actions based on "generic" (i.e., 30%) thresholds, or thresholds recorded from a study system that is not the one to which the action is being applied.

AUTHORS' CONTRIBUTIONS

J.S.S., M.M., B.J.v.R., and A.I.T.T. developed conceptual framework for study. J.S. conducted the data analysis and wrote the manuscript. All authors contributed critically to drafts of the manuscript and gave final approval for its submission.

DATA ACCESSIBILITY

Links to all spatial datasets used in this analysis, as described in Section 2, are provided in the reference list, with relevant citations

also provided in the manuscript. The raw Australian Bird Atlas data are available under licence from BirdLife Australia and can be requested at: http://birdlife.org.au/projects/atlas-and-birdata/data-extractions-atl. Data used for this analysis, including bird species richness estimates derived from the raw Australian Bird Atlas data, and spatial landscape data for the 251,100 km^2 landscapes analysed, are available via the Dryad Digital Repository, https://doi.org/10.5061/dryad.6pp21np (Simmonds, van Rensburg, Tulloch, & Maron, 2018).

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