



THE UNIVERSITY OF QUEENSLAND
AUSTRALIA

**IMPLICATIONS OF VEGETATION CLEARING BIASES FOR THE
INTERPRETATION OF LANDSCAPE-SCALE SPECIES-AREA
RELATIONSHIPS**

Jeremy Scott Simmonds
BSc, MEnvMan



*A thesis submitted for the degree of Doctor of Philosophy at
The University of Queensland in 2016*

School of Geography, Planning and Environmental Management

Abstract

Vegetation clearing results in the loss of species from landscapes. Indeed, the area of remaining native vegetation is an important determinant of species richness in human-modified mosaics. Of interest to ecologists and landscape managers is the effect of area—that is, how the number of species a landscape supports changes with the amount of native vegetation, as revealed by the shape and functional form of the species-area relationship. Understanding this is vital for guiding conservation interventions such as setting limits to vegetation clearing or establishing revegetation targets.

Crucially though, it is not only vegetation area that affects patterns of species richness at the landscape level—so do environmental attributes such as soil properties and topography. Complicating the matter is the fact that these attributes tend to be correlated with landscape-level vegetation area, because humans preferentially remove vegetation from landscapes suited to land uses such as agriculture. However, this interplay between vegetation area, other landscape attributes, and biased patterns of vegetation loss/retention is infrequently considered in landscape-level species-area analyses. If unaccounted for, these confounding factors may result in erroneous interpretations of the effect of area, leading to suboptimal management actions.

The aim of this thesis was to examine how attributes of landscapes affect the relationship between species richness and vegetation area. Through four specific research questions, I explored in detail the hypothesis that attributes of human-modified landscapes that bias vegetation clearing also interact with vegetation area to produce landscape-specific area effects on species richness.

First, I quantified correlates of vegetation clearing/retention in two regions of the southern hemisphere, and reviewed the literature to determine how often, and in what ways, biased clearing patterns are accounted for in studies relating vegetation area to an ecological response. I demonstrated that soil properties and range in elevation are reliably associated with the amount of remaining native vegetation across ~18,000 100 km² landscapes in Australia and South Africa. Importantly though, I found that clearing biases were explicitly acknowledged in only 15 of the 118 reviewed studies. If the area of native vegetation in landscapes is a legacy of biased clearing, confounding factors like soil properties should be accounted for in analyses of area effects.

Second, I explored the extent to which the effect of native vegetation area on species richness differed in 100 km² landscapes categorised by attributes such as soil fertility, range in elevation or matrix land use. Using a case study of south-east Australian birds, I found that the shape of the species-area relationship varied substantially depending on whether landscapes were, for example, more- or less-topographically variable, or had higher or lower soil fertility. While threshold models depicting a point of sudden change in the effect of area emerged consistently, the amount of vegetation corresponding with observed thresholds differed considerably among landscape types. Therefore, aggregating and analysing species-area data from different landscape types is likely to misrepresent how species richness is affected by vegetation area. This will be exacerbated by clearing biases, because heavily cleared landscapes tend to be characterised by very different attributes to high cover landscapes.

Third, I compared the effect of vegetation area on bird species richness at three scales of analysis (landscapes of 25 km², 100 km², 400 km²) for two regions of south-east Australia. When data for the entire study extent were analysed, a remarkable degree of scale-invariance was observed—namely, a threshold relationship with a change-point at approximately 30% vegetation cover. However, when data were analysed for two regional subsets of the overall dataset, the effect of vegetation area, and the factors moderating this relationship, were scale-dependent. Given this finding, observed thresholds can only reliably be used to guide landscape management at the scale and in the region where the relationship was observed.

Finally, I evaluated the implications of accounting for clearing biases when using species-area relationships to guide conservation, focussing on a region of Australia undergoing rapid landscape transformation. I found that using observed thresholds from species-area models that do and do not account for landscape attributes yielded different outcomes for landscape-scale species richness conservation, given a scenario of future vegetation loss. Specifically, the number and location of landscapes that could be prioritised for conservation actions varied considerably depending on the species-area model used.

This research demonstrates that the effect of area on species richness differs substantially as a function of the attributes of landscapes. Crucially, clearing biases underpinned by these same attributes can confound analyses of the species-area relationship. Accounting

for landscape attributes will allow for a more rigorous understanding of how species richness varies among landscapes with different amounts of native vegetation. A robust appreciation of the effect of area will provide more certainty around how much vegetation needs to be managed (i.e. protected, revegetated), and where this should occur among multiple landscapes, to avert the loss of, or enhance, landscape-scale species richness.

Declaration by author

This thesis is composed of my original work, and contains no material previously published or written by another person except where due reference has been made in the text. I have clearly stated the contribution by others to jointly-authored works that I have included in my thesis.

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Publications during candidature

Peer-reviewed papers:

Chapter 2: Simmonds, J.S., van Rensburg, B.J. & Maron, M. Non-random patterns of vegetation clearing and potential biases in studies of habitat area effects. Accepted for publication in *Landscape Ecology*.

Conference abstracts:

Simmonds, J.S., van Rensburg, B.J. & Maron, M. Not all landscapes are the same – non-random clearing and the confounded area metric. Ecological Society of Australia Conference, Alice Springs, September 2014.

Simmonds, J.S., van Rensburg, B.J. & Maron, M. Not all landscapes are the same – non-random clearing and the confounded area metric. Student Conference on Conservation Science, Brisbane, January 2015.

Simmonds, J.S., van Rensburg, B.J., Tulloch, A.I.T. & Maron, M. Accounting for abiotic correlates in landscape-scale species-area relationships. International Congress for Conservation Biology, Montpellier, France, August 2015.

Simmonds, J.S., van Rensburg, B.J., Tulloch, A.I.T. & Maron, M. Variability in the relationship between bird species richness and landscape-scale vegetation area. Australasian Ornithological Conference, Adelaide, November 2015.

Simmonds, J.S., van Rensburg, B.J. & Maron, M. Using species-area relationships to inform conservation actions in modified landscapes. Society for Conservation Biology Oceania Conference, Brisbane, July 2016.

Publications included in this thesis

Chapter 2: Simmonds, J.S., van Rensburg, B.J. & Maron, M. Non-random patterns of vegetation clearing and potential biases in studies of habitat area effects. Accepted for publication in *Landscape Ecology*.

Contributor	Statement of contribution
Jeremy Simmonds (Candidate)	Designed study (70%) Performed literature review (100%) Data extraction and analysis (100%) Wrote the paper (100%) Edited paper (80%)
Berndt van Rensburg	Designed study (15%) Edited paper (10%)
Martine Maron	Designed study (15%) Edited paper (10%)

Contributions by others to the thesis

Chapters 2-5 have been accepted in, or prepared for submission to peer-reviewed journals. I developed the research questions in collaboration with my PhD supervisors (Martine Maron and Berndt van Rensburg), conducted all data analyses and wrote the chapters/manuscripts. In all four chapters, Martine Maron and Berndt van Rensburg contributed to the development of ideas, provided guidance on statistical procedures, and provided feedback on drafts. Additionally, Ayesha Tulloch provided guidance on statistical procedures, and gave feedback on drafts of Chapter 3.

Statement of parts of the thesis submitted to qualify for the award of another degree

None.

Acknowledgements

As I near the end of my PhD studies, I take this opportunity to reflect back on what has been a wonderful experience. First and foremost, I acknowledge the funding that allowed me to undertake this research—an Australian Postgraduate Award provided by The University of Queensland (UQ), a top-up scholarship provided by the National Environmental Research Program, and travel support from the School of Geography, Planning and Environmental Management (GPEM).

I have learned so much in these three and a half years, and feel immensely grateful to have had the opportunity to conduct research at UQ. Beyond the incredible scientific training and technical and personal development that I have been fortunate enough to receive, the countless fantastic people I have met along the way will be my enduring memory of this experience. All have contributed to me getting to this point in one way or another, and I thank you.

I express my sincerest gratitude to my primary supervisor, Martine Maron, without whom this would not have been possible. I thank you for entrusting me with your brilliant idea, for your unfailing enthusiasm and positivity, and your patience and dedication in mentoring me and developing my research skills. You have challenged me to think critically, contest ideas, and communicate clearly. I am extremely grateful for your guidance, and feel privileged to have worked with you on this project. Thank you also to my co-supervisor Berndt van Rensburg for your tremendous support throughout. I thank you for encouraging me to explore ideas from different perspectives, distil complex concepts into simple language, and for your detailed guidance on the South African component of my project. I have greatly benefited from your input into my research.

Numerous other people provided varying degrees of input into my research. I particularly want to acknowledge Ayesha Tulloch and Claire Runge, who both provided important technical advice, and whose interest and enthusiasm about my project translated to numerous thought-provoking and stimulating conversations. I thank James Watson for his input in the early stages of my project, and Talitha Santini for invaluable advice about soil properties. I benefited greatly from conversations with David Currie about my research, and am particularly grateful for the feedback he provided on my work. More broadly, I derived great value from the countless conversations in the hallway, over lunch or at

conferences with colleagues about not only my project, but the amazing array of research in the fields of landscape ecology and conservation science being done in Australia and around the world. Also, thanks to the thousands of birdwatchers whose carefully collected data formed the foundation of a large component of my research.

Conducting my research in a school as supportive and friendly as GPEM has greatly enhanced my PhD experience. In particular, I thank Judy Nankiville for assisting with postgraduate administration, Jurgen Overheu for fixing (always urgent!) IT problems, and the finance team for guiding me through the university travel system. It has been a pleasure being a part of such a vibrant and positive school. Being a member of the wider Centre for Biodiversity and Conservation Science at UQ has exposed me to a large group of incredible researchers. Thanks to you all for the friendship, good humour and inspiring conservation work.

My earliest memories are of a curiosity about nature, and a fascination with birds. Thanks to my parents and extended family for nurturing and facilitating this interest. Special mention to my mum, who, despite being so afraid of birds that she doesn't eat poultry, still took me out birdwatching as a little kid! These childhood memories instilled a passion for wild animals and wild places in me. Thanks for your genuine interest in my PhD project, and for your ever-dependable support.

Finally, I could not have done this without my partner, Kath. Thanks for your positivity and enthusiasm, for your patience, for reading countless drafts, and for the numerous pep talks. While this project has been my (our?) baby for the last few years, welcoming our first child into the world earlier this year changed that perspective. Thanks for balancing being a wonderful mum to Josie and supporting me over these final few months—it's definitely my turn to change a few more nappies! Josie – this is for you.

Keywords

abiotic, area effects, Australian birds, heterogeneity, landscape scale, native vegetation, non-random clearing, species-area relationship, species richness, threshold

Australian and New Zealand Standard Research Classifications (ANZSRC)

ANZSRC code: 050104, Landscape Ecology, 70%

ANZSRC code: 050202, Conservation and Biodiversity, 20%

ANZSRC code: 050211, Wildlife and Habitat Management, 10%

Fields of Research (FoR) Classification

FoR code: 0501, Ecological Applications, 70%

FoR code: 0502, Environmental Science and Management, 30%

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CHAPTER 1

INTRODUCTION

1.1 Background to the problem

The near-ubiquitous positive relationship between the number of species and area is well established in biogeography and ecology (MacArthur & Wilson, 1967; Rosenzweig, 1995; Lomolino, 2000; Lazarina *et al.*, 2014), and has been cited as one of ecology's few laws (Whittaker & Triantis, 2012). The species-area relationship has attracted significant research interest over many decades, not least because of its utility for describing patterns of species occurrence in a world that is undergoing rapid transformation. Analysis of the species-area relationship can inform predictions about how changes in habitat area will influence species richness (Drakare *et al.*, 2006; Scheiner *et al.*, 2011; Proenca & Pereira, 2013), and can guide management interventions that seek to arrest the decline of biodiversity in modified environments (Desmet & Cowling, 2004; Huth & Possingham, 2011; Possingham *et al.*, 2015).

In the case of landscapes—mosaics of natural vegetation cover and human land use covering hundreds to thousands of hectares—species richness is expected to be higher in landscapes that have a greater area of habitat (Fahrig, 2013). Of significant interest is the shape of the curve that describes the landscape-level species-area relationship, as this illustrates *how* richness varies along a gradient of habitat cover among multiple landscapes. Indeed, studies at the landscape level have variously revealed that richness increases as a monotonic function of habitat area (De Camargo & Currie, 2015), that the relationship exhibits a 'peak' whereby richness is maximised at intermediate levels of habitat cover (Desrochers *et al.*, 2011), or that there is a threshold in the relationship, about which the effect of area on richness suddenly changes (Radford *et al.*, 2005; Ochoa-Quintero *et al.*, 2015). Consensus on how habitat area affects species richness at the landscape level is lacking.

Given that the implications of future habitat loss can be revealed by the shape of the relationship (Tjørve, 2003; Whittaker & Triantis, 2012), resolving uncertainty about the effect of habitat area on species richness is of pressing importance. A key approach to addressing this uncertainty is identifying and accounting for attributes of landscapes that potentially act on the shape of observed species-area relationships. For example, abiotic

attributes of landscapes such as soil fertility and topography are often correlated with habitat area because of biases in where humans clear and retain native vegetation (Seabloom *et al.*, 2002; Rouget *et al.*, 2003). Moreover, these same attributes may interact with habitat area to affect patterns of species occurrence (Lindenmayer & Luck, 2005; Maron *et al.*, 2012). If unaccounted for, these confounding factors may distort the shape of the landscape-level species-area relationship.

A species-area relationship that is distorted by the confounding influence of landscape attributes diminishes our understanding of the response of biodiversity to landscape modification. It could lead to inaccurate predictions and ineffective conservation interventions that are focussed on habitat area.

1.2 Species richness and area

Larger areas tend to have more species. This is one of the most widely recognised patterns in ecology and biogeography, and is encapsulated by the species-area relationship (Rosenzweig, 1995; Triantis *et al.*, 2008). The most straightforward mechanism explaining the species-area relationship is that larger areas contain more individuals, and, assuming individuals are distributed randomly, a greater likelihood of more species—a concept that has been captured by an array of terms, including ‘passive sampling’ (Connor & McCoy, 1979), ‘random placement’ (Turner & Tjørve, 2005) and ‘more individuals’ (Scheiner *et al.*, 2011). A second mechanism is that species richness is positively correlated with area because larger areas contain a greater diversity of habitats, which facilitates the co-occurrence of more species (Turner & Tjørve, 2005; Drakare *et al.*, 2006; Báldi, 2008; Scheiner *et al.*, 2011; Giladi *et al.*, 2014). The interplay between area, population sizes and likelihood of extinction further underpins the relationship between species richness and area (MacArthur & Wilson, 1967; Gaston, 2000; Scheiner *et al.*, 2011). Notably, Triantis *et al.* (2008) highlighted that the species-area relationship represents a generalisation of the substantial complexity that drives ecological systems. Thus, while various mutually-exclusive mechanisms have been proposed to explain the relationship, deriving a more nuanced appreciation of the effect of area requires examination of factors that interact to influence the occurrence, persistence and distribution of species (Turner & Tjørve, 2005; Tjørve & Turner, 2009; Scheiner *et al.*, 2011).

The approach to modelling species-area relationships has received considerable attention, both from a theoretical perspective, and with regards to what this relationship reveals about ecological and biogeographical patterns (Dengler, 2009). While the power and logarithmic (or exponential) models—represented by convex, upward shaped curves—have been widely used to examine the relationship between species richness and area (Dengler, 2009; Scheiner *et al.*, 2011), a number of authors have highlighted the pitfalls of not critically analysing model choice, given that the relationship may be better explained by other functions (Lomolino, 2000; Turner & Tjørve, 2005; Smith, 2010; Scheiner *et al.*, 2011; Proenca & Pereira, 2013). For example, species-area relationships for islands or other isolates, where some but not all species potentially exhibit minimum area requirements, may be better represented by sigmoid models (Tjørve & Turner, 2009). Quadratic models may be appropriate where richness is a peaked function of area (Desrochers *et al.*, 2011; De Camargo & Currie, 2015). Where the relationship is characterised by a sudden change point, threshold models may best represent the shape of the relationship between species richness and area (Ficetola & Denoël, 2009; Matthews *et al.*, 2014a).

The substantial emphasis that has been placed on understanding the factors that underpin the species-area relationship, and what mathematical function best represents it, is due to the tremendous utility of the relationship for revealing how species richness may be affected by changes to area. In particular, MacArthur and Wilson's (1967) theory of island biogeography spawned significant interest in how an understanding of the species-area relationship can translate to predictions about the implications of habitat loss in mainland environments (Giladi *et al.*, 2014). Indeed, the species-area relationship is one of the cornerstones of conservation biogeography (Matthews *et al.*, 2016). It has been employed to predict species extinctions resulting from habitat loss (Pereira & Daily, 2006; Pimm *et al.*, 2006; Hubbell *et al.*, 2008; Koh *et al.*, 2010; He & Hubbell, 2011; Bogich *et al.*, 2012; Kitzes & Harte, 2014), and guide conservation actions that seek to maintain or enhance species richness (Desmet & Cowling, 2004; Wilson *et al.*, 2006; Wilson *et al.*, 2007; Evans *et al.*, 2011; Possingham *et al.*, 2015).

In mainland applications of the species-area relationship, there has been a particular focus on the effect of patch area on species richness. Patches, or 'habitat islands' (*sensu* Matthews *et al.*, 2016) occurring within a matrix of human land use, have frequently been considered as analogues to 'true' (oceanic) islands (Fahrig, 2013). However, there is

considerable conjecture about the appropriateness of applying the island paradigm to fragmented mainland systems (Laurance, 2008; Mendenhall *et al.*, 2012; Fahrig, 2013). Of note is the recognition that the effects of habitat loss on patterns of species richness manifest at a scale beyond that of individual patches (Fahrig, 2013). This has generated an increased focus on exploring the effects of habitat loss at the scale at which local assemblages are likely to respond to the transformation—that is in ‘whole landscapes’ (Radford & Bennett, 2007). As such, understanding how species are affected by the amount of habitat at the landscape level has been advocated (Radford *et al.*, 2005; Thornton *et al.*, 2011), and has resulted in a substantial recent body of literature on landscape-scale species-area relationships.

1.2.1 The relationship between species richness and habitat area in modified landscapes

Habitat amount and configuration

Unlike islands or habitat patches, modified landscape mosaics contain both habitat and non-habitat (in accordance with the widely used patch-corridor-matrix conceptualisation of landscapes (Forman, 1995; Fahrig, 2013)—although see Bennett *et al.* (2006); Lindenmayer and Fischer (2007); Laurance (2008) for critique of this approach). Using this conceptualisation of modified landscapes, there has been extensive exploration of how species richness is affected by both the amount of habitat in a landscape, and how this habitat is configured (Parker & Mac Nally, 2002; Radford *et al.*, 2005; Pardini *et al.*, 2010; Smith *et al.*, 2011; Hanski *et al.*, 2013; Rybicki & Hanski, 2013). Much of the interest in configuration effects in human-modified landscapes was spawned by the ‘fragmentation threshold’ hypothesis (Andrén, 1994), which proposed that the (negative) influence of habitat configuration on populations in a given landscape becomes stronger as habitat amount decreases. Specifically, Andrén (1994) suggested that habitat loss is the primary cause of species richness declines where habitat extent for a given landscape is above 30%, but that below this level, fragmentation effects exacerbate the adverse impact of habitat loss.

While some landscape-scale studies have detected an influence of habitat configuration on species occurrence patterns (Trzcinski *et al.*, 1999; Villard *et al.*, 1999; Pardini *et al.*, 2010; Smith *et al.*, 2011; Haddad *et al.*, 2016), analyses at the landscape level have consistently revealed that habitat amount is a fundamental driver of species richness in

human-modified mosaics (Radford *et al.*, 2005; Martensen *et al.*, 2012; Cunningham *et al.*, 2014a; Ochoa-Quintero *et al.*, 2015). These conclusions are supported by Fahrig, whose review of empirical studies (Fahrig, 2003) and comparative analysis of modelling and empirical data (Fahrig, 2002) provided strong support to the notion that habitat amount is a far more important driver of species occurrence, than habitat configuration. Fahrig (2013) formalised this view with the 'habitat amount hypothesis', which suggests that species richness in patches of habitat in a modified matrix is neither a function of patch size nor isolation, but rather, the total amount of habitat in the local landscape. This hypothesis is underpinned by the sample area effect, whereby larger sample areas contain more individuals, and generally as a result, more species (Fahrig, 2013).

Abiotic landscape attributes and non-random clearing

In addition to the oft-analysed influence of habitat configuration, various abiotic attributes have also been incorporated into landscape-level species-area studies. This is because elements of environmental heterogeneity—topographic variation, soil properties and climatic factors—are important determinants of spatial patterns of species occurrence (van Rensburg *et al.*, 2002; Davies *et al.*, 2007; Allouche *et al.*, 2012; Fitterer *et al.*, 2013; Stein *et al.*, 2014; Chocron *et al.*, 2015), and have the potential to interact with habitat area to affect species richness (Lindenmayer & Luck, 2005). Although focussing on islands, Triantis *et al.* (2008) noted that the consideration of other variables which contribute to the occurrence of species in space and time, such as productivity and environmental heterogeneity, can allow for an improved understanding of the effect of area on biodiversity as revealed by the species-area relationship.

Indeed, the influence of abiotic attributes has been considered in a range of examinations of the effect of area on biodiversity. Storch *et al.* (2005) highlighted that energy availability—associated with abiotic factors such as rainfall—moderates the slope of broadscale species-area relationships. While focused on the cumulative area of sample grid cells rather than habitat area within landscapes, Storch *et al.* (2005) noted that the effect of area on bird species richness in South Africa and Great Britain was significantly reduced where energy availability was higher (i.e. a negative interaction). Kisel *et al.* (2011) documented that area was a key driver of regional-scale species-area relationships, although interactions between area and abiotic variables including range in elevation and energy availability were found to be significant. Radford *et al.* (2005) found

that within-landscape altitudinal variation contributed additional explanatory power (to that provided by habitat area) of observed patterns of woodland bird species richness in south-east Australia. This result was attributed to the positive correlation between topographic variation and heterogeneity in vegetation (habitat) types (Radford *et al.*, 2005). Yamaura *et al.* (2011) explored how rainfall, topography and productivity interacted with human land use (and associated habitat loss) to explain patterns of Japanese forest bird species richness at various scales. The existence of a correlation between abiotic attributes and habitat loss, whereby productive lowlands have been more heavily cleared, was highlighted by Yamaura *et al.* (2011) to explain variation in the relationship between species richness and habitat area.

As touched on by Yamaura *et al.* (2011), abiotic factors can affect both patterns of species occurrence in interaction or association with area, and the amount of habitat in landscapes by biasing where native vegetation is cleared and retained. Such non-random patterns of vegetation clearing, driven by abiotic landscape attributes, are ubiquitous in many parts of the world (Lindenmayer & Fischer, 2006). However, these biases in patterns of vegetation clearing (habitat loss) are rarely explicitly accounted for in studies of the effect of habitat area on species richness (but see Seabloom *et al.* (2002); Rompré *et al.* (2009)).

The significance of non-random clearing for studies of biodiversity in human-modified landscapes is captured by Watson's (2011, p. 16) simple, yet highly pertinent observation of Australian woodland systems:

"...not all woodlands are the same. Woodland on a stony ridge and woodland on a floodplain provide very different resources for plants and animals, and exhibit very different fluctuations in resource availability through time – soils that grow more wheat and wool originally grew more robins and babblers."

The flat, fertile landscapes such as floodplains, evoked by Watson (2011) as the best-quality woodland bird habitat, are also the most attractive areas for agriculture. Because these landscapes are preferentially cleared of native vegetation, while vegetation is retained in landscapes that are less suitable for human land use, the amount of habitat (as represented by native vegetation cover) among multiple landscape mosaics is potentially confounded by abiotic factors which also affect the occurrence of species (Lindenmayer & Luck, 2005; Lindenmayer & Fischer, 2006). For example, more heavily cleared landscapes

are frequently more productive, which means that the number of individuals (and species) that can be supported per unit area of habitat is potentially higher than habitat occurring in a less-productive landscape (Lindenmayer & Fischer, 2006; Maron, 2008). The confounding effect of non-random clearing entails substantial ramifications for analyses of the effect of area on species richness in human-modified landscapes.

The spurious thresholds hypothesis

Maron *et al.* (2012) explored how accounting for non-random vegetation clearing affected the shape of landscape-scale species-area relationships. Using woodland birds of eastern Australia as a case study assemblage, species-area relationships were constructed for all landscapes in the study extent, and for subsets of landscapes categorised by soil productivity (higher and lower productivity landscapes) (Maron *et al.*, 2012). This landscape-specific subsetting was conducted to examine the confounding effect of soil productivity on the amount of native vegetation in landscapes.

The hypothesis under examination was that relating species richness to area where data were combined from the two broadly different landscape types would misrepresent the species-area relationship, due to the inherent bias associated with non-random clearing patterns (Maron *et al.*, 2012). Specifically, Maron *et al.* (2012) hypothesised that this bias may manifest in a threshold relationship, where two separate species-area relationships representing the different landscape types intersect, erroneously indicating that the effect of area on species richness exhibits a sharp change. Indeed, Maron *et al.* (2012) demonstrated that segregation of the data by landscape type yielded a very different representation of how species richness varied with habitat area in contrast to the shape of the relationship for the aggregated dataset, implying that landscape-specific species-area relationships (for higher- and lower-productivity landscapes) were evident.

The potential for misleading patterns to be described from landscapes that vary fundamentally in their underlying abiotic characteristics was captured in the 'spurious thresholds hypothesis' (Maron *et al.*, 2012). A graphical depiction of how combining data from different landscape types subject to vegetation clearing bias can affect the shape of observed species-area relationships is presented in Figure 1.1 (reproduced from Maron *et al.* (2012)). Thresholds, which were a key focus of the analysis, represent a highly attractive management tool, especially for establishing conservation targets (Swift &

Hannon, 2010), and have been identified from a number of landscape-scale studies of the relationship between species richness and habitat area (Radford *et al.*, 2005; Banks-Leite *et al.*, 2014; Ochoa-Quintero *et al.*, 2015; Richmond *et al.*, 2015). Spurious thresholds, which arise as a function of the confounding effect of vegetation clearing bias, undermine the applied value of the concept for guiding conservation actions such as vegetation protection or restoration targets. The spurious thresholds hypothesis, with its basis in the non-random nature of vegetation clearing and retention in human-modified landscapes, has significant implications for interpreting and managing patterns of species richness, thus warranting more detailed and widespread investigation (Maron *et al.*, 2012).

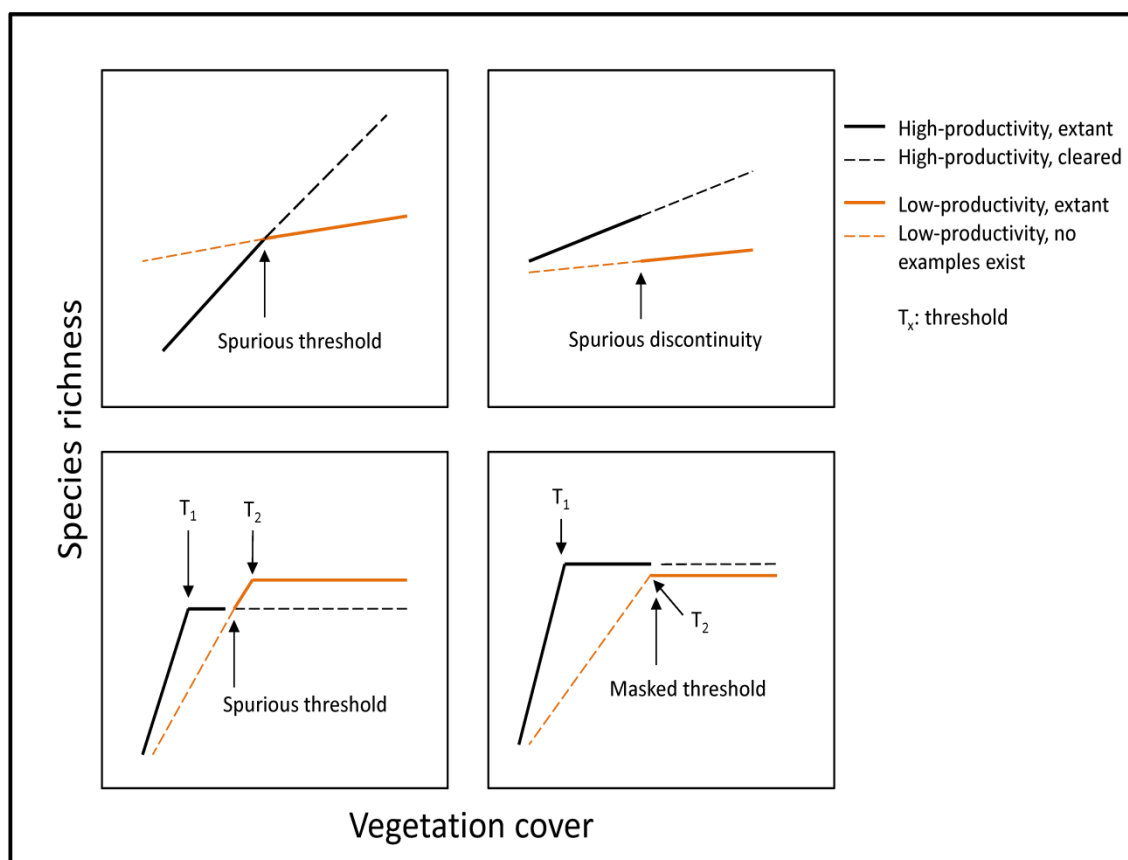


Figure 1.1 Graphical depiction of the spurious thresholds hypothesis (figure reproduced and modified from Maron *et al.* (2012, p. 684))

1.2.2 Ecological thresholds

Overview

In reviewing the applicability of the threshold concept for landscape planning, Kato and Ahern (2011) (p. 276) defined a threshold (in the natural sciences) “as a point or zone of the value of an independent parameter where a small, additional change in the independent parameter causes sudden, large changes in the state of the dependent parameter”. The manifestation of the relationship between the two variables as a discontinuity or nonlinearity is characteristic of a threshold (Muradian, 2001). It is because of the rapidity of the change in the way that one variable relates to another that the threshold concept is important and attractive from an applied conservation perspective: important because it allows for the identification of critical changes that can potentially disrupt system dynamics, and attractive, because it can provide tangible targets for protecting and enhancing biodiversity.

Causes of thresholds

Habitat configuration is the most commonly proposed driver of landscape-scale ecological thresholds (Swift & Hannon, 2010). At low levels of habitat cover, the negative effects of reduced habitat availability are potentially compounded by the spatial distribution of this habitat (Andr n, 1994; Hanski, 2015). In particular, at low levels of habitat cover, the ability of organisms to disperse between habitats, and habitat quality within remnant fragments, are potentially compromised (Swift & Hannon, 2010). The composition of the matrix, that is ‘non-preferred’ habitat type(s) that dominate the mosaic, potentially influences these fragmentation effects (Watson *et al.*, 2005; Swift & Hannon, 2010; Villard & Metzger, 2014). For example, in assessing how forest bird species richness varied with habitat amount and configuration in Brazilian Atlantic Forest mosaics, Martensen *et al.* (2012) attributed an observed threshold level of forest cover to the dominance of specialist species in the community, which in combination with their sensitivity to habitat loss, were less able to disperse through the matrix than generalist species.

Other factors that may promote thresholds in species-habitat (i.e. species-specific response to habitat) and species-area (i.e. species assemblage response to habitat) relationships include Allee effects and time-lags (Swift & Hannon, 2010). Allee effects refer

to a reduction in the viability of a population at low numbers, given the positive relationship between density and population growth rate (Courchamp *et al.*, 1999; Berec *et al.*, 2007). Factors that combine to reduce individual fitness, and thus population viability at low densities include inbreeding depression and loss of heterozygosity, demographic stochasticity (sex ratio fluctuations) and social-system dysfunction (reduced mutually-beneficial interactions) (Courchamp *et al.*, 1999). These factors, individually or in concert, may promote non-linear changes in occurrence (i.e. of a population of an individual species, or of constituent species in an assemblage), where factors such as habitat loss and/or fragmentation (independent of habitat loss) drive populations to low enough levels (Swift & Hannon, 2010).

Time lags, relating to the rate and timing of habitat loss, may contribute to nonlinear species responses to habitat area in modified landscapes. Where clearing is rapid initially, species may crowd into remnants in the landscape (Swift & Hannon, 2010), with the effect of temporarily dampening the impact of habitat loss. However, with time, and the ongoing loss of habitat, the ability of species to persist is compromised, including potentially by other factors such as fragmentation and Allee effects, thereby incurring 'payment' of the so-called 'extinction debt' (Tilman *et al.*, 1994; Swift & Hannon, 2010). A threshold in the relationship between species richness and area may result from the 'payment' of the extinction debt, whereby the negative effects of habitat loss are realised and species are rapidly lost ('relaxation') below a certain amount of habitat (Swift & Hannon, 2010; Halley *et al.*, 2014).

Importantly, interpretation of how habitat loss influences biodiversity in human-modified landscapes must be cognisant of the potential occurrence of extinction debts, as the time since clearing has the potential to distort patterns. Namely, recent, rapid habitat loss may mean that the remaining habitat is carrying an extinction debt, and thus, the true relationship between species occurrence and habitat amount is obscured by the time lag in loss of species (Halley *et al.*, 2014). For example, Radford *et al.* (2005) explored how time since clearing may have influenced their interpretation of an observed threshold in the species-area relationship of woodland birds from agricultural landscapes in south-east Australia. Finding that many species had smaller populations in low-cover landscapes, the authors suggested that an extinction debt may be evident in these landscapes (Radford *et al.*, 2005). With respect to the threshold value they identified, Radford *et al.* (2005) hypothesised that 'repayment' of the extinction debt via the loss of those low-population

species would, with time, shift the species-area threshold towards higher levels of habitat cover.

Thresholds in landscape-scale species-area studies

A number of studies that have examined how landscape-scale habitat area affects species richness have noted the occurrence of a threshold in the relationship. In the aforementioned study conducted by Radford *et al.* (2005), a rapid loss of species was observed in landscapes with less than 10% native vegetation cover. Above this value, the amount of vegetation in the landscape had little effect on species richness (Radford *et al.*, 2005). Ochoa-Quintero *et al.* (2015) noted a much higher threshold value—approximately 43% forest cover—when relating the richness of birds and mammals to forest cover in landscapes in the Amazon region of Brazil. In a study on the response of forest-specialist mammals to habitat loss in the Atlantic Forest of Brazil, Estavillo *et al.* (2013) reported that a rapid decline in species richness was observed in landscapes with less than 30% forest cover. In other studies from the Atlantic Forest, thresholds of landscape-scale forest cover below which species richness exhibited a sharp decline were observed at approximately 30-50% for birds (Martensen *et al.*, 2012), 50% for forest-specialist birds (Morante-Filho *et al.*, 2015), 47% for bats (Muylaert *et al.*, 2016), 30% for forest trees of the family Sapotaceae (Lima & Mariano-Neto, 2014) and 10-30% for small mammals (Pardini *et al.*, 2010). Richmond *et al.* (2015) noted a broad range in observed thresholds in the relationship between forest bird richness and different types of landscape-scale forest cover in two regions of Canada. These values ranged from approximately 4-28% cover (Richmond *et al.*, 2015).

Utility and limitations of thresholds for informing conservation

Ecological thresholds—including those in the relationship between species richness and habitat area—can act as explicit targets upon which conservation measures such as habitat protection or restoration can be based (Huggett, 2005; Luck, 2005; Ficetola & Denoël, 2009; Kato & Ahern, 2011; Kelly *et al.*, 2014). For example, Ochoa-Quintero *et al.* (2015) identified landscapes in the Amazon region of Brazil that should be prioritised for conservation interventions under a scenario of future habitat loss. The prioritisation was guided by an observed threshold in the species-area relationship of 43% forest cover, below which species richness rapidly declined (Ochoa-Quintero *et al.*, 2015). Banks-Leite

et al. (2014) explored how enhancing landscape-scale forest cover above a threshold of 30%—a value derived from several aggregated datasets on the response of forest-specialist and disturbance-adapted species to forest loss—could guide the management of 143 million hectares of land in the Atlantic Forest region of Brazil. In particular, a focus on restoring forest in landscapes close to, but below, the threshold value of cover was advocated as a means by which to prioritise management actions to achieve a maximum biodiversity benefit (Banks-Leite *et al.*, 2014). In observing a sharp decline of woodland bird species richness below 10% vegetation cover, Radford *et al.* (2005) advocated that landscape-scale native vegetation extent be maintained at well above 10% to avoid the rapid species loss associated with this threshold being breached.

Nonetheless, a number of flaws have been highlighted regarding the uncritical application of thresholds for guiding management. As exemplified by various studies of landscape-scale relationships between species richness and area, there is considerable variation in observed threshold values. Notwithstanding the fact that these thresholds have been observed for different taxa in landscapes of varying sizes across an array of regions, the lack of consistency in the point at which species richness suddenly declines has been highlighted as a potential limitation of the threshold concept for informing applied conservation (Huggett, 2005; Johnson, 2013; van der Hoek *et al.*, 2015).

In particular, the application of an observed threshold from one system to guide the management of a different assemblage/system/region has been strongly discouraged (Huggett, 2005; Johnson, 2013; van der Hoek *et al.*, 2015). This is because the factors underpinning a threshold response are likely to be highly species-, system-, and scale-specific (Huggett, 2005; Lindenmayer & Luck, 2005; van der Hoek *et al.*, 2015). The application of thresholds may also mean that units of analysis (i.e. landscapes) that fall well below an observed threshold value will be neglected or under-valued in terms of management intervention, even though such actions would entail a biodiversity benefit (Huggett, 2005; Bestelmeyer, 2006). Finally, managing habitat area such that it remains above an observed threshold does not necessarily correspond with the ongoing persistence of all species in the assemblage. This is because some species may be on a trajectory towards local extinction, even where habitat cover is above an observed threshold (Radford *et al.*, 2005; van der Hoek *et al.*, 2015).

These limitations underscore the importance of deriving a more nuanced understanding of the effect of area on species richness. Without a more detailed appreciation of why, and how consistently, thresholds occur, they will remain merely descriptive with limited applied utility. The exploration of factors that potentially interact to effect patterns of species richness represents an avenue by which to resolve some of the uncertainty about thresholds in landscape-level species-area relationships. Huggett (2005), Lindenmayer and Luck (2005), and Ewers and Didham (2006) highlighted that thresholds may manifest as a result of landscape attributes interacting with habitat area to affect the occurrence of species. Swift and Hannon (2010) noted that thresholds are likely to vary in different types of landscape—implying that landscape-specific species-area relationships occur. Indeed, Maron *et al.* (2012) demonstrated that the effect of area on species richness differs in different landscape types, and linked this to the interaction between landscape attributes (such as soil productivity) and habitat amount. Crucially, in recognising that these same landscape attributes are frequently correlated with habitat area due to non-random patterns of vegetation clearing, Maron *et al.* (2012) presented a foundation upon which a more thorough interrogation of thresholds in landscape-scale species-area relationships could be based. Further exploration of the spurious thresholds hypothesis will address some of the recognised limitations of the applied utility of ecological thresholds for guiding landscape management.

1.3 Summary of problem

Attributes of human-modified landscapes have the potential to confound analyses of the species-area relationship. Abiotic attributes like soil properties and topography may affect patterns of species occurrence independently of, or in interaction with habitat area. For example, flat and fertile landscapes may be able to support more species for a given area of habitat than hilly, infertile landscapes with the same amount of habitat, because the flat, fertile habitat potentially provides more resources and can support larger populations of multiple species. Furthermore, landscape attributes like soil properties and topography frequently underpin non-random patterns of habitat clearing and retention, and thus may exhibit a strong correlation with the amount of habitat in a landscape.

Failure to account for these interacting and confounding factors has the potential to distort observed species-area relationships, and may explain why substantial variation in the shape of this relationship has been recorded among various landscape-level studies. In particular, the enigmatic occurrence and nature of thresholds—a potentially valuable tool

for landscape managers and policy makers—may reflect this. In order to improve our understanding of how species richness varies with habitat area at the landscape level, it is crucial that factors that interact with and/or are correlated with area are accounted for. Only then will a more accurate representation of the way in which richness changes with area—the shape of the relationship—be gained, with significant implications for the predictive and conservation utility of the species-area relationship in modified landscapes.

1.4 Thesis aims and objectives

The overall aim of this thesis is to examine how accounting for landscape attributes that potentially bias patterns of clearing, and interact with area to drive the occurrence of species, affects interpretation of the species-area relationship in human-modified landscapes. To achieve this, I explore the ubiquity of non-random vegetation clearing in two parts of the world (Australia and South Africa), and review how the confounding effect of biased clearing patterns has been addressed in the landscape ecology literature. I then focus on how the shape and functional form of the species-area relationship, and particularly the occurrence and value of thresholds, varies in landscapes characterised by specific attributes, and in landscapes of different sizes. The focus of these analyses is on the avifauna of heavily modified woodlands and forests of south-east Australia. To explore the applied utility of the species-area relationship, I incorporate the findings of these analyses in a case study of the potential impacts of future vegetation loss in a region of eastern Australia that is subject to ongoing, rapid transformation in a dynamic policy environment.

The four key questions that I examine in this thesis are:

1. Are patterns of remnant native vegetation extent consistently non-random with respect to abiotic attributes such as soil properties in human-modified landscapes, and what are the implications of this for studies that use native vegetation extent to explore ecological patterns?
2. How does the shape of the relationship between species richness and native vegetation extent vary when landscapes are categorised by specific abiotic and anthropogenic attributes?

3. Does the shape of the relationship between species richness and native vegetation extent vary in landscape units of different sizes?
4. What can landscape-specific species-area relationships reveal about how future changes in native vegetation extent may affect bird species richness, and how can these relationships guide conservation interventions?

1.5 Thesis approach

In this thesis, I have considered the key components of landscape ecology—pattern, process, scale and heterogeneity (Wu, 2013)—to explore how species richness is affected by anthropogenic transformation of landscapes. In short, I have expanded upon the examination of simple patterns—relating species richness to native vegetation area, as per an island biogeography approach—by delving into the processes that potentially affect this relationship. By focussing on the complexity subsumed within the metric ‘area’, and particularly, how its effect may be moderated by other attributes of landscapes in a non-random clearing context, I have sought to derive a more comprehensive understanding of variation in species richness in human-modified landscapes. Specifically, the recognition that the effect of area is likely to differ among heterogeneous landscapes because of the interactive effect of abiotic attributes which act on the occurrence of individuals and species, underpins this more detailed exploration of the response of species richness to landscape transformation. Because the case study assemblage in this thesis is the avifauna of heavily modified woodlands and forests of south-east Australia, any reference to ‘landscape’ for these analyses is at a scale relevant to this bird community – namely thousands to tens of thousands of hectares.

1.6 Thesis outline

This thesis comprises six chapters: this introductory chapter outlining the background to the problem and objectives of the research; four core chapters addressing each of the specific research questions posed in section 1.4; and a conclusion chapter where the main findings, conservation implications, limitations and future research directions arising from this research are synthesised. The core analysis chapters (2 to 5) have been accepted for publication in or prepared for submission to peer-reviewed journals. As such, these chapters have been compiled as stand-alone manuscripts, entailing some repetition of key themes and methods among these four chapters.

A brief overview of the six chapters is presented below, and depicted visually in Figure 1.2.

Chapter 1 *Introduction*. This chapter provides an overview of the key topics being explored in this thesis—biased patterns of vegetation clearing, landscape-scale species-area relationships, and ecological thresholds—and outlines the overarching objective and specific questions being addressed by this research.

Chapter 2 *Non-random patterns of vegetation clearing and potential biases in studies of habitat area effects*. In this chapter, I provide an in-depth exploration of non-random patterns of vegetation clearing, and what these may mean for the study of ecological phenomena in human-modified landscapes. First, I present the results of a review of the literature, where the objective was to determine how the issue of non-random clearing has been addressed in studies of human-modified environments. Second, I examine correlations between remnant (uncleared) native vegetation extent and a range of abiotic attributes in 100 km² landscapes, and compare the findings for different regions of Australia and South Africa. This chapter establishes the foundation for the ensuing analyses that focus on the relationship between species richness and vegetation extent at the landscape level.

This chapter has been accepted for publication in *Landscape Ecology*.

Chapter 3 *Landscape-specific effects and the relationship between species richness and native vegetation extent*. Chapter 2 established the prevalence of non-random vegetation clearing, and the pitfalls of not considering these biases when relating an ecological response to area. In this chapter, I examine the relationship between the species richness of woodland and forest birds and remnant native vegetation extent in 100 km² landscapes of south-east Australia, while accounting for potential biases associated with non-random clearing. By exploring landscape-specific species-area relationships, whereby attributes of landscapes like soil fertility and topography are controlled for, I demonstrate that the shape of the species-area relationship, and particularly the occurrence and value of thresholds, varies for different landscape types. This analysis represents an exploration of the key themes of the spurious threshold hypothesis (Maron *et al.*, 2012), and highlights the importance of considering interactions between habitat area and other attributes of landscapes.

This chapter has been prepared for submission to *Ecography*.

Chapter 4 *The effect of scale on how habitat area influences landscape-level species richness.* Building upon the findings presented in Chapter 3, I explore how the shape of the landscape-scale species-area relationship, including the occurrence and value of thresholds, varies at different scales—that is, in landscapes of different sizes. While numerous studies have explored the scale of effect by varying the scale at which predictor variables are measured and related to a response, I take a ‘whole landscapes’ approach (Radford & Bennett, 2007) of measuring both the predictor variables (vegetation extent, as well as other potentially influential landscape attributes) and the response (estimates of species richness) at different scales—landscapes of 25 km², 100 km², and 400 km². I show that there is scale invariance in the relationship across a broad geographical extent, although this breaks down when the data are subset regionally. I infer processes underpinning the potential scale-dependence of species-area relationships in two regions of south-east Australia.

This chapter has been prepared for submission to *Landscape Ecology*.

Chapter 5 *The implications of using thresholds from landscape-specific species-area relationships to guide conservation actions.* In this chapter I use observed landscape-specific species-area relationships to explore the potential ramifications of future remnant vegetation loss in a region experiencing rapid change. In particular, I examine how accounting for landscape attributes (soil fertility and topography) in species-area relationships (as performed in Chapter 3) affects both predictions of changes to species richness, and potential conservation interventions based on observed thresholds. This case study is focussed on southern Queensland, Australia—a region that has undergone rapid and extensive landscape transformation, and for which future clearing trends are uncertain due to a dynamic and changing policy environment.

This chapter will be prepared for submission to *Biological Conservation*.

Chapter 6 *Thesis synthesis and conclusion.* In this final chapter, I summarise the key findings of my research, with a major focus on how interpretation of the effect of habitat area on patterns of species richness is affected by landscape attributes. I outline the contribution that this research makes to the fields of landscape ecology and conservation

biogeography. I address key limitations, both in the research approach, and in the interpretation and application of the findings presented. Additionally, I detail a suite of recommendations relating to future research directions that can build upon the foundation presented in this thesis.

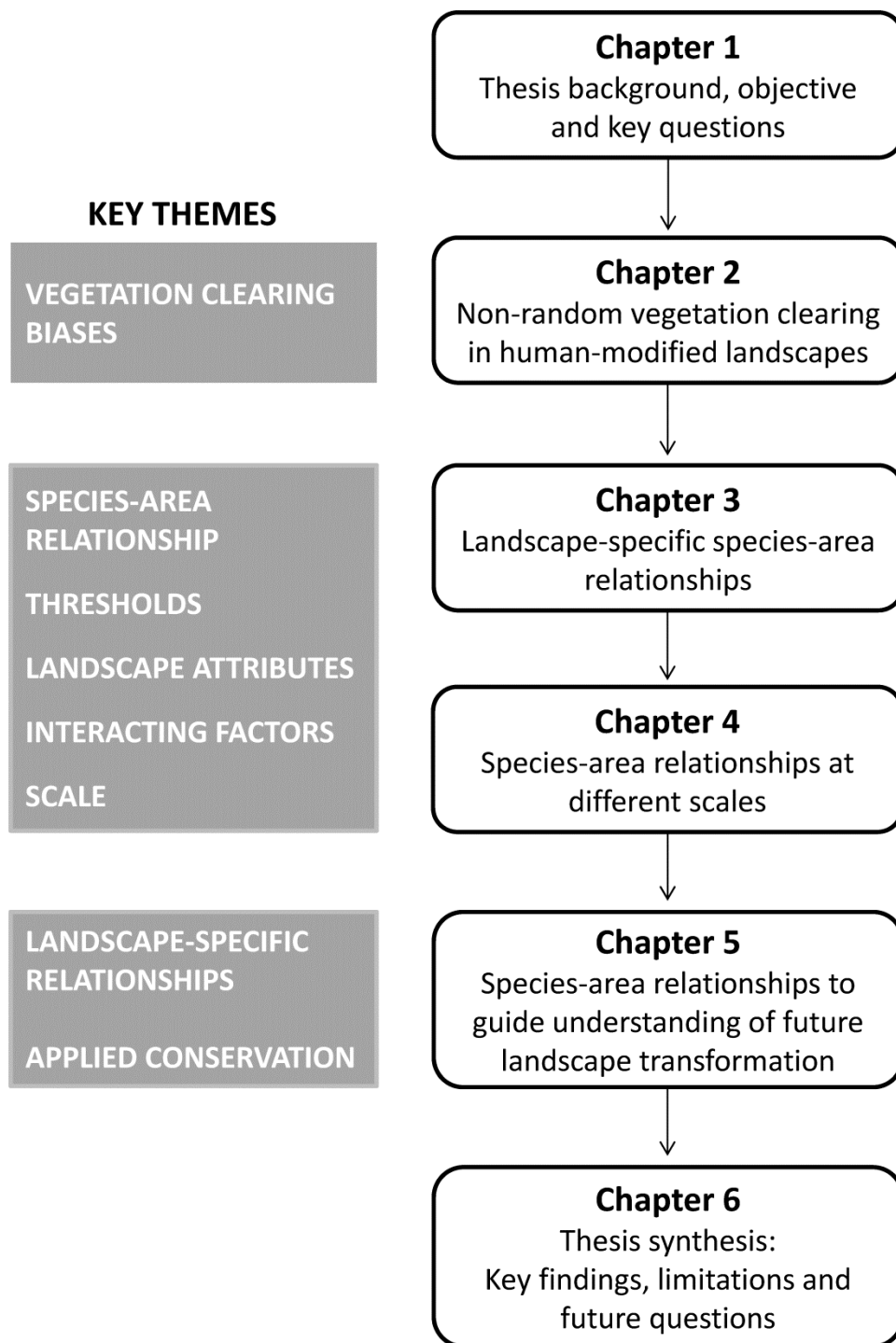


Figure 1.2 Thesis outline with key research themes highlighted

CHAPTER 2

NON-RANDOM PATTERNS OF VEGETATION CLEARING AND POTENTIAL BIASES IN STUDIES OF HABITAT AREA EFFECTS

Accepted for publication in *Landscape Ecology*

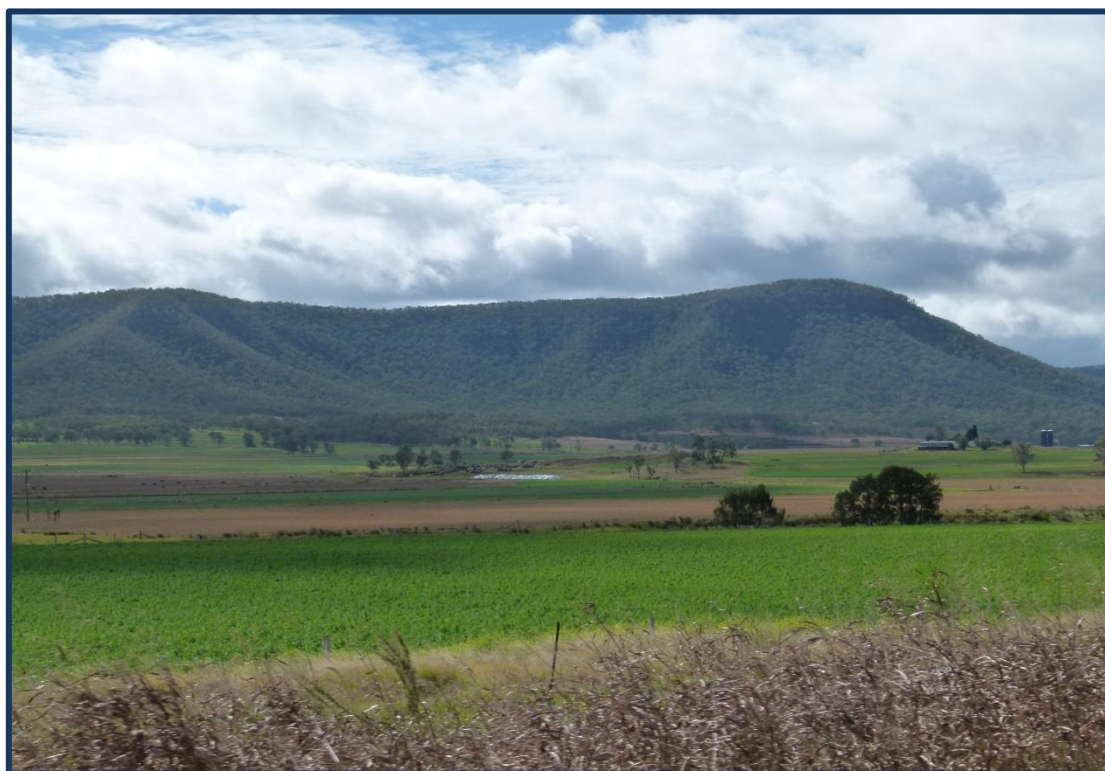


Plate 1 Native vegetation cleared on a fertile plain and retained in surrounding hills—
Darling Downs, southern Queensland

2.1 Abstract

Native vegetation extent is often a proxy for habitat area in studies of human-modified landscapes. However, the loss and retention of native vegetation is rarely random among landscapes. Instead, the extent of native vegetation in landscapes may be correlated with abiotic factors, thereby obscuring or distorting relationships between ecological phenomena and area. We asked: (1) How has the potential for non-random vegetation loss to confound area effects been addressed in the landscape ecology literature? (2) Are consistent patterns of non-random vegetation loss and retention evident from modified regions of two countries? We reviewed 118 papers that related area to an ecological response, to determine whether potential biases associated with non-random vegetation loss and retention were considered. We then analysed ~18,000 100 km² landscape units in Australia and South Africa to identify how different abiotic factors correlate with the extent of native vegetation retained in those landscapes. Only 21% of the studies we reviewed explicitly or implicitly considered spatial biases in vegetation clearing. Yet, across modified regions of Australia and South Africa, landscape-scale native vegetation extent was consistently and often strongly related to abiotic factors, particularly soil properties and topographic variability. Patterns of vegetation clearing and retention commonly reflect underlying abiotic heterogeneity. These biases, which are infrequently highlighted in studies focussing on area effects, have implications for how we assess the importance of vegetation extent for species and assemblages. Failure to account for correlates of vegetation extent risks erroneous area-based conservation prescriptions in human-modified environments.

2.2 Introduction

The role of habitat area is central to ecology's most fundamental and enduring concepts, including the species-area relationship (Rosenzweig, 1995; Whittaker & Triantis, 2012) and metapopulation theory (Hanski, 1998). Habitat area affects patterns of species distribution through its effects on colonisation, persistence and local extinction (Kisel *et al.*, 2011) via its correlation with habitat diversity (Turner & Tjørve, 2005), its association with fragmentation (Andrén, 1994; Crouzeilles *et al.*, 2014; Hanski, 2015), and its influence on the abundance of individuals (Connor & McCoy, 1979). For example, more colonists arriving at, or individuals persisting within, larger areas of habitat imply greater species richness, as more individuals will generally include more species (Connor & McCoy, 1979).

Habitat area effects have been explored at various spatial scales in human-modified systems. Approaches include assessing how organisms respond to habitat area within a set radius of sampling sites (Polyakov *et al.*, 2013; Carrara *et al.*, 2015), comparing the effect of patch size (Nufio *et al.*, 2011; Hadley *et al.*, 2014), and analysing the influence of habitat amount in pre-defined landscape-units (Harrisson *et al.*, 2012; Lima & Mariano-Neto, 2014). In such studies, area of habitat is often defined as the total extent of native vegetation cover, or cover of a particular vegetation type, within or relating to the sampling units.

The contemporary spatial extent and distribution of native vegetation in human-modified systems is generally a legacy of historical decisions about which land should be cleared (Lindenmayer *et al.*, 2010). Frequently, land is cleared of its native vegetation based on its potential to support land uses such as agriculture (Lunt & Spooner, 2005; Laurance, 2008; Watson, 2011), so the spatial pattern of vegetation clearing reflects heterogeneity in the biophysical and socioeconomic factors that promote such land use (Rompré *et al.*, 2009). It follows that the amount of native vegetation retained in a particular place will exhibit correlations with those same biophysical factors, such as soil properties and topography, which create suitable conditions for human-dominated land uses (Seabloom *et al.*, 2002).

Spatial biases in the location of terrestrial protected areas—often in unproductive, steep, and/or remote places that are unsuitable for human developmental needs such as agriculture or urban development—have been repeatedly identified in the literature (Margules & Pressey, 2000; Cowling & Pressey, 2003; Watson *et al.*, 2014). The ramifications of such biases are clear—a lack of representation of habitats and species in reserve systems (Watson *et al.*, 2014). A related, yet less-well studied issue is that of biases in patterns of vegetation clearing and retention, and the ramifications of these biases—especially where vegetation area is used to explain how species and assemblages respond to landscape modification. If vegetation area is consistently correlated with particular abiotic factors, what does this mean for conclusions drawn about the effect of area?

Recognising that abiotic properties potentially interact with area to affect ecological processes that underpin the spatial occurrence of species and assemblages (Hawkins *et al.*, 2003; Lindenmayer & Luck, 2005) underscores the need to consider biases in clearing patterns when exploring the effect of area. Indeed, accounting for factors that both interact

with area to affect the response, and are correlated with area because of non-random clearing, will allow for a more nuanced understanding of area effects. Conversely, failure to account for a confounding abiotic variable may result in erroneous conclusions about the influence of area (Lindenmayer & Fischer, 2006).

The confounding effect of non-random vegetation clearing has important implications for key ecological patterns and principles that are underpinned by area effects. For example, clearing biases may affect the shape of an observed species-area relationship. This is because the area of patches, or of native vegetation in landscapes, will be correlated with factors like soil fertility and/or topographic variability, which may also act on patterns of species richness via mechanisms like resource availability (Maron *et al.*, 2012). If the bias is not accounted for, the shape of the species-area relationship will not be an accurate representation of the effect of area *per se* on species richness.

Clearing biases may also obscure a real effect of area *per se* on an ecological response like species occurrence or abundance. In such an instance, an (expected) positive effect of habitat area on the response variable may be dampened by the confounding effect of an abiotic property like soil fertility. For example, large patches of habitat may be less productive, given their association with poorer quality soils that are unsuited to agriculture, while small patches may be more fertile. The confounding effect of productivity, and its association with resource availability (Watson, 2011), may mean that species occurrence or abundance is similar in small and large patches, thereby masking a real area effect that may exist where the confounding effect of productivity is controlled for. In an applied conservation context, such a finding may devalue larger areas, given a lack of observed area effect. However, accounting for the confounding effect of the abiotic attribute may reveal that area is indeed important, with its effect dependent on the abiotic attribute (i.e. an interaction).

Resolving uncertainty around how species and assemblages respond to native vegetation area is particularly important when conservation decisions, such as the setting of targets for vegetation retention and restoration, are based upon observed area effects such as the species-area relationship (Maron *et al.*, 2012). In light of this, to our knowledge, no comprehensive multi-regional examination of the types and importance of factors confounding remnant vegetation area in modified environments has yet been done. In this study we examine how the phenomenon of non-random vegetation clearing may confound

the effect of area on ecological responses, through both a review of the global landscape ecology literature and an empirical case study of data from almost 18,000 100 km² landscape units from two continents. We ask: (1) how do studies that use area to explore an ecological response account for potential non-randomness in patterns of vegetation extent? And (2) how is the extent of native vegetation at the landscape scale correlated with abiotic factors across human-modified regions in Australia and South Africa? In undertaking these analyses, we seek to provide a more detailed understanding of how non-random patterns of vegetation clearing affect our interpretation of area effects, and how these biases may impact conservation actions that rely on the effect of area to conserve biodiversity.

2.3 Methods

2.3.1 Literature review

We used a systematic literature review to examine how non-random vegetation clearing patterns have been addressed in studies that explored the relationship between vegetation area and an ecological response in human-modified environments (i.e. those that have been altered by the clearing and, often, the fragmentation of native vegetation). The review incorporated studies where the replicate sampling units were sites (with buffers), patches or landscapes. It was global in its coverage, and included papers published 2005-2014 inclusive. The following three exact key word combinations were searched separately in two online databases (Scopus and Web of Science): (1) “independent variable” or predictor and habitat and fragment*; (2) “habitat area” and “area of habitat” and fragment*; (3) “habitat cover” or “vegetation cover” and fragment*. Titles and abstracts of studies from these database searches were screened to identify potentially relevant papers, returning a total of 172 and 180 potential candidate papers for the two databases, respectively (including 113 duplicates). From this subset of 239 unique papers, we retained those which: (1) focussed on an empirical analysis of human-modified terrestrial systems; and (2) incorporated a measure of terrestrial habitat (vegetation) area as a predictor of a species- or assemblage-level response. The entire text of articles that satisfied these selection criteria (n=118) was examined to determine whether spatial heterogeneity in abiotic factors was considered, and particularly, whether the potential for abiotic factors to confound habitat area due to non-random vegetation clearing was: (a) explicitly controlled for in study design; (b) accounted or controlled for as part of data analysis; (c) considered in the interpretation and discussion of results; (d) not explicitly acknowledged, although

spatial homogeneity in abiotic factors was identified as a feature of the study extent; or (e) not acknowledged.

2.3.2 Empirical case study

Study extent

We quantified relationships between the extent of native vegetation and various abiotic factors from modified landscapes across different regions of Australia and South Africa. A landscape-level approach was taken as vegetation extent in a landscape has been advocated as a key determinant of species richness (Fahrig, 2013), and this scale—several to several hundred square kilometres (Fischer & Lindenmayer, 2007)—has been widely used to explore biodiversity patterns in modified environments (Radford *et al.*, 2005; Maron *et al.*, 2012). Australia and South Africa were selected for this analysis because they are both large, span several climatic zones and numerous landforms, and parts of each have been heavily modified. However, their contrasting landscape transformation histories allowed some exploration of the generality of any patterns detected.

Because abiotic factors that may introduce spatial bias to patterns of anthropogenic vegetation clearing were our focus, we considered only regions that have experienced substantial landscape alteration. In each country, bioregions (or subregions) in which at least 25% of the land cover was non-native vegetation (i.e. cleared, built-up, forestry plantations) formed the study extent. Bioregions were based on the Interim Biogeographic Regionalisation for Australia (Department of the Environment, 2012a) and the Bioregions of South Africa, Lesotho and Swaziland (Mucina & Rutherford, 2006). Within each study extent, a 10 km x 10 km grid was overlaid, and any incomplete (i.e. <100 km²) grid cells (such as those overlapping the study extent's boundaries or the coast) were removed. Each grid cell represented a 'landscape unit'. The Australian study extent included 13,230 landscape units and the South African study extent had 4564 landscape units.

Landscape units within the Australian and South African study extents were subset into broad geographic categories (Australia: south west, south east, central east, north east; South Africa: south west, central east, north east). Each category comprised 3-9 whole bioregions (see Appendix A: Table A1) for identity of bioregions corresponding with each broad geographic category). These geographic categories were further subdivided based

on climate zone (temperate or arid), using a global Koppen-Geiger climate classification (Peel *et al.*, 2007) (Figure 2.1).

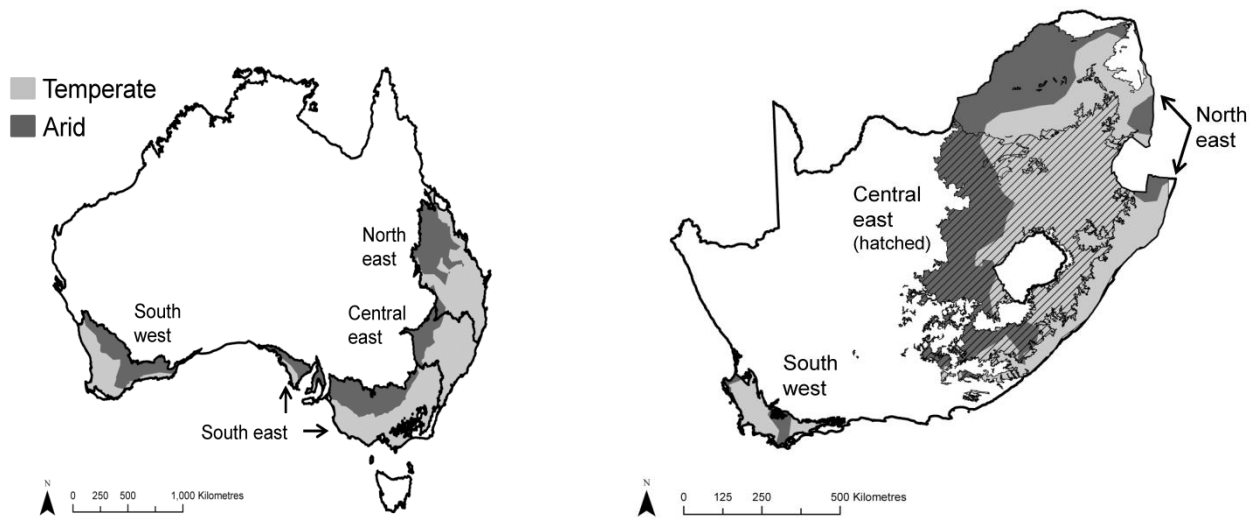


Figure 2.1 Australia (left) and South Africa (right) study extents with regional and climate zone categories displayed. Australian regions: north east (n = 2434 landscape units, n = 1551 landscape units—temperate and arid, respectively); central east (n = 1956, n = 566); south east (n = 2595, n = 1723); south west (n = 1219, n = 1186). South African regions: north east (n = 1161 landscape units, n = 799 landscape units); central east (n = 1582, n = 931); south west (n = 141, n = 40)

Response and predictor variables

National vegetation datasets were used to quantify the extent of native vegetation in each landscape. For Australia, we used the Commonwealth Government’s National Vegetation Information System major vegetation groups map version 4.1 (Department of the Environment, 2012b). This product identifies the contemporary distribution of major native vegetation groups at a 100 m raster pixel resolution, and is a summary of mapping produced by various State and Territory agencies, as at 2012. The input datasets that were incorporated into the mapping were updated during the period 2009-2011. For South Africa, the Vegetation Map of South Africa, Lesotho and Swaziland (Mucina & Rutherford, 2006) was used. This vector map, produced at a resolution of 1:250,000, represents the pre-clearing extent of vegetation types. It was converted to a 30 m raster and intersected with the 30 m pixel resolution 2009 National Land Cover map (South African National

Biodiversity Institute, 2009) to identify natural vegetation compared with areas of transformed land cover (cultivation, degraded, urban built-up, mines, plantations). In this analysis, we considered all native vegetation types (i.e. forest, woodland, shrubland, grassland), such that our measures of landscape-scale native vegetation—the amount of native vegetation retained in a landscape as a proportion of the total area of the landscape (100 km²)—represented the (aggregated) extent of all native vegetation types (not just forest).

To explore patterns in native vegetation extent among landscapes, we collated data on abiotic factors relating to three key elements of landscape heterogeneity: soil, climate and topography (Stein *et al.*, 2014). Average landscape values were obtained for three soil attributes that contribute to soil fertility via nutrient storage/availability and mediation of chemical processes (Hazelton & Murphy, 2007): pH, cation exchange capacity (cmol/kg) (CEC) and clay content mass fraction (%) (clay content). Climate data included annual mean temperature and annual rainfall, with landscape-scale average values derived for both variables. The difference between the highest and lowest points in a landscape unit was used to determine range in elevation values. Details about the datasets used for this analysis are summarised in Table 2.1. Geospatial data processing and extraction was done using ArcMap10.1 (ESRI, 2012) and Geospatial Modelling Environment (Beyer, 2012). Spatial datasets were reprojected using an Albers equal-area projection.

Table 2.1 Summary of variables and associated datasets used to explore patterns of landscape-scale vegetation extent in Australia and South Africa

Variable	Dataset (source)	Scale
Soil		
Cation exchange capacity (cmol/kg)	International Soil Reference and Information Centre (ISRIC) Soil Grids 1 km dataset (ISRIC - World Soil Information, 2013; Hengl <i>et al.</i> , 2014) – mean estimates for the 0-5 cm soil depth range were extracted	1 km
pH		
Clay content mass fraction (%)		
Climate		
Annual mean temperature (°C)	WorldClim database (Hijmans <i>et al.</i> , 2005)	1 km
Annual rainfall (mm)		
Topography		
Range in elevation (m)	Consultative Group on International Agricultural Research's version of NASA's Shuttle Radar Topography Mission 90 m resolution v.4 digital elevation model (Jarvis <i>et al.</i> , 2008)	90 m
Productivity		
Enhanced Vegetation Index (EVI)	Australian and South African continental mosaic datasets (Paget & King, 2008; TERN/AusCover, 2013) of the Moderate Resolution Imaging Spectroradiometer (MODIS) 16-day L3 Global 250 m EVI dataset (MOD13Q1: https://lpdaac.usgs.gov/dataset_discovery/modis/modis_products_table/mod13q1)	250 m

In addition, we hypothesised that if clearing patterns are biased by abiotic factors linked to agricultural potential, then landscapes that retain more native vegetation might be expected to be characterised by lower-productivity native vegetation. The Enhanced Vegetation Index (EVI) was used to provide a proxy for the productivity of remaining native vegetation in a landscape. Average EVI values were derived for the remaining native vegetation in a landscape unit, rather than for the entire landscape unit, because in modified environments, landscape-level EVI measures are likely to be strongly affected by land use and may not reflect intrinsic landscape conditions that preceded vegetation

clearing. Further information about how the EVI data were processed is provided in Appendix A1.

Data analysis

Univariate ordinary least squares (OLS) linear regressions were examined to explore the direction, shape and strength of relationships between landscape-scale native vegetation area and abiotic factors in different geographic and climate zone regions of the Australian and South African study extents. Where an inspection of scatter plots indicated nonlinearity in the relationship, a quadratic term was included in models. The response variable—proportion of native vegetation retained in a landscape—was logit transformed (Equation 1) prior to these regression analyses using the approach presented by Warton and Hui (2011), to allow for the approximate fulfilment of linear modelling assumptions.

$$\text{Equation 1: } \log(y+e / 1-y+e)$$

An added constant (e) was incorporated into the logit transformation (Equation 1). This value allowed for sample proportions equal to 0 and 1 to be transformed, without introducing substantial bias (Warton & Hui, 2011). The smallest non-zero proportion values (to three decimal places) were identified for each of the Australian and South African datasets, and this value (0.001 and 0.002, respectively) was used to represent the constant e in logit transformations for data from each country. All analyses were done in R (R Core Team, 2013).

Spatial autocorrelation may arise in models where spatial patterning in the response variable is not wholly accounted for by the spatial structuring of the model's predictor variables (Beale *et al.*, 2010). This lack of independence between data points may inflate Type I errors (Diniz-Filho *et al.*, 2003). A multivariate analysis using generalised least squares (GLS) regression to account for spatial autocorrelation was used to explore how three abiotic factors representing soil fertility (CEC), climate variability (annual rainfall) and topographic heterogeneity (range in elevation), and each two way interaction, related to (logit) native vegetation proportion. GLS regression, undertaken using the nlme package in R (Pinheiro *et al.*, 2013), allows for the incorporation of a residual spatial correlation structure into the model (Dormann *et al.*, 2007). Collinearity in input variables was checked prior to the multivariate modelling using variance inflation factors (Zuur *et al.*, 2010). Using

the approach of Rhodes *et al.* (2009), we found that variance inflation factors were well below 10, indicating collinearity was not likely to affect the multivariate analyses. All predictor variables were standardized to z-scores to allow for comparison of coefficients among regions. For each region, six alternative GLS regression models were evaluated. Each was a global model, but five incorporated a different spatial correlation structure (exponential, Gaussian, linear, rational quadratic, spherical (Zuur *et al.*, 2009)), and the sixth incorporated no spatial correlation structure (i.e. a non-spatial model). The model with the lowest Akaike information criterion (AIC) value was retained for further examination. Inspection of bubble plots, and variograms of normalised residuals, was performed to determine whether residual spatial autocorrelation was still present after the inclusion of the spatial correlation structure.

2.4 Results

2.4.1 Literature review

Of the 118 studies reviewed in detail, only 15 considered how non-random vegetation clearing influenced the effect that area had on the response variable in question. One of these 15 studies was designed to control (in part) for spatial biases in vegetation extent with respect to abiotic factors, five sought to account for confounding factors in the analysis of data, and nine acknowledged the influence of non-random clearing in the interpretation of study results.

A number of key conclusions about the implications of non-random clearing were highlighted by these studies. For example, Polyakov *et al.* (2013) noted that the predictive capacity of models of woodland bird occurrence focussing on vegetation extent may be affected by clearing biases, because landscapes with high vegetation cover differ in soil properties and vegetation type compared to low cover landscapes. They found that including vegetation composition, as well as extent, resulted in an improvement in the explanatory power of models of species occurrence, and highlighted the need to focus restoration efforts at sites with fertile soils (Polyakov *et al.*, 2013). Maron *et al.* (2012) demonstrated that clearing biases distort the shape of the relationship between woodland bird species richness and native vegetation extent at the landscape scale. Drinnan (2005) found that the positive effect of vegetation connectivity on several taxa was difficult to distinguish from the effect of remnant area, and acknowledged that biases in clearing, whereby larger and more connected remnants occurred in hilly parts of an urban matrix, underpinned this correlation.

Furthermore, several studies highlighted that an expected positive effect of area was not realised, and associated this lack of effect with non-random patterns of clearing. Basham *et al.* (2011) reported lower bat activity in well-vegetated protected areas compared with less-vegetated urban areas in the Sydney region of eastern Australia, and suggested that the confounding effects of soil fertility on vegetation extent—a legacy of non-random clearing—may be responsible for this result. Looney *et al.* (2009) proposed that biases in clearing leading to a negative association between remnant area and soil fertility underpinned the lack of relationship between grassland beetle community structure and patch size in prairie remnants in a heavily modified agricultural matrix in the north-west United States. The lack of an effect of forest area on koalas (*Phascolarctos cinereus*) in southern Australia was associated with biased clearing patterns by Januchowski *et al.* (2008), who suggested that the higher soil fertility associated with smaller habitat fragments in a heavily cleared agricultural and urban matrix was a more influential driver of koala occurrence than forest area.

While not explicitly outlining efforts to account for non-random vegetation clearing, ten studies noted that the focal study system was spatially homogeneous with respect to abiotic factors, implying that the effect of non-random vegetation clearing was unlikely to be an issue in these studies. A further nine studies were designed such that one or more elements of spatial abiotic heterogeneity were controlled for, although this was not explicitly associated with controlling for the confounding effect of non-random vegetation clearing. While 28 studies used predictor variables capturing spatial variation in abiotic factors, the potential for correlations between these variables and vegetation extent to modify the apparent effects of area was not explored. The full list of papers reviewed, and the category to which they were assigned as part of the review process, is provided in Appendix A: Table A2.

2.4.2 Empirical analysis

Relationships between the proportion of native vegetation retained in a landscape and several abiotic factors emerged repeatedly across regions in both Australia and South Africa (Table 2.2; for all univariate graphs see Appendix A: Figure A1). In temperate landscapes of Australia, the proportion of native vegetation retained in a landscape (hereafter, 'native vegetation extent') was inversely related to average CEC. Landscapes with a greater range in elevation and higher average annual rainfall tended to have more

native vegetation. These patterns held for each of the four Australian regions analysed, and were evident when data from all temperate landscapes across these four regions were combined (Figure 2.2). Native vegetation extent was also generally higher in temperate landscapes characterised by soils with lower average clay content and pH values, which, like CEC, are factors associated with soil fertility. This result likely reflects the strong correlations among the various soil properties. In arid Australian regions, landscapes with more native vegetation were typified by lower values of average CEC, average clay content and average pH, although the shape and goodness-of-fit of these relationships varied among regions. Average annual temperature was generally negatively related to native vegetation extent, although these relationships were typically weak ($R^2 < 0.10$). The strength and direction of the relationship between native vegetation extent and mean EVI of remaining native vegetation varied among geographic regions and climate zones.

The range in elevation was related positively to native vegetation extent in temperate and arid landscapes of all three South African regions, although this relationship was weak in the central east and north east ($R^2 < 0.15$). In contrast to the results for Australia, soil properties were not consistently negatively related to native vegetation extent. Model fit was low when data for all South African temperate landscapes were combined (Figure 2.2). EVI was generally lower in landscapes where more native vegetation was retained, as predicted.

Table 2.2 Direction and significance of univariate ordinary least squares (OLS) regression coefficients for the relationship between the proportion of native vegetation in a landscape (logit transformed) and abiotic factors. CEC = average cation exchange capacity (cmol/kg); Clay = average clay content mass fraction (%); pH = average pH; Elevation = range in elevation (m); Rainfall = average annual rainfall (mm); Temperature = average annual temperature (°C); EVI = average enhanced vegetation index of native vegetation

	Temperate landscapes				Arid landscapes				
	North east	Central east	South east	South west	North east	Central east	South east	South west	
Australia	CEC	---	---	---	---	---	---	---	
	Clay	---	---	---	---	n.s	---	---	
	pH	---	---	---	---	---	---	---	
	Elevation	+++	+++	+++	+++	+++	n.s	--	n.s
	Rainfall	+++	+++	+++	+++	+++	---	---	+++
	Temperature	n.s	---	---	---	---	+	n.s	---
	EVI	+++	+++	---	+++	+++	---	---	n.s
South Africa	CEC	n.s	+++		n.s	---	+++		n.s
	Clay	+	n.s		n.s	---	+++		n.s
	pH	++	+		---	---	+++		---
	Elevation	+++	+++		+++	+	+++		+++
	Rainfall	---	+++		+++	n.s	---		n.s
	Temperature	n.s	---		---	+++	---		-
	EVI	---	n.s		---	n.s	---		--

+ <0.05; ++ <0.01; +++ <0.001; n.s not significant

Grey shading: a quadratic term in the model due to evidence of nonlinearity in the relationship – see Appendix A: Figure A1 for all univariate graphs

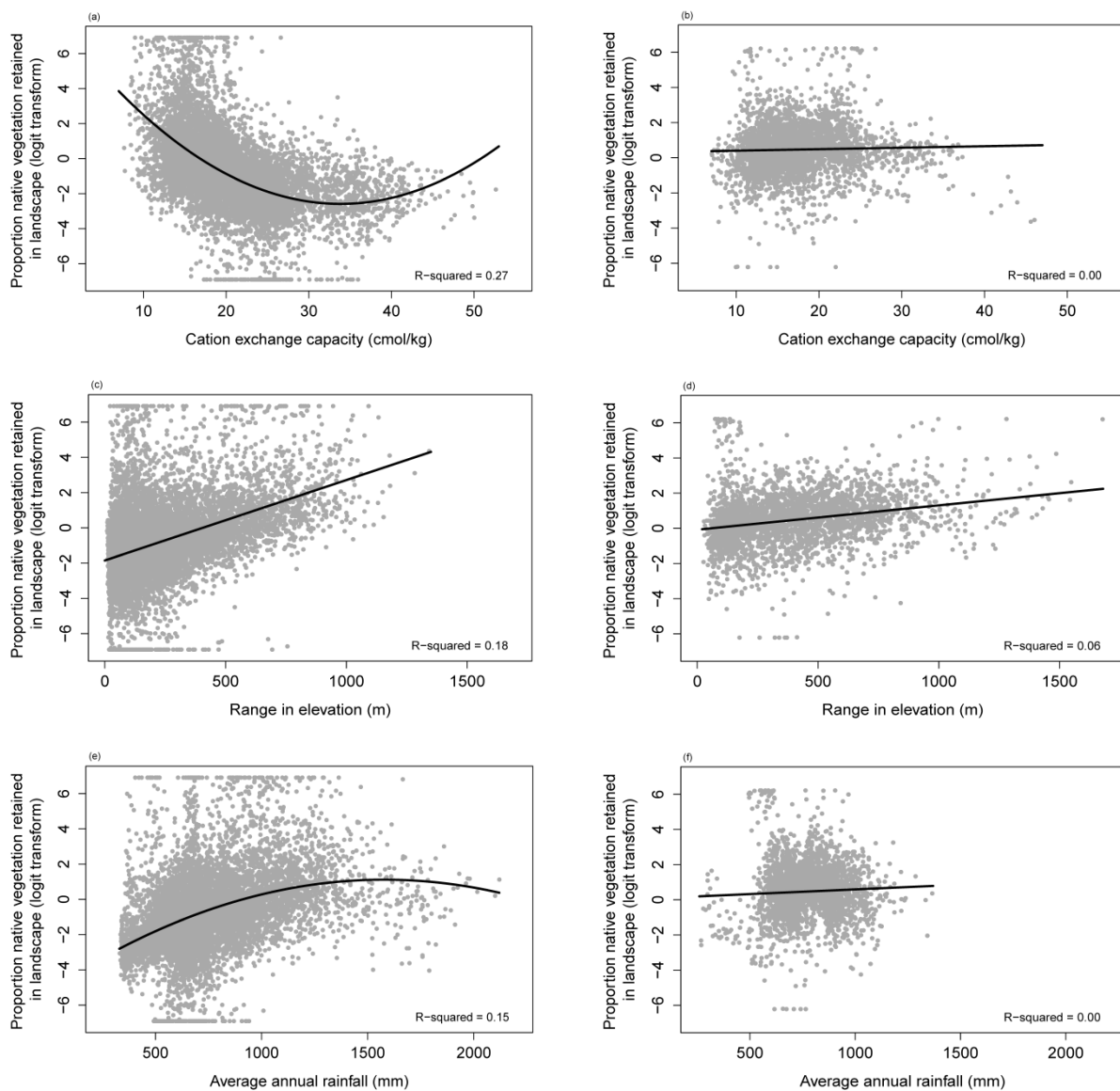


Figure 2.2 Ordinary least squares relationship between the proportion of native vegetation retained in a landscape (logit transformed) and three abiotic factors—average cation exchange capacity (a, b), range in elevation (c, d) and average annual rainfall (e, f)—for all temperate landscapes across the four Australian regions (left column, n=8204 landscape units) and the three South African regions (right column, n=2884 landscape units) examined

The relationships identified from the univariate analysis also emerged in multivariate GLS regression models which accounted for spatial autocorrelation (Table 2.3). In temperate and arid landscapes of all four Australian regions, higher native vegetation extent was associated with lower average CEC values ($p < 0.05$). Furthermore, higher range in elevation and average annual rainfall values were always significant predictors ($p < 0.05$) of

greater vegetation extent across temperate Australian regions. The relative strength of these effects varied within and among regions. In South Africa, range in elevation had a significant ($p < 0.05$) positive influence on vegetation extent across all regions and climate zones. However, unlike Australia, higher native vegetation extent was associated with higher values of average CEC in some regions of South Africa. Inspection of bubble plots and variograms of normalised residuals revealed that spatial autocorrelation was reduced substantially, but was still present in spatial models for some regions. This may have been a function of autocorrelation occurring at different scales among the predictors (i.e. range in elevation = small-scale correlation vs annual rainfall = large-scale correlation) (Dormann *et al.*, 2007).

Table 2.3 Standardised generalised least squares (GLS) multiple regression coefficients, significance at $p < 0.05$ and standard errors in parentheses, for the relationship between the proportion of native vegetation in a landscape (logit transformed) and abiotic factors. CEC = average cation exchange capacity (cmol/kg); Elev. = range in elevation (m); Rain = average annual rainfall (mm). The spatial correlation structure (Corr) of the model for which results are reported (model with lowest AIC for each region) is presented

		Temperate landscapes				Arid landscapes			
		North east	Central east	South east	South west	North east	Central east	South east	South west
Corr [#]		RQ	SPH	EXP	EXP	EXP.	RQ	EXP	EXP
	Australia	CEC	-0.63 *** (±0.06)	-0.48 *** (±0.07)	-0.69 *** (±0.05)	-1.14 *** (±0.07)	-0.75 *** (±0.06)	-0.49 *** (±0.10)	-0.98 *** (±0.08)
Elev.		0.67 *** (±0.06)	0.71 *** (±0.07)	0.63 *** (±0.06)	0.30 *** (±0.05)	0.45 *** (±0.06)	-0.04 (±0.06)	0.03 (±0.06)	0.01 (±0.06)
Rain		0.28 * (±0.12)	2.18 *** (±0.20)	1.11 *** (±0.12)	0.78 * (±0.31)	0.89 *** (±0.18)	-1.13 *** (±0.20)	-0.70 ** (±0.21)	0.61 (±0.37)
CEC x Elev.		0.14 ** (±0.05)	0.22 *** (±0.06)	-0.08 (±0.06)	0.16 ** (±0.06)	-0.14 ** (±0.05)	0.01 (±0.05)	-0.12 * (±0.05)	0.09 * (±0.04)
CEC x Rain		0.34 *** (±0.07)	-0.15 (±0.09)	0.26 *** (±0.06)	-0.47 *** (±0.08)	0.01 (±0.06)	-0.01 (±0.10)	0.12 (±0.07)	-0.38 *** (±0.06)
Elev. x Rain		0.02 (0.04)	0.03 (±0.05)	-0.02 (±0.05)	-0.20 *** (±0.05)	0.02 (±0.06)	0.06 (±0.06)	0.15 ** (±0.05)	0.02 (±0.04)

		Temperate landscapes				Arid landscapes			
		North east	Central east	South east	South west	North east	Central east	South east	South west
South Africa	Corr [#]	EXP	RQ		SPH	EXP	EXP		RQ
	CEC	0.32 ^{***}	0.33 ^{***}		0.06	-0.23 ^{**}	0.44 ^{***}		-0.45
		(±0.07)	(±0.03)		(±0.14)	(±0.08)	(±0.05)		(±0.26)
	Elev.	0.50 ^{***}	0.46 ^{***}		0.65 ^{**}	0.28 ^{***}	0.38 ^{***}		1.76 ^{***}
		(±0.07)	(±0.04)		(±0.21)	(±0.08)	(±0.07)		(±0.42)
	Rain	-0.07	0.09		0.19	0.99 ^{***}	0.65 ^{***}		-0.20
		(±0.14)	(±0.07)		(±0.34)	(±0.20)	(±0.18)		(±0.52)
	CEC x	0.27 ^{***}	-0.002		0.40 [*]	0.11	-0.08		-0.30
		(±0.06)	(±0.04)		(±0.19)	(±0.07)	(±0.06)		(±0.38)
	CEC x	0.11	0.03		0.53 ^{**}	-0.11	0.10		0.32
	(±0.07)	(±0.05)		(±0.20)	(±0.11)	(±0.06)		(±0.34)	
Elev. x	0.06	-0.04		0.56 ^{**}	-0.06	-0.03		-0.15	
	(±0.06)	(±0.03)		(±0.19)	(±0.07)	(±0.05)		(±0.37)	

Significance levels * <0.05; ** <0.01; *** <0.001

Spatial correlation structure in generalised least squares regression model with lowest AIC value. Note RQ = rational quadratic correlation structure; SPH = spherical correlation structure; EXP = exponential spatial correlation structure

2.5 Discussion

We conducted the first cross-continental evaluation of factors confounding vegetation extent in regions highly modified by anthropogenic activities. The extent of native vegetation retained in human-modified landscapes was consistently, and often strongly, related to particular abiotic factors of the landscapes examined. This evidence of non-random vegetation clearing across broad spatial extents has important implications for studies in modified environments, as these patterns may confound the observed effect of habitat area on ecological responses such as the persistence or richness of species. Yet, our literature review highlighted that such non-random vegetation clearing patterns and their ecological ramifications are infrequently considered in landscape ecological studies.

2.5.1 *Native vegetation extent is often correlated with abiotic factors*

In our Australian study extent, landscapes characterised by soils with relatively lower CEC, pH and clay values (i.e. less fertile soils) generally had more native vegetation. Agriculture has been the major driver of vegetation clearing in the Australian regions examined (Bennett & Watson, 2011), so soils suited to agricultural production are expected to retain less native vegetation. Similarly, hilly landscapes in temperate Australia are less conducive to agricultural and other anthropogenic land uses, and so retain more native vegetation. A bias towards vegetation clearing in flatter terrain was also shown by Seabloom *et al.* (2002) across broad regions of California. The topographic homogeneity of three of the four the arid Australian regions analysed in this study may explain why no consistent pattern in the relationship between vegetation extent and range in elevation was noted among arid Australian regions.

While abiotic factors were consistently associated with patterns of native vegetation retention in Australian landscapes, in some regions of South Africa this signal was less clear. Differing agricultural land use practices in the two countries—particularly the occurrence of an agricultural sector that comprises commercial and subsistence components in South Africa (Kirsten & Moldenhauer, 2006)—potentially underpins this cross-continental inconsistency. Subsistence/smallholder cultivation occurs in many parts of South Africa, including in eastern and northern regions of the country (Baiphethi & Jacobs, 2009). Compared to areas dominated by commercial agriculture, subsistence agriculture often occurs in marginal environments (Morton, 2007), which may be characterised by abiotic attributes like shallow soils and steep slopes (Lal, 2000). This may partly explain why the observed relationships between native vegetation extent and soil

and topography variables in the north east and central east regions of South Africa were inconsistent with patterns observed in the Australian study extent, and indeed, in south west South Africa. In south west South Africa, patterns of vegetation extent with respect to soil properties—particularly pH—and range in elevation, resembled those seen in Australia. In this part of South Africa, cultivation for commercial agriculture and forestry are the dominant agents of land transformation, which has resulted in substantial alteration to flat and fertile areas (Rouget *et al.*, 2003).

Interestingly, across Australia and South Africa, the relationship between native vegetation productivity (EVI) and the extent of native vegetation at the landscape scale was weak. In some heavily cleared heterogeneous landscapes, it is possible that less-productive native vegetation may have been preferentially retained while more-productive vegetation was removed. Such retention of less-productive vegetation in low cover landscapes resulting from finer-scale (i.e. within-landscape) clearing biases may dampen any relationship between vegetation productivity and vegetation extent at the landscape scale. Within-landscape biases in clearing patterns have ramifications for studies conducted at finer scales, including patch- and site-level studies.

2.5.2 *When do biases in vegetation retention matter?*

Environmental heterogeneity, including spatial variability in abiotic factors such as soil, topography and climate, is a key driver of biodiversity patterns (Seabloom *et al.*, 2002; Stein *et al.*, 2014). While abiotic heterogeneity was considered in more than half of the studies assessed as part of our literature review, few linked this heterogeneity with patterns of vegetation clearing, or considered the implications for the area effects being examined. There are several possible reasons why this link was not made, including (i) non-random vegetation clearing associated with spatial abiotic heterogeneity was not a characteristic of the study extent, (ii) the scale of the analysis was not congruent with the scale of (non-random) vegetation clearing patterns in the study extent, (iii) variability in the ecological response was not influenced by spatial abiotic heterogeneity, or (iv) sample units for which area was examined were spatially homogenous.

Furthermore, in many instances, abiotic heterogeneity (and its correlation with patterns of clearing) may be incidentally or indirectly controlled for in studies, without this explicitly being stated. For example, analytical techniques employed to control for spatial autocorrelation, or the use of measures of area which are correlated with, or proxies, for

abiotic heterogeneity (i.e. specific vegetation types that are associated with particular abiotic conditions, rather than a broader conceptualisation like native vegetation extent), may account for spatial abiotic heterogeneity. Such approaches would reduce the confounding effect of biased clearing patterns in studies examining the effect of area.

Of the 15 studies that did consider the potential influence of non-random vegetation clearing (Appendix A: Table A2), 11 focussed on the effect of soil properties. Several of these studies (Januchowski *et al.*, 2008; Looney *et al.*, 2009; Basham *et al.*, 2011) highlighted that a lack of an area effect was due to biased vegetation clearing patterns, whereby soil fertility/productivity was negatively correlated with habitat area. Because bigger remnants were associated with poorer quality soils, a positive effect of area on the response variable was not realised in these studies. Enhanced habitat quality, associated with access to foraging resources, was invoked to explain these findings (Januchowski *et al.*, 2008; Looney *et al.*, 2009; Basham *et al.*, 2011). Indeed, Lindenmayer and Luck (2005) proposed that in a scenario where patterns of vegetation clearing are non-random, the response of species and assemblages to landscape modification may in fact be an interaction between habitat quantity and quality. Storch *et al.* (2005) documented that the effect of area exhibits an interaction with one such measure of habitat quality—environmental energy availability—such that the positive effect of area is depressed because increased energy availability promotes greater species occupancy per unit area.

Expanding upon the concept that the effect of area is dependent on abiotic properties, Maron *et al.* (2012) demonstrated that biased clearing patterns can affect interpretation of the species-area relationship. In their study of the effect of native vegetation extent on bird species richness, Maron *et al.* (2012) highlighted that (1) high cover landscapes and low cover landscapes tend to be characterised by different attributes (i.e. lower and higher productivity soils, respectively), and (2) the effect of area on species richness differs as a function of landscape productivity. The authors concluded that the shape of the observed species-area relationship was not a valid representation of the effect of area, because of the confounding effect of soil productivity on vegetation extent (Maron *et al.*, 2012). This conclusion was based upon the finding that landscapes which have been extensively cleared tended to be more fertile, which may imply that retained vegetation in these low cover landscapes is relatively more productive, and thus able to support a higher density of individuals and more species per unit area (Maron *et al.*, 2012).

As revealed by our literature review, non-random clearing associated with abiotic factors may manifest in the lack of an observed area effect, or a distorted species-area relationship. Although not noted in the studies we reviewed, an apparent area effect may also reflect a positive correlation between area and another factor that positively affects species occurrence—for example, habitat heterogeneity that is associated with increased topographic variability. A study extent—regardless of the scale (sites with buffer, patches, landscapes) of the study units for which vegetation extent is being analysed—that encompasses heterogeneity in abiotic factors and biased patterns of vegetation removal clearly warrants special consideration, as there is potential for inaccurate conclusions to be drawn about the effects of area *per se*.

2.5.3 Conservation implications

Erroneous interpretations about the effect of area on species and assemblages can adversely affect conservation prescriptions that seek to achieve a biodiversity outcome by protecting or restoring native vegetation. For example, observed area effects in which biases associated with non-random clearing are unaccounted for may result in (1) actions that protect or restore too little habitat to achieve a specific goal, (2) actions that protect more habitat than is necessary to achieve a specific goal, and/or (3) activities in which efforts are concentrated in the wrong locations (with respect to abiotic properties).

Specifically, the value of large areas may be undervalued, where an uncontrolled bias obscures the effect of area. Conversely, a confounding factor like topographic variation and associated habitat heterogeneity may indicate (erroneously) that area is influential, thereby overstating the importance of large areas. An assumption that larger areas are more valuable than smaller areas, may overlook the fact that smaller areas are often of higher quality, because of their association with abiotic factors like enhanced soil fertility. Interpretations of the species-area relationship, such as the occurrence and position of a threshold (Swift & Hannon, 2010), will be constrained by the confounding effect of abiotic factors that potentially interact with area to affect species richness. This limits the utility of this relationship for informing conservation actions.

The potential existence of system-specific area effects—whereby the effect of area is different depending on whether the habitat is associated with a particular abiotic attribute like higher or lower soil fertility—should be considered in conservation actions that focus on area. Such system-specific relationships imply that the amount of habitat that needs to

be protected or restored to achieve a particular biodiversity outcome will differ depending on the underlying abiotic attribute(s) of the area that is the focus of the conservation action (Maron *et al.*, 2012). For example, a target to maintain the amount of habitat above a minimum threshold, based on an observed area effect derived from one system (i.e. fertile, productive habitat), may not achieve the desired outcome if it were translated to infertile habitat, because a greater area of this relatively less-productive habitat type may be needed to achieve a comparable biodiversity outcome. Conversely, applying a habitat protection (or restoration) target to a fertile system, based on an observed area effect from an infertile system, may overestimate the area required to achieve the desired biodiversity outcome, representing a potentially inefficient use of limited conservation resources.

2.5.4 Conclusion

Notwithstanding some notable exceptions such as the Biological Dynamics of Forest Fragments project (Laurance *et al.*, 2011), analyses of human-modified landscapes generally involve ‘natural experiments’—relating observed, as opposed to experimentally-created, patterns to ecological phenomena. The difficulty in controlling confounding factors experimentally is a fundamental limitation of such studies, underscoring the need for careful consideration where predictor variables may be correlated (McGarigal & Cushman, 2002). Here, we have highlighted that native vegetation extent is frequently correlated with a range of abiotic factors linked to non-random vegetation clearing, and that the occurrence of such correlations may lead to erroneous conclusions about the effect of area on an ecological response. In exploring ecological patterns in modified environments, such as the response of species and assemblages to area, it is crucial that the mechanisms acting on the response, including those associated with area by virtue of non-random vegetation clearing, are taken into account.

CHAPTER 3

LANDSCAPE-SPECIFIC EFFECTS AND THE RELATIONSHIP BETWEEN SPECIES RICHNESS AND NATIVE VEGETATION EXTENT

To be submitted to *Ecography*

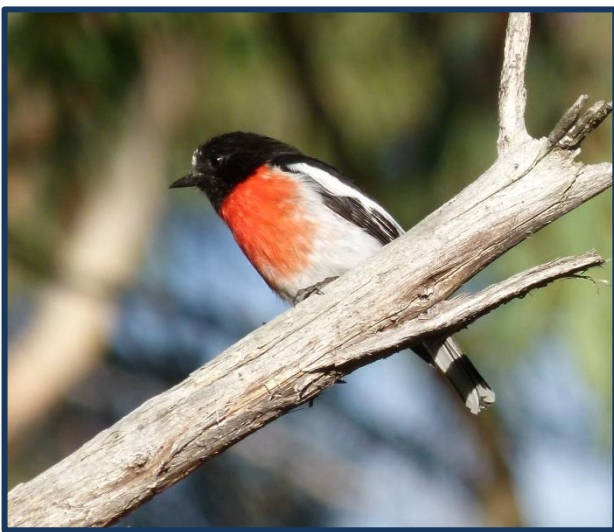


Plate 2 Woodland birds that occur in south-east Australia—scarlet robin (*Petroica boodang*) (left); and noisy miner (*Manorina melanocephala*) (right)

3.1 Abstract

The shape of the landscape-scale species-area relationship can inform habitat protection and restoration targets. However, differences in abiotic and anthropogenic attributes among landscapes could lead to erroneous conclusions about the shape of this relationship, if these attributes interact with habitat area to affect the occurrence of species at the landscape level. We examined the extent to which species-area relationships differ in shape where landscapes were categorised by particular abiotic and anthropogenic attributes. Species richness estimates of birds associated with woodland and forest were derived for 251 100 km² landscapes in south-east Australia. We compared the fit of alternative models, including traditional exponential, linear, quadratic and piecewise (threshold) models, to the relationship between estimated species richness and the area of woody native vegetation among different landscape types. Landscapes were categorised by abiotic properties, the occurrence of hyperaggressive native bird species, vegetation configuration and matrix land use. Employing generalised linear mixed modelling and model averaging, we ascertained how vegetation area interacted with different landscape attributes to explain estimated species richness. Thresholds were consistently observed in species-area relationships among different landscape types; however the position of thresholds varied markedly from 21-51% native vegetation cover. Vegetation area was the most important predictor of species richness, but interacted strongly with other landscape attributes, including range in elevation and the occurrence of highly competitive native birds of the genus *Manorina*. We demonstrate that the effect of vegetation area on Australian woodland bird species richness varies markedly with landscape type. Accounting for differences in landscape type has important implications for accurately informing both conservation decisions based on the shape of this relationship, and ecological theory around the form of landscape-scale species-area relationships.

3.2 Introduction

The removal of native vegetation, and the habitat that it provides, affects patterns of species richness at the landscape level (Fahrig, 2013; Cunningham *et al.*, 2014a; Hanski, 2015; Morante-Filho *et al.*, 2015). Substantial attention has been focussed on the relationship between species richness and the amount of vegetation in 'landscapes'—that is, mosaics of thousands to tens of thousands of hectares (McAlpine *et al.*, 2016), featuring a mix of elements including habitat (i.e. native vegetation) and non-habitat (i.e. human land uses) (Tscharrntke *et al.*, 2012). In particular, the shape and functional form of the curve fitted to this relationship has received considerable attention, as this can guide

predictions about how species richness will vary in response to changes in vegetation area (Whittaker & Triantis, 2012; De Camargo & Currie, 2015).

It is increasingly evident from landscape-scale species-area studies that the shape of this relationship exhibits substantial variation (Radford *et al.*, 2005; Desrochers *et al.*, 2011; De Camargo & Currie, 2015). Of note has been the observation of a threshold in this relationship from a number of studies conducted at the landscape level, where the effect of habitat area on species richness exhibits a sudden change (Radford *et al.*, 2005; Maron *et al.*, 2012; Lima & Mariano-Neto, 2014; Morante-Filho *et al.*, 2015; Ochoa-Quintero *et al.*, 2015; Richmond *et al.*, 2015). This contrasts with an expected monotonic increase in richness, as revealed by traditional species-area models such as the exponential (or logarithmic) function (Gleason, 1922), or the power function (Arrhenius, 1921). Because the species-area relationship reveals how assemblages respond to changes in vegetation extent, and can inform decision-making about where to protect or manage biodiversity (Desmet & Cowling, 2004; Possingham *et al.*, 2015), it is important to understand the factors that potentially underpin such variation in the effect of area on species richness, including the occurrence of sudden thresholds of change. In this study we ask: how do different attributes of landscapes, including abiotic properties and factors associated with anthropogenic land use, interact with vegetation extent to affect the shape of the landscape-scale species-area relationship?

If landscape attributes such as abiotic properties or factors associated with human land use interact with vegetation area to affect how many species a landscape can support, then the shape of the relationship between species richness and vegetation area will potentially vary among different landscape types (Lindenmayer & Luck, 2005). For example, species richness may vary in response to both vegetation area and other landscape attributes, such as soil fertility which affects resource availability (Watson, 2011), or topographic variation which is often correlated with habitat heterogeneity and niche availability (Stein *et al.*, 2014). These same landscape attributes may also underpin differences in patterns of vegetation clearing and anthropogenic land use (Seabrook *et al.*, 2006; Cattarino *et al.*, 2014), and in consequence, may act indirectly on species via their association with the configuration and condition of remnant vegetation (and the matrix) (Figure 3.1).

Maron *et al.* (2012) demonstrated that the effect of native vegetation area on Australian woodland bird species richness in 100 km² mosaics differed where landscapes were categorised by soil fertility. They hypothesised that this difference arose because landscapes with fertile soils may be able to support more species per unit area of native vegetation than less fertile landscapes, due to an interaction between vegetation area and resource availability (Maron *et al.*, 2012). The identification of landscape-specific area effects led Maron *et al.* (2012) to warn that aggregating species-area data from landscapes with different attributes may provide a misleading representation of how species richness relates to vegetation extent, as revealed by the shape of the species-area relationship.

Aggregating data from landscape types in which the effect of area differs is particularly problematic where the amount of vegetation in landscapes is correlated with abiotic attributes like soil fertility and/or topography because of non-random patterns of vegetation clearing (Lindenmayer & Luck, 2005; Rompré *et al.*, 2009; Maron *et al.*, 2012). The real effect of area will be obscured in such instances, because landscapes with less remnant native vegetation will predominantly be characterised by one suite of attributes (e.g. fertile soils; flat topography), while landscapes that retain more native vegetation will have different attributes (e.g. infertile soils; hilly topography) (Lindenmayer & Fischer, 2006).

A failure to account for these interactions and associations between vegetation area and landscape attributes has the potential to distort our understanding of patterns of species richness at the landscape level. This could compromise the effectiveness of area-based management actions that are informed by the shape of landscape-scale species-area relationships (Maron *et al.*, 2012). In this study, we examine the extent to which the effect of vegetation area on Australian bird species richness differs in 100 km² landscapes broadly characterised by particular abiotic and anthropogenic attributes. We address two key questions: (1) is the effect of vegetation area landscape-specific, whereby factors such as abiotic attributes, human land use and interspecific competition moderate the effect of vegetation area on species richness?; and (2) what ecological mechanisms potentially underpin landscape-specific area effects? Expanding upon the results presented by Maron *et al.* (2012), we consider the implications of landscape-specific area effects for analyses of patterns of species richness, and management actions that are informed by such analyses. In particular, we explore how landscape-specific area effects may distort

species-area analyses, particularly where the amount of vegetation in landscapes is biased by attributes such as soil fertility or topography.

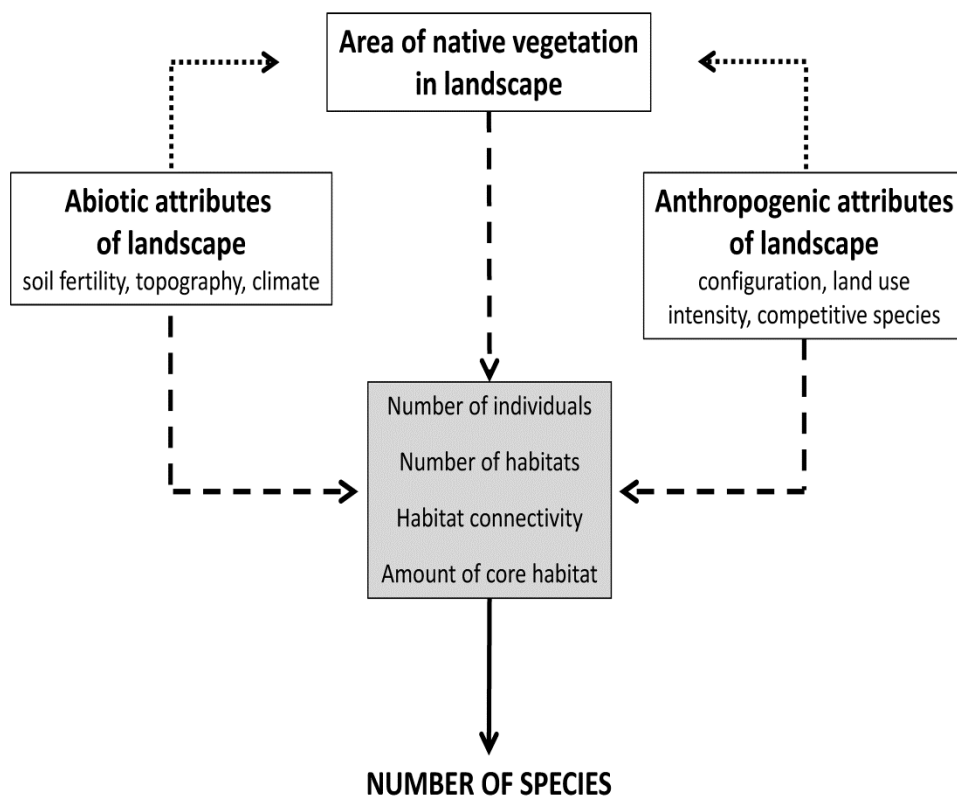


Figure 3.1 A conceptual framework of this study. The number of species in a landscape is frequently modelled as a function of native vegetation area. Vegetation area *per se* does not influence the occurrence of species, but rather, it is those variables that are (typically positively) associated with area (grey box) that underpin variation in species richness (solid arrow). Importantly, both area of vegetation, and other landscape attributes, can affect these variables (dashed lines with arrows). Therefore, the effect of area will depend on other attributes of landscapes, which also influence the occurrence of species. Controlling for variation in landscape attributes will provide a more accurate representation of the effect of area on species richness, as revealed by the shape of the species-area relationship. This will also remove the confounding effect of non-random patterns of vegetation clearing, whereby the amount of vegetation in a landscape is correlated with abiotic attributes like soil fertility and topography, and anthropogenic landscape attributes such as land use intensity (dotted lines)

3.3 Methods

3.3.1 Study region

Extensive areas of south-east Australia have been substantially modified, mainly to facilitate agricultural production (Lunt & Spooner, 2005). These high rates of clearing and landscape transformation have had profound adverse impacts on the biodiversity of the region (Lindenmayer *et al.*, 2010). To explore the implications of landscape modification on bird species richness in this highly transformed region of Australia, we restricted our analysis to those parts of south-east Australia that (1) are broadly characterised by native vegetation that is woody (i.e. various forms of shrubland, woodland and forest, but dominated by vegetation communities characterised by *Eucalyptus spp.* and other associated genera), and (2) have been subject to substantial anthropogenic modification (bioregions (or subregions) based on the Interim Biogeographic Regionalisation of Australia (IBRA) (Department of the Environment, 2012a) where at least 25% of the area has been transformed). A 10 x 10 km grid was overlaid on those parts of south-east Australia that satisfied the above criteria, with each complete grid cell (i.e. not overlapping the coastline) representing a landscape unit. We used a grain size of 100 km² to represent landscape-scale patterns in bird species richness, as this scale has been widely investigated in previous studies (Radford *et al.*, 2005; Maron *et al.*, 2012; De Camargo & Currie, 2015). Radford *et al.* (2005) employed this scale to represent replicate landscape units in their study of the response of Australian woodland bird species richness to the amount of native vegetation in agricultural mosaics, because this size captured the daily dispersal movements (home ranges) of the focal assemblage, and encompassed various attributes of landscape heterogeneity.

3.3.2 Bird data

As we were interested in the effect of landscape-scale woody vegetation area 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 members of this broad assemblage utilise a range of structurally-varied woody vegetation types, albeit typified by *Eucalyptus spp.* and other associated genera. We included species that can also utilise 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 characterised by woody vegetation—

were confirmed using the Handbook of Australian, New Zealand and Antarctic Birds (as summarised by Garnett *et al.* (2015)).

Occurrence data for the focal suite of species for the period 1998 to 2014 were extracted from BirdLife Australia's New Atlas of Australian Birds (Barrett *et al.*, 2003) database. To allow for estimates of species richness to be obtained from the Atlas dataset, we identified 100 km² landscape units from our grid in which at least 20 bird surveys (of the standardised 20 minute/2ha protocol (Loyn, 1986)) had been conducted (n=746). Because there was substantial variation in the number of surveys conducted in landscape units (ranging from 20 to 2057), we derived estimates of asymptotic species richness using the program EstimateS Version 9 (Colwell, 2013). Estimates were considered to be robust where the asymptotic estimator (Chao2 bias-corrected, or when indicated by the software, Chao2 classic or ICE classic) varied by fewer than 2 species in the last five surveys of the total set of samples (as per Maron *et al.* (2012)). This exercise yielded a list of 440 landscape units with robust asymptotic estimates based on a minimum of 20 surveys.

Despite this procedure to help minimise the effect of sampling bias, we found a positive correlation between the number of surveys in a landscape unit and the asymptotic estimates of richness (Spearman's rank correlation = 0.55, p-value <0.01). The effect of sampling effort on estimates of species richness has been cited as a potential issue, even where asymptotic estimators are used to derive richness estimates (Reese *et al.*, 2014; Engemann *et al.*, 2015). If a correlation exists, it becomes difficult to ascertain whether differences in estimated richness are real, or are an artefact of the confounding influence of sampling effort. Therefore, we used the unified rarefaction/extrapolation approach (Colwell *et al.*, 2012) to obtain comparable values of expected species richness at a standardised level of survey effort (Colwell & Elsensohn, 2014). This approach uses an analytical formula to either rarefy the species accumulation curve to a level of effort that is less than the total number of samples (i.e. for a particular landscape unit), or extrapolate the species accumulation curve beyond the total number of samples, where an asymptotic estimate of species richness is used as the 'target' for the extrapolation (Colwell *et al.*, 2012). Given the recommendation of 20 samples as a minimum number for rarefaction (Gotelli & Colwell, 2011), and the conservative suggestion to extrapolate only to twice the number of samples (Colwell *et al.*, 2012), we standardised sampling effort at 40 surveys, and obtained expected measures of species richness for landscape units at this level of sampling. These estimates were weakly correlated with the total number of surveys in a

landscape unit (Spearman's rank correlation = 0.09, p-value = 0.05), and provided us with a species richness estimate for each landscape unit that was not confounded by variable sampling effort.

Because larger or more species-rich areas could require greater sampling effort compared with smaller or species-poor areas (Watson, 2003), it is possible that standardised estimates of species richness for more diverse landscapes could underestimate true species richness, while less-rich landscapes would boast more complete inventories. We therefore tested whether setting a standardised level of sampling (40 surveys) was sufficient to characterise the richness of both species-rich and species-poor landscapes and led to estimates that were equivalently complete. To do this, we derived estimates of richness at 60 surveys (using the unified rarefaction/extrapolation approach (Colwell *et al.* (2012)), and examined whether the proportional increase in richness at 60 surveys was greater in landscapes that had higher estimated richness at 40 surveys. Landscapes with higher estimated richness at 40 surveys did not show a proportionally greater increase in estimated richness than lower richness landscapes at 60 surveys, indicating that standardisation to 40 samples was not suppressing approximations of richness in these landscapes.

In selecting a final set of landscape units for the analysis, we applied a number of criteria to account for within-landscape spatial and temporal variability in sampling, and temporal changes in land cover over the period for which bird data were collected. The criteria we selected sought to strike a balance between satisfactorily controlling for spatial and temporal variation, while still allowing for a sufficient number of landscape units to test our hypothesis and explore our study questions. Thus, to be included in this analysis, landscape units needed to satisfy the following criteria: (1) surveys from at least five unique locations in at least two different quadrants of a landscape; (2) at least five surveys from each half of the Atlas data collection period (1998-2014); (3) at least five surveys in each half of the year (April-September, October-March); (4) 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 met the criteria and were used for the analysis (Figure 3.2). This final set of landscape units comprised estimates of species richness derived from a total of 32,160 individual bird

surveys, and incorporated records of 232 unique species (see Appendix B: Table B1 for list of species).

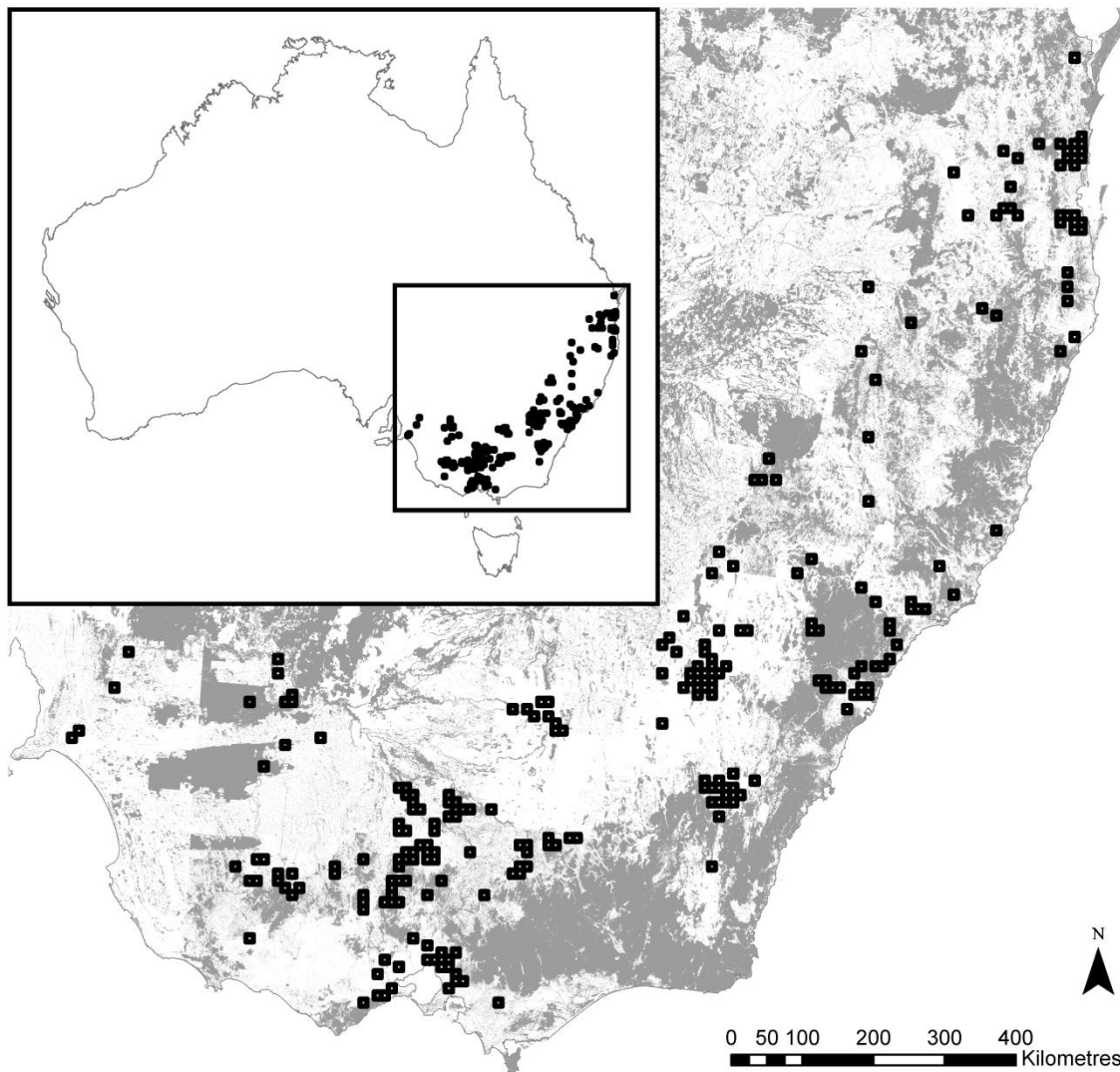


Figure 3.2 South-east Australian landscapes units (n=251) with native remnant woody vegetation layer (based on NVIS v 4.1) shown as dark grey layer

3.3.3 *Landscape data*

We used the Australian Government’s National Vegetation Information System (NVIS) version 4.1 (Department of the Environment, 2012b) to map the contemporary distribution of remnant native vegetation and determine the area of native woody vegetation in our landscape units. From this 100 m pixel resolution dataset of 33 major vegetation groups (MVGs), we identified MVGs that were characterised by remnant woody vegetation (i.e. woodland and forest), and aggregated these to calculate the percentage cover of woody vegetation area for each landscape unit. These values were related to estimates of species richness for each landscape unit, to explore the shape of landscape-scale

species-area relationships. As such, the species-area relationships examined focus on the effect of percentage woody vegetation cover (representing 'area') on species richness in 100 km² landscapes.

Additionally, we derived information on six abiotic and anthropogenic attributes for each landscape unit, by which to categorise landscapes (Table 3.1). These attributes were selected based on their potential to affect patterns of species occurrence at the landscape scale. The soil attribute we selected was cation exchange capacity (CEC), which contributes to fertility via nutrient storage and availability (Hazelton & Murphy, 2007). Mean annual rainfall and range in elevation were used to explore the effect of climate and topographic heterogeneity, respectively. Two native Australian bird species in the genus *Manorina*—the noisy miner (*M. melanocephala*), and the yellow-throated miner (*M. flavigula*)—can have substantial impacts on the richness of smaller-bodied native birds through competitive exclusion in modified environments, leading to shifts in assemblages (Maron *et al.*, 2013; Mac Nally *et al.*, 2014a). We determined the proportion of surveys in which one or both of these species was recorded in a landscape unit (i.e. a reporting rate (Watson, 2003)), to explore how the occurrence of these species affected the response of species richness to vegetation area. We calculated two measures of anthropogenic landscape modification—mean patch size and matrix land use intensity. Geospatial data processing and extraction was done using ArcMap10.1 (ESRI, 2012), and Geospatial Modelling Environment (Beyer, 2012).

Table 3.1 Landscape attribute data used to categorise landscapes

Attribute	Description	Source	Range (median)
Cation exchange capacity (cmol/kg)	Mean value derived for each landscape unit from 0-5 cm soil depth range data layer	International Soil Reference and Information Centre (ISRIC) Soil Grids 1 km dataset (ISRIC - World Soil Information, 2013; Hengl <i>et al.</i> , 2014)	10.91-50.03 cmol/kg (20.6 cmol/kg)
Annual rainfall (mm)	Mean value derived for each landscape unit	WorldClim database (Hijmans <i>et al.</i> , 2005)	268-1800 mm (682 mm)
Range in elevation (m)	Range in elevation calculated as difference between highest and lowest point in landscape unit	Consultative Group on International Agricultural Research's version of NASA's Shuttle Radar Topography Mission 90 m resolution v.4 digital elevation model (Jarvis <i>et al.</i> , 2008)	18-1000 m (213 m)
<i>Manorina</i> honeyeaters (reporting rate %)	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	Based on 20 minute/2 ha bird surveys for landscape units	0-100% (18%)
Mean patch size (ha)	Area of mapped woody vegetation divided by number of patches (equal to or greater than 1 ha) in a landscape unit	Based on NVIS v 4.1 mapping of MVGs (woody native vegetation)	0-9915 ha (62 ha)
Matrix land use intensity (ha)	Area of the matrix that is characterised by intensive land use (i.e. irrigated production agriculture, irrigated plantations, urban, industrial, extraction)	Australian land use dataset: Catchment Scale Land Use of Australia – Updated March 2015 (Australian Bureau of Agricultural and Resource Economics and Sciences (ABARES), 2015)	0-9867 ha (1011 ha)

3.3.4 Data analysis

While numerous approaches have been advocated to model the species-area relationship (Tjørve, 2003; Turner & Tjørve, 2005; Scheiner *et al.*, 2011), it has typically been examined using convex increasing curves such as the exponential (or logarithmic) function (Gleason, 1922) or the power function (Arrhenius, 1921). In landscape-scale studies, polynomial (Desrochers *et al.*, 2011; De Camargo & Currie, 2015) and piecewise (Lima & Mariano-Neto, 2014; Richmond *et al.*, 2015) regressions have also been used to describe the relationship. Piecewise regressions identify a threshold, or ‘point of abrupt change’ (Ficetola & Denoël, 2009), below which the rate of decline in species richness with decline in vegetation area changes. Such thresholds have the potential to act as explicit reference points upon which vegetation clearing or revegetation targets can be based (Huggett, 2005; Swift & Hannon, 2010), and have been identified from several studies examining species-area relationships at the landscape level (Radford *et al.*, 2005; Banks-Leite *et al.*, 2014; Ochoa-Quintero *et al.*, 2015; Richmond *et al.*, 2015). However, a lack of consistency in threshold values across different studies has been cited as a limitation of the generality of thresholds for informing applied conservation (Johnson, 2013; Matthews *et al.*, 2014a).

We built univariate generalised linear models (GLMs) with a Poisson error distribution in R (R Core Team, 2013) to explore the shape of the relationship between estimates of species richness and woody vegetation area. We compared the fit of four different models—exponential (to approximate a ‘traditional’ convex upward curve), linear, polynomial (quadratic) and threshold—using Akaike’s Information Criterion (AIC). The threshold model was constructed using the R package ‘segmented’ (Muggeo, 2008). For this modelling, we used the percentage of woody vegetation cover as the predictor variable, and our estimates of species richness as the response variable. To examine whether aggregating data from multiple landscapes that exhibit heterogeneity in abiotic and anthropogenic attributes is likely to result in a distortion of the true effect of vegetation area, we first built the four different models for the entire aggregated dataset using all 251 landscapes. This preliminary step allowed us to compare the shape of a relationship summarising all 251 landscapes with subsets of the data representing specific landscape types.

To address our first question of determining if the shape of the relationship varies among different landscape types, we subset the 251 landscape units according to our six abiotic and anthropogenic attributes. Landscape units were categorised based on the median

value of each landscape attribute (either below or above median (Table 3.1)) resulting in 12 landscape types, and separate GLMs for the four species-area curves were built for each landscape type (48 models in total). We identified which of the four models had the lowest AIC value for each landscape type, and calculated the Nagelkerke R^2 (pseudo- R^2) (Nagelkerke, 1991) to determine the deviance explained by each GLM.

Our second question was to explore the ecological mechanisms associated with particular landscape attributes that potentially underpin variation in the relationship between estimated species richness and woody vegetation area. To achieve this, we sought to determine the relative influence of native vegetation area and other landscape attributes on estimated species richness. We first modelled variability in estimated species richness for the aggregated dataset of all 251 landscape units, using generalised linear mixed models (GLMM) constructed in the R package 'lme4' (Bates *et al.*, 2014). The predictor variables were vegetation area, mean CEC, mean annual rainfall, range in elevation, *Manorina* reporting rate, mean patch size and matrix land use intensity, as well as two-way interactions among vegetation area and the other attributes. To account for potential differences in the level of species richness across our study extent (i.e. due to bioregional differences, and differences in clearance histories), the IBRA bioregion in which each landscape unit occurs was included as a random intercept. While some predictors exhibited moderate (>0.5) two-way Spearman's rank correlations (i.e. the three abiotic attributes; vegetation area and mean patch size), a check of variance inflation factors (<2 for all predictors) indicated that collinearity was not likely to be an issue in this analysis (Zuur *et al.*, 2010). All predictor variables were standardised (mean = 0, standard deviation = 1) prior to this analysis to allow for comparison of parameter coefficients.

We then conducted model averaging and multimodel inference, using the R package 'MuMIn' (Barton, 2015), to determine the relative importance of vegetation area versus the various landscape attributes in explaining variation in estimated species richness. From a global model that contained all seven predictor variables (as well as all two-way interactions between vegetation area and the other six landscape attributes (six interaction terms)), a set of top models—those within 2AICc values of the best model in the set—was identified (Grueber *et al.*, 2011). From this set, model-averaged parameter estimates, unconditional standard errors and 95% confidence intervals were derived, as was the relative importance of each predictor based on the sum of the Akaike weights for all models in the top set in which the predictor occurred (Grueber *et al.*, 2011). We checked

for spatial autocorrelation in the residuals of the global model, using a spline correlogram produced via the R package 'nfc' (Bjornstad, 2013).

3.4 Results

A comparison of models fitted to the relationship between estimated species richness and native woody vegetation area for all 251 landscape units revealed that the threshold model was more parsimonious than the exponential, linear and quadratic models (Table 3.2). Estimated richness increased with woody vegetation area to a threshold value of approximately 28% cover, beyond which vegetation area had little effect (Figure 3.3a).

When we classified the landscapes into subsets according to particular abiotic and anthropogenic attributes (Table 3.1) to address our first research question, threshold models were the best supported for 7 out of 12 landscape categories ($\Delta AIC > 2$) (Table 3.2; Figure 3.3). The area of remnant woody vegetation leading to a threshold response in species richness varied considerably among different landscape types, from 21% of woody vegetation cover in lower rainfall landscapes (Figure 3.3d) to 51% in less fragmented landscapes (Figure 3.3f). In most cases, the effect of area was strongest below the threshold value, with a reduced effect, and in some instances, a plateau, above the threshold. The value of the threshold with respect to estimated species richness (i.e. the 'maxima' where the change point or plateau corresponded with the y-axis) also differed between landscapes classified by different attributes. For example, the threshold point for lower fertility landscapes occurred at a higher level of estimated richness than for higher fertility landscapes (approximately 65 species compared with approximately 55 species, respectively (Figure 3.3c)).

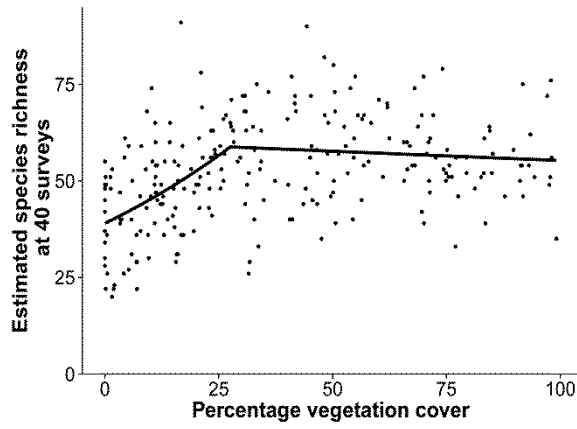
In three landscape types—those characterised by a higher reporting rate of *Manorina* honeyeaters (Figure 3.3e), lower mean patch size (Figure 3.3f), and by lower matrix land use intensity (Figure 3.3g)—quadratic models indicated that estimated richness was highest at intermediate levels of woody vegetation area. However, support for quadratic models in these three landscape types was only marginally better ($\Delta AIC < 2$) than that for a threshold relationship (Table 3.2).

Table 3.2 Summary of univariate generalised linear models with the lowest AIC value for each category of landscape

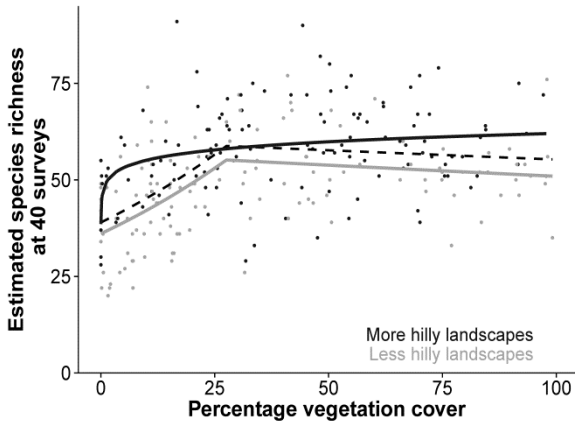
Landscape category	Best supported functional form*	ΔAIC top two models	Estimated threshold[#]	Nagelkerke pseudo-R²
All landscapes	Threshold	11.29	27.6 (\pm 2.2)	0.59
<i>Range in elevation</i>				
More hilly	Exponential	8.45	NA	0.46
Less hilly	Threshold	8.12	27.6 (\pm 3.5)	0.59
<i>Soil</i>				
Higher soil fertility	Threshold	15.60	22.1 (\pm 2.6)	0.56
Lower soil fertility	Threshold	5.74	41.8 (\pm 4.2)	0.47
<i>Rainfall</i>				
Higher rainfall	Threshold (Quadratic)	0.32	36.0 (\pm 4.1)	0.51
Lower rainfall	Threshold	21.54	21.0 (\pm 2.5)	0.63
<i>Manorina honeyeaters</i>				
Higher <i>Manorina</i> reporting rate	Quadratic (Threshold)	0.65	NA	0.75
Lower <i>Manorina</i> reporting rate	Threshold	9.82	22.0 (\pm 3.4)	0.45
<i>Vegetation configuration</i>				
Higher mean patch size	Threshold	3.39	50.7 (\pm 5.6)	0.19
Lower mean patch size	Quadratic (Threshold)	0.11	NA	0.66
<i>Matrix land use</i>				
Higher matrix land use intensity	Threshold	5.43	27.8 (\pm 2.7)	0.63
Lower matrix land use intensity	Quadratic (Threshold)	0.65	NA	0.53

* Where Δ AIC top two models <2 , next best model type presented in parentheses

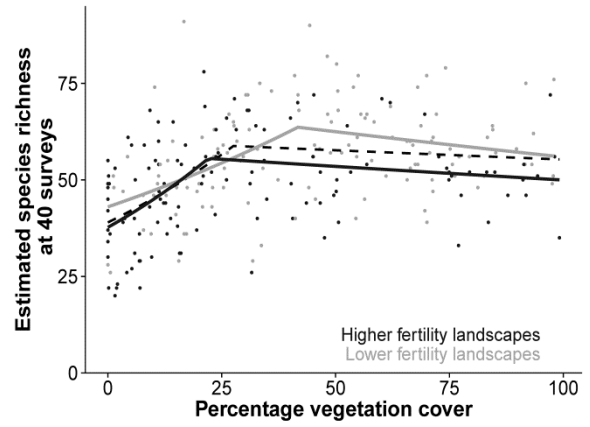
Percentage landscape woody vegetation area at which threshold occurs (\pm error around threshold estimate)



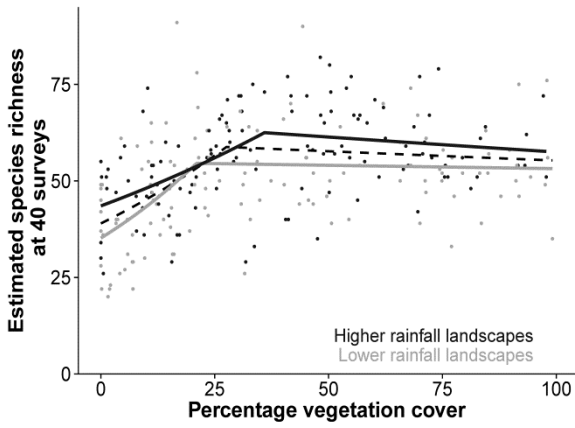
(a)



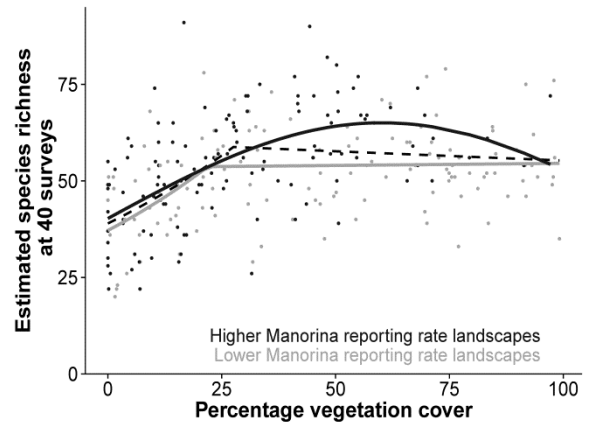
(b)



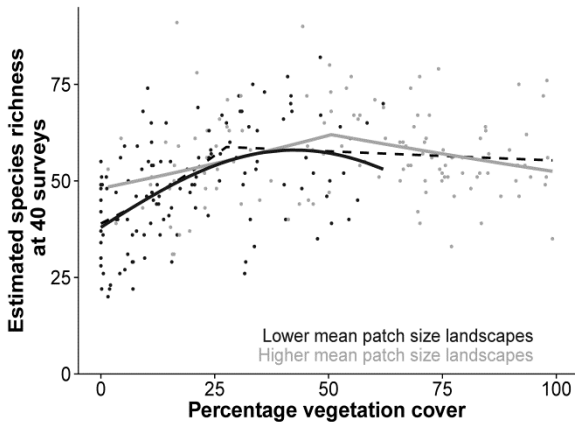
(c)



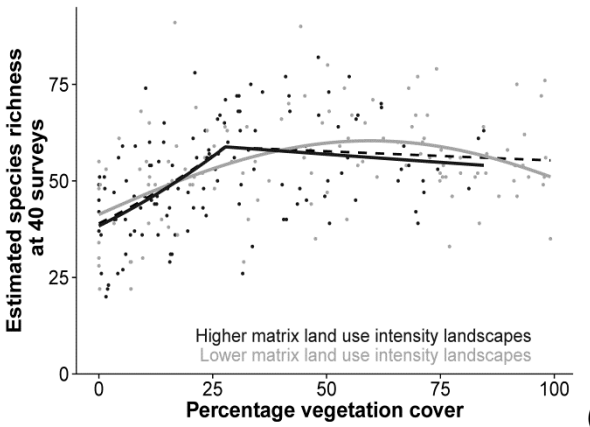
(d)



(e)



(f)



(g)

Figure 3.3 Landscape-specific models for the relationship between estimated species richness and the area of mapped remnant woody vegetation (percentage vegetation cover). The top plot (3.3a) shows the most parsimonious model fitted to all 251 landscape units. Each of the remaining six plots (3.3b-3.3g) exhibits three separate species-area models: the dashed line represents the most parsimonious model fitted to all 251 landscape units; while the grey and black curves (associated with the grey and black data points) represent the model of best fit (based on lowest AIC value for four different fitted models) for each specific landscape type. The landscape types presented in each plot are: more hilly and less hilly landscapes (3.3b); higher fertility and lower fertility landscapes (3.3c); higher rainfall and lower rainfall landscapes (3.3d); higher *Manorina* reporting rate and lower *Manorina* reporting rate landscapes (3.3e); lower mean patch size and higher mean patch size landscape (3.3f); and higher matrix land use intensity and lower matrix land use intensity landscapes (3.3g). These landscape categories were derived by subsetting the overall dataset (251 landscapes) based on median values (i.e. above or below median) for each of the six landscape attributes under examination

Model averaging revealed that the positive effect of woody vegetation area was of greatest importance in explaining estimated species richness (Figure 3.4). Range in elevation also had a positive effect on species richness, while negative independent effects were detected for soil fertility (CEC), mean patch size, and matrix land use intensity. These variables all had summed Akaike weights of 1 (Figure 3.5). Significant interactions between woody vegetation area and range in elevation, and woody vegetation area and *Manorina* reporting rate were detected (Figure 3.4; Figure 3.5), indicating that the effect of area on species richness was moderated by landscape attributes. Vegetation area had a weaker effect on species richness in landscapes with greater range in elevation (i.e. more hilly landscapes). The effect of area on species richness was stronger, and the positive effect was evident up to a higher value of vegetation cover, in landscapes with high *Manorina* reporting rates.

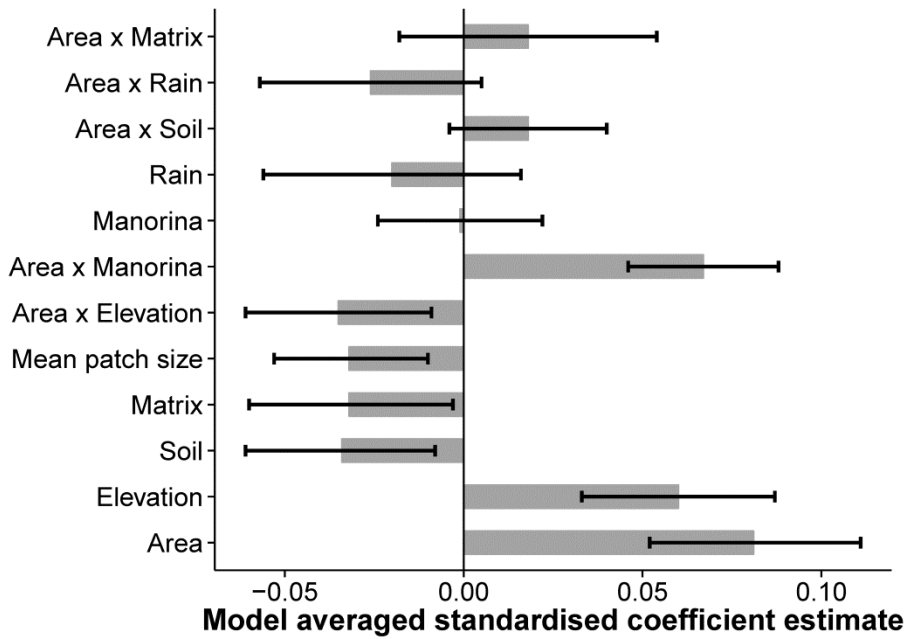


Figure 3.4 Model averaged coefficients (error bars = 95% confidence intervals) across the top set of models ($\Delta 2AICc$ values) for all predictor variables, where estimated species richness was the response variable. The predictor Area x Mean patch size was not included in any of the models in the top model set

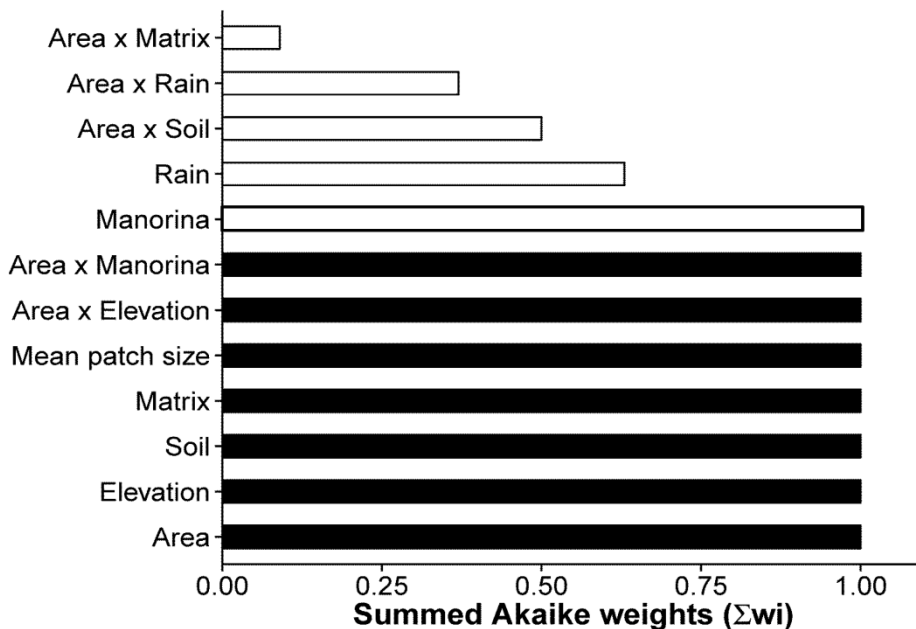


Figure 3.5 Ranked importance of predictor variables in the top set of models ($\Delta 2AICc$ values) – filled bars denote variables for which model-averaged parameter estimate coefficient confidence intervals do not overlap zero

3.5 Discussion

Native vegetation area is a key determinant of patterns of landscape-scale bird species richness (Radford *et al.*, 2005; Desrochers *et al.*, 2011). However, our analysis revealed that the effect of woody vegetation area on Australian woodland bird species richness differs in landscapes characterised by certain abiotic and anthropogenic attributes. For example, while we found evidence for the occurrence of thresholds of abrupt change in the relationship between species richness and native vegetation area, the amount of vegetation corresponding with these thresholds varied considerably among landscapes characterised by different attributes. This identification of landscape-specific area effects has important implications for the exploration of species-area relationships. Most notably, deriving an accurate representation of the effect of area necessitates that factors that confound species-area analyses, such as landscape attributes, and the associated ecological mechanisms which moderate the effect of area, be accounted for. This is particularly important where vegetation area is also cofounded with landscape attributes due to biased patterns of anthropogenic vegetation clearing. A more nuanced understanding of the effect of vegetation area, as revealed by the species-area relationship, is integral to informing conservation management and policy, where area-based vegetation protection or restoration targets are set based on the expectation that their achievement will maintain or enhance landscape-scale species richness.

3.5.1 *Thresholds vary for different landscape types*

We recorded a threshold in the species-area relationship at approximately 28% woody vegetation cover when data from all landscapes were aggregated. This is remarkably consistent with the predictions of Andr en (1994), who postulated that the configuration of habitat in a landscape is particularly influential below 30% cover, thereby explaining the non-linear response of species richness to habitat extent at low levels of cover. This non-linear response may also reflect a point below which individual fitness and population processes are impaired (Swift & Hannon, 2010), resulting in more rapid loss of species.

When landscapes were classified by particular abiotic and anthropogenic attributes, a threshold relationship was found more often than other curve types, but the position of the threshold varied depending on the landscape attributes considered (21-51% native vegetation cover). Furthermore, the estimated number of species at which a change in the relationship between species richness and area was observed also exhibited variation among the different landscape types examined, indicating that landscape attributes act on

both how richness changes with area, as well as how many species a particular landscape type can support. Taken together, these results highlight that the effect of woody vegetation area on woodland bird species richness in south-east Australia varies as a function of landscape attributes. As proposed by Maron *et al.* (2012), and emphasised by our results, aggregating data from multiple landscapes that exhibit heterogeneity in abiotic and anthropogenic attributes is likely to result in a distortion of the true effect of habitat area. Furthermore, these findings reinforce a key criticism of the use of thresholds for establishing targets such as landscape-level vegetation clearing limits—that is, the existence of landscape-specific threshold values, reflecting landscape-specific area effects, hampers our ability to generalise about the ubiquity and causes of thresholds, therefore precluding their broad application for conservation target setting.

Richmond *et al.* (2015) found that thresholds in the relationship between landscape-scale forest cover and forest bird species richness varied from approximately 4 to 28% cover among different forest types, ecozones and spatial scales. In a review of studies that examined landscape-scale species richness and the occurrence of specific species, Swift and Hannon (2010) noted substantial variation in threshold values, and emphasised that thresholds are likely to vary in different landscape types. In studies of woodland birds in south-east Australia, thresholds in the relationship between vegetation area and species richness were identified at approximately 10% cover (Radford *et al.*, 2005) and 35% cover (Maron *et al.*, 2012). While such variation in threshold values across studies is a potential impediment to their utility for informing landscape management (Lindenmayer & Luck, 2005; van der Hoek *et al.*, 2015), these threshold analyses, and indeed the results we present, highlight that the rate at which species are lost (or gained) with reduced (or enhanced) vegetation extent is often greatest at lower levels of landscape vegetation cover (Fischer & Lindenmayer, 2007). Understanding what factors interact with vegetation area to drive threshold responses in different types of landscapes is important (Swift & Hannon, 2010) and warrants further exploration, as this knowledge may help maximise the impact of conservation interventions such as restoration in low cover landscapes.

3.5.2 *Ecological mechanisms moderate the effect of vegetation area on species richness*

We recorded a significant negative interaction between vegetation area and range in elevation. More topographically diverse landscapes are likely to capture a wider array of habitats and associated niches (Bennett *et al.*, 2006; Stein *et al.*, 2014) per unit area of native vegetation, which may moderate the effect of area *per se* (Kallimanis *et al.*, 2008).

The effect of vegetation area may also be moderated by topography because of an association between slope/terrain ruggedness and land use intensity. For example, if hilly landscapes that are characterised by steeper slopes are less conducive to intensive agricultural production, this may mean that the matrix permeability is enhanced in such landscapes. In turn, this may allow for enhanced opportunities for dispersal across the matrix (Prevedello & Vieira, 2010), even where landscape-level native vegetation cover is low. In less hilly landscapes, species richness may respond more strongly to area as increases in vegetation extent potentially buffer species from the adverse impacts of habitat degradation (i.e. edge effects) that are associated with intensive land use (Watson *et al.*, 2005; Lindenmayer & Fischer, 2006), as well as provide for enhanced connectivity (Hanski, 2015).

The disruptive effect that hyperaggressive native competitors (either noisy or yellow-throated miners) have on Australian native bird assemblages is typically greatest in modified and fragmented woodlands and forests (Maron *et al.*, 2013; Kutt *et al.*, 2015). In particular, these two species of *Manorina* honeyeater favour edge habitats (Maron *et al.*, 2013; Thomson *et al.*, 2015), where they cooperate to exclude other species—especially smaller birds—to the extent that large shifts in community composition occur (Mac Nally *et al.*, 2014b). We found that vegetation area had a stronger effect on species richness in landscapes where *Manorina* honeyeaters were more prevalent (i.e. a positive interaction between vegetation area and *Manorina* reporting rate). In landscapes with many *Manorina* honeyeaters, the role of increasing vegetation cover is likely to be particularly important as it correlates with larger remnants, more core habitat and proportionally less edge habitat (Fahrig, 2003; Ewers & Didham, 2006), the latter of which these aggressive competitors preferentially occupy (Maron *et al.*, 2013; Thomson *et al.*, 2015).

The quadratic fit for higher *Manorina* reporting rate landscapes (Figure 3.3e) had only marginally better support than the threshold model (Table 3.2), which revealed a plateau in the relationship between species richness and area above approximately 21% native vegetation cover. In low cover landscapes (less than 20% cover), the effect of vegetation area on species richness was similar for lower and higher *Manorina* reporting rate landscapes. Surprisingly, richness tended to be higher in higher *Manorina* reporting rate landscapes beyond low levels of cover (Figure 3.3e). This may reflect the fact that *Manorina* honeyeaters often favour more productive areas (Maron *et al.*, 2013), which may support more individuals and therefore more species through greater energy and resource

availability (Storch *et al.*, 2005; Watson, 2011). Furthermore, noisy and yellow-throated miners tend to have their strongest adverse effects on smaller birds, although they are also associated with increases in larger birds (Howes *et al.*, 2014; Kutt *et al.*, 2015). Thus, it may be that undesirable compositional differences such as site-scale homogenisation of bird communities arise as a result of *Manorina* occurrence (Howes *et al.*, 2014; Kutt *et al.*, 2015), but that landscape-level species richness may not necessarily be reduced in landscapes with many *Manorina* honeyeaters.

Factors such as habitat heterogeneity or land use intensity associated with topographic variation, or the disruptive influence of highly competitive *Manorina* honeyeaters, should be considered in studies of the response of Australian woodland birds to landscape-scale vegetation area. Failure to consider these factors may entail erroneous interpretations of the effect of area. For example, vegetation area is frequently correlated with range in elevation at the landscape level, whereby flat landscapes are typically more heavily cleared than hilly landscapes (Seabloom *et al.*, 2002). If this confounding factor is not accounted for, an analysis of the effect of area that is based upon an aggregation of lower cover landscapes that are flat, and higher cover landscapes that are hilly, where each of the two landscape types has its own landscape-specific area effect as demonstrated here, will manifest in a species-area relationship that is not representative of either landscape type. Similarly, and uniquely applicable to Australian woodland birds, *Manorina* honeyeater occurrence should be acknowledged and accounted for, because the number of species occurring per unit area of vegetation in landscapes potentially differs depending on the occurrence of these hyperaggressive native competitors.

3.5.3 *Additional considerations for landscape-level analyses of species richness*

Here, we have considered landscape-specific effects in the relationship between the species richness of a broad assemblage of birds and landscape-scale native vegetation cover. We note that within this broad assemblage, individual species will exhibit varying degrees of tolerance to landscape modification and habitat loss. Given that various studies have revealed differential responses of assemblages to landscape-scale vegetation cover where 'forest' species have been subset by disturbance tolerance (i.e. 'forest specialist' vs 'disturbance tolerant') (Pardini *et al.*, 2010; Banks-Leite *et al.*, 2012; De Camargo & Currie, 2015), it would be a useful next step to examine the landscape-specific relationships we present here for subsets of our broad bird community. In particular, observations that sensitive species decline and are lost from landscapes at higher levels of vegetation cover

than observed thresholds reflecting the response of the broader assemblage (Banks-Leite *et al.*, 2014), underscores the importance of considering groups of species with different levels of sensitivity/tolerance to disturbance.

Our analysis focussed on relating the richness of a broad assemblage of species that are dependent on woody vegetation, to the amount of native vegetation (woodland) in landscapes. This followed the widely used habit/non-habitat approach (Radford *et al.*, 2005; Haslem & Bennett, 2008; Desrochers *et al.*, 2011; Smith *et al.*, 2011; Maron *et al.*, 2012; Cunningham *et al.*, 2014a) to exploring landscape-level responses of biodiversity to anthropogenic modification, whereby mapped native vegetation is used to represent habitat for the assemblage being examined. We acknowledge that a potential flaw in this approach is that individual species within an assemblage may respond differently to specific vegetation types that are captured within a broad characterisation of habitat such as 'woodland' (Fischer & Lindenmayer, 2007; Fahrig *et al.*, 2011; Betts *et al.*, 2014; Matthews *et al.*, 2014b; Almeida-Gomes *et al.*, 2015). However, in light of the findings we present here, we advocate that studies exploring area effects using a habitat/non-habitat conceptualisation may be enhanced by considering other attributes of landscapes that potentially reflect and/or act on the quality of native vegetation for various species in an assemblage. For example, our results indicate that species in the assemblage we considered respond to fertile, productive woodlands differently to infertile woodlands, or that the effect of woodland area in flat, homogenous landscapes may be different to woodland occurring in a hilly, heterogeneous landscape. Incorporating attributes of vegetation quality into analyses of the effect of vegetation quantity can allow for a more nuanced appreciation of how biodiversity responds to landscape change when using a habitat/non-habitat approach.

The dichotomous approach that we used to classify landscapes by particular attributes allowed us to confirm two key aspects of the spurious thresholds hypothesis (Maron *et al.* 2012)—(1) that the effect of vegetation area depends on broad attributes of landscapes, and (2) this may result in a distorted representation of the species-area relationship if data are aggregated from broadly different landscape types in a non-random clearing context. We recognise that the attributes we used to classify landscapes do not necessarily act in isolation from one another on species-area relationships; rather these broad attributes, and the ecological mechanisms associated with them, exhibit interactions and correlations among landscapes. To test this, we explored how various attributes (and the mechanisms

they subsume) interact to affect patterns of species richness using multivariate mixed modelling. This revealed, for example, that the effect of vegetation area differs as function of landscape topography, and we infer that this may be due to differences in land use intensity, habitat configuration and habitat heterogeneity among landscape that broadly differ in topography (i.e. flat and hilly). While we note that other approaches, such as using an ordination procedure, could be used to group landscapes for the purposes of exploring variation in the shape of the species-area relationship, our dichotomous classification is advantageous in that it allows for clear links between (non-random) patterns of anthropogenic clearing and the response of biodiversity to be made, and provides simple, intuitive guidance for both assessing patterns of species richness in modified landscapes and informing landscape management using broad and easily translatable landscape classifications.

3.5.4 Conclusion

We highlight that the effect of woody vegetation area on woodland birds of south-east Australia varies as a function of the attributes of landscapes, and that these differences likely reflect ecological mechanisms which interact with area to affect the occurrence of species. Recognising that the effect of area is not the same among different landscape types is important for analyses of species-area relationships in modified landscape mosaics. In particular, we advocate the importance of identifying which attributes of landscapes may interact with area to affect species richness, and accounting/controlling for these in species-area analyses. In short, it is important to compare 'like with like', so as to remove the confounding effect of landscape attributes that may distort observed area effects. This is particularly crucial where non-random clearing introduces substantial bias into analyses of area effects in modified environments. Given that habitat loss is a landscape-level process (Radford & Bennett, 2007) with landscape-scale effects (Fahrig, 2013), it is vital that management actions focussing on species richness are undertaken at this scale. Deriving an accurate representation of the relationship between species richness and vegetation area is therefore fundamental for planning conservation or restoration interventions that seek to maximise the number of species a landscape can support.

CHAPTER 4

THE EFFECT OF SCALE ON HOW HABITAT AREA INFLUENCES LANDSCAPE- LEVEL SPECIES RICHNESS

To be submitted to *Landscape Ecology*

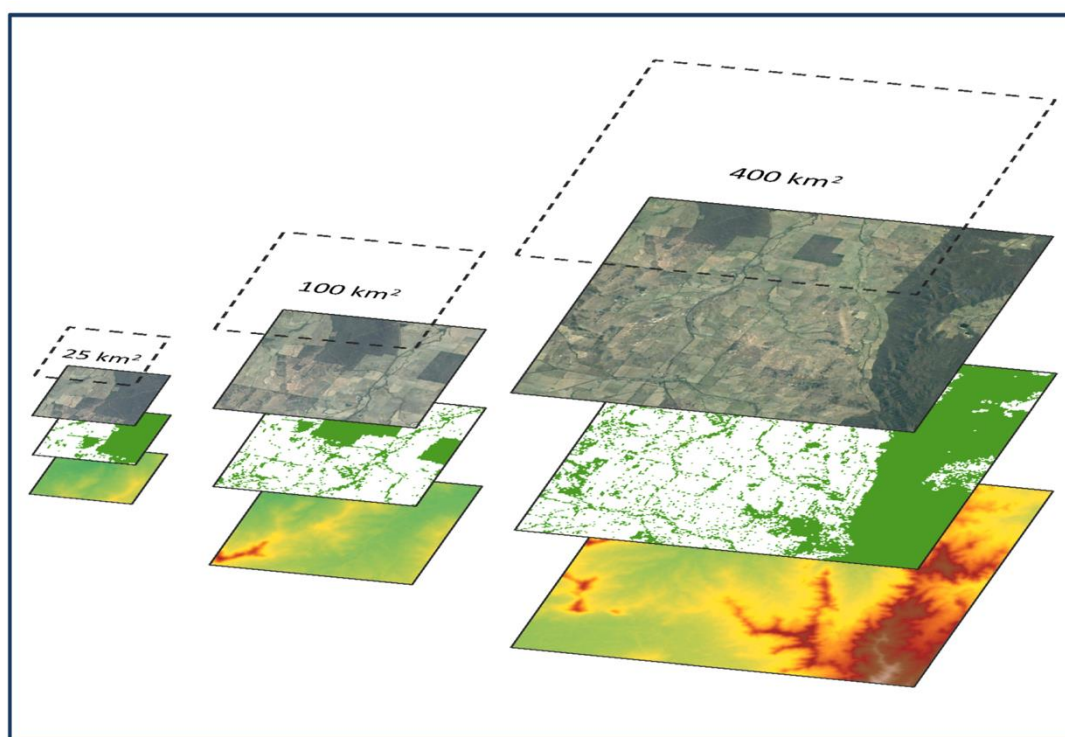


Plate 3 Example of landscape units at scales of analysis considered in this chapter

4.1 Abstract

We examined whether the shape of the species-area relationship differed in landscapes at three scales of analysis. Given scale-dependence in factors that moderate the species-area relationship, we predicted that the shape of the relationship would vary in landscapes of different sizes. We compared the effect of native vegetation area on estimates of Australian woodland bird species richness, among landscapes of three sizes—25 km², 100 km² and 400 km². The fit of four different univariate models describing the species-area relationship at each scale was compared, both for our overall dataset and for two regional subsets of our data. We examined generalized linear mixed models to determine whether two attributes of landscapes—range in elevation and the occurrence of highly competitive native birds of the genus *Manorina*—interacted with vegetation area to explain variation in species richness, and whether these interactions were scale-dependent. At all three scales, the best-supported model describing the landscape-level species-area relationship was a threshold. Furthermore, the location of the threshold value—at approximately 30% vegetation cover—was remarkably similar among the three scales. However, when the relationship was examined separately for northern and southern regions of our study extent, this scale-invariance in the shape of the species-area relationship broke down. Range in elevation and *Manorina* occurrence interacted with vegetation area to explain variation in patterns of species richness, although the effects of these interactions varied among scales. Our results highlight the importance of accounting for scale in studies of landscape-level species richness, particularly where an understanding of the effect of area underpins conservation actions that seek to enhance richness.

4.2 Introduction

Habitat area is a key determinant of the number of species that occur in a landscape (Fahrig, 2013). The effect of area on species richness—the species-area relationship—has frequently been examined by relating measures of both habitat amount and species richness derived at the landscape level. This approach has allowed for exploration of the effect of habitat area in ‘whole landscapes’ (*sensu* Radford and Bennett (2007)), thus providing insights about broad patterns of species richness among human-modified mosaics (Haslem & Bennett, 2008; Desrochers *et al.*, 2011; De Camargo & Currie, 2015; Ochoa-Quintero *et al.*, 2015). For example, studies by Radford *et al.* (2005) and Maron *et al.* (2012) from different parts of south-east Australia explored how the amount of native vegetation in 100 km² landscape units affected the richness of woodland bird species measured at this scale. Both studies found that a threshold model—with a rapid change-

point beyond which the effect of vegetation extent was minimal—had the most parsimonious fit.

Jackson and Fahrig (2015) highlighted that the inferred effects of landscape properties (i.e. habitat area) on an ecological response may be affected by the scale(s) at which they are measured. Indeed, several authors have proposed that the shape of the species-area relationship may vary depending on the scale of analysis (Whittaker *et al.*, 2001; Turner & Tjørve, 2005; Triantis *et al.*, 2012). Turner and Tjørve (2005) noted that the relative effects of factors that influence the relationship between species richness and area vary among scales ranging from metres to biogeographical provinces. Within the range of scales encompassed by ‘landscapes’—mosaics of thousands to tens of thousands of hectares (McAlpine *et al.*, 2016), featuring a mix of elements including habitat (i.e. native vegetation) and non-habitat (i.e. human land uses) (Tscharrntke *et al.*, 2012)—a number of factors influence how species richness responds to habitat area, and that influence may be expected to be scale-dependent.

First, landscape heterogeneity, such as topographic variation, tends to be greater in larger extents (van Rensburg *et al.*, 2002; Báldi, 2008). This correlation may drive scale-dependence in the species-area relationship, as heterogeneity increases species richness (Turner & Tjørve, 2005). Second, biotic interactions, such as competitive exclusion and predation, can exhibit scale-dependent effects on the spatial distribution of species (Araújo & Rozenfeld, 2014; Belmaker *et al.*, 2015). Such scale-dependent biotic interactions may underpin differences in how species richness is affected by area (Scheiner *et al.*, 2011). Third, habitat fragmentation—a process that potentially underpins non-linear species-area relationships (Andrén, 1994; Hanski, 2015)—also exhibits scale-dependent effects on species (Lindenmayer & Fischer, 2007; Jarzyna *et al.*, 2015; Miguet *et al.*, 2015). In recognition of these potentially scale-dependent mechanisms, Turner and Tjørve (2005) emphasised the importance of exploring how the shape of the species-area relationship varies at different spatial scales.

Studies that have related species richness measured at two or more scales (i.e. site and landscape) to habitat area have provided important insights into the effect of area on richness at different scales of analysis (Cunningham *et al.*, 2014a; Burgess & Maron, 2015; Richmond *et al.*, 2015; With, 2016). While some studies have considered how the size of landscapes affects species-specific factors such as population density (Pulliam *et*

al., 1995), we know of no studies focussing specifically on how patterns of landscape-level richness vary among landscapes of different sizes. If the relationship between landscape-level species richness and habitat area varies depending on the size of the landscape under consideration, predictions about patterns of richness, and resultant conservation prescriptions such as habitat protection targets, will only be applicable to the scale at which the relationship was explored. As such, it is imperative to resolve whether landscape-level species-area relationships exhibit scale-dependence.

Using woodland birds of south-east Australia as a focal taxon, we explore how the shape of the relationship between species richness and native vegetation area compares among landscapes that vary in size. Radford *et al.* (2005) examined the effect of vegetation extent on woodland bird species richness in southern Australian landscape units of 100 km², because this size was large enough to encompass the daily movements (home ranges) of the focal assemblage, captured heterogeneity in landscape elements, was of a scale applicable to land managers, and allowed for sufficient replication. Here, we assess landscapes of three sizes – 25 km², 100 km² and 400 km²—to (a) determine whether the shape of landscape-scale species-area relationships vary with landscape size; and (b) draw inferences about how factors such as landscape heterogeneity, the incidence of highly competitive species, and time since clearing, underpin observed scale-dependent area effects. Furthermore, we consider how the shape of species-area relationships for landscapes of different sizes vary regionally, given that differences in the response of woodland birds to native vegetation area have been observed from previous studies that correspond with the southern (Radford *et al.*, 2005) and northern (Maron *et al.*, 2012) parts of our broad study area.

We hypothesise that a threshold will emerge in the species-area relationship, as this has been documented in other landscape-scale studies of bird species richness (Radford *et al.*, 2005; Ochoa-Quintero *et al.*, 2015; Richmond *et al.*, 2015). However, we expect to see differences in the threshold position, or at least in the shape of the relationship among the three landscape sizes, because of geographic and scale-dependent differences in the factors that moderate the effect of area on species richness. In particular, we predict that there will be an interaction between native vegetation area and the occurrence of hyperaggressive native birds of the genus *Manorina* in small landscapes (25 km²), as these aggressive competitors have been shown to substantially affect the composition of woodland bird communities at localised (site, patch, small landscape) scales. As

landscape size increases (100 km²; 400 km²), we expect that the interaction between vegetation area and range in elevation (a proxy for landscape heterogeneity) will become increasingly important, as more habitat types associated with topographic variation are likely to be captured in these larger landscapes.

4.3 Methods

4.3.1 Study area and landscape units

Our study focussed on how bird species richness is affected by the amount of native woody vegetation—a proxy for habitat extent (Radford *et al.*, 2005; Smith *et al.*, 2011; Maron *et al.*, 2012; Cunningham *et al.*, 2014b)—in landscapes of different sizes across a broad region of south-east Australia. The study area comprised those mapped bioregions (or subregions) (based on the Interim Bioregionalisation of Australia (Department of the Environment, 2012a), that have been subject to extensive anthropogenic modification (i.e. at least 25% of the area has been transformed). Clearing of native woodland and forest to facilitate agricultural and urban development has had a profound impact on the avifauna of this part of Australia (Ford, 2011).

For each landscape size (25 km², 100 km² and 400 km²), a corresponding grid (5 x 5 km, 10 x 10 km, 20 x 20 km) spanning our entire study area was overlaid in a geospatial information system (GIS – ArcMap 10.1(ESRI, 2012)). Any incomplete grid cells (those overlapping the coastline) were removed, such that each complete grid cell at each resolution represented a landscape unit.

Radford *et al.* (2005) and Maron *et al.* (2012) detected a threshold in the species-area relationship for woodland birds in 100 km² landscapes in different parts of south-east Australia. However, the percentage cover of native woodland in a landscape corresponding with the observed thresholds differed markedly between the two studies (Radford *et al.*, 2005; Maron *et al.*, 2012). In light of the different results of these studies, we also consider subsets of landscapes from our overall dataset corresponding with bioregions that centre on the location of these two studies. These subsets, which we identify as ‘southern’ and ‘northern’ landscapes (Figure 4.1), encompass the extents of the Radford *et al.* (2005) and Maron *et al.* (2012) studies, respectively. We note however that the extents considered here are considerably broader than those explored in the two previous studies.

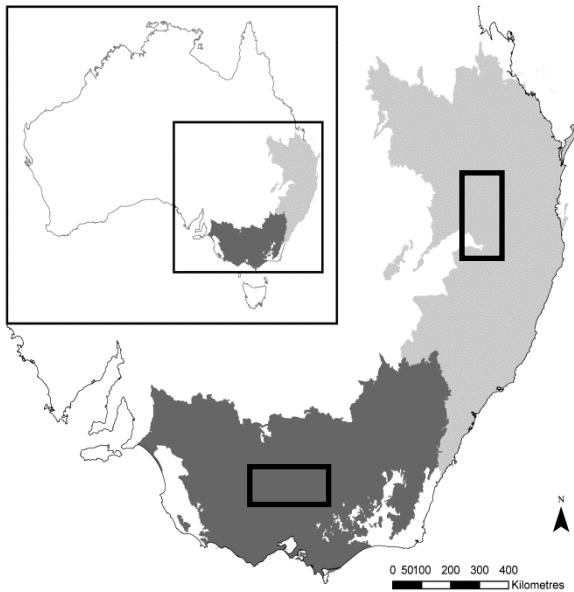


Figure 4.1 Northern (light grey) and southern (dark grey) subset of our overall study area. Bioregion boundaries (as per the Interim Bioregionalisation of Australia) were used to distinguish the two regional subsets, with bioregions (and the landscape units that they contained) occurring in the northern part of the study area being allocated to the northern subset, and bioregions (and associated landscape units) in the southern part of the study area being allocated to the southern subset. The approximate locations of the Maron *et al.* (2012) and Radford *et al.* (2005) study extents (corresponding with the northern and southern subsets, respectively) are highlighted by black rectangles

4.3.2 Bird data

Our focal assemblage was native woodland and forest birds: species that are dependent on woody vegetation (hereafter, ‘woodland birds’), but not waterbirds, or birds that can persist entirely in open environments where trees are very widely scattered or absent. Using data from BirdLife Australia’s New Atlas of Australian Birds database 20 minute/2ha (Loyn, 1986) standardised surveys, we overlaid survey location points on each of our three landscape grids in ArcMap 10.1 (ESRI, 2012). Landscape units at each scale in which at least 20 bird surveys had been conducted were identified ($n=720, 746, 565$, for 25 km^2 , 100 km^2 , 400 km^2 landscapes, respectively). This process allowed us to determine the observed species richness of woodland birds for landscape units at each landscape size in which at least 20 standardised surveys had been performed.

Because there was substantial variation in the number of surveys conducted in landscape units, we used a three-step approach for deriving comparable estimates of species

richness that were not biased by variable survey effort. First, we used non-parametric asymptotic estimators in the program EstimateS Version 9 (Colwell, 2013) to derive estimates of species richness for landscape units at each of the three scales being investigated. We retained landscape units at each scale where estimated richness varied by less than two species in the last five surveys of the total set of samples (i.e. the estimator had stabilised (as per Maron *et al.* (2012))).

Second, for landscapes with stable estimates of richness ($n=480, 450, 400$, for the 25 km^2 , 100 km^2 , 400 km^2 landscape sizes, respectively), we then checked whether the asymptotic estimation process had removed the positive correlation between number of surveys and (estimated) species richness. Upon finding a moderate positive correlation at each landscape size, we used the unified rarefaction/extrapolation approach (Colwell *et al.*, 2012) to obtain comparable values of expected species richness at a standardised level of survey effort (Colwell & Elsensohn, 2014). Given the recommendation of 20 samples as a minimum number for rarefaction (Gotelli & Colwell, 2011), and the conservative suggestion to extrapolate only to twice the number of samples (Colwell *et al.*, 2012), we standardised sampling effort at 40 surveys, and obtained expected measures of species richness for landscape units at each landscape size at this level of sampling. These estimates were weakly correlated with the total number of surveys in a landscape unit, and provided us with species richness estimates for landscape units that were not confounded by variable sampling effort.

Third, we checked whether estimates of richness at 40 surveys at each landscape size were equivalently complete (Watson, 2003) for more-species rich landscapes as compared with species-poor landscapes. To do this, we examined estimates of richness at 60 surveys, derived using the unified rarefaction/extrapolation approach (Colwell *et al.*, 2012). Landscapes with higher estimated richness at 40 surveys did not show a proportionally greater increase in estimated richness than lower richness landscapes at 60 surveys, indicating that standardisation to 40 samples was not systematically reducing estimates of richness in more-diverse landscapes.

In selecting a final set of landscape units at each landscape size, we applied a number of criteria to account for within-landscape spatial and temporal variability in sampling effort, and temporal changes in the amount of woody vegetation cover over the period for which bird data were collected. The criteria we selected sought to strike a balance between

satisfactorily controlling for spatial and temporal variation, while still allowing for a sufficient number of landscape units at each landscape size to explore our study questions. Thus, for a landscape unit to be included in this analysis, units at each landscape size needed to satisfy the following criteria: (1) surveys from at least five unique locations in at least two different quadrants of a landscape; (2) at least five surveys from each half of the Atlas data collection period (1998-2014); (3) at least five surveys in each half of the year (April-September, October-March); and (4) less than a 5% change in total 'forest' cover for the period 2000-2012 based on the 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 176, 238 and 250 landscape units for the 25 km², 100 km², 400 km² landscape sizes, respectively, met the criteria and were used for the analysis (Figure 4.2) (See Appendix C: Table C1 for an overview of the bird data used in analysis).

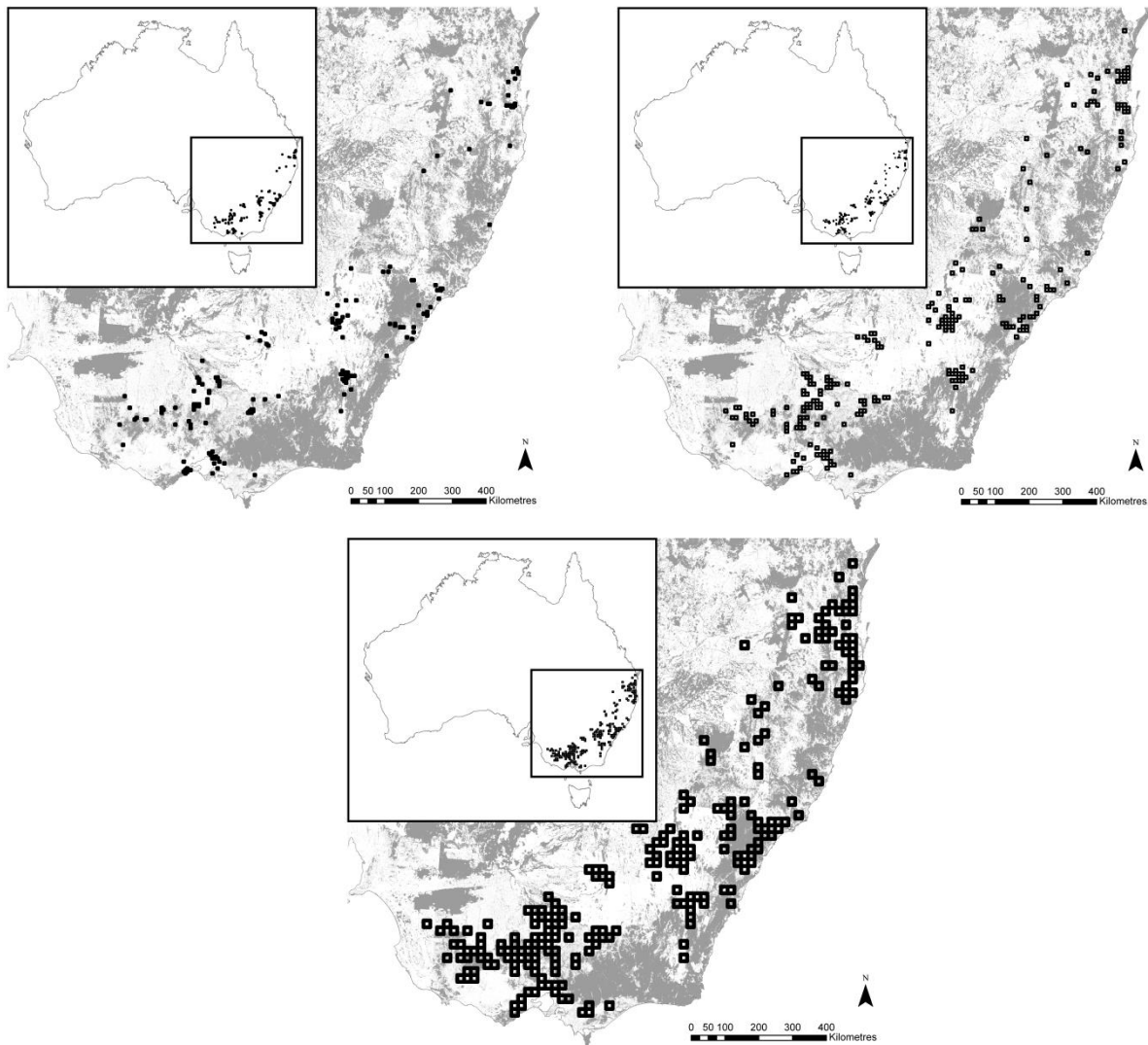


Figure 4.2 Location of landscape units in south-east Australian study area – 25 km² (top left), 100 km² (top right), and 400 km² (bottom). Remnant native woody vegetation is depicted by the grey shading

4.3.3 Landscape data

We used the Australian Government’s National Vegetation Information System (NVIS) version 4.1 (Department of the Environment, 2012b), which maps the contemporary distribution of remnant native vegetation in Australia, to determine the area of native woody vegetation in landscape units. From this 100 m pixel resolution dataset of 33 major vegetation groups, we identified vegetation types that were characterised by remnant woody vegetation, and determined the percentage cover of woody vegetation area for landscape units at each of the three landscape sizes. *Eucalyptus* woodlands and forests are the dominant vegetation types in our south-east Australian study area. The percentage cover of woody vegetation was related to the estimate of bird species richness for each

landscape unit, to explore the shape of landscape-level species-area relationships at the three different scales.

We extracted data on two attributes of landscapes that act on the occurrence of birds, and have the potential to interact with area to affect landscape-scale species richness. This was undertaken to explore whether the interactive effect with area differed in landscapes of different sizes. First, we calculated the range in elevation in landscape units at each landscape size, using a 90 m resolution digital elevation model (Jarvis *et al.*, 2008). Range in elevation is an oft-used proxy for topographic variability in a landscape (Belmaker & Jetz, 2011), and is known to positively correlate with both species richness (Jetz *et al.*, 2004; van Rensburg *et al.*, 2009; Stein *et al.*, 2014; Burgess & Maron, 2015) and non-random patterns of vegetation clearing (Seabloom *et al.*, 2002; Maron *et al.*, 2015a). Here, we use range in elevation to represent landscape heterogeneity. Second, we extracted data on the relative occurrence of two native bird species that are known to affect the composition of bird assemblages within our study area. These colony-forming birds of the genus *Manorina*—the noisy miner (*M. melanocephala*), and the yellow-throated miner (*M. flavigula*)—can have dramatic impacts on the occurrence of smaller-bodied native birds through aggressive competitive exclusion, leading to shifts in assemblages within their colonies (Maron *et al.*, 2013; Mac Nally *et al.*, 2014a). For landscape units at each scale, we determined the proportion of surveys in which one or both of these species was recorded (i.e. a reporting rate (Watson, 2003)). Geospatial data processing and extraction was done using ArcMap10.1 (ESRI, 2012) and Geospatial Modelling Environment (Beyer, 2012).

This exploration of interactions also allowed us to (in part) account for how the effect of native vegetation area—a broad proxy for habitat extent for the assemblage of birds under examination—differed as a function of attributes of landscapes that act on the quality of native vegetation for woodland and forest birds. While the species we examined may respond differently to specific vegetation types that are captured within the broad characterisation of habitat (woody vegetation cover) that we used, consideration of the interactive effects of attributes of landscape quality that may be associated with topographic heterogeneity and/or the occurrence of hypercompetitive species, allowed us to draw inferences about how habitat quality may underpin differential responses to habitat quantity.

4.3.4 Data analysis

We built univariate generalised linear models (GLMs) with a Poisson error distribution in R (R Core Team, 2013) to explore the shape of the relationship between estimates of species richness and woody vegetation area for all landscape units from our study area, at each of the three landscape sizes. The fit of four different models—exponential (to approximate a traditional convex upward species-area curve), linear, polynomial (quadratic) and threshold—was compared using Akaike’s Information Criterion (AIC). We included a threshold model, as previous landscape-scale studies have recorded a sudden change in the relationship between species richness and vegetation extent (Banks-Leite *et al.*, 2014; Ochoa-Quintero *et al.*, 2015; Richmond *et al.*, 2015), including two from within our study area (Radford *et al.*, 2005; Maron *et al.*, 2012). Threshold models were constructed using the R package ‘segmented’ (Muggeo, 2008). For this modelling, we used the percentage of woody vegetation area as the predictor variable, and our estimates of species richness as the response variable. To explore the generality of the shape of the species-area relationship at each landscape size, we repeated the model-fitting exercise on southern and northern subsets of the data (Figure 4.1). This allowed us to explore whether the relationship between species richness and area at each landscape size differed between the two regions, as well as how these ‘region-specific’ relationships compared to that of the aggregated dataset for the entire study area.

We then explored how landscape heterogeneity and *Manorina* reporting rate interacted with vegetation area to affect species richness in landscapes of different sizes. To do this, we used generalised linear mixed models (GLMM) constructed in the R package ‘lme4’ (Bates *et al.*, 2014). For northern and southern landscapes at each landscape size, we considered how species richness varied as a function of vegetation area, range in elevation, and *Manorina* reporting rate, as well as interaction terms between vegetation area and the other two landscape attributes. The inclusion of the range in elevation parameter in our models not only allowed us to explore how the effect of area is moderated by landscape heterogeneity, but also allowed us to derive inferences about how non-random patterns of vegetation clearing may confound species-area analyses in landscapes of different sizes. All predictor variables were standardised (mean = 0, standard deviation = 1) prior to this analysis. The bioregion in which each landscape unit occurred was included as a random intercept to account for potential spatial autocorrelation. This modelling exercise allowed us to examine how landscape

heterogeneity and biotic moderators of localised bird assemblages interact with area to affect species richness in landscapes of different sizes.

4.4 Results

We found that the shape of the species-area relationship for landscapes across our study extent was remarkably similar irrespective of the size of the landscape under analysis (Figure 4.3a-c). First, for 25 km², 100 km² and 400 km² landscape units, a threshold model was found to be the most parsimonious fit (Table 4.1). Second, at all three landscape sizes, the value of percent native woody vegetation area that corresponded with a change in the rate at which species richness varied with area was approximately 30% (Table 4.1). Above this value, estimated species richness changed little with increasing vegetation area in 25 km² and 100 km² landscapes, although continued to increase slightly in 400 km² landscapes.

When landscapes were subset into northern and southern regions, different patterns emerged in the species-area relationship (Figure 4.3d-f, Table 4.1). Threshold models were best supported for northern and southern landscapes at the 25 km² and 100 km² landscape size. However, the percent cover of woody native vegetation at which these thresholds emerged differed between regions at each landscape size, and between landscape sizes within regions. We recorded a threshold at approximately 17% and 36% cover, for southern and northern landscapes respectively, at the 100 km² landscape size. However, at the 25 km² landscape size, the observed threshold value was higher in southern landscapes (approximately 37%, compared with 15% for northern landscapes). At the largest landscape size, threshold models were no longer best-supported; species richness tended to increase with vegetation area up to at least 50% in northern and southern landscapes, with richness tending to plateau or decline above this value. However, the support for the quadratic models in northern and southern landscapes at 400 km² was only marginally stronger than that for other models (Table 4.1).

The mixed modelling revealed that in both northern and southern landscapes, native vegetation area was generally a significant positive predictor of estimated species richness, irrespective of the scale of analysis (Table 4.2). The one exception was southern landscapes at the 25 km² landscape size, where vegetation area was not significant. Range in elevation typically had a significant positive independent effect on species richness, while *Manorina* reporting rate was rarely influential (Table 4.2). The effect of

vegetation area was moderated by range in elevation, as revealed by the significant negative interaction term between the two variables, at all three landscape sizes in southern landscapes (Table 4.2). In northern landscapes, a positive interaction between vegetation area and *Manorina* reporting rate was recorded at all three landscape sizes (Table 4.2).

Table 4.1 Summary of univariate generalised linear models for the relationship between estimated species richness and vegetation area at each landscape size for the entire study area, and for regional subsets (northern and southern). Italicised rows indicates the model of best fit (lowest AIC value) for each landscape size

	% Deviance explained	Nagelkerke R²	ΔAIC	Threshold value*
25 km²				
All landscapes (n= 176)				
Exponential	12.8	0.40	41.2	
Linear	10.7	0.35	55.8	
Quadratic	17.7	0.51	10.2	
<i>Segmented</i>	<i>19.5</i>	<i>0.54</i>	<i>0</i>	<i>31% (±3.7)</i>
Northern landscapes (n= 52)				
Exponential	33.9	0.71	6.5	
Linear	17.4	0.47	36.2	
Quadratic	34.9	0.72	6.7	
<i>Segmented</i>	<i>39.8</i>	<i>0.77</i>	<i>0</i>	<i>15% (±2.5)</i>
Southern landscapes (n= 124)				
Exponential	7.6	0.25	19.2	
Linear	8.2	0.26	16.7	
Quadratic	11.1	0.34	5.7	
<i>Segmented</i>	<i>12.8</i>	<i>0.38</i>	<i>0</i>	<i>37% (±7.0)</i>
100 km²				
All landscapes (n= 238)				
Exponential	17.6	0.47	56.3	
Linear	13.8	0.39	87.4	
Quadratic	22.9	0.56	14.7	
<i>Segmented</i>	<i>25.0</i>	<i>0.60</i>	<i>0</i>	<i>27% (±2.4)</i>
Northern landscapes (n= 80)				
Exponential	15.4	0.31	17.7	
Linear	7.0	0.15	31.3	
Quadratic	22.7	0.42	8.1	
<i>Segmented</i>	<i>29.1</i>	<i>0.51</i>	<i>0</i>	<i>36% (±3.7)</i>

	% Deviance explained	Nagelkerke R²	ΔAIC	Threshold value*
Southern landscapes (n= 158)				
Exponential	13.6	0.38	29.5	
Linear	12.6	0.35	34.7	
Quadratic	17.6	0.46	10.5	
<i>Segmented</i>	<i>20.0</i>	<i>0.50</i>	<i>0</i>	<i>17% (±2.7)</i>
400 km²				
All landscapes (n= 250)				
Exponential	16.7	0.48	81.1	
Linear	22.6	0.59	24.5	
Quadratic	25.1	0.63	2.7	
<i>Segmented</i>	<i>25.6</i>	<i>0.64</i>	<i>0</i>	<i>31% (±4.0)</i>
Northern landscapes (n= 94)				
Exponential	30.7	0.60	2.9	
Linear	20.4	0.45	28.6	
<i>Quadratic</i>	<i>32.7</i>	<i>0.62</i>	<i>0</i>	
Segmented	31.9	0.61	4.0	32% (±3.6)
Southern landscapes (n= 156)				
Exponential	7.5	0.22	36.1	
Linear	14.1	0.38	2.4	
<i>Quadratic</i>	<i>15.0</i>	<i>0.40</i>	<i>0</i>	
Segmented	15.4	0.41	0.1	41% (±8.6)

* % landscape woody vegetation area (rounded to nearest 1%) at which change in rate of species loss/gain as a function of woody vegetation area occurs (± error around threshold estimate)

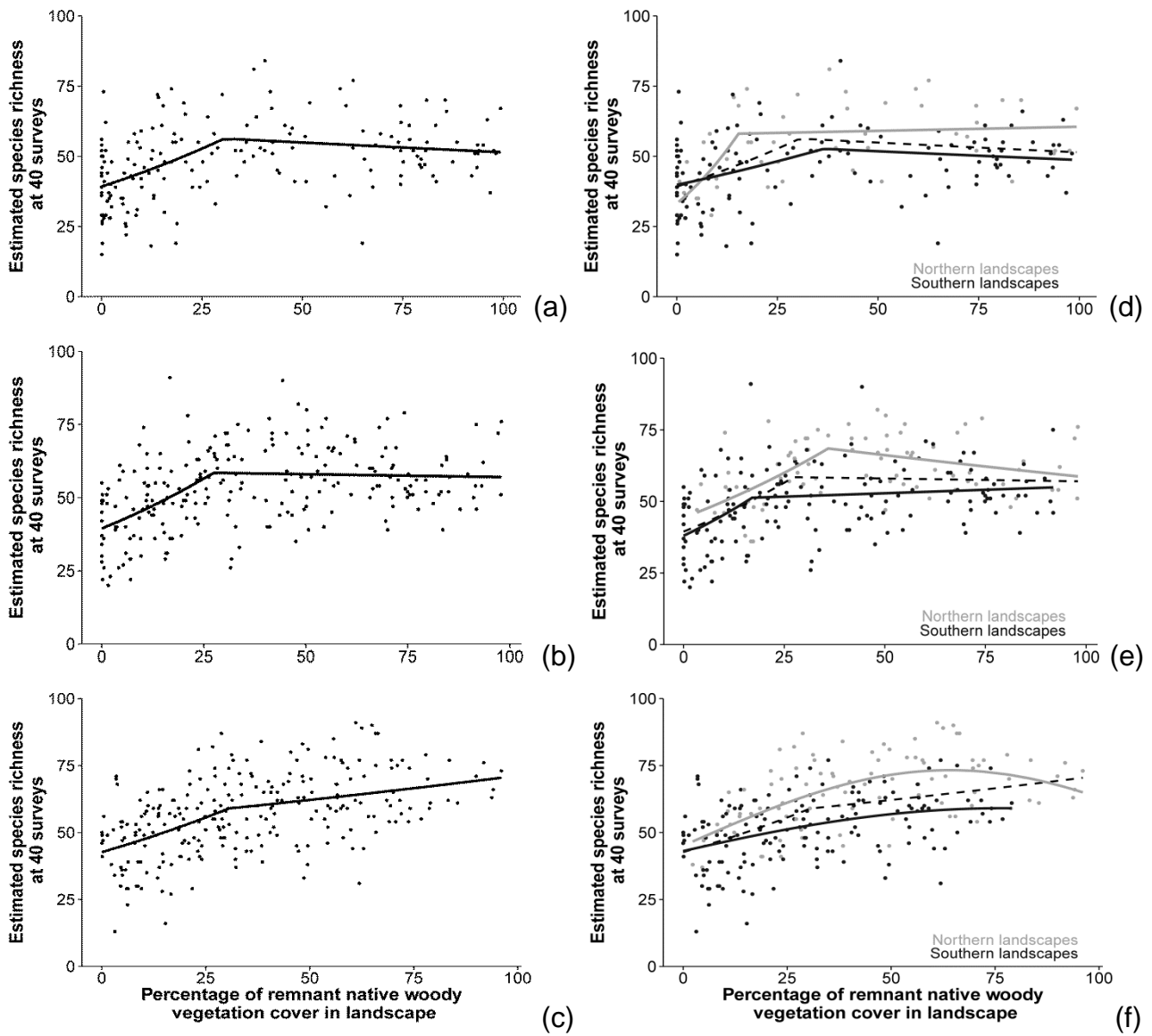


Figure 4.3 Relationship of best fit for all landscape units in south-east Australia study area (left column) at 25 km² (n=176; top (4.3a)), 100 km² (n=238; middle (4.3b)) and 400 km² (n=250; bottom(4.3c)); Relationship of best fit for landscape units categorised by region (right column) at 25 km² (n=52, n=124 (northern and southern, respectively); top (4.3d)), 100 km² (n=80 n=158; middle (4.3e)) and 400 km² (n=94, n=156; bottom (4.3f))

Table 4.2 Standardised parameter estimates (and standard errors in parentheses) for generalised linear mixed models for northern and southern landscapes. Estimated species richness is the response variable, and landscape attributes including vegetation area, range in elevation and *Manorina* reporting rate, as well as two way interactions between vegetation area and the other two landscape attributes, are the predictor variables. Bold parameter estimates significant at $p < 0.05$

	Vegetation area	Range in elevation	<i>Manorina</i> occurrence	Area x Elevation	Area x <i>Manorina</i>
25 km²					
	0.085	0.120	-0.035	-0.109	0.062
Northern	(0.025)	(0.025)	(0.023)	(0.023)	(0.023)
	0.023	0.067	-0.057	-0.042	0.001
Southern	(0.021)	(0.019)	(0.019)	(0.015)	(0.019)
100 km²					
	0.062	0.024	0.023	-0.030	0.090
Northern	(0.018)	(0.018)	(0.019)	(0.016)	(0.017)
	0.110	0.085	-0.024	-0.038	0.064
Southern	(0.016)	(0.016)	(0.015)	(0.013)	(0.014)
400 km²					
	0.087	0.077	0.034	-0.028	0.070
Northern	(0.019)	(0.020)	(0.017)	(0.016)	(0.017)
	0.090	0.078	-0.020	-0.025	0.025
Southern	(0.015)	(0.016)	(0.014)	(0.012)	(0.014)

4.5 Discussion

When data were aggregated across a broad region of south-east Australia, we recorded marked scale-invariance in the landscape-level relationship between estimates of woodland bird species richness and vegetation area. Threshold models, with a very similar change point, were always best-supported, regardless of the landscape size. However, when relationships were analysed for two separate regions of our overall study area, scale-specific patterns in the shape of the species-area relationship emerged. Our findings have important implications for the interpretation and application of landscape-level species-area analyses, especially where the objective is to inform actions seeking to maintain or enhance species richness in human-modified landscapes.

4.5.1 *Threshold relationships in landscapes of different sizes*

As hypothesised, we consistently recorded a threshold in the relationship between estimates of species richness and vegetation area, irrespective of both the size of the landscape units, and how the data were aggregated/subset. Thresholds of vegetation extent have been observed in a number of landscape-scale studies that have examined the relationship between species richness and vegetation area (Radford *et al.*, 2005; Maron *et al.*, 2012; Morante-Filho *et al.*, 2015; Ochoa-Quintero *et al.*, 2015; Richmond *et al.*, 2015). These studies have highlighted that vegetation area has reduced or no effect on species richness above the threshold point, contrasting with the expected monotonic increase in richness associated with a traditional (power or exponential) species-area model (De Camargo & Currie, 2015).

A key mechanism that has been proposed to explain thresholds in the relationship between species richness and vegetation extent relates to the configuration of habitat in a landscape (Swift & Hannon, 2010). Andrén (1994) hypothesised that the deleterious effects of habitat fragmentation may exacerbate the adverse impact of habitat loss at low levels of habitat cover (<30%) in landscapes, thereby explaining the occurrence of a sudden change (threshold) in the rate at which species richness varies with area. The threshold values we recorded at each landscape size for our entire study extent corresponded with the 30% 'fragmentation threshold' value proposed by Andrén (1994). If the configuration of habitat in low cover landscapes is the major determinant of the threshold patterns we observed at the 25 km², 100 km² and 400 km² landscape sizes, this would suggest that the effects of fragmentation on our focal assemblage are scale invariant.

However, a notable finding of our study was that apparent scale-invariance in the relationship at different landscape sizes broke down when data were subset into regions. This finding indicates that different processes are potentially acting on the species-area relationship in different-sized landscapes in the regional subsets we examined. One such mechanism may relate to differences in temporal patterns of vegetation clearing. Radford *et al.* (2005) highlighted that the value corresponding with a threshold would be expected to shift to a higher level of (landscape-scale) vegetation area as the extinction debt carried by landscapes is 'paid'. Extinction debt reflects the occurrence of species post-vegetation clearing (habitat loss), which are ultimately on a trajectory towards local extinction (Tilman *et al.*, 1994; Ford *et al.*, 2009; Swift & Hannon, 2010). This process was ruled out by

Maron *et al.* (2012) as explaining the difference in threshold values recorded in their study of woodland birds in 100 km² landscapes, compared with the study of Radford *et al.* (2005), because the former study recorded a higher threshold value from a region in which broadscale clearing was more recent.

Our results for 100 km² landscapes are consistent with the findings of Maron *et al.* (2012) and Radford *et al.* (2005). However, we recorded the reverse pattern in 25 km² landscapes; a higher threshold value from southern landscapes (approximately 37% vegetation cover) compared with northern landscapes (approximately 15% cover). Part of our northern subset includes landscapes that have experienced Australia's greatest rates of deforestation in recent decades—namely northern New South Wales and southern Queensland (Bradshaw, 2012). By contrast, historical clearing in the extent covered by our southern subset—largely corresponding with the state of Victoria—generally occurred over 100 years ago (Bradshaw, 2012), with comparatively much lower forest loss since the 1970s (Evans, 2016). The different threshold values for 25 km² landscapes may in part reflect different stages of the 'payment' of the extinction debt, with the influence of recently cleared (<50 years) landscapes in part of the northern subset acting to reduce the level of vegetation cover at which a threshold is realised. If this is the case, it highlights that the effect of extinction debt on landscape-level species richness may be prominent at finer scales of analysis, with other factors moderating the relationship between species richness and vegetation area at coarser scales.

4.5.2 *Influence of landscape attributes on species richness at different scales*

Turner and Tjørve (2005) proposed that the scale at which landscape heterogeneity is most likely to influence species-area relationships ranges over several orders of magnitude, encompassing the landscape sizes we have analysed here. Indeed, we found that native vegetation area had a weaker effect on species richness as range in elevation (a proxy for landscape heterogeneity (Belmaker & Jetz, 2011)) increased, and that this was evident at all three landscape sizes across the northern and southern regions. However, contrary to our expectation, this interaction was not significant in 100 km² and 400 km² landscapes from our northern subset. We expected that in larger landscapes, increasing range in elevation would dampen the effect of area *per se*, as species richness would reflect a response to the greater heterogeneity of these landscapes. This is because high species turnover (i.e. greater beta diversity) between habitat types in heterogeneous landscapes may contribute to increased landscape-scale richness (i.e. gamma diversity)

(Fahrig *et al.*, 2011; Burgess & Maron, 2015), thereby moderating the effect of habitat area *per se*. In other words, for the same amount of habitat, more heterogeneous landscapes may be expected to support more species. The significant negative interaction between vegetation area and range in elevation in southern landscapes of all three sizes indicates that beta diversity associated with habitat heterogeneity may contribute strongly to landscape-scale patterns of richness, and that the moderating effect of landscape heterogeneity on the effect of area is scale invariant in this region. Notably, the fact that the moderating effect of range in elevation on vegetation area was not significant in 100 km² and 400 km² landscapes from our northern subset indicates that clearing biases associated with non-random clearing may not always confound observed area effects.

The effect of vegetation area was also moderated by *Manorina* occurrence in our northern and southern subsets, at all three landscape sizes. We expected that this interaction would be important at the finest scale of analysis (25 km²), given a large body of research has documented that these highly-competitive native species are important drivers of bird assemblages in sites (Mac Nally *et al.*, 2014a; Mac Nally *et al.*, 2014b), patches (Maron *et al.*, 2011) and (small) landscapes (25 km²) (Robertson *et al.*, 2013). However, our results did not support this prediction. The positive interaction term was significant at all three landscape sizes in northern landscapes, although it was only significant in 100 km² landscapes from our southern landscapes.

This result potentially underscores the importance of increasing vegetation extent (including more core habitat) for woodland birds, given the preference of *Manorina* honeyeaters for edge habitats (Maron *et al.*, 2013; Thomson *et al.*, 2015). We expected that this association would become less important at coarser scales, because, for a given percent cover of native vegetation extent, larger landscapes (i.e. 100 km², 400 km²) would be expected to have more core habitat. However, it may be that an increase in the amount of edge habitat for a given percent cover of native vegetation extent underpins the significant positive interaction between vegetation area and *Manorina* reporting rate at coarser scales. Alternatively, the results we obtained may be a reflection of the confounding influence of other landscape attributes, such as productivity (and associated energy availability), which may be positively correlated with both increased species richness (Storch *et al.*, 2005; Symonds & Johnson, 2008; Luck *et al.*, 2010) and *Manorina* occurrence (Montague-Drake *et al.*, 2011; Maron *et al.*, 2013).

4.5.3 Conclusion

Our study took the novel approach of exploring the relationship between bird species richness and native vegetation area in landscape units of different sizes. In general, we found that the relationship reflected a threshold value of vegetation extent, irrespective of the size of the landscape examined. However, the threshold value differed depending on how data were aggregated/subset. These differences in the relationship potentially represent a complex interaction of factors that have differing effects on the species-area relationship among scales and regions.

We highlight two key messages from this study. First, extrapolating the findings of species-area studies to other scales and systems is likely to result in a misrepresentation of the effect of area on species richness. This is because of scale- and geographical-dependence in factors that act on the landscape-level species-area relationship. Second, we reiterate a message that has been highlighted by others (Lindenmayer *et al.*, 2005; Johnson, 2013; Toms & Villard, 2015), in urging caution in the interpretation and use of thresholds for guiding the management of landscapes. Accordingly, the application of thresholds to inform vegetation protection or restoration targets that seek to maximise species richness, should be underpinned by analyses of the focal system and assemblage at the grain size in which management actions will take place.

CHAPTER 5

THE IMPLICATIONS OF USING THRESHOLDS FROM LANDSCAPE-SPECIFIC SPECIES-AREA RELATIONSHIPS TO GUIDE CONSERVATION ACTIONS

To be prepared for submission to *Biological Conservation*



Plate 4 Brigalow (*Acacia harpophylla*) woodland adjacent to a cleared pasture—Brigalow Belt South (Darling Downs), southern Queensland (photo: M. Maron)

5.1 Abstract

Observed thresholds in the relationship between species richness and native vegetation extent can guide conservation actions in human-modified landscapes. For example, particular landscapes could be targeted for native vegetation protection and/or restoration to prevent precipitous species declines. However, this approach may be ineffective if observed thresholds do not accurately represent the manner in which species richness responds to habitat amount at the landscape level. Accounting for landscape attributes that confound identification of thresholds in the species-area relationship may allow for a more thorough understanding of the effect of vegetation area, thereby enhancing the utility of thresholds for incorporation into conservation target setting. Using a case study of woodland birds in a rapidly changing region of eastern Australia, I explore how accounting for landscape-specific differences in species-area relationships can alter the prioritisation of landscapes for conservation actions such as vegetation protection or restoration. Observed thresholds in species-area relationships, where landscape attributes such as topography and soil fertility were accounted for, implied different prospective conservation actions to those informed by a threshold derived from a non-landscape-specific species-area model. Specifically, the number and location of landscapes that could be the focus of conservation interventions differed depending on the species-area model used to guide the prioritisation. Accounting for landscape attributes that potentially confound species-area analyses is important where thresholds are to be used to guide actions that seek to maintain or enhance species richness in human-modified landscapes.

5.2 Introduction

The species-area relationship is an important tool for informing conservation actions that aim to address or predict the impacts of habitat loss (Desmet & Cowling, 2004; Kitzes & Harte, 2014; Matthews *et al.*, 2014b). Of particular interest is the functional form and shape of the relationship, as this reveals the rate at which species richness changes with habitat area (Whittaker & Triantis, 2012). Interpretation of the form and shape of the relationship can underpin management interventions that focus on mitigating species loss via habitat protection and/or restoration (Radford *et al.*, 2005; Possingham *et al.*, 2015), as well as guide predictions about how future changes to habitat area may affect patterns of species richness (Kitzes & Harte, 2014; Ochoa-Quintero *et al.*, 2015).

In 'landscapes'—mosaics of thousands to tens of thousands of hectares (McAlpine *et al.*, 2016), featuring a mix of elements including habitat (i.e. native vegetation) and non-habitat

(i.e. human land uses) (Tscharrntke *et al.*, 2012)—habitat area is a key determinant of species richness (Pardini *et al.*, 2010; Fahrig, 2013; Cunningham *et al.*, 2014a). Notably, a number of recent studies have detected a threshold in the relationship between species richness and habitat area at the landscape level, where, unlike a classic power or exponential species-area curve, the slope suddenly changes at a particular amount of habitat (Radford *et al.*, 2005; Lima & Mariano-Neto, 2014; Morante-Filho *et al.*, 2015; Ochoa-Quintero *et al.*, 2015; Richmond *et al.*, 2015). Generally, these threshold models reveal that the loss of species is much more rapid below the threshold value of habitat area (Swift & Hannon, 2010).

Thresholds are an important concept from an applied conservation perspective, as they represent potential ‘targets’ upon which conservation actions and predictions can be based (Guénette & Villard, 2005; Huggett, 2005; Rhodes *et al.*, 2008). For example, in landscape units of 100 km² located in south-east Australia, Radford *et al.* (2005) found that woodland bird species richness exhibited a sharp decline with habitat area in landscapes with less than 10% native vegetation cover, but was not affected by habitat area above this threshold. Based on this finding, Radford *et al.* (2005) advocated that landscape-scale native vegetation cover in their study area be maintained at well over 10% to avoid species richness declining to the low values observed where this threshold was breached. Ochoa-Quintero *et al.* (2015) recorded a much higher threshold value when relating the species richness of Brazilian forest birds and mammals to forest area in 100 km² landscape units. Using an observed threshold value of 43% forest cover as the point below which species richness declined sharply with forest area, Ochoa-Quintero *et al.* (2015) predicted how future forest loss may affect species richness at the landscape scale.

Despite the promise of using thresholds to guide management actions and inform predictions of future change, the concept is not without limitations. For example, variation in observed thresholds among different taxa and regions precludes generalities from being derived about what threshold value should be used to underpin conservation actions (Lindenmayer & Luck, 2005; Johnson, 2013; van der Hoek *et al.*, 2013). Moreover, from a landscape ecological perspective, observed thresholds may be an artefact of confounding factors that distort the relationship between species richness and area. The ‘spurious thresholds hypothesis’ (Maron *et al.*, 2012) suggests that thresholds may arise because of the intersection of separate species-area relationships for landscapes with different attributes (i.e. differences in soil fertility). This hypothesis draws on two interrelated

themes, both of which I have explored in earlier chapters of this thesis: (1) that the amount of habitat in a landscape is correlated with abiotic attributes like soil fertility because anthropogenic patterns of vegetation clearing are non-random (Chapter 2); and (2) that the effect of habitat area on species richness differs in landscapes with different attributes (i.e. there is an interaction between area and attributes like soil fertility or topography) (Chapters 3 and 4). A failure to account for potentially confounding factors such as soil fertility and topography may translate to inaccurate habitat protection or restoration prescriptions, if they are informed by observed thresholds (Maron *et al.*, 2012).

In this chapter, I examine the implications of accounting for landscape attributes when using species-area relationships to inform landscape-scale conservation actions. I test how observed thresholds could guide conservation actions aiming to maintain landscape-scale species richness under two scenarios of future vegetation clearing. I use the case study of woodland bird species richness in the Brigalow Belt South bioregion of southern Queensland, Australia—a heavily modified region that has experienced a recent increase in rates of vegetation loss—to explore these questions. This analysis draws upon the two key themes of the spurious thresholds hypothesis: (1) patterns of vegetation loss and retention at the landscape-level are non-random, and are correlated with abiotic landscape attributes; and (2) the shape of the relationship between species richness and native vegetation area differs depending on landscape attributes. The aim of this study is to examine the extent to which using observed threshold values from different species-area models—including landscape-specific models—yields different outcomes in terms of (1) informing potential conservation actions such as the spatial distribution of landscapes that should be the focus of vegetation protection/restoration to avoid sharp declines in species richness; and (2) predictions of the response of species richness to current and future landscape-scale habitat amount.

5.3 Methods

5.3.1 Study region

The Brigalow Belt South (BBS) bioregion covers approximately 12.5% (215,967 km²) of Queensland (Queensland Department of Environment and Heritage Protection, 2016) (Figure 5.1). It is one of 89 bioregions in Australia, with each defined based on attributes associated with climate, geology, landform and biodiversity (Department of the Environment, 2012a). Historically, the BBS bioregion was characterised by extensive forests of brigalow (*Acacia harpophylla*), as well as various woodland communities

dominated by eucalypts (*Eucalyptus spp.*) (Seabrook *et al.*, 2006). Substantial landscape transformation, including rapid and extensive clearing of woodlands and forests to facilitate agricultural production, has occurred in the BBS bioregion since the 1950s (McAlpine *et al.*, 2002; Seabrook *et al.*, 2006). More than 60% of the native vegetation of the bioregion has been cleared, with a particular focus on fertile areas (Seabrook *et al.*, 2006; Eyre *et al.*, 2009).

Unregulated broadscale clearing of native vegetation in Queensland ended in 2006. This resulted in a substantial reduction in annual clearing rates of remnant (previously uncleared) native vegetation. Furthermore, provisions were introduced in 2009 to protect non-remnant vegetation classified as 'high-value regrowth', identified as vegetation communities that have not been cleared since at least 1989. The mean rate of remnant vegetation clearing for the period 2009-2011 in the BBS bioregion was approximately 3,500 ha/year (Queensland Government, 2015). However, upon changes to the vegetation management framework in Queensland in 2013, rates of remnant and high-value regrowth vegetation clearing increased. Across Queensland, approximately four times (397%) more remnant woody vegetation was cleared during the period 2013-2014 compared with 2010-11 (Queensland Department of Science, Information Technology, Innovation and the Arts, 2014; Queensland Department of Science, Information Technology and Innovation, 2015). In the Queensland Brigalow Belt (comprising the BBS and Brigalow Belt North bioregions), clearing rates of remnant woody vegetation increased by approximately two and a half times (267%) over the same period (Queensland Department of Science, Information Technology, Innovation and the Arts, 2014; Queensland Department of Science, Information Technology and Innovation, 2015). In 2016, amendments to Queensland's *Vegetation Management Act 1999* were being considered, whereby protection for remnant and high-value regrowth vegetation would (again) be strengthened. In the context of its extensive historical modification, and the recent policy changes (and proposed changes) to the management of native vegetation in Queensland, the BBS bioregion represents a highly relevant case study region by which to showcase how different observed thresholds in the species-area relationships can guide our understanding of (and response to) the effects of habitat loss.

In the preceding chapters of this thesis, I explored non-random patterns of vegetation clearing (Chapter 2), and landscape-specific species-area relationships (Chapter 3), using 100 km² landscape units. In Chapter 4, I demonstrated scale-dependence in these

relationships. The BBS bioregion was a part of the study extent in all of these analyses. While the results of these previous analyses were derived for broader extents (albeit, encompassing the BBS bioregion), I use these results here to exemplify how different landscape-scale species-area relationships (and associated threshold values) potentially entail different predictions and conservation outcomes, in a region subject to rapid and ongoing change. For the purposes of this analysis, I consider the form and shape of the species-area relationships observed for south-east Australian woodland birds (Chapter 3) to be representative of how woodland bird richness varies with area in the BBS bioregion. It is important to note that the study presented in the chapter represents a demonstration of the utility and potential limitations of the threshold concept for informing the management of landscapes, rather than an exhaustive analysis of bird species richness in the BBS bioregion.

For this analysis, I overlaid a 100 km² grid on the BBS bioregion, and discarded all grid cells ('landscape units') that overlapped the boundary of the bioregion. A total of 1904 complete 100 km² landscape units were incorporated into this analysis (Figure 5.1).

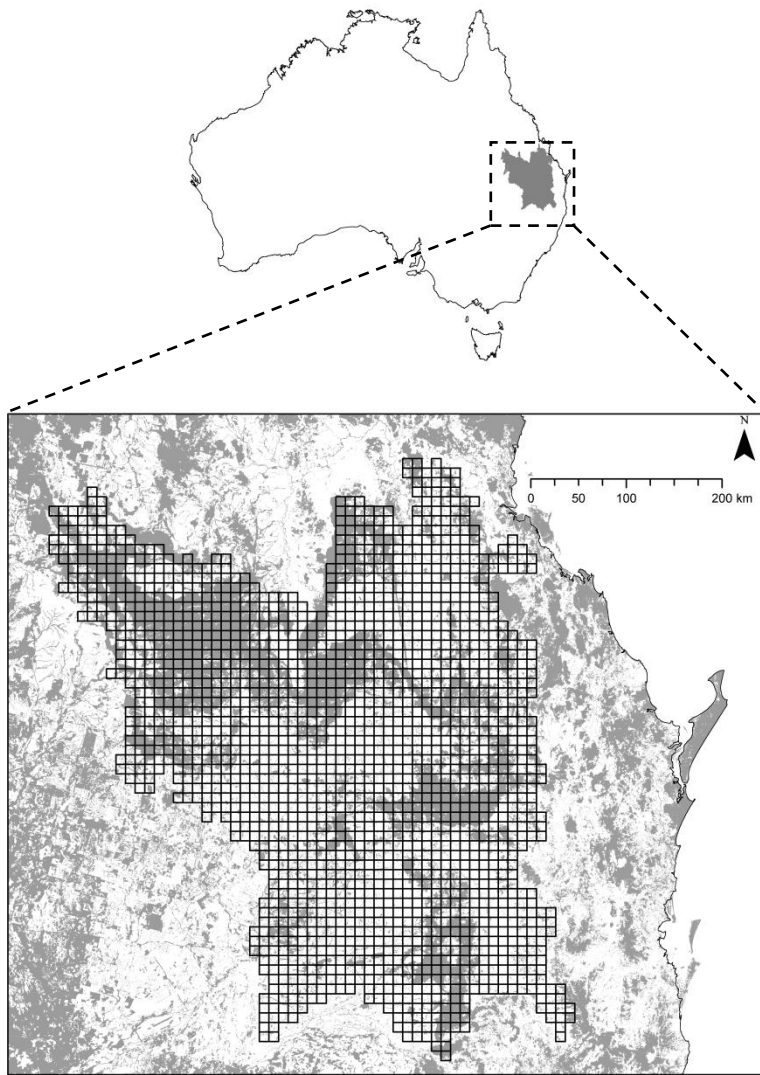


Figure 5.1 Brigalow Belt South study extent, showing the 1904 x 100 km² landscape units

5.3.2 Data extraction

I extracted data on the area of native remnant woodland/forest vegetation in each landscape unit, using the Queensland Herbarium's Regional Ecosystems version 9.0 mapping (Queensland Department of Science, Information Technology and Innovation, 2016). This dataset, mapped at a scale of 1:100,000, identifies the extent of remnant native vegetation as at 2013. The Queensland Regional Ecosystem mapping underpins the native vegetation mapping that was used in preceding chapters of this thesis (the Australian Government's National Vegetation Information System map version 4.1 (Department of the Environment, 2012b)). A comparison of the similarity of the two datasets revealed a strong correlation in terms of mapped remnant woody vegetation extent (Pearson's correlation coefficient = 0.99). Additionally, I used the Queensland Government's proposed regulated vegetation management map (Queensland Department

of Natural Resources and Mines, 2016) to identify the area of each landscape mapped as high-value regrowth vegetation (including areas that are currently mapped, and those that are proposed to be included in the regulated vegetation mapping dataset, should amendments to Queensland's vegetation management framework be enacted).

To account for landscape attributes known to influence both patterns of clearing (Chapter 2), and the form and shape of the species-area relationship (Chapter 3), I extracted information about the topographic and soil properties of each landscape unit. The range in elevation, representing the difference between the highest and lowest point in each landscape, was calculated using a 90 m digital elevation model (Jarvis *et al.*, 2008). A proxy for landscape-scale soil fertility was determined by identifying the proportional area of each landscape unit that was mapped as a high fertility landzone. Landzone refers to the underlying geological characteristics of mapped (pre-clearance) vegetation communities under the Queensland Regional Ecosystem framework, and this measure was used by Maron *et al.* (2012) to characterise landscape productivity in the BBS bioregion. Landzone measures were strongly correlated (Pearson's correlation coefficient = 0.70) with mean soil cation exchange capacity of landscapes—the proxy for soil fertility that was used in the exploration of landscape-scale species-area relationships in Chapter 3.

As noted in Chapters 3 and 4, consideration of landscape attributes such as topographic heterogeneity and soil fertility allowed for a more refined exploration of the effect of 'habitat' area (by way of the proxy native remnant woody vegetation area). Specifically, this approach recognised that species within the broad assemblage of birds under examination may respond differently to vegetation types subsumed within the overall characterisation of habitat extent (native remnant woody vegetation area), and that these differential responses may be predictably related to landscape attributes such as topography or soil fertility which likely act on the type and quality of vegetation occurring in these different landscape types.

5.3.3 *Effect of current vegetation extent on species richness*

I examined how observed landscape-scale species-area relationships can inform conservation actions based on current patterns of remnant woody vegetation extent in the BBS bioregion. In Chapter 3 of this thesis, I highlighted that the shape of the species-area relationship was different depending on the particular attributes of landscapes. Of note

was the prevalence of a threshold in these relationships, although the amount of native vegetation cover corresponding with the threshold varied depending on the attributes of the landscapes under consideration. To highlight this, the modelled species-area relationships from the Chapter 3 analysis when 'all landscapes' were aggregated (n=251), and for two landscape-specific subsets (landscapes categorised by soil fertility and range in elevation), are presented in Figure 5.2.

Ochoa-Quintero *et al.* (2015) explored how an observed threshold in the landscape-scale species-area relationship could be used to prioritise landscapes for conservation actions in northern Brazil. Based on an observed threshold of approximately 43% forest cover, Ochoa-Quintero *et al.* (2015) identified landscapes with vegetation extent that was below this value, as well as landscapes with intermediate (up to 70%) and high (above 70%) forest cover. By mapping landscapes according to these classifications, Ochoa-Quintero *et al.* (2015) were able to compare how many landscapes breached the threshold under a probabilistic model of deforestation, thereby allowing for the identification of landscapes that should be prioritised for protection.

Using a similar approach to Ochoa-Quintero *et al.* (2015), I identified landscapes in the BBS bioregion where native remnant woody vegetation area was considerably above, marginally above and below threshold values observed in Chapter 3. I define 'considerably above' as a landscape in which current vegetation area is at least 10% above the threshold, and 'marginally above' as a landscape with vegetation area within 10% of the threshold value. Initially, I used the observed threshold value from the species-area relationship describing 'all landscapes' (from the Chapter 3 analysis)—approximately 28% remnant vegetation area (Figure 5.2a)—to conduct this exercise. Expanding upon the work of Ochoa-Quintero *et al.* (2015), I also explored how the number of landscapes in each of these categories compared when landscape-specific thresholds were used to guide the classification. This was based on observed species-area relationships for landscapes with higher and lower soil fertility (Figure 5.2b) and landscapes that were less hilly and more hilly (Figure 5.2c). I used the median value of range in elevation from the analysis in Chapter 3 (213 m asl) to distinguish less hilly and more hilly landscapes in the BBS bioregion, and fertile landzone area to distinguish higher and lower fertility landscapes (>50% and <50% of landscape mapped as fertile landzone, respectively).

Additionally, I used the various species-area models to generate predictions of mean species richness based on current woody vegetation cover in landscapes of the BBS bioregion. Importantly, the species-area models from Chapter 3 (Figure 5.2) described estimates of species richness at a standardised level of sampling, and do not represent estimates of total richness. As such, mean predicted richness based on habitat amount in landscapes of the BBS bioregion should be viewed as a comparable index of richness that is not confounded by variable sampling effort.

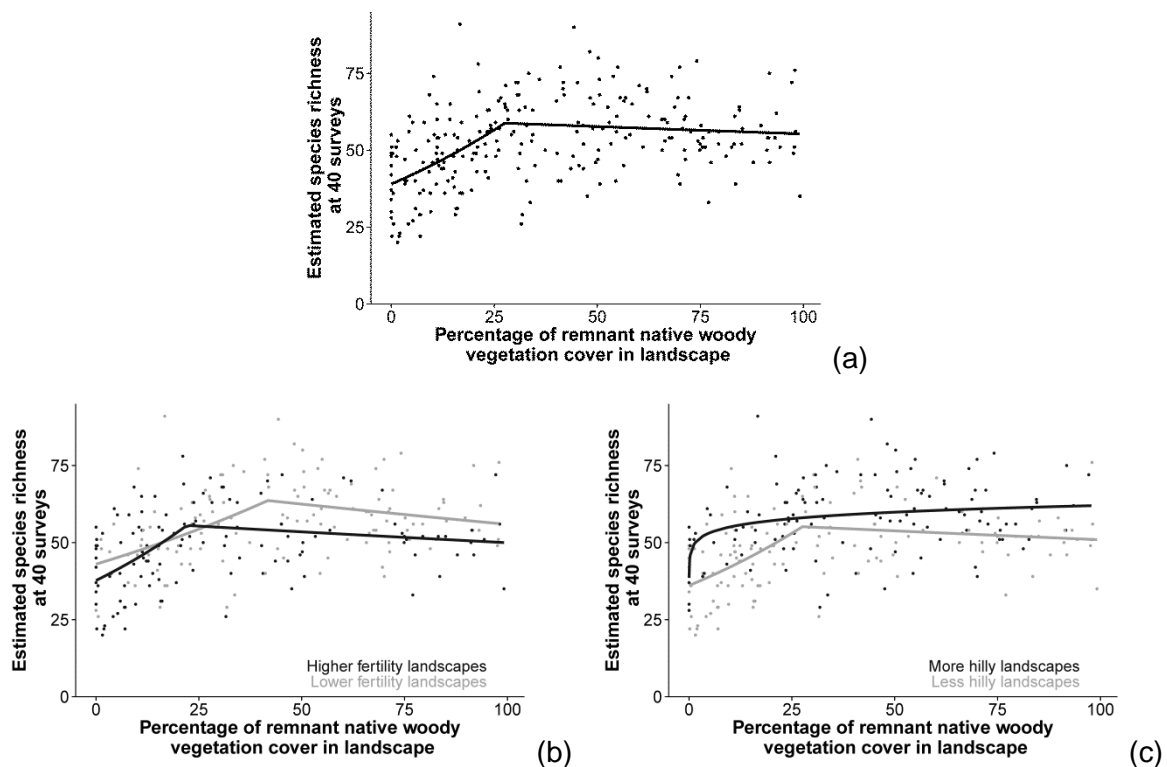


Figure 5.2 The most parsimonious models describing the relationship between estimates of woodland bird species richness and vegetation area in 251 100 km² landscapes in south-east Australia. The top plot (Figure 5.2a) shows the relationship for ‘all landscapes’ (n=251), while the bottom plots display landscape-specific relationships, where landscape units were categorised by soil fertility (left) (Figure 5.2b) and elevation (right) (Figure 5.2c)

5.3.4 Projected effect of future clearing on species richness

I generated two scenarios of future vegetation loss in the BBS bioregion, and used different observed species-area thresholds to explore how bird species richness may be affected. Seabrook *et al.* (2006) noted that clearing in the bioregion has been concentrated in areas with fertile soils, with larger remnants of native vegetation restricted to areas of lower production value. This evidence for non-random patterns of vegetation clearing is in

accordance with the results presented in Chapter 2 of this thesis, whereby in eastern parts of Australia, remnant native vegetation extent at the landscape scale tended to be lower in landscapes that were (1) more fertile, and (2) flatter. Indeed, the amount of remnant woody vegetation remaining in landscapes in the BBS bioregion being analysed here is correlated with both of these landscape attributes—negatively with fertile landzone area (Pearson's correlation coefficient = -0.64), and positively with range in elevation (Pearson's correlation coefficient = 0.38). As non-random vegetation loss is clearly evident in this bioregion, I restricted the future clearing scenarios to landscapes classified as both higher fertility (>50% mapped as fertile landzone) and less hilly (range in elevation <213 m) ($n = 825$ landscapes, hereafter, 'fertile and flat landscapes').

Based on recent trends in clearing, I developed two scenarios of future vegetation loss to apply to fertile and flat landscapes. The first, the 'lower rate of clearing scenario', is represented by the annual clearing rate of 3,500 ha/year, corresponding with the average amount during the period of lower clearing rates in the study area (2009-2011). The second, the 'higher rate of clearing scenario', applies a conservative multiplier of 2.5 to the lower rate of clearing scenario figure of 3,500 ha/year. This is intended to simulate a continuation of more recent land clearing rates, which increased by approximately 2.67 times between the 2009-2011 period and the 2013-2014 period. As such, the higher rate of clearing scenario corresponds with the loss of 8,750 ha/year of remnant woody vegetation.

Using ArcGIS version 10.1 (ESRI, 2012) and Geospatial Modelling Environment (Beyer, 2012), I generated predictions of vegetation loss over a 20 year period. This translates to a total loss of 70,000 ha and 175,000 ha of remnant woody vegetation for the lower and higher rate of clearing scenarios, respectively. I converted the polygon map of remnant woody vegetation extent to a raster with 100 m (1 ha) pixel resolution, and randomly generated points—each of which represented 1 ha of clearing—within the extent of remnant vegetation occurring in the 825 fertile and flat landscapes, up to a total amount of 70,000 and 175,000 ha for the two scenarios. Remnant woody vegetation occurring within protected areas mapped by the Queensland Government was excluded from future clearing. The random point generation was repeated 100 times, and the average amount of vegetation loss in each landscape was subsequently calculated.

I explored how many landscapes breached observed thresholds of vegetation extent under each of the future clearing scenarios, using two different species-area models. I applied the ‘all landscapes’ model, with its 28% threshold (Figure 5.2a), and a threshold more specific to the landscapes in which the clearing scenarios were focussed—namely a threshold of 22% associated with fertile landscapes (Figure 5.2b) (flat landscapes had a threshold of 28%). Adapting the approach used by Ochoa-Quintero *et al.* (2015), and focussing on the higher rate of clearing scenario, I examined how observed thresholds of vegetation extent could inform the identification of landscapes for conservation interventions given projections of future habitat loss. Finally, I compared how mean landscape-scale species richness for the BBS bioregion compared when using the ‘all landscapes’ and soil fertility species-area models to generate predictions of richness based on future habitat amount under the two clearing scenarios.

5.4 Results

5.4.1 Current patterns of vegetation extent

Based on 2013 remnant vegetation mapping, approximately half (52%) of the landscape units in the BBS bioregion have less than 28% native remnant woody vegetation extent (Table 5.1; Table 5.2), the threshold for ‘all landscapes’ combined. However, the proportion of landscapes with remnant vegetation extent below a threshold differed by up to 5% (96 landscapes), depending on the landscape type and the associated threshold(s) used to guide the classification (Table 5.1; Figure 5.3). This equates to a land area of almost 1 million hectares for which there is a discrepancy regarding whether a landscape-scale threshold of vegetation extent has been breached.

Landscape-specific species-area models revealed contrasting results. For example, in higher fertility landscapes, 71% of landscapes have remnant vegetation extent below the recorded threshold value of 22% cover for this landscape type (Table 5.2). Conversely, only 37% of lower fertility landscapes have remnant vegetation extent below the landscape-specific threshold value of 42% cover (Table 5.2). Similarly, relatively more flat landscapes (57%) have remnant vegetation extent below the threshold value for this landscape type compared with hilly landscapes (17%) (Table 5.2).

Despite differences in the relative number of landscapes falling below thresholds of vegetation extent, estimates of mean landscape-scale species richness for the BBS bioregion were similar irrespective of the species-area model(s) used to generate

predictions (Table 5.3). Indeed, predictions of richness based on the ‘all landscapes’ model, and the landscape-specific models associated with soil fertility and elevation, differed by only two species (Table 5.3).

Table 5.1 Summary of landscape classifications, based on observed thresholds from ‘all landscapes’ and landscape-specific species-area models. The percentage of landscapes aligning with each of the three classifications (current remnant vegetation extent below, marginally above, considerably above threshold) was summed for landscapes categorised by soil fertility (lower and higher fertility landscapes), and for landscapes categorised by range in elevation (more and less hilly landscapes). All percentage values have been rounded to the nearest whole number

Model(s) used to guide landscape classification*	% landscapes below threshold	% landscapes marginally above threshold	% landscapes considerably above threshold
‘All landscapes’ species-area model	52 (n=984)	8 (n=144)	41 (n=776)
Soil fertility species-area models (higher and lower fertility landscapes)	54 (n=1027)	9 (n=180)	37 (n=697)
Elevation species-area models (more and less hilly landscapes)	49 (n=931)	8 (n=158)	43 (n=815)

* Based on species-area relationships presented in Chapter 3 of this thesis. Note that the most parsimonious model for more hilly landscapes was an exponential model (see Figure 5.2c), although the level of support and explained variation in this model was similar to that of the threshold model. I have estimated a threshold value of 17% cover for hilly landscapes, corresponding with the threshold value detected for this landscape type in the Chapter 2 analysis

Table 5.2 Classification of landscapes in the BBS bioregion by current remnant woody vegetation extent, according to threshold values observed from different species-area relationships. All percentage values have been rounded to the nearest whole number

Model used to guide landscape classification (number of landscapes)	Threshold value (% cover)	% landscapes below threshold	% landscapes marginally above threshold	% landscapes considerably above threshold
'All landscapes' species-area model (n=1904)	28	52	8	41
Lower fertility landscapes species-area model (n=930)	42	37	8	55
Higher fertility landscapes species-area model (n=974)	22	71	11	19
Less hilly landscapes species-area model (n=1499)	28	57	7	35
More hilly landscapes species-area model (n=405)	17	17	12	71

Table 5.3 Predicted estimates of mean landscape-scale species richness for the BBS bioregion based on current habitat amount. The 'all landscapes' and landscape-specific species-area models (Figure 5.2) were used to generate predictions of richness

Model(s) used to generate species richness prediction	Mean richness	Minimum richness	Maximum richness
'All landscapes' species-area model	51	39	59
Soil fertility species-area models (higher and lower fertility landscapes)	52	38	64
Elevation species-area models (more and less hilly landscapes)	50	36	61

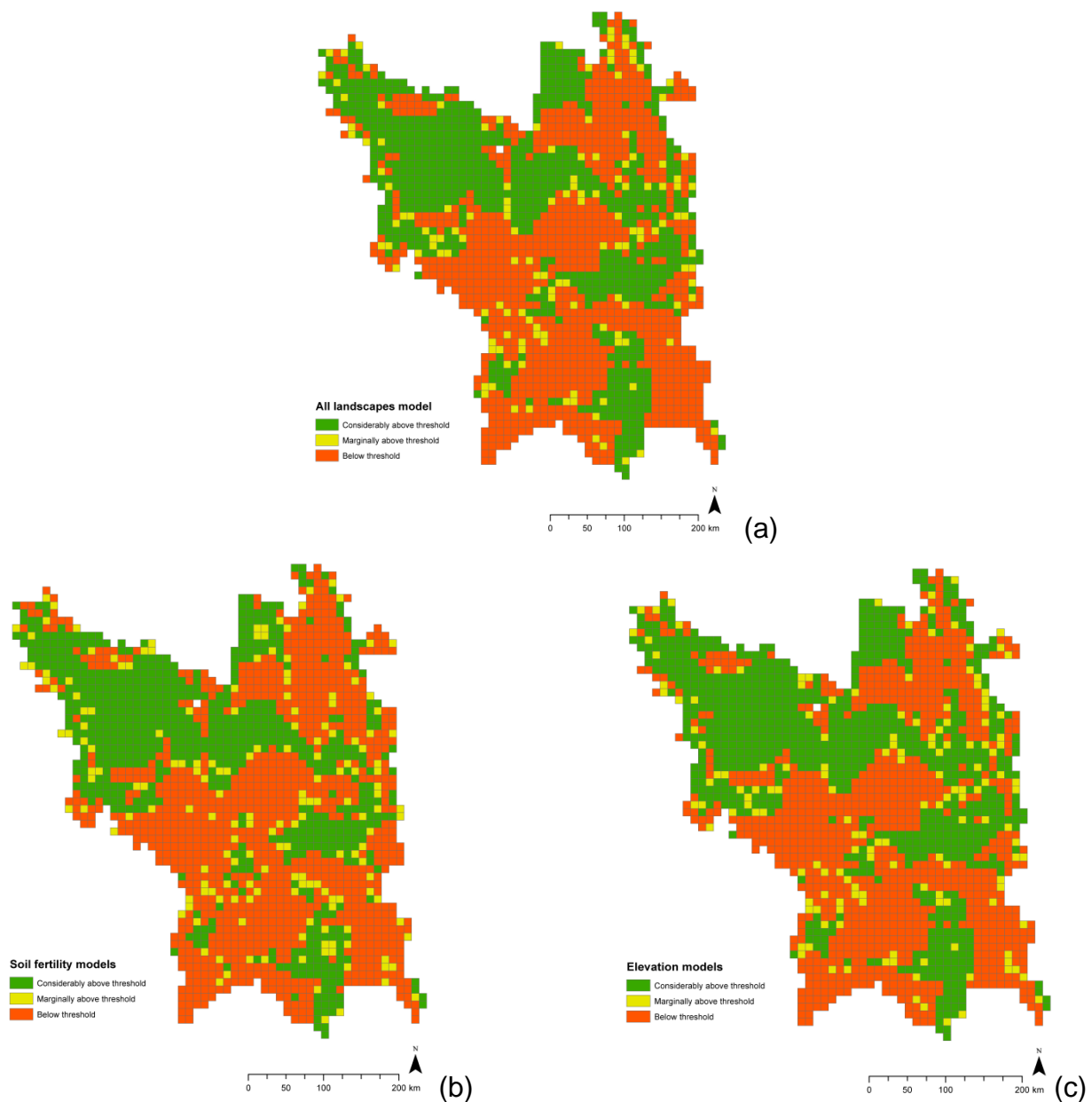


Figure 5.3 Classification of landscapes as ‘considerably above threshold’ (green), ‘marginally above threshold’ (yellow), or ‘below threshold’ (orange) based on current remnant woody vegetation extent, using threshold values from different species-area models: (a) species-area model that does not account for landscape attributes (‘all landscapes’ model); (b) species-area models for higher and lower fertility landscapes; (c) species-area models for more and less hilly landscapes

5.4.2 Future patterns of vegetation extent

Under the higher rate of clearing scenario, native vegetation extent was projected to decline below a threshold of 28% in 27 of the 825 fertile and flat landscapes (Figure 5.4). However, the number and location of landscapes breaching a threshold differed when a

22% cut-off—derived from a species-area model for fertile landscapes—was used to guide the classification. In this instance, 47 fertile and flat landscapes breached the 22% threshold (Figure 5.4). Similarly, the number and location of landscapes breaching thresholds under the lower rate of clearing scenario differed depending on the threshold value used, with seven and 15 landscapes declining below 28% and 22% vegetation extent, respectively (Figure 5.4).

Interestingly though, predictions of mean landscape-scale species richness for the 1904 landscapes of the BBS bioregion were similar for the higher and lower clearing scenarios, despite these scenarios reducing the extent of woody vegetation by 175,000 and 70,000 ha, respectively. Using the ‘all landscapes’ species-area model to generate predictions of richness yielded the same estimated mean richness for both scenarios: 51 species. Indeed, this corresponds with the mean predicted richness of landscapes based on current vegetation extent in the BBS bioregion (Table 5.3). When focussing specifically on the 825 fertile and flat landscapes that were subject to vegetation removal, the higher clearing scenario implied a reduction of mean species richness from 46 (based on current vegetation extent) to 45 species in these landscapes.

Using different species-area models to guide the identification of landscapes for conservation actions yielded different outcomes (Figure 5.5). In addition to the discrepancy in the number and location of ‘Highest priority’ landscapes—that is, those that will breach a threshold of vegetation extent (27 or 47 under the higher rate of clearing scenario, depending on the threshold value used)—the number and spatial distribution of landscapes in other priority categories varied. For example, the number of landscapes that could be the focus of vegetation protection so that a threshold is not breached given continued future clearing (‘Intermediate priority – above threshold’) was 133 when using the 28% threshold derived from the ‘all landscapes’ species-area model. However, 157 landscapes were assigned to this priority category when landscape-specific (soil fertility) species-area models were used. The number of landscapes in which a combination of vegetation protection and active (and/or passive) revegetation could be undertaken to increase landscape-scale vegetation extent above a threshold value (‘Intermediate priority – below threshold’) was 215 and 273, where the ‘all landscapes’ and soil fertility model threshold values were used to guide the classification. Applying thresholds derived from the soil fertility species-area models revealed that 97 fewer landscapes had vegetation extent that was at least 10% above the threshold (‘Lower priority – high cover’) for these

landscape types, as compared with the prioritisation based on the all landscapes model and its 28% threshold.

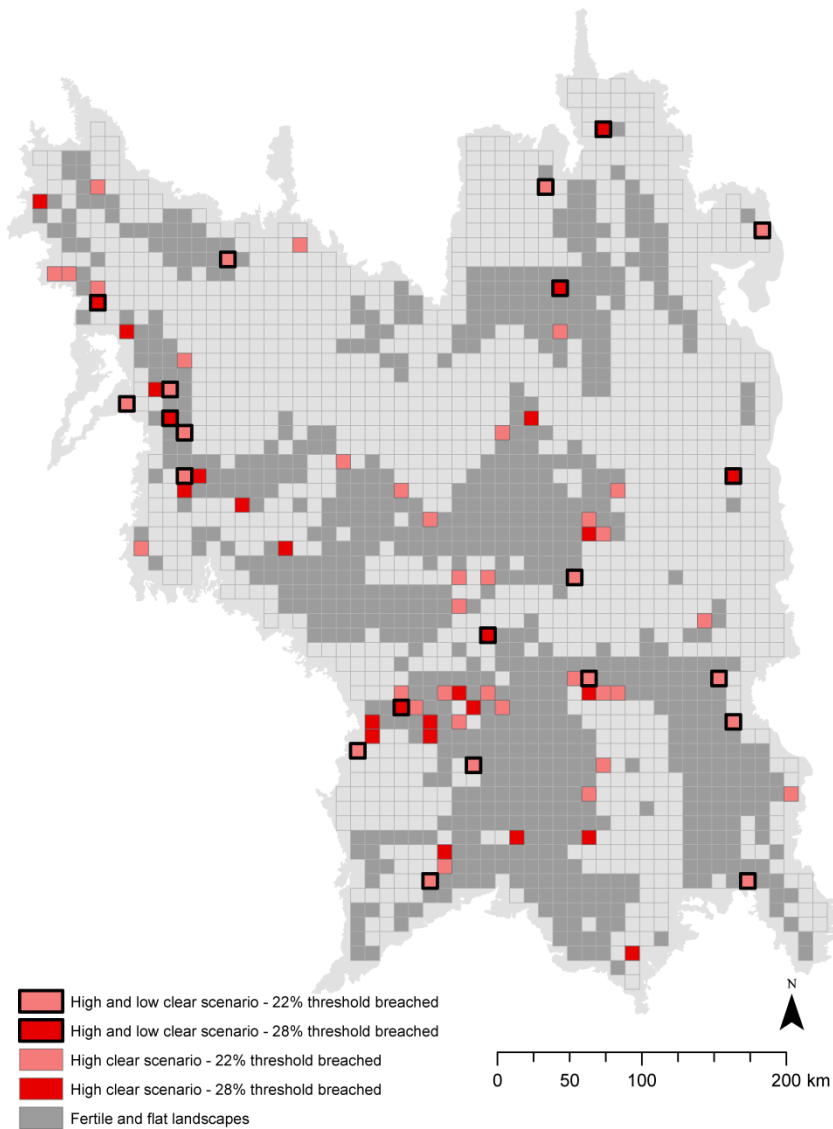


Figure 5.4 Landscapes where a threshold of vegetation extent will be breached under higher and lower scenarios of future clearing in fertile and flat landscapes. Two threshold values were applied – a 28% threshold identified from the ‘all landscapes’ species-area model, and 22% threshold that was identified for fertile landscapes. Landscapes that breached a threshold in the lower clearing scenario also breached the threshold in the higher clearing scenario (identified by bold black outline)

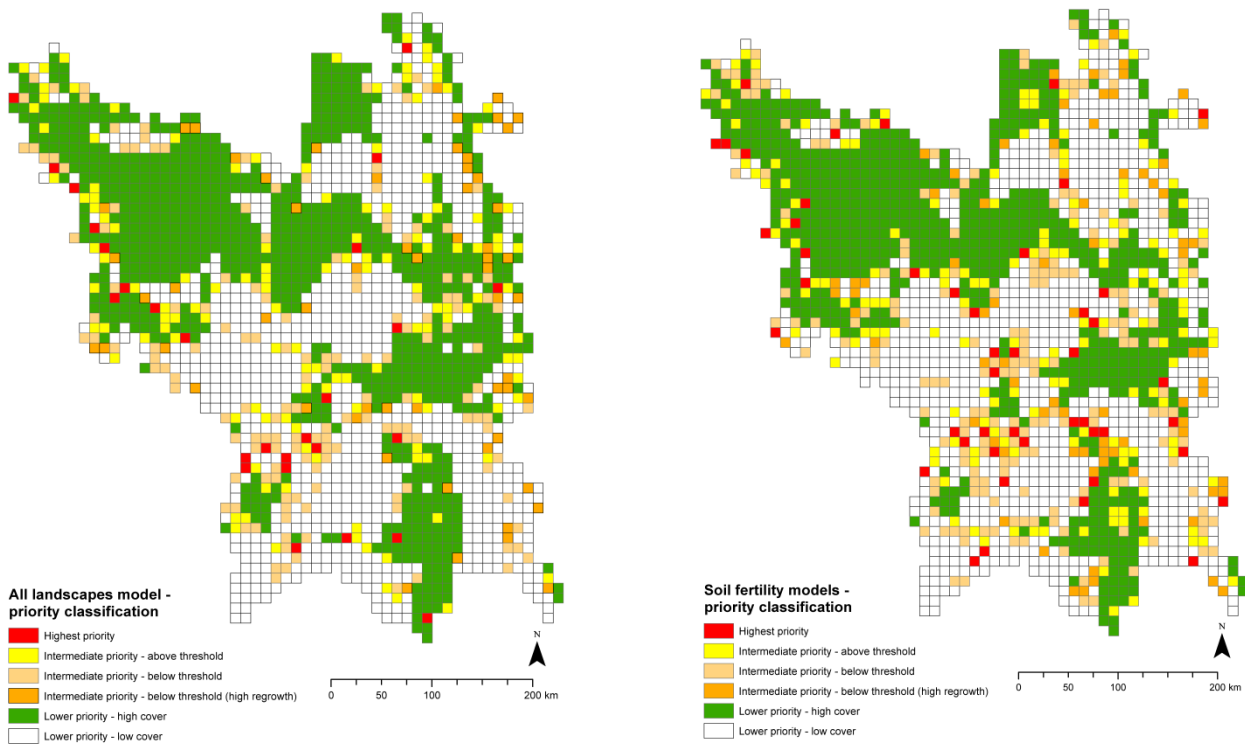


Figure 5.5 Example of identification of landscapes for conservation actions to mitigate impacts of future woodland and forest loss in the BBS bioregion. The classification of landscapes has been guided by thresholds in observed species-area relationships: the ‘all landscapes’ model, with a 28% threshold (left); and landscape-specific species-area models that accounted for soil fertility (higher fertility landscapes threshold 22%; lower fertility landscapes threshold 42%) (right). ‘Highest priority’ landscapes are those that will breach a threshold under the higher rate of clearing scenario. ‘Intermediate priority—above threshold’ are landscapes where vegetation extent will be $\leq 10\%$ above a threshold post-clearing; ‘Intermediate priority—below threshold’ are landscapes where vegetation extent is currently $\leq 10\%$ below a threshold. ‘Lower priority’ landscapes are either high or low cover, where vegetation extent will be $> 10\%$ above a threshold post-clearing, or is currently $> 10\%$ below a threshold

5.5 Discussion

Using landscape-specific species-area models changed the spatial distribution of priority landscapes for maintaining or increasing remnant vegetation cover. Interestingly though, different species-area models generated similar predictions of mean landscape-scale richness based on existing remnant vegetation extent, and indicated that mean richness only exhibited a marginal decline with the projected loss of 175,000 ha of habitat across the BBS bioregion. These results highlight the potential utility of the threshold concept for

guiding landscape-scale conservation, yet also underscore the need for caution when interpreting landscape-scale species-area relationships. Specifically, uncritical application of an observed threshold may lead to ineffective conservation outcomes, such as protecting vegetation in landscapes where species are not at risk of imminent decline. Moreover, predictions of mean landscape-level richness should be interpreted with care, as these may mask important impacts to biodiversity arising from landscape change.

5.5.1 Using thresholds in the species-area relationship to classify and prioritise landscapes

The spatially-explicit, non-random scenarios of habitat loss explored, provide an example of how observed thresholds can be used to guide landscape management in a region facing ongoing change. In particular, I highlight that landscapes shown in Figure 5.5 that will breach an observed threshold ('highest priority'), as well as those marginally above or marginally below ('intermediate priority'), could be the focus for management actions that seek to avert the rapid loss of species associated with a decline in vegetation extent below a threshold. For example, regrowth vegetation could be protected and/or restoration activities prioritised in landscapes with remnant vegetation extent marginally below an observed threshold. Complementing this, the protection of remnant vegetation in these landscapes could be strengthened to minimise further loss. Additionally, active replanting could be undertaken to provide additional habitat in the longer term. Such actions may prevent the rapid loss of species that would occur if vegetation was to be cleared from these below-threshold landscapes, and result in gains in species richness as vegetation extent increases.

However, a key finding of these analyses is that the spatial distribution of landscapes classified as above or below an observed threshold differed based on the species-area model used to guide the classification. This has important implications for the utility of thresholds in the species-area relationship for guiding the management of landscapes. In particular, actions that seek to avoid a threshold being breached, or enhance vegetation extent above a threshold, may fail to achieve an objective of maintaining or enhancing species richness if an erroneous or artefactual threshold is used to guide the identification of priority landscapes.

In light of this, which landscapes should be prioritised for habitat interventions (protection/restoration) to avoid a rapid decline in species richness associated with a

threshold being breached? For example, should a 28% threshold, derived from a species-area model that does not account for landscape attributes ('all landscapes'), be used to prioritise landscapes for vegetation protection? Or are threshold values derived from models that account for landscape attributes more appropriate? Indeed, we know from the BBS bioregion that landscape factors like topographic heterogeneity (Burgess & Maron, 2015) and soil fertility (Maron *et al.*, 2012) act on patterns of bird species richness. Moreover, vegetation clearing (and thus, the amount of habitat in landscapes) in the bioregion is biased by these same landscape attributes. As such, using thresholds identified from landscape-specific species-area models to guide landscape prioritisation would address the key issues raised by Maron *et al.* (2012) regarding thresholds in the species-area relationship; namely: (1) the need to account for the confounding effect of non-random patterns of clearing, whereby habitat amount is correlated with abiotic landscape attributes; and (2) the importance of recognising that the effect of area is different in different landscape types, because of ecological factors like resource availability or habitat heterogeneity which interact with area to act on species richness.

Where the resources available to undertake landscape-level conservation are limited, it is beneficial to identify those landscapes (or parts thereof) in which actions are expected to have the greatest effect (Hobbs & Kristjanson, 2003; Bennett & Mac Nally, 2004). For example, landscapes with intermediate levels of cover may provide the best cost-benefit ratio with respect to conservation action such as vegetation protection and restoration (Tambosi *et al.*, 2014; Rappaport *et al.*, 2015). Because thresholds entail a discrete point at which species loss accelerates with habitat loss, they are a useful basis upon which to define habitat protection and restoration targets. As such, landscapes in which protection and/or revegetation actions will prevent a threshold from being breached, or enhance habitat extent above a threshold, may be ideal candidates for priority management and/or policy interventions (Banks-Leite *et al.*, 2014).

Moreover, implementing management actions in landscapes where they are unlikely to achieve the desired outcomes represents a waste of limited conservation funds (Carwardine *et al.*, 2008). Replanting vegetation is an expensive undertaking (Lindenmayer *et al.*, 2012; Smallbone *et al.*, 2014; Ikin *et al.*, 2016). For example, approximately AU\$2 million was spent on replanting 2000 ha of vegetation in the heavily cleared Holbrook region of southern New South Wales, Australia (Barrett *et al.*, 2008). Furthermore, opportunities for management interventions are particularly constrained

where such actions may conflict with agricultural land use in productive environments (Vesk & Mac Nally, 2006). This is highly pertinent for Australian woodland birds, as productive landscapes are the priority for the implementation of conservation actions (Watson, 2011).

It is vital that conservation actions are underpinned by an accurate understanding of the effect of area on biodiversity. Accounting for those factors which may distort the shape of the species-area relationship—namely abiotic factors which are both correlated with vegetation extent, and interact with habitat amount to affect the occurrence of species—will contribute to a more robust understanding of the effect of area. This entails clear benefits for conservation actions focussed on managing habitat area at the landscape level.

5.5.2 Predicted species richness using different species-area models

Predictions of mean landscape-scale richness, based on existing remnant vegetation extent, were surprisingly consistent among different species-area models. This may be partly explained by the fact that, irrespective of what model(s) were used to generate predictions—be it the ‘all landscapes’ model, or landscape-specific models associated with soil fertility or topography—vegetation extent had little effect on richness at higher levels of cover. That is, in higher cover landscapes, loss of habitat had little effect on landscape-scale richness. Moreover, the range in predicted richness was similar among the different landscape types. While area clearly has contrasting effects in different landscape types at particular levels of cover—namely, at and below threshold values of vegetation extent—this did not translate to differences in predictions of species richness when averaged across over 1900 landscapes at the regional scale.

Even with the removal of up to 175,000 ha of remnant woody vegetation, predictions of mean species richness among the 1904 landscapes of the BBS bioregion remained largely unchanged from predictions based on current vegetation extent. However, in the 825 fertile and flat landscapes in which the simulated removal occurred, an average of one species was lost per landscape. While this appears a small impact arising from the loss of a large amount of habitat, there are several important considerations relating to this finding. First, the species-area models used to generate predictions of species richness in fertile and flat landscapes exhibit a very slight decline in species richness above recorded threshold values. This is somewhat analogous to the finding of De Camargo and Currie

(2015), who noted a peak in a landscape-scale species-area relationship, whereby richness was highest at an intermediate level of habitat cover, and declined towards lower and higher levels of habitat amount. While the thresholds I identified clearly illustrate that habitat area has its strongest effect at low levels of cover, the slight decline in richness with habitat area above the observed thresholds entails that a loss of vegetation in landscapes with current vegetation extent above a threshold actually results in a very slight increase in species richness. The marginal gains in predicted richness with habitat loss in higher cover landscapes may represent a slight offset to the loss of species with habitat removal in landscapes below a threshold of vegetation extent, or in landscapes where a threshold is breached.

Second, it is important to note that among the 825 fertile and flat landscapes that were the focus of the scenario analysis, only a small proportion (approximately 2% on average) of remnant woody vegetation cover was removed from any one landscape. This approach likely spread the impact of the projected landscape-scale loss, and could be refined by using a more sophisticated probabilistic model of loss. For example, Ochoa-Quintero *et al.* (2015) considered various correlates of forest loss in their Amazon study area, including proximity of previous deforestation, distance to roads, rivers and settlements, abiotic attributes associated with topography, soil and climate, and location of protected areas, to predict where future forest loss would be most likely to occur.

Third, similar predictions of mean landscape-scale species richness potentially obscure a key finding of this study. That is, it is important to explore how the shape of the species-area relationship can guide the interpretation of patterns of richness among multiple landscapes. A measure of mean landscape-level richness reveals nothing about how richness varies with area among multiple landscapes, whereas the shape of the relationship, including the occurrence and position of thresholds, illustrates the manner in which richness changes along a gradient of landscape-level habitat cover from entirely cleared to entirely vegetated.

Furthermore, an average value of species richness may mask the fact that certain species are being disproportionately affected and potentially lost, due to their occurrence in landscapes which may be more exposed to the impacts of habitat loss. For example, species that preferentially inhabit productive woodlands may be more severely affected by habitat loss in a non-random clearing scenario (Lindenmayer & Luck, 2005; Lindenmayer

et al., 2010), yet this is not borne out in an average value of species richness among multiple landscapes across an entire region because other species may benefit from a more open mosaic (De Camargo & Currie, 2015). Indeed, the loss of woodlands on fertile soils has been implicated in the decline of species including the hooded robin (*Melanodryas cucullata*) (Priday, 2010) and the regent honeyeater (*Anthochaera phrygia*) (Kvistad *et al.*, 2015), while the importance of these productive habitats for a broader ensemble of declining woodland species in south-east Australia has been widely reported (Watson, 2011; Stevens & Watson, 2013; Bennett *et al.*, 2014). Moreover, non-random habitat loss may indirectly act on woodland birds via the domination of fertile remnants by *Manorina* honeyeaters, which have a strong effect on the composition of bird communities in modified environments (Maron & Kennedy, 2007; Mac Nally *et al.*, 2014a; Thomson *et al.*, 2015). The (average) loss of one species from fertile and flat landscapes is noteworthy, and likely masks the far more severe disruption to the composition of communities in these landscapes.

From the perspective of guiding the management and conservation of landscapes, a complementary approach in which predictions about richness and changes thereto are considered alongside interpretation of the shape of the species-area relationship, should be undertaken. This would allow for the impact of habitat loss to be quantified both regionally (how many species are expected to be lost/gained on average among all landscapes, or subsets of landscapes), and for individual landscapes (in which landscapes are changes to species richness expected to be greatest).

5.5.3 Conclusion

This analysis demonstrates that the utility of the threshold concept for guiding management actions such as the establishment of minimum landscape-level habitat area targets can be enhanced by examining landscape-specific species-area models. More importantly, it highlights the potential pitfalls of uncritically using thresholds, given that different observed threshold values yielded different outcomes relating to potential conservation responses to current and future habitat amount and predictions of richness. As noted, this case study does not represent a definitive examination of patterns of woodland bird species richness in the BBS bioregion; rather, it exemplifies how different landscape-scale species-area relationships can be applied to guide the interpretation and management of broadscale patterns of species richness in a region exposed to substantial, ongoing change. Indeed, other factors, such as extinction debt (see Chapter

4), and the suitability of the matrix (including regrowth vegetation), likely contribute to landscape-scale patterns of richness in this region. Nonetheless, given the undoubted importance of remnant vegetation as a key determinant of species richness at the landscape level, considering landscape-specific relationships between species richness and remnant vegetation area should be undertaken when the species-area relationship is used to guide management actions and predictions of species richness.

CHAPTER 6

THESIS SYNTHESIS AND CONCLUSION



Plate 5 Native woodland retained in hilly, rocky landscape that is unsuited to agricultural production—New England Tablelands, Queensland/New South Wales border

6.1 Thesis overview

Fundamental questions that conservation scientists and managers seek to address in the face of ongoing biodiversity loss include:

- how much habitat must be conserved or restored/rehabilitated to avert or reverse declines in biodiversity?;
- in which landscapes should these interventions be focussed?; and
- what are the implications of future reductions or gains in area of native vegetation?

Detailed knowledge of how the extent of native vegetation (and changes thereto) affects patterns of biodiversity is critical for addressing these pressing conservation questions. The species-area relationship describes how one of the most widely used biodiversity metrics—species richness—varies with vegetation area in modified landscapes. Yet, factors that potentially distort the relationship between species richness and vegetation extent at the landscape level are infrequently accounted for.

In this thesis, I examined the interplay between landscape attributes such as topography and soil properties, the area of native vegetation that is retained in human-modified landscapes, and patterns of species richness. I have shown that attributes of landscapes that both underpin where humans clear and retain vegetation, and potentially act on patterns of species occurrence, should be considered in landscape-level species-area analyses. If such attributes are not accounted for, observed species-area relationships may incorrectly represent the effect of area. Conservation actions based on species-area analyses that are confounded by landscape attributes may fail to arrest or reverse declines in species richness, representing an ineffectual use of limited resources and funds.

The following key findings emerge from this thesis, all of which are highly relevant to ecologists, biogeographers and practitioners/managers with an interest in the effect of area in human-modified landscapes:

- 1. Non-random patterns of vegetation clearing can confound the exploration and interpretation of the effect of area.**
- 2. The effect of area was landscape-specific, and aggregating species-area data from different landscape types in a non-random clearing context may distort observed species-area relationships.**

3. **The effect of area, including its interaction with landscape attributes, was scale-dependent, although scale invariance was noted when data were aggregated across a broad region.**

4. **The uncritical application of observed thresholds as targets for protecting or restoring vegetation among multiple landscape mosaics may lead to ineffective conservation outcomes.**

These key findings were arrived at by exploring four specific research questions, each of which contributed to addressing the overall aim of this thesis:

How does accounting for landscape attributes that bias vegetation clearing, and interact with area to drive the occurrence of species, affect interpretation of the species-area relationship in human-modified landscapes?

A brief overview of the findings of each research question is presented below, with the main conclusions highlighted in Table 6.1.

In **Chapter 2**, I performed a review of studies that related native vegetation area to a response such as species richness, and conducted an empirical analysis of correlates of vegetation retention and clearing at the landscape scale. My literature review highlighted that the confounding effect of non-random vegetation clearing patterns was rarely considered or accounted for in studies of the effect of vegetation area in modified environments. This finding was put sharply into focus by my empirical analysis, which indicated that the area of native vegetation retained in landscapes in transformed regions of Australia and South Africa was consistently correlated with abiotic attributes—namely, soil properties associated with fertility, and range in elevation. This study highlights that accounting for vegetation clearing biases remains a gap in the practice of landscape ecology and biogeography.

Consideration of the biasing effect of non-random clearing is particularly vital where the effect of vegetation area differs in landscapes characterised by particular attributes. This is because, in a non-random clearing context, landscapes with less native vegetation tend to be characterised by particular, predictable attributes such as fertile soils and flat

topography, while landscapes that retain more native vegetation will have different attributes (e.g. hilly and infertile). If the effect of area on species richness differs as a function of the attributes of landscapes, aggregating data from low cover landscapes that are flat and fertile, with data from high cover landscapes that are hilly and infertile, is likely to misrepresent how species richness is affected by vegetation extent at the landscape scale.

Given that landscape-specific area effects may confound species-area analyses, I sought to quantify how species richness was affected by vegetation area in landscapes characterised by specific abiotic or anthropogenic attributes (**Chapter 3**). Specifically, I examined the extent to which the shape of the relationship between Australian woodland bird species richness and vegetation area differed when particular attributes of 100 km² landscapes were controlled for. I showed that the effect of native vegetation extent on species richness, as revealed by the shape of the species-area relationship, differed for landscapes characterised by (for example) higher soil fertility, flatter topography or higher incidence of competitive native bird species. I suggested that mechanisms such as topographic variability and its association with habitat heterogeneity, or the disruptive effect that aggressive *Manorina* honeyeaters have on woodland bird community composition, could explain why the effect of area differed in landscapes with particular attributes.

Importantly, this analysis of landscape-specific area effects was conducted at a single spatial scale (100 km² landscapes). However, conservation actions that are informed by observed ecological relationships may be ineffective if they are applied at the incorrect scale. Thus, it is crucial to determine whether ecological effects, such as that of vegetation area on species richness, exhibit scale-dependence or invariance. In **Chapter 4**, I took the novel approach of deriving estimates of Australian woodland bird species richness in landscapes at three scales of analysis (25 km², 100 km² and 400 km²), and relating these estimates to vegetation extent in each respective landscape size, so as to determine whether the effect of area on species richness was scale invariant. Indeed, the shape of the relationship—characterised by a threshold with a sudden change point at approximately 30% vegetation cover—was similar at all three scales. However, when two regional subsets of the data were analysed, scale-specific species-area relationships were apparent. Attributes of landscapes that interacted with vegetation area—namely, range in elevation, and the occurrence of *Manorina* honeyeaters—exhibited scale-specific effects

on species richness in the two regional subsets explored. This finding indicates that the moderating influence of landscape attributes such as topography on the effect of area exhibits scale-dependence.

In **Chapter 5**, I examined the implications of accounting for non-random clearing (Chapter 2) and landscape-specific area effects (Chapter 3) when using observed thresholds in species-area relationships to guide the management of landscapes. Using a case study of the Brigalow Belt South bioregion (BBS) of southern Queensland, Australia, I compared predictions of species richness, and the spatial distribution of landscapes that could be prioritised for conservation action, where these were generated by species-area models that did and did not account for landscape attributes. Landscapes that were identified as potential candidates for management actions (such as habitat protection or restoration) varied in location depending on what species-area model was used to guide the classification. Given the history of non-random vegetation clearing in the BBS bioregion, and the fact that the scenarios of future vegetation loss that were examined represented ongoing non-random loss (i.e. in flat and fertile landscapes), the importance of using landscape-specific species-area models was demonstrated through this case study.

Table 6.1 Main conclusions emanating from this thesis

Research question	Main conclusions
<p>Chapter 2</p> <p>(Research question 1)</p> <p><i>Do landscape ecological studies typically consider non-random vegetation clearing when examining area effects, and what attributes bias patterns of vegetation clearing at the landscape scale?</i></p>	<ul style="list-style-type: none">• The biasing effect of non-random vegetation clearing is rarely considered in the landscape ecology literature.• The amount of native vegetation remaining in landscapes in human-modified regions of Australia and South Africa is frequently correlated with attributes of landscapes such as soil properties and topography.• A failure to consider the correlation between vegetation area and landscape attributes may distort analyses of the effect of vegetation area.
<p>Chapter 3</p> <p>(Research question 2)</p> <p><i>Does the shape of the relationship between species richness and area differ depending on the attributes of landscapes?</i></p>	<ul style="list-style-type: none">• The response of Australian woodland birds to vegetation area at the landscape scale varies depending on attributes of landscapes.• Landscape-specific area effects potentially reflect interactions between habitat amount, and other mechanisms which act on species, such as habitat heterogeneity or interspecific competition.• Combining data from different landscape types that exhibit landscape-specific area effects may misrepresent how species respond to vegetation extent. This will be exacerbated where vegetation extent is correlated with landscape attributes due to biased patterns of clearing.
<p>Chapter 4</p> <p>(Research question 3)</p> <p><i>Is the effect of vegetation area on species richness scale invariant?</i></p>	<ul style="list-style-type: none">• The effect of vegetation area on Australian woodland birds differs in landscapes of different sizes, although scale invariance was noted across a broad region.• Scale-dependence in factors that moderate patterns of richness in interaction with vegetation

Research question	Main conclusions
	<p>extent, such as topography, highlights the need to consider the potential for landscape-specific species-area relationships at multiple scales.</p> <ul style="list-style-type: none"> • Extrapolating results of studies between different locations and scales should be undertaken with caution. This is especially pertinent to viewing observed thresholds as ‘targets’ to guide conservation actions, beyond the location and scale at which they were observed.
<p>Chapter 5</p> <p>(Research question 4)</p> <p><i>How can the landscape-scale species-area relationship guide broadscale conservation measures?</i></p>	<ul style="list-style-type: none"> • The number and location of landscapes identified for conservation interventions varied considerably depending on whether the species-area model used to guide the prioritisation accounted for landscape attributes like soil fertility or range in elevation. • Where clearing patterns are non-random, landscape-specific species-area models may provide a more accurate basis by which to explore the implications of future landscape change. • The uncritical application of thresholds as targets upon which to base conservation interventions may yield ineffectual outcomes for biodiversity. For example, this may entail wasted management effort in landscapes for which an intervention such as revegetation will not have the desired outcome (i.e. a gain in species richness).

6.1.1 Key findings in the context of existing research

In this thesis, I have shown that the area of native vegetation in landscapes is often correlated with factors that also have the potential to act on patterns of species richness. While non-random patterns of vegetation clearing, and the interaction between landscape attributes and area, are both concepts that are known to ecologists and biogeographers, consideration of the interplay between the two remains a key gap in the exploration of area

effects in modified landscapes. Addressing this gap acknowledges the biogeographic underpinnings of the species-area relationship, while allowing for a more nuanced appreciation of the effect of area that draws upon the key tenets of landscape ecology.

The implications of non-random patterns of vegetation removal and retention are widely recognised with respect to the location of protected areas (Margules & Pressey, 2000; Pressey *et al.*, 2002; Cowling & Pressey, 2003; Watson *et al.*, 2014). Reserved lands frequently occur in areas where native vegetation is uncleared because of a lack of suitability for human land use (Margules & Pressey, 2000; Pressey *et al.*, 2002; Cowling & Pressey, 2003; Watson *et al.*, 2014). This bias potentially undermines the effectiveness of protected area networks, given a lack of representativeness in reserved lands (Joppa & Pfaff, 2009; Barr *et al.*, 2011; Watson *et al.*, 2014; Barnes, 2015; Butchart *et al.*, 2015; Kuempel *et al.*, 2016; Watson *et al.*, 2016).

Yet, the implications of non-random vegetation clearing and retention have received far less attention in analyses of the response of biodiversity to landscape modification (although see Seabloom *et al.* (2002); Rompré *et al.* (2009); Fischer *et al.* (2010a)), as compared with the widespread acknowledgement of vegetation clearing and retention biases in studies on the location and effectiveness of protected area networks. As outlined in Chapter 2, such biases can distort our understanding of the effect of area. For example, the importance of small areas of habitat (i.e. low cover landscapes) may be undervalued, if there is an implicit assumption that 'bigger is better' (Looney *et al.*, 2009). However, a correlation between vegetation area and soil fertility associated with biased clearing, may mean that smaller areas are actually disproportionately important (Lindenmayer & Fischer, 2006; Tulloch *et al.*, 2015). To exemplify, small, productive habitats that support higher reproductive output may act as source habitats for the surrounding landscape, and be of great value for maintaining landscape-level populations, relative to larger, less-productive sink habitats (Pulliam, 1988).

There are various reasons why the confounding effect of biased clearing patterns may not be applicable to analyses of area effects in modified landscapes—the effect of area may not be moderated by landscape attributes that are correlated with the amount of remaining native vegetation, or biased clearing patterns may not be a feature of the study extent. Nonetheless, just as biases in protected area locations can detract from the effectiveness

of reserve networks, so too can biases in landscape-level vegetation extent detract from our understanding of how species are affected by the transformation of landscapes.

Taken together, the findings of Chapters 3 and 4 highlight the need for caution when interpreting the effect of vegetation extent on species richness in modified landscapes. In these chapters, I demonstrate that the effect of area differs by landscape type and by spatial scale. Particular care is required where a threshold presents in this relationship, given that thresholds are an intuitive and simple metric upon which to base landscape management actions. A key criticism of thresholds is a lack of generality in the amount of vegetation corresponding with a sudden change in the ecological response (Huggett, 2005; Lindenmayer & Luck, 2005; Bestelmeyer, 2006; Groffman *et al.*, 2006; Rhodes *et al.*, 2008; Johnson, 2013; van der Hoek *et al.*, 2013; van der Hoek *et al.*, 2015). This precludes widespread application of 'generic' targets upon which to base landscape-level habitat protection or revegetation actions.

My findings lend weight to this cited limitation in the applied utility of thresholds, given that the threshold values I recorded varied considerably depending on the attributes and size of landscapes under examination. As shown in Chapter 5, differences in observed thresholds can have large implications for applied conservation, such as the identification of landscapes in which to prioritise vegetation protection or restoration. Nonetheless, a threshold identified from an analysis in which the confounding effects of biased clearing patterns and landscape-specific area effects are controlled for, does represent a potentially useful measure upon which to base applied conservation interventions. Importantly though, such application must be restricted to the specific assemblage, scale and study extent from which the threshold was observed, and should not be generalised to other assemblages, scales and/or geographic localities (van der Hoek *et al.*, 2015).

Using a case study of Australian birds allowed me to explore how competitive native species act on landscape-level species-area effects. *Manorina* honeyeaters are a unique and exceptional example of hypercompetitive native species, which have benefited greatly from landscape modification (Howes & Maron, 2009; Montague-Drake *et al.*, 2011; Maron *et al.*, 2013; Robertson *et al.*, 2013; Howes *et al.*, 2014; Mac Nally *et al.*, 2014a; Kutt *et al.*, 2015; Thomson *et al.*, 2015). Indeed, Mac Nally *et al.* (2014a, pg. 1080) claimed "The ecological despotism of the genus *Manorina* amounts to one of the most powerful controllers of the constitution of avian assemblages anywhere on earth". I found that

woodland bird species richness responded differently to vegetation extent depending on the occurrence of noisy miners (*Manorina melanocephala*) and/or yellow throated miners (*M. flavigula*) (Chapters 3 and 4). However, surprisingly, species richness tended to be higher in landscapes with a higher incidence of these species, with richness peaking at intermediate levels of vegetation cover (Chapter 3). I propose that *Manorina* occurrence moderates the effect of landscape-level vegetation extent on species richness, and that this is underpinned by mechanisms including resource availability (i.e. soil fertility), habitat configuration (i.e. edge length) and/or habitat degradation/simplification. For example, in landscapes where *Manorina* honeyeaters are prevalent, enhanced productivity and resource availability (per unit area of habitat) may be offset by the adverse impacts that *Manorina* honeyeaters, which favour edge habitats in productive woodlands and forests, have on many species.

While there is a large body of research on the adverse effect of *Manorina* honeyeaters on woodland birds at the site and patch scale, less is known about how these species affect assemblages at the landscape level. My unexpected finding that richness was higher in landscapes where these birds were more prevalent underscores a need to derive a more detailed understanding of how woodland birds are affected by *Manorina* honeyeaters, in interaction with habitat area, at the scale of entire mosaics. This knowledge could guide landscape-level approaches to addressing the adverse impacts of *Manorina* honeyeaters, such as where revegetation could be prioritised to reduce the strong influence these species have on the occurrence of a large suite of woodland birds.

The questions explored in this thesis represent a thorough interrogation of the key themes of the 'spurious thresholds hypothesis', proposed by Maron *et al.* (2012). I have shown empirically that patterns of vegetation clearing are frequently biased by abiotic attributes, and that the shape of the relationship between species richness and vegetation area varies in landscapes characterised by these same attributes. As such, it is conceivable that aggregating data from different landscape types in a non-random clearing context could indeed present as an artefactual threshold. Since the hypothesis was introduced by Maron *et al.* in 2012, a number of landscape-level investigations have reported thresholds in the relationship between species richness and vegetation area. Notably, Lima and Mariano-Neto (2014) highlighted a lack of correlation between soil fertility and forest area, thereby excluding biased clearing as a confounding factor in their identification of a threshold in the relationship between forest tree species richness and landscape-scale

forest cover in the Atlantic Forest of Brazil. Yet, the potential for the confounding effect of non-random patterns of vegetation clearing to bias these observed relationships remains largely unacknowledged (Estavillo *et al.*, 2013; Morante-Filho *et al.*, 2015; Ochoa-Quintero *et al.*, 2015; Richmond *et al.*, 2015; Muylaert *et al.*, 2016). Given the conjecture about the threshold concept for informing management, my research emphatically supports Maron *et al.*'s (2012) message that biased clearing patterns should be a central consideration in the examination of area effects in modified landscapes.

6.2 Implications of this research

6.2.1 Key implications for analyses of the effect of area

The process of, and impacts arising from, habitat loss occur at the scale of entire landscape mosaics (Radford & Bennett, 2007; MacRaild *et al.*, 2010). Increasingly, efforts to address biodiversity declines in modified environments are being undertaken at the landscape level (Radford *et al.*, 2005; Fischer & Lindenmayer, 2006; Tschardtke *et al.*, 2012; Bennett, 2016). Thus, understanding the response of biodiversity to habitat loss among entire mosaics is of fundamental importance. Supported by the results presented in this thesis, I advocate that researchers engaged in studies of the effect of habitat area at the landscape level consider and account for potential confounding effects of non-random clearing. Additionally, I encourage ecologists and biogeographers to consider the complexity—namely the key (broad) ecological mechanisms/processes that underpin patterns of species occurrence—subsumed within measures of vegetation area among landscapes that differ broadly in their attributes. To guide future studies of area effects in modified landscapes, I provide a simple flowchart checklist to indicate when biased clearing patterns and landscape-specific relationships should be considered (Figure 6.1).

While the focus of this research has been on the response of Australian woodland bird species richness to landscape-scale habitat area, I note that the key findings of this thesis are applicable to a range of other ecological responses and geographic locations. Biased clearing patterns and landscape-specific area effects are likely to be just as relevant to investigations where vegetation area is related to the occurrence of individual species (including threatened species), reproductive success, elements of behaviour/activity, or individual health/physiology. Indeed, studies that I reviewed in Chapter 2 that did consider the confounding influence of non-random clearing included examinations of the effect of area on the occurrence of individual woodland bird species (Polyakov *et al.*, 2013), bat

activity patterns (Basham *et al.*, 2011), beetle community structure (Looney *et al.*, 2009), and koala (*Phascolarctos cinereus*) presence (Januchowski *et al.*, 2008).

For example, Looney *et al.* (2009) highlighted that grassland beetle community composition and abundance was largely driven by soil fertility in habitat remnants. They concluded that an expected positive effect of vegetation area (patch size) was moderated by soil fertility, because smaller remnants were on fertile soils (Looney *et al.*, 2009). This underscores another important consideration: if non-random clearing is evident at the scale of individual patches—that is, a correlation exists between patch size and (for example) soil fertility—then the key findings and implications outlined herein would translate to analyses of the effect of patch area. In summary, where the ecological mechanisms underpinning a particular response (i.e. breeding success, behaviour, occurrence) vary spatially as a function of landscape attributes, it is likely that the effect of habitat area will be moderated by these same landscape attributes.

6.2.2 *Key implications for applied landscape management*

Conservation interventions that focus on native vegetation area (or changes thereto) should be underpinned by an understanding of the effect of area that is not confounded by clearing biases and landscape-specific area effects. As emphasised in this thesis, actions that are focussed on averting declines in, maintaining or enhancing species richness at the landscape level can be informed by observed species-area relationships. These actions include the establishment of clearing limits in landscapes to avoid an observed threshold being breached, the strategic protection of vegetation in landscapes with vegetation cover that is near an observed threshold, or revegetation actions that seek to enhance landscape-level vegetation cover. A robust understanding of the effect of area, where confounding factors are accounted for, will allow for two key questions relating to such actions to be addressed:

1. How much vegetation needs to be protected/revegetated in a landscape to achieve a particular biodiversity objective (reverse decline of/enhance species richness)?; and
2. Given current patterns of landscape-level vegetation extent (or projected future changes to vegetation extent), in which landscapes should particular actions be focussed?

It is vital that we can accurately address these two questions. Given the constraints on conservation funding and resources (Carwardine *et al.*, 2008), and to improve transparency between conservation objectives and the ongoing demand for land clearing associated with human development needs, we need to ensure that any interventions are implemented in a targeted and strategic way, so as to maximise the likelihood that they achieve an objective such as enhancing landscape-level richness. To exemplify, undertaking expensive revegetation activities in higher-cover landscapes where species richness varies little with changes to vegetation cover is unlikely to have an effect on landscape-level richness (Cunningham *et al.*, 2014a). Conversely, establishing limits to further clearing in low cover landscapes may yield a large benefit, by preventing rapid declines in species richness associated with small losses of habitat (Radford *et al.*, 2005; Ochoa-Quintero *et al.*, 2015). Critically, a robust appreciation of the effect of area will provide more certainty around **how much** vegetation needs to be managed, and **where** this should occur among multiple landscapes.

A detailed knowledge of the response of a specific assemblage of conservation concern to landscape-level vegetation extent can also inform other management actions. For example, such knowledge could be used to guide conservation measures incorporated into national planning instruments, such as the Brazil Forest Code which establishes limits to clearing on private land (Soares-Filho *et al.*, 2014), or to inform regional policy decisions relating to vegetation management. This latter point is particularly pertinent in Australia currently, given active debates about changes to vegetation management laws in the states of New South Wales (relaxing) and Queensland (strengthening). A detailed understanding of how an assemblage responds to changes in native vegetation extent could also inform the assessment of impacts arising from proposed developments. Where an assemblage is of conservation concern, the significance of habitat loss needs to be quantified as part of the environmental impact assessment process (Wintle *et al.*, 2012). Associated with this, determining the area of habitat that needs to be offset as part of the management of impacts stemming from development (Maron *et al.*, 2015b) would benefit from a detailed understanding of the effect of area on the assemblage exposed to the impact.

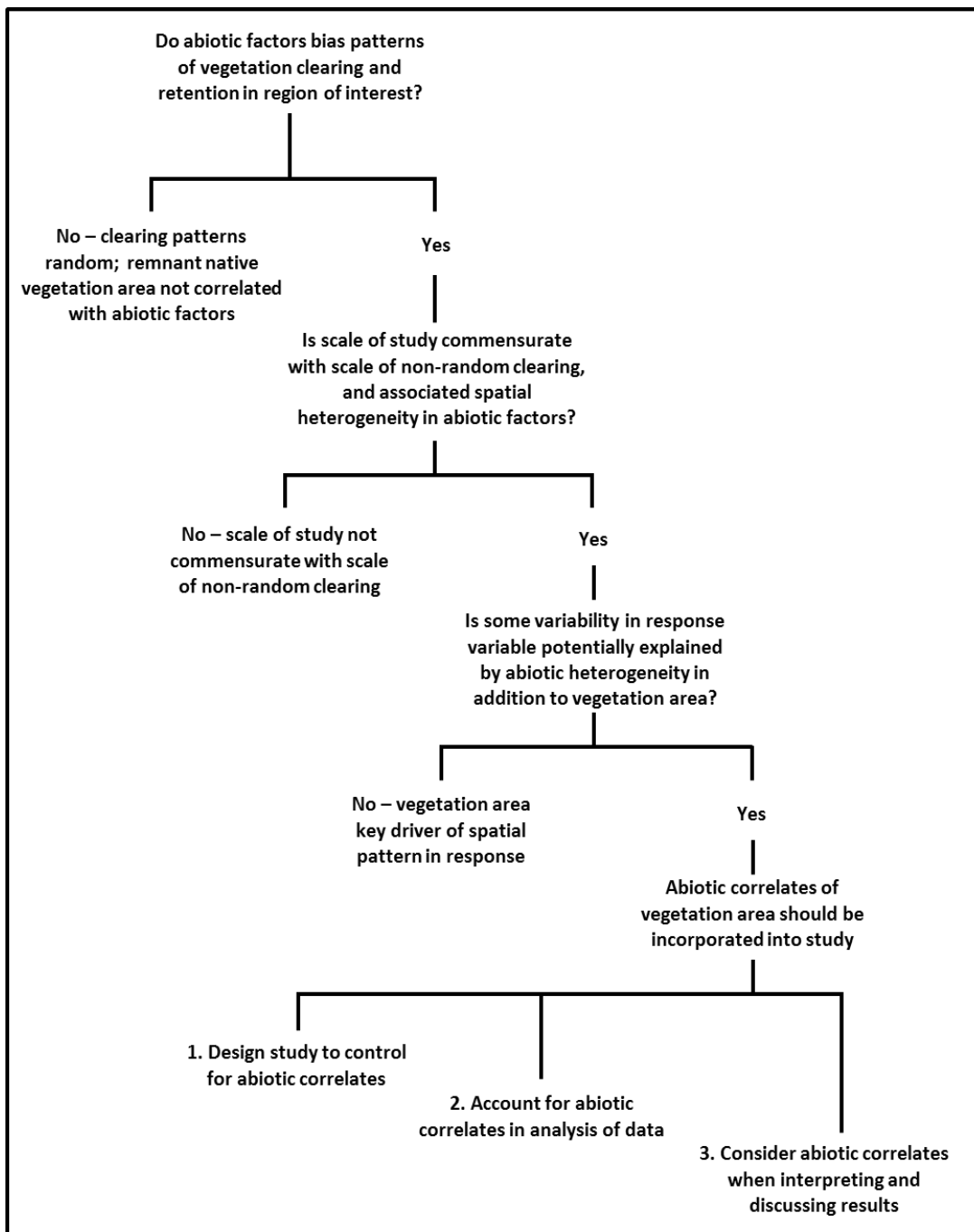


Figure 6.1 Framework to guide studies of area effects in modified landscapes. This decision tree focusses on landscape attributes—broad characteristics of landscapes such as the fertility of the soil, or range in elevation—and how these attributes may correlate with vegetation extent (non-random clearing) and moderate the effect of area (landscape-specific area effects)

6.3 Limitations, caveats and future research directions

There are several important limitations and caveats associated with the findings of this research. First, collecting species occurrence data to address landscape-level questions for numerous landscapes across a broad extent is time consuming, expensive and labour-

intensive. As such, I drew upon species occurrence records contained within BirdLife Australia's New Atlas of Australian Birds to examine how vegetation extent affected patterns of species richness among over 200 landscape units. A clear advantage of collecting data in the field is that it allows for biases associated with sampling, such as the number, timing and spatial distribution of surveys to be controlled for. I sought to minimise sampling bias in the estimates of species richness I used in this thesis, by enacting a number of hierarchical rules. In summary, this approach sought to ensure that estimates were not confounded by variable sampling protocols, survey effort (number of surveys in a landscape), the location of surveys in a landscape, or the timing of surveys in a landscape. This latter point is noteworthy in the context of south-east Australia—it ensured that seasonal (native) migrants were represented in the data, and allowed for temporal variation in climatic conditions (i.e. drought/very wet periods) across the duration of the Atlas project from which data were extracted, to be captured.

Second, this research explored broad ecological patterns over a large extent. The data used to examine how species richness responds to native vegetation area, as well as attributes of landscapes that potentially influence this relationship, were selected such that the resolution of the datasets was appropriate to address the questions being posed. While some datasets were relatively coarse (i.e. climate and soil data at a resolution of approximately 1 km), an average value of these datasets was derived for landscape units of 100 km² to explore how the effect of area is moderated by broad attributes of landscapes. Moreover, the vegetation data used in this research—namely the Australian Government National Vegetation Information System mapping—was at a finer scale of 100 m.

I also highlight four general considerations associated with investigations of species-area patterns that are pertinent to this research. **(1)** While species richness is a ubiquitous measure of biodiversity, it is not without inherent limitations. As has been highlighted by numerous authors, measures of species richness (and analyses of changes thereto) can mask how the composition of assemblages compare, or vary in response to environmental change (i.e. vegetation clearing) (Radford *et al.*, 2005; Bennett *et al.*, 2006; Fleishman *et al.*, 2006; Villalobos *et al.*, 2013; Matthews *et al.*, 2014b; Lindenmayer *et al.*, 2015; Yong *et al.*, 2016). This is potentially problematic because a small (or no) change in species richness may obscure a large conservation impact, such as compositional changes that mask the loss of highly-sensitive species (Radford *et al.*, 2005), or species that have

disproportionately important functional roles in an assemblage (Banks-Leite *et al.*, 2012; De Coster *et al.*, 2015). Furthermore, a measure of species richness is not indicative of the viability of populations of species (Radford *et al.*, 2005; Fleishman *et al.*, 2006; Fattorini & Borges, 2012). To exemplify, a single individual which is representative of a species on a trajectory towards (local) extinction contributes equally to an aggregate measure of richness as do records of species which have numerous individuals and secure populations (Radford *et al.*, 2005; Kitzes & Harte, 2014).

As discussed in this thesis, attributes of landscapes such as the occurrence of highly competitive *Manorina* honeyeaters may cause undesirable changes to landscape-level woodland bird communities (Chapter 3). However, this may not dramatically alter species richness (and if unaccounted for, potentially distort observed species-area relationships) because of compositional changes that are associated with the occurrence of noisy and/or yellow-throated miners (Howes *et al.*, 2014; Kutt *et al.*, 2015). Additionally, the loss of vegetation across multiple landscapes may only result in the (average) loss of a small number of species (Chapter 5). The significance of this habitat loss can be difficult to assess without knowing the identity of the lost species (Banks-Leite *et al.*, 2012). An enhanced understanding of the effect of area on species richness, as explored in this thesis, will be particularly beneficial for the analysis and management of landscapes where it is used as a complement to other ecological information (i.e. the composition, viability and functional role of species in an assemblage).

(2) In this thesis, I have focussed primarily on spatial patterns. However, a key component of the analysis of landscapes, and the fields of landscape ecology and conservation biogeography, is the influence of temporal factors (Whittaker *et al.*, 2005; Bennett *et al.*, 2006; Lindenmayer *et al.*, 2008; Szabo *et al.*, 2011; Wu, 2013; Kitzes & Harte, 2015). I touch on extinction debt in Chapter 4, when inferring potential mechanisms explaining regional differences in the observed effect of vegetation area on species richness. An important follow up to the analyses outlined in this thesis would be to explore how landscape attributes moderate species-area relationships, where the potential effects of extinction debt (i.e. time lags in the loss of species post-vegetation clearing) are explicitly accounted for.

(3) Native vegetation extent, such as woodland or forest cover, is widely used as a broad proxy for habitat in studies of area effects in modified landscapes (Radford *et al.*, 2005;

Haslem & Bennett, 2008; Desrochers *et al.*, 2011; Smith *et al.*, 2011; Maron *et al.*, 2012; Cunningham *et al.*, 2014a). I have taken such an approach in this thesis, whereby the focal assemblage was related to the area of native woody vegetation (woodland/forest). The broad bird assemblage considered was restricted to species that are associated with woodland and forest habitat, and excluded species that can occur and persist in cleared environments lacking woody vegetation. While variation in woodland and forest types occurs across the extent that I examined, in broad terms, the habitat type is typified by woodlands and forests dominated by trees of the genus *Eucalyptus*. Nonetheless, other woodland and forest types, which also provide habitat resources for numerous members of the focal bird assemblage, do occur throughout the study region, albeit, as a much smaller fraction of the overall extent of remnant native vegetation. Aggregating these different woodland/forest types into a single 'habitat' class meant that I was unable to explicitly account for potential differential effects of specific vegetation types on the focal assemblage. Importantly though, the landscape attributes I considered, such as topographic variation or soil fertility, may have indirectly accounted for heterogeneity in woodland types, and the contribution they made to patterns of species richness.

I used a binary habitat/non-habitat conceptualisation of landscapes (Forman, 1995; Lindenmayer *et al.*, 2008; Fahrig, 2013) to explore the effect of native vegetation cover on bird species richness. I note however that the habitat/non-habitat approach has attendant caveats. First, this approach tends to de-emphasise the role of the matrix (the 'non-habitat') in shaping ecological responses in fragmented landscapes (Ricketts, 2001; Ewers & Didham, 2006; Koh & Ghazoul, 2010; Mendenhall *et al.*, 2014). To address this, I considered whether matrix land use intensity moderated the effect of native vegetation area on species richness in Chapter 3. My results indicated that the shape of the relationship between species richness and native vegetation area differed for high- versus low-intensity matrix land use landscapes, although in a multivariate mixed model, the interaction between vegetation area and matrix land use intensity was not important. Nonetheless, I hypothesise that matrix land use intensity does potentially moderate area effects in landscapes, and this effect may be captured by other attributes of landscapes. For example, fertile and flat landscapes may facilitate more intensive land use (i.e. mechanised irrigated monocultures as compared with livestock grazing of native pastures), while land use in hilly, infertile is less intensive. If dispersal across the matrix is a function of land use intensity (Maron & Fitzsimons, 2007; Attwood *et al.*, 2009), this may serve to moderate the effect of vegetation area. The interplay between land use intensity, broad

attributes of landscapes like soil fertility, and the effect of native vegetation area on biodiversity, warrants further examination. Indeed, this may be conceptualised as ‘non-random land use’ and its confounding influence on observed area effects—an extension of the exploration of the implications of non-random clearing.

Second, it has been highlighted in the landscape ecology literature that habitat is a species-specific concept (Hobbs, 2005; Fischer & Lindenmayer, 2006; Lindenmayer & Fischer, 2007; Radford & Bennett, 2007; Price *et al.*, 2009; Ockinger *et al.*, 2010; Betts *et al.*, 2014). A criticism of the habitat/non-habitat approach is that individual species will have different responses to spatial patterns (amount and configuration) of a broad characterisation of habitat such as ‘woodland’ in modified landscapes (Fischer & Lindenmayer, 2007; Fahrig *et al.*, 2011; Betts *et al.*, 2014; Matthews *et al.*, 2014b; Almeida-Gomes *et al.*, 2015). I propose that studies exploring area effects using a habitat/non-habitat conceptualisation may benefit from consideration of landscape attributes which potentially moderate the response of assemblages to landscape patterns. Such an approach acknowledges that the effect of a broad conceptualisation of habitat area (i.e. woodland cover) potentially differs depending on attributes of a landscape. That is, rather than all woodland being considered of ‘equal’ habitat value for the focal assemblage, it recognises that species in an assemblage may perceive and respond to fertile, productive woodlands differently to infertile woodlands, or that the effect of woodland area in flat, homogenous landscapes may be different to woodland occurring in a hilly, heterogeneous landscape, or that species richness may respond differently to woodland area in landscapes in which *Manorina* honeyeaters are prevalent.

(4) In this thesis, I focussed on how the effect of area is potentially moderated by broad attributes of landscapes. These attributes were selected given that they have been shown to affect the occurrence of Australian woodland birds, and included soil properties (Thomson *et al.*, 2007; Watson, 2011; Stevens & Watson, 2013; Razeng & Watson, 2015), topographic heterogeneity (Radford *et al.*, 2005; Burgess & Maron, 2015), and the occurrence of *Manorina* honeyeaters (Kutt *et al.*, 2015; Thomson *et al.*, 2015).

However, there is substantial evidence that spatial patterns in Australian woodland birds are underpinned by a raft of factors at multiple scales. For example, site attributes such as the occurrence of woody debris (Antos *et al.*, 2008; Ikin *et al.*, 2015), leaf litter (Montague-Drake *et al.*, 2009; Ikin *et al.*, 2014), and the occurrence of hemiparasitic mistletoe plants

(Bowen *et al.*, 2009a; Watson & Herring, 2012) variously influence the occurrence of birds in modified landscapes. Moreover, geomorphological features such as creek lines, and associated riparian vegetation have been shown to be a disproportionately important driver of bird occurrence (Bennett *et al.*, 2014; Haslem *et al.*, 2015; Nimmo *et al.*, 2015). Indeed, this may in part relate to an association between creeks, riparian/floodplain vegetation and enhanced soil fertility and vegetation productivity (Bennett *et al.*, 2014). Fire is an important driver of the occurrence of birds in Australian woodlands and forests, given its influence on the age and structure of vegetation (Barton *et al.*, 2014; Burgess & Maron, 2015; Haslem *et al.*, 2016). Scattered paddock trees (Fischer *et al.*, 2010b; Hanspach *et al.*, 2011), and regrowth vegetation (Bowen *et al.*, 2009b; Lindenmayer *et al.*, 2012; Smallbone *et al.*, 2014) have also been shown to affect the spatial composition of bird communities, due to the habitat resources they provide as a complement to remnant native vegetation.

It would be interesting to explore how these various factors potentially moderate area effects in modified landscapes where patterns of vegetation retention are non-random. Indeed, this may provide a more detailed level of understanding about why the effect of area differs in landscapes broadly characterised by, for example, fertile soils or hilly topography. For example, increased resource availability in remnant vegetation occurring in fertile landscapes may be underpinned by mistletoe density, or the presence of productive riparian vegetation; hilly landscapes may be more exposed to fire impacts, which may serve to increase the structural heterogeneity of vegetation remnants; or the effect of remnant vegetation may be moderated by the occurrence of scattered trees or regrowth vegetation, in heavily cleared production environments. There are numerous opportunities and directions by which to explore not only how Australian birds relate to native remnant vegetation extent, as examined in this thesis, but why the effect differs in different landscape types.

6.4 Concluding remarks

As quoted in the Introduction of this thesis, Watson (2011) stated that the value of remnant woodland patches for Australian birds differs based on their position within a landscape, because of the different abiotic properties that characterise the remnants. Just as Watson (2011) noted that “not all woodlands are the same”, I use the results of this thesis to highlight that not all landscapes are the same. Both the amount of habitat in a landscape, and its effect on species richness, can be moderated by the attributes of the landscape.

Recognising this variability among multiple landscapes should be a key focus of future studies of the effect of area in human-modified environments.

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APPENDICES

Appendix A

Chapter 2

Appendix A: Table A1 Bioregions aligning with each of the broad geographic categories explored in the empirical analysis. Bioregions were based on the Interim Biogeographic Regionalisation for Australia (Department of the Environment, 2012a) and the Bioregions of South Africa, Lesotho and Swaziland (Mucina and Rutherford, 2006)

	Broad geographic category	Bioregions
Australia	North east	Brigalow Belt North, Brigalow Belt South*, Central Mackay Coast, South Eastern Queensland
	Central east	Brigalow Belt South*, Darling Riverine Plains, Nandewar, New England Tablelands, New South Wales North Coast, Sydney Basin
	South east	Eyre Yorke Block, Murray Darling Depression, Naracoorte Coastal Plain, New South Wales South Western Slopes, Riverina, South East Coastal Plain, South Eastern Highlands, Southern Volcanic Plain, Victorian Midlands
	South west	Avon Wheatbelt, Esperance Plains, Geraldton Sandplains, Jarrah Forest, Mallee, Swan Coastal Plain
South Africa	North east	Central Bushveld, Indian Ocean Coastal Belt, Lowveld, Sub-Escarpment Savanna
	Central east	Dry Highveld Grassland, Mesic Highveld Grassland, Sub-Escarpment Grassland
	South west	East Coast Renosterveld, Southwest Fynbos, West Coast Renosterveld, West Strandveld

* note the Brigalow Belt South bioregion of eastern Australia was split across two broad geographic categories (North east and Central east) due to its size and north-south orientation

Appendix A1

The Enhanced Vegetation Index (EVI) was used to provide a proxy for the productivity of remaining native vegetation in a landscape for this analysis. Australian and South African continental mosaic datasets (Paget & King, 2008) of the Moderate Resolution Imaging Spectroradiometer (MODIS) 16-day L3 Global 250 m EVI data (https://lpdaac.usgs.gov/dataset_discovery/modis/modis_products_table/mod13q1) were obtained to examine this productivity relationship. Six mosaic datasets corresponding with the first 16-day mosaic available for each alternate month were acquired for each year for the period 2004-2013. Each EVI mosaic dataset was processed using its accompanying quality assurance (QA) dataset, whereby only pixels ascribed a QA rating of 'good data – use with confidence' were retained. Upon processing, the 60 individual mosaics were overlaid to determine an average EVI value for each pixel. The EVI data was resampled in ArcMap to a pixel size of 100 m and 30 m for Australia and South Africa respectively, to allow for congruence between the pixel sizes of the vegetation and EVI data for the two countries. This allowed for the derivation of an approximate EVI value for each native vegetation pixel, which could then be used to calculate the average EVI of all native vegetation in a landscape.

Appendix A: Table A2 Summary of literature review identifying whether studies that used vegetation area to explore an ecological response considered spatial abiotic heterogeneity, and whether such heterogeneity was linked to non-random patterns of vegetation clearing and retention. Full reference list for reviewed literature is provided below table.

Author(s) (year)	Abiotic heterogeneity considered – linked to non-random patterns of vegetation clearing and confounding effect on area			Abiotic heterogeneity considered – not linked to non-random patterns of vegetation clearing			Abiotic heterogeneity not considered in analysis
	Controlled for in study design	Controlled or accounted for in data analysis	Considered in interpretation and discussion of results	Abiotic homogeneity in study system	Efforts to control heterogeneity in study design	Abiotic factor(s) as explanatory variables in addition to area	
Gonclaves <i>et al.</i> (2014)							x
Hadley <i>et al.</i> (2014)	x						
Ikin <i>et al.</i> (2014)							x
Inclan <i>et al.</i> (2014)							x
Johnstone <i>et al.</i> (2014)						x	
Lima and Mariano-Neto (2014)			x				
Martins <i>et al.</i> (2014)							x
Robinson <i>et al.</i> (2014)							x
Wulf and Kolk (2014)						x	
Zulka <i>et al.</i> (2014)						x	
Broughton <i>et al.</i> (2013)							x
Davis <i>et al.</i> (2013)							x
García-Marmolejo <i>et al.</i> (2013)						x	
Jauker <i>et al.</i> (2013)				x			
Marchi <i>et al.</i> (2013)							x
Oliver <i>et al.</i> (2013)						x	
Polyakov <i>et al.</i> (2013)			x				
Reino <i>et al.</i> (2013)			x				

Author(s) (year)	Abiotic heterogeneity considered – linked to non-random patterns of vegetation clearing and confounding effect on area			Abiotic heterogeneity considered – not linked to non-random patterns of vegetation clearing			Abiotic heterogeneity not considered in analysis
	Controlled for in study design	Controlled or accounted for in data analysis	Considered in interpretation and discussion of results	Abiotic homogeneity in study system	Efforts to control heterogeneity in study design	Abiotic factor(s) as explanatory variables in addition to area	
Robertson <i>et al.</i> (2013)			x				
Banks-Leite <i>et al.</i> (2012)							x
Graham <i>et al.</i> (2012)							x
Harrisson <i>et al.</i> (2012)							x
Hinners <i>et al.</i> (2012)							x
Knappova <i>et al.</i> (2012)						x	
Maron <i>et al.</i> (2012)		x					
Mathewson <i>et al.</i> (2012)							x
Melles <i>et al.</i> (2012)							x
Reitalu <i>et al.</i> (2012)					x		
Ribeiro <i>et al.</i> (2012)					x		
Sugiura and Taki (2012)							x
Basham <i>et al.</i> (2011)		x					
Bollmann <i>et al.</i> (2011)						x	
Brückmann <i>et al.</i> (2011)					x		
Duggan <i>et al.</i> (2011)						x	
Haslem and Bennett (2011)							x
Jamoneau <i>et al.</i> (2011)			x				
Moxham and Turner (2011)						x	
Nufio <i>et al.</i> (2011)							x
Oliver <i>et al.</i> (2011)							x
Peña <i>et al.</i> (2011)						x	
Poulin and Villard (2011)							x

Author(s) (year)	Abiotic heterogeneity considered – linked to non-random patterns of vegetation clearing and confounding effect on area			Abiotic heterogeneity considered – not linked to non-random patterns of vegetation clearing			Abiotic heterogeneity not considered in analysis
	Controlled for in study design	Controlled or accounted for in data analysis	Considered in interpretation and discussion of results	Abiotic homogeneity in study system	Efforts to control heterogeneity in study design	Abiotic factor(s) as explanatory variables in addition to area	
Püttker <i>et al.</i> (2011)				x			
Shanahan <i>et al.</i> (2011)							x
Yen <i>et al.</i> (2011)				x			
Cerezo <i>et al.</i> (2010)							x
De Sanctis <i>et al.</i> (2010)						x	
Desrochers <i>et al.</i> (2010)							x
González-Varo (2010)							x
Lasky and Keitt (2010)							x
Lees and Peres (2010)				x			
Leyequien <i>et al.</i> (2010)							x
Lindenmayer <i>et al.</i> (2010)						x	
Marshall <i>et al.</i> (2010)			x				
Mezquida and Benkman (2010)						x	
Norris <i>et al.</i> (2010)						x	
Pardini <i>et al.</i> (2010)				x			
Priday (2010)		x					
Stiles and Scheiner (2010)						x	
Vergara <i>et al.</i> (2010)						x	
Zurita and Bellocq (2010)							x
Cagnolo <i>et al.</i> (2009)							x
Caprio <i>et al.</i> (2009a)							x
Caprio <i>et al.</i> (2009b)							x

Author(s) (year)	Abiotic heterogeneity considered – linked to non-random patterns of vegetation clearing and confounding effect on area			Abiotic heterogeneity considered – not linked to non-random patterns of vegetation clearing			Abiotic heterogeneity not considered in analysis
	Controlled for in study design	Controlled or accounted for in data analysis	Considered in interpretation and discussion of results	Abiotic homogeneity in study system	Efforts to control heterogeneity in study design	Abiotic factor(s) as explanatory variables in addition to area	
Carrete <i>et al.</i> (2009)							x
Cherkaoui <i>et al.</i> (2009)							x
Debuse <i>et al.</i> (2009)		x					
Ewers <i>et al.</i> (2009)							x
Holland and Bennett (2009)							x
Horváth <i>et al.</i> (2009)							x
Kath <i>et al.</i> (2009)							x
Looney <i>et al.</i> (2009)		x					
Magle and Crooks (2009)						x	
Mapelli and Kittlein (2009)						x	
Nufio <i>et al.</i> (2009)							x
Raatikainen <i>et al.</i> (2009)						x	
Rogers <i>et al.</i> (2009)						x	
Sutton and Morgan (2009)							x
Urquiza-Haas <i>et al.</i> (2009)						x	
Aparicio <i>et al.</i> (2008)						x	
Boulton <i>et al.</i> (2008)							x
Cunningham <i>et al.</i> (2008)					x		
Götmark <i>et al.</i> (2008)						x	
Haslem and Bennett (2008)							x
Januchowski <i>et al.</i> (2008)			x				
Ktitorov <i>et al.</i> (2008)						x	
Liira <i>et al.</i> (2008)							x

Author(s) (year)	Abiotic heterogeneity considered – linked to non-random patterns of vegetation clearing and confounding effect on area			Abiotic heterogeneity considered – not linked to non-random patterns of vegetation clearing			Abiotic heterogeneity not considered in analysis
	Controlled for in study design	Controlled or accounted for in data analysis	Considered in interpretation and discussion of results	Abiotic homogeneity in study system	Efforts to control heterogeneity in study design	Abiotic factor(s) as explanatory variables in addition to area	
Martensen <i>et al.</i> (2008)							x
Renfrew and Ribic (2008)							x
Struebig <i>et al.</i> (2008)							x
Brown (2007)				x			
Bulman <i>et al.</i> (2007)			x				
dos Santos <i>et al.</i> (2007)					x		
Ewers <i>et al.</i> (2007)					x		
Gardner and Heinsohn (2007)							x
Michalski and Peres (2007)				x			
Taki <i>et al.</i> (2007)				x			
Arroyo-Rodríguez and Mandujano (2006)							x
Cagnolo <i>et al.</i> (2006)						x	
Castellon and Sieving (2006)							x
Davis <i>et al.</i> (2006)							x
Ernault <i>et al.</i> (2006)							x
Hamer <i>et al.</i> (2006)							x
Husté <i>et al.</i> (2006)							x
Lees and Peres (2006)				x			
Magness <i>et al.</i> (2006)							x
McAlpine <i>et al.</i> (2006)						x	
Morimoto <i>et al.</i> (2006)							x
Öckinger and Smith (2006)					x		

Author(s) (year)	Abiotic heterogeneity considered – linked to non-random patterns of vegetation clearing and confounding effect on area			Abiotic heterogeneity considered – not linked to non-random patterns of vegetation clearing			Abiotic heterogeneity not considered in analysis
	Controlled for in study design	Controlled or accounted for in data analysis	Considered in interpretation and discussion of results	Abiotic homogeneity in study system	Efforts to control heterogeneity in study design	Abiotic factor(s) as explanatory variables in addition to area	
Swihart <i>et al.</i> (2006)							x
Cristóbal-Azkarate <i>et al.</i> (2005)							x
Drinnan (2005)			x				
Driscoll <i>et al.</i> (2005)							x
Heikkinen <i>et al.</i> (2005)						x	
Jiguet <i>et al.</i> (2005)							x
Lindenmayer <i>et al.</i> (2005)							x
Michalski and Peres (2005)				x			
Nol <i>et al.</i> (2005)					x		
Radford <i>et al.</i> (2005)					x	x	

Appendix A: Table A2 references

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Appendix A: Figure A1

AUSTRALIA – top to bottom: north east region, central east region, south east region, south west region; left column: temperate landscapes, right column: arid landscapes

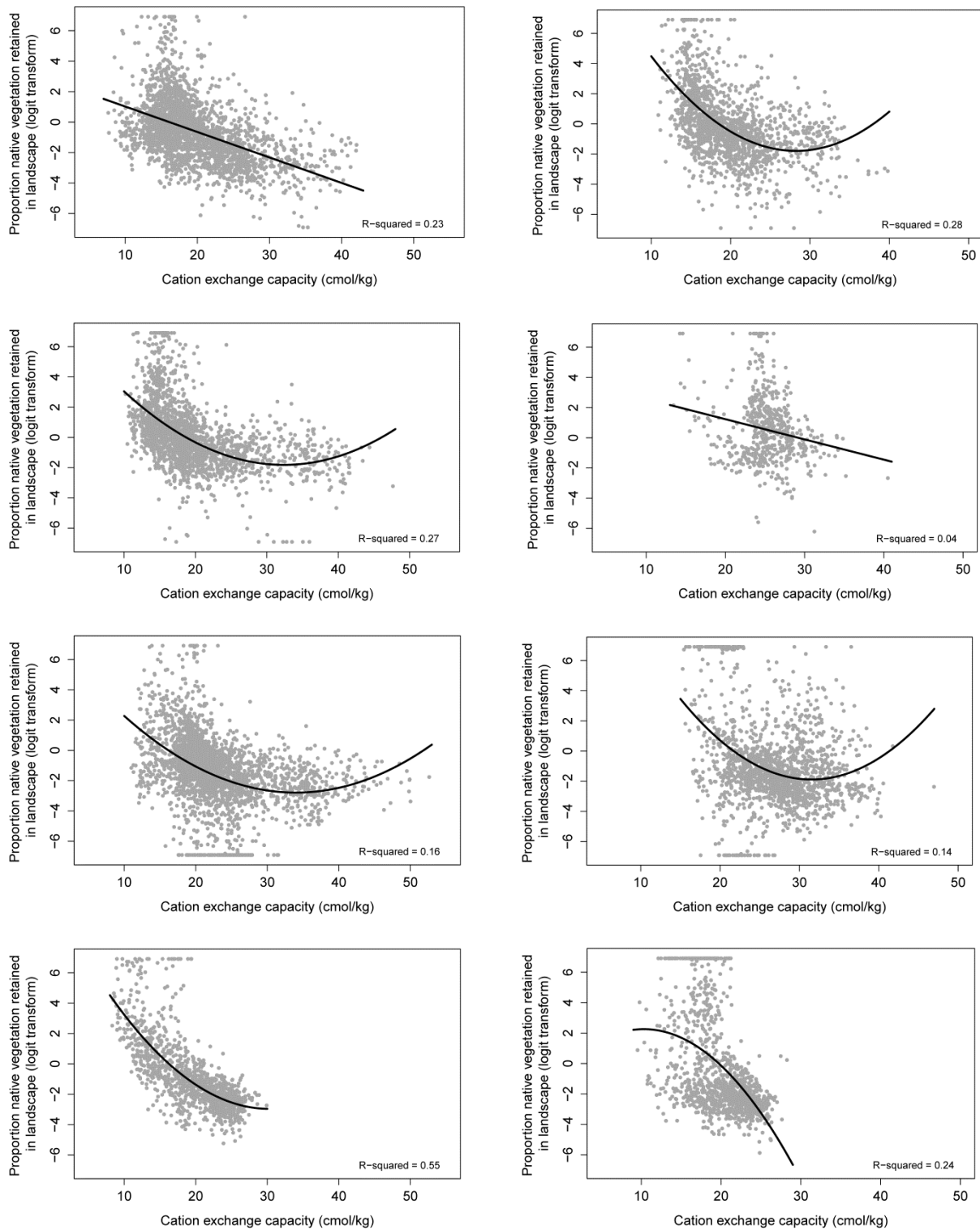


Figure A1.1 Univariate relationship between average cation exchange capacity and proportion native vegetation retained in landscape (logit transformed)

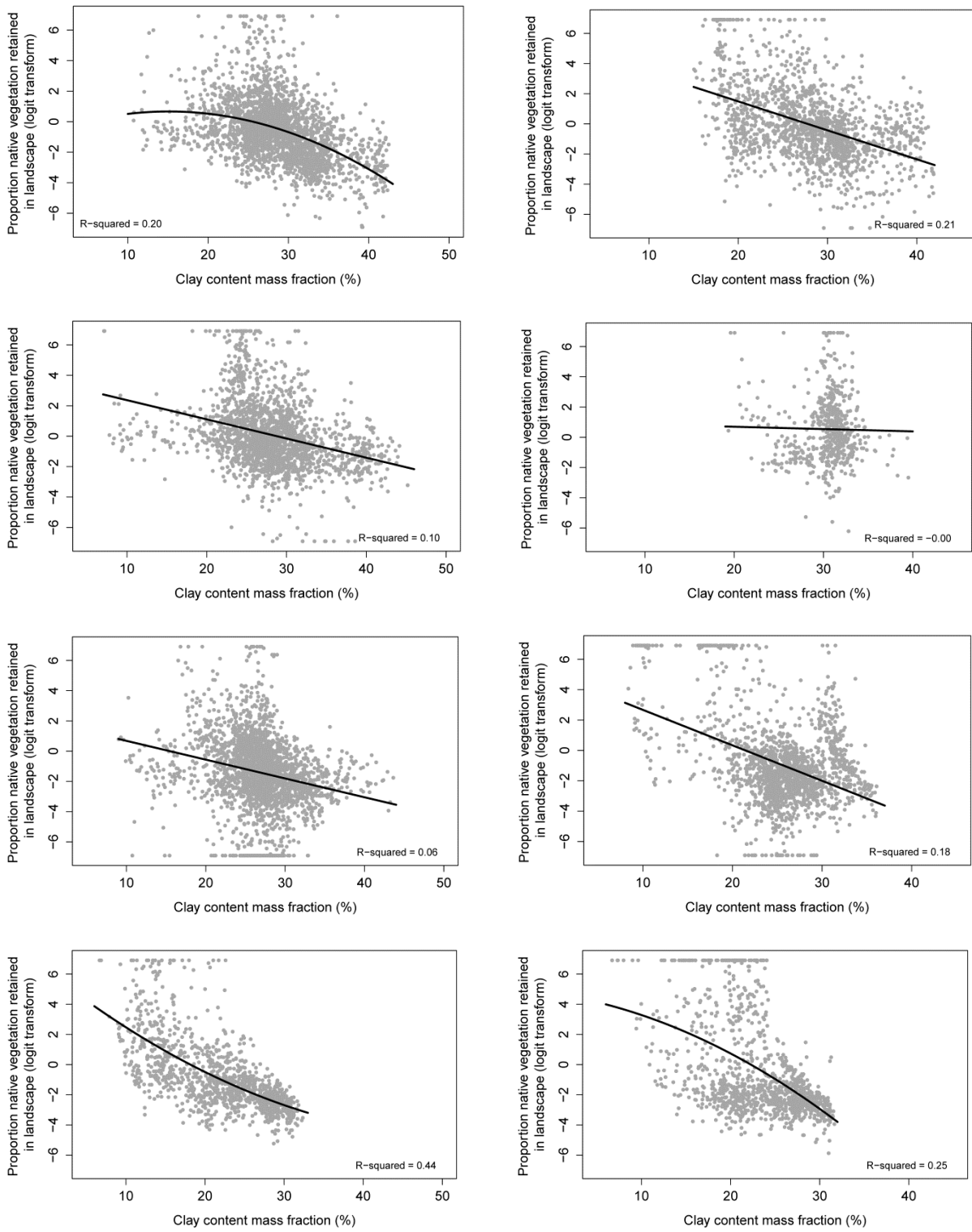


Figure A1.2 Univariate relationship between average clay content mass fraction and proportion native vegetation retained in landscape (logit transformed)

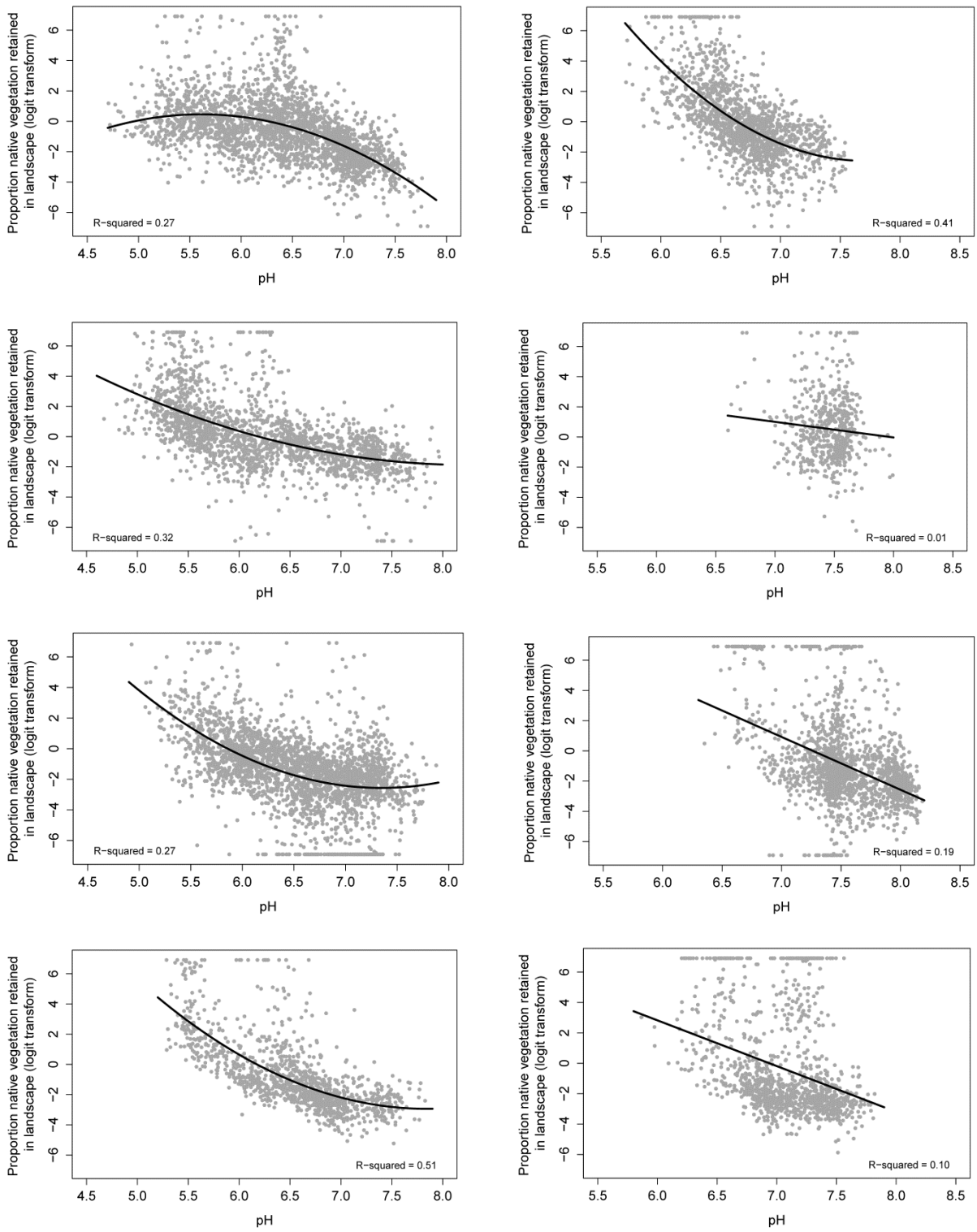


Figure A1.3 Univariate relationship between average pH and proportion native vegetation retained in landscape (logit transformed)

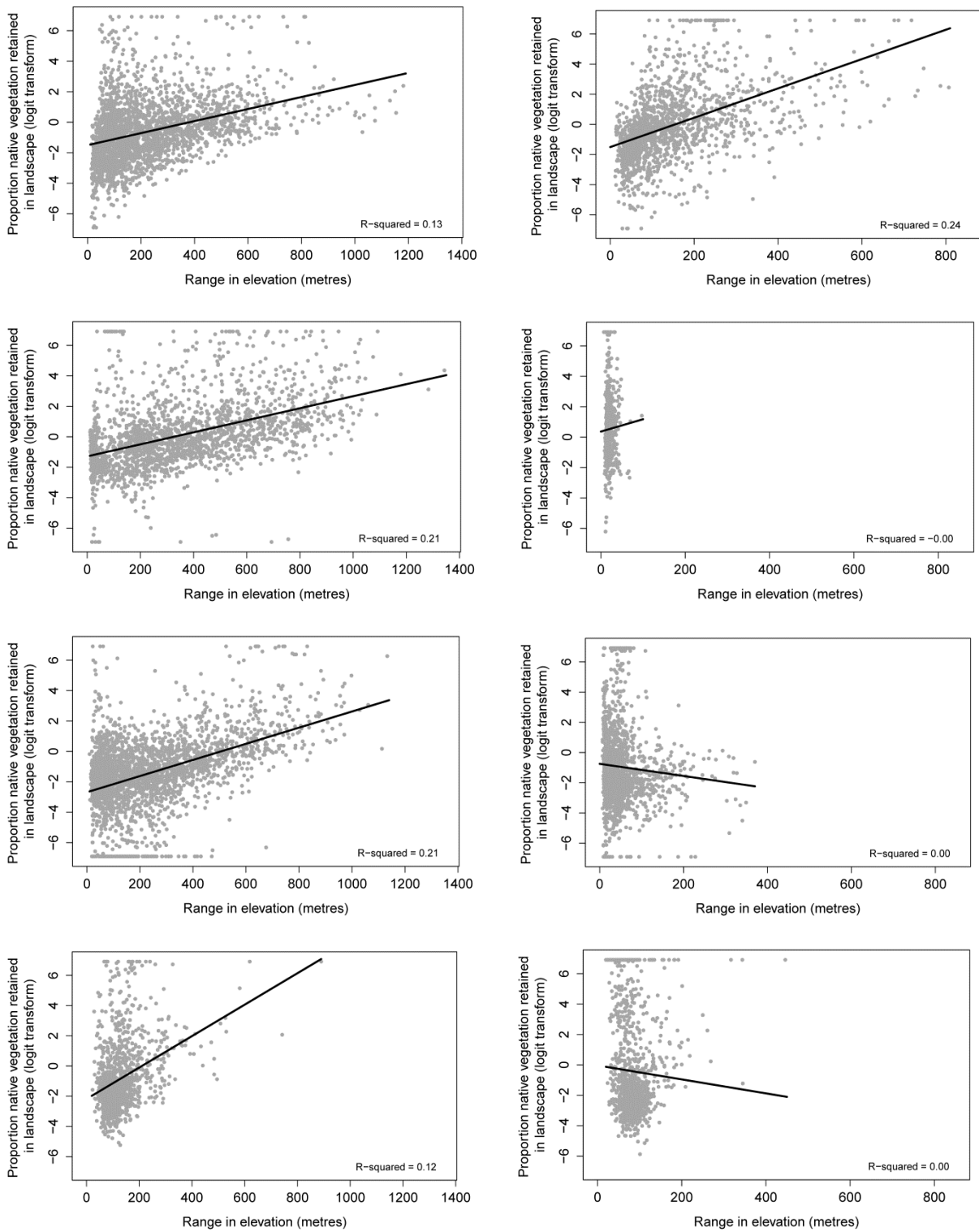


Figure A1.4 Univariate relationship between range in elevation and proportion native vegetation retained in landscape (logit transformed)

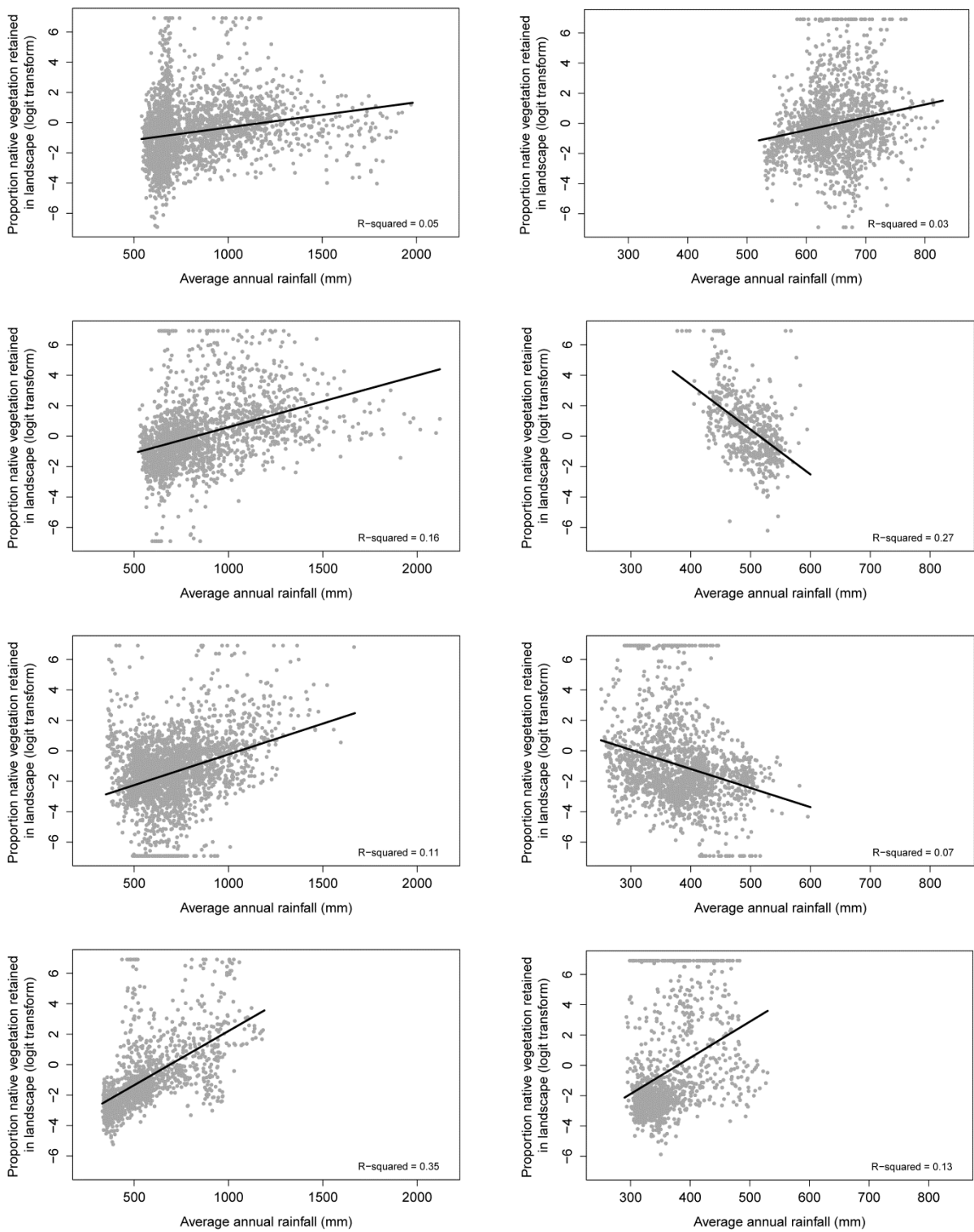


Figure A1.5 Univariate relationship between average annual rainfall and proportion native vegetation retained in landscape (logit transformed)

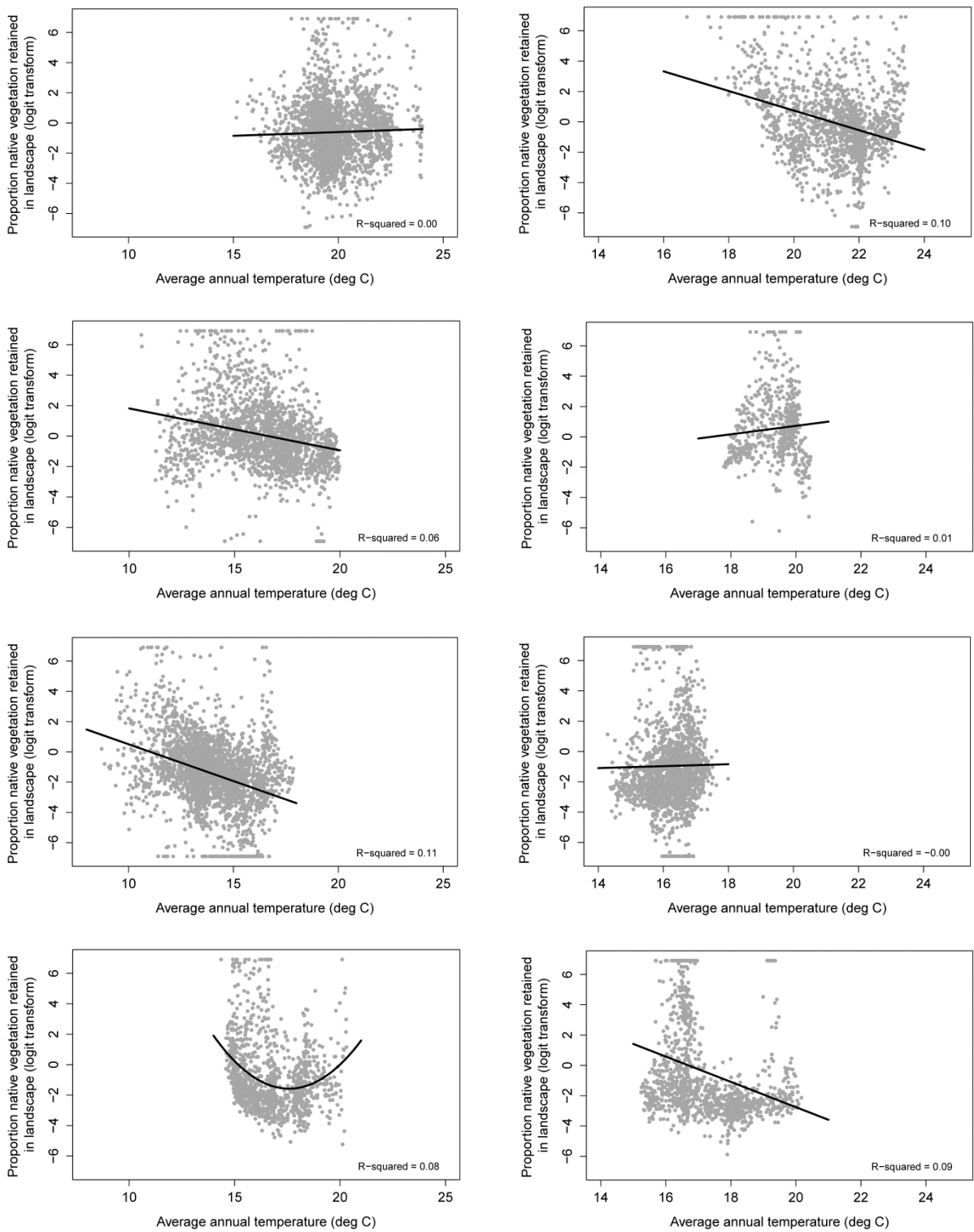


Figure A1.6 Univariate relationship between average annual temperature and proportion native vegetation retained in landscape (logit transformed)

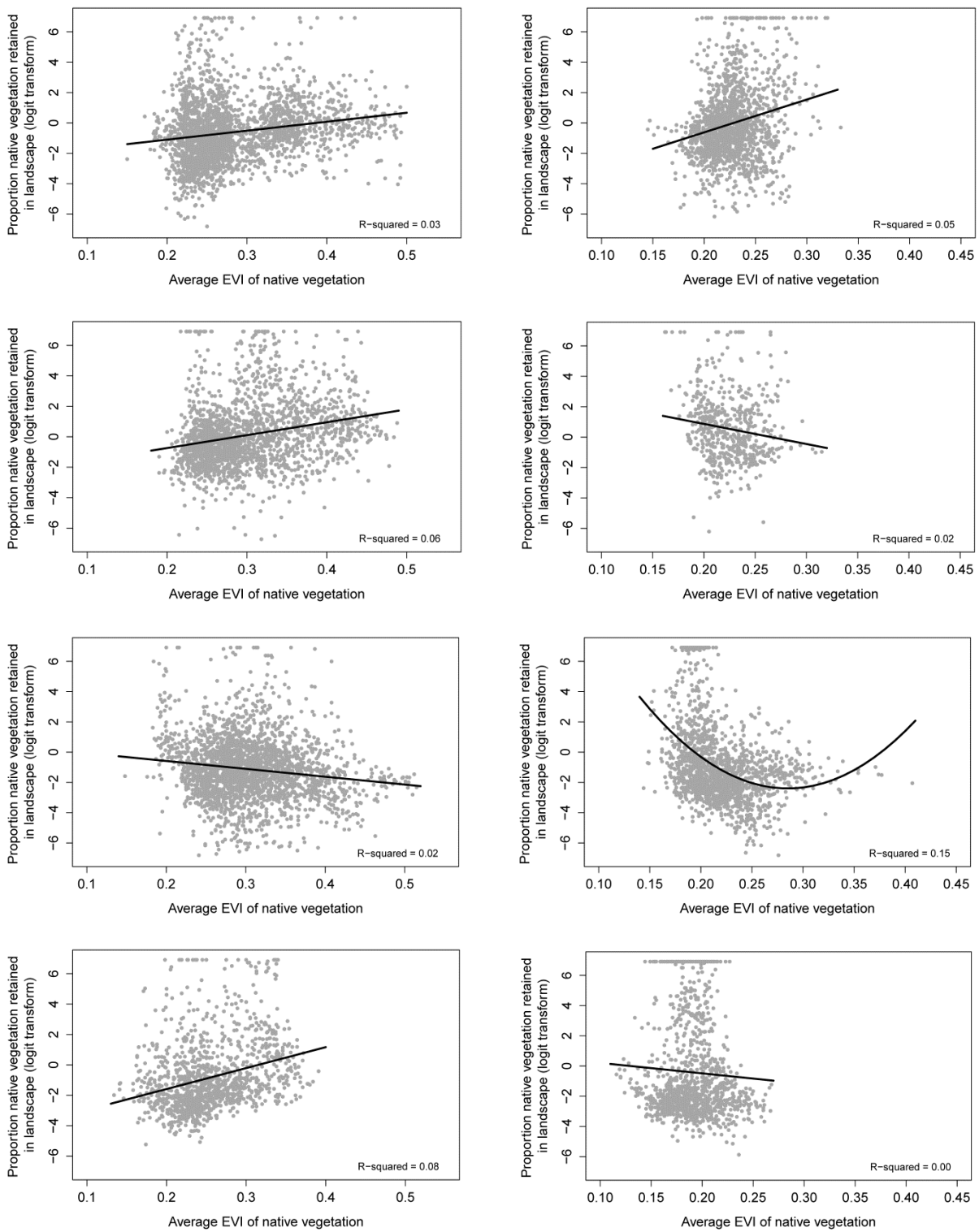


Figure A1.7 Univariate relationship between average EVI of native vegetation and proportion native vegetation retained in landscape (logit transformed)

SOUTH AFRICA – top to bottom: north east region, central east region, south west region;
left column: temperate landscapes, right column: arid landscapes

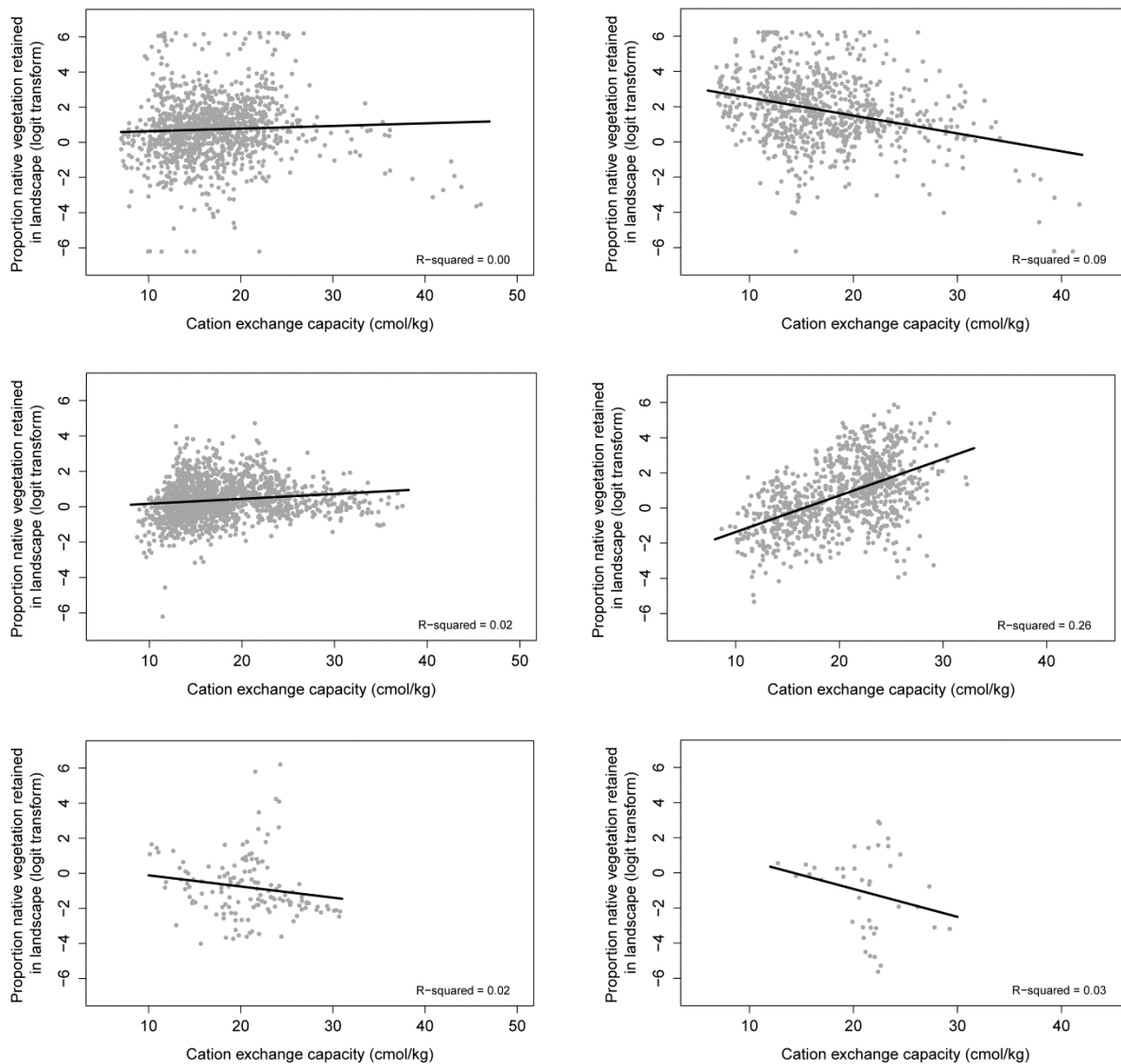


Figure A1.8 Univariate relationship between average cation exchange capacity and proportion native vegetation retained in landscape (logit transformed)

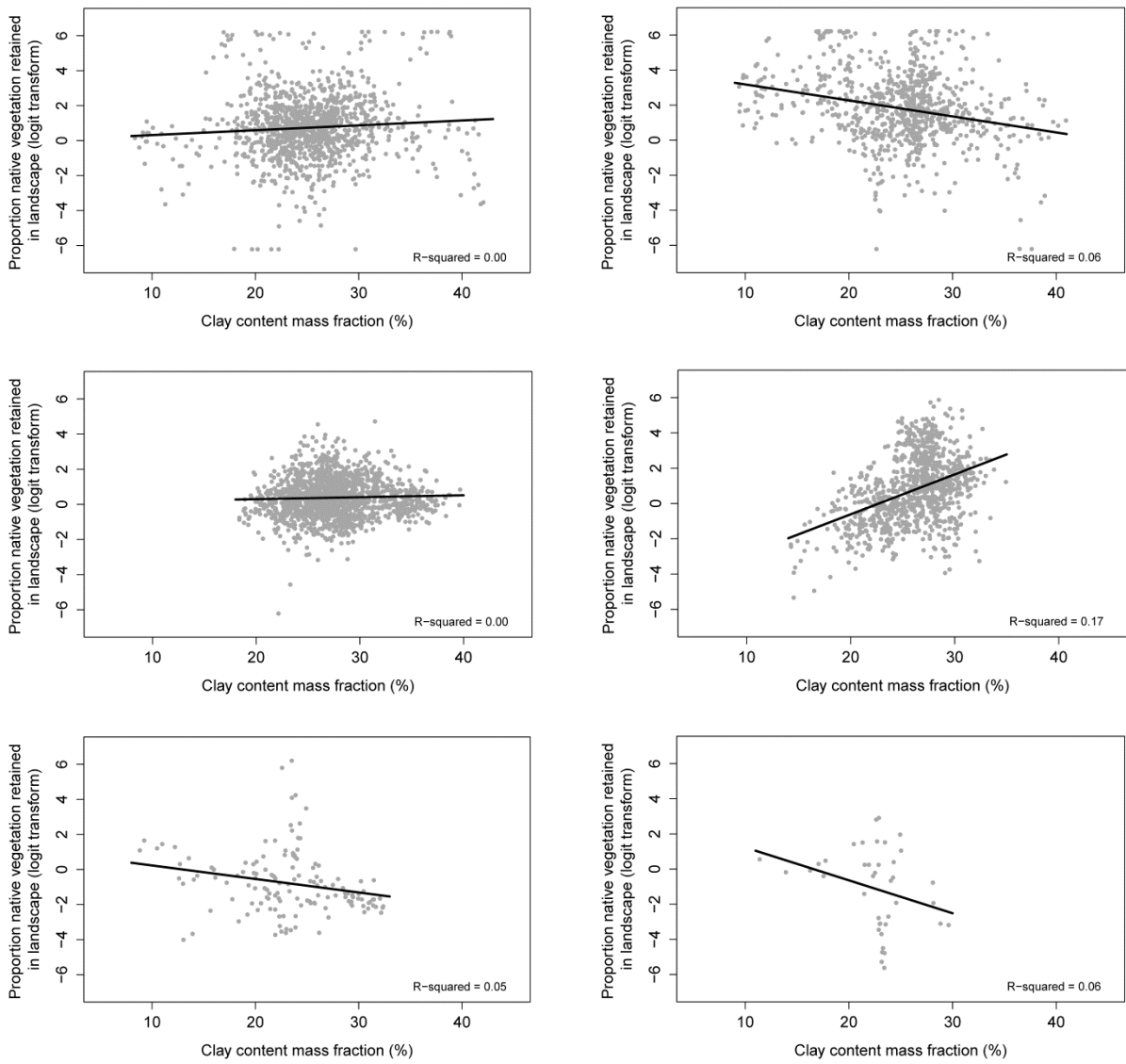


Figure A1.9 Univariate relationship between average clay content mass fraction and proportion native vegetation retained in landscape (logit transformed)

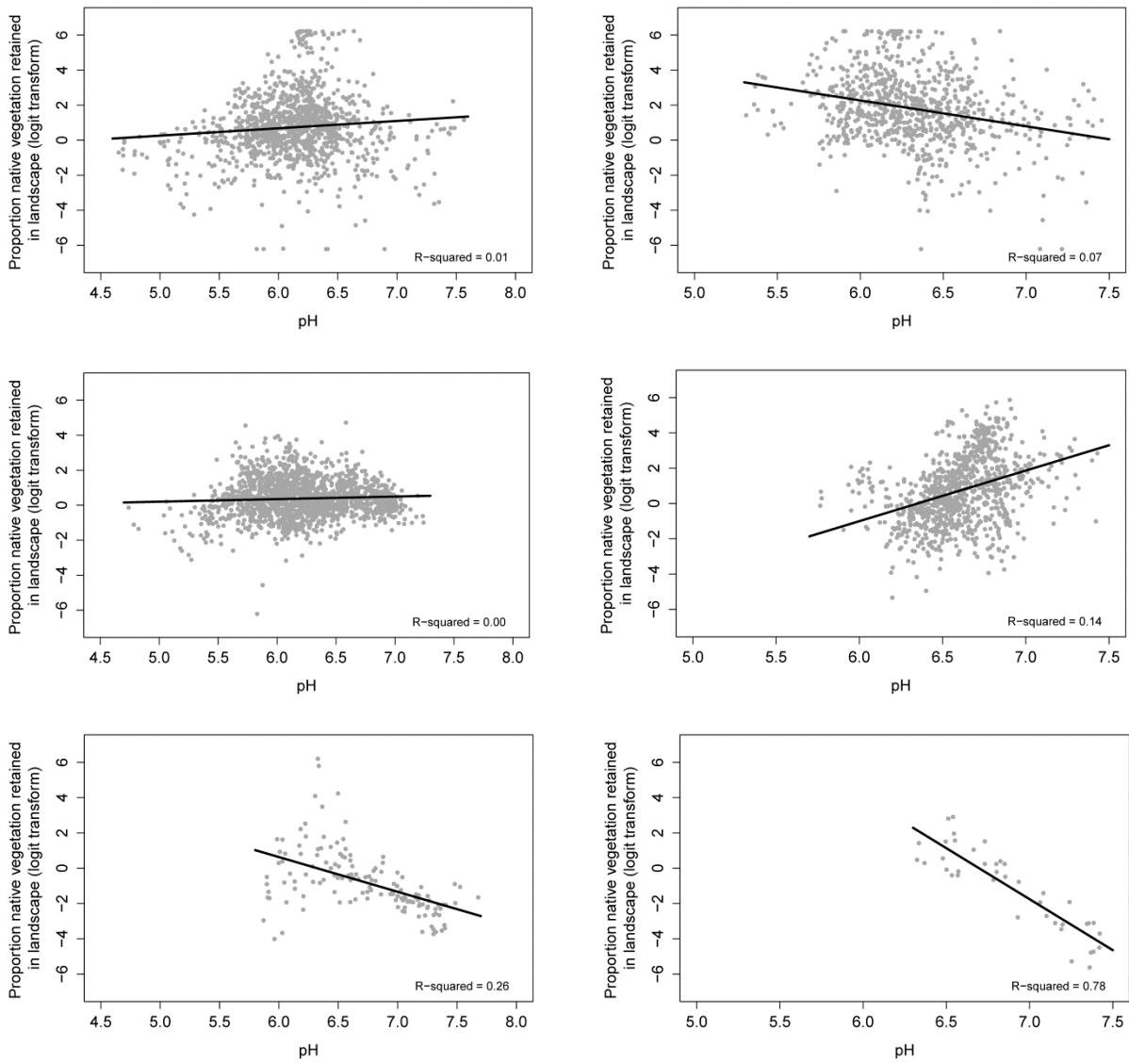


Figure A1.10 Univariate relationship between average pH and proportion native vegetation retained in landscape (logit transformed)

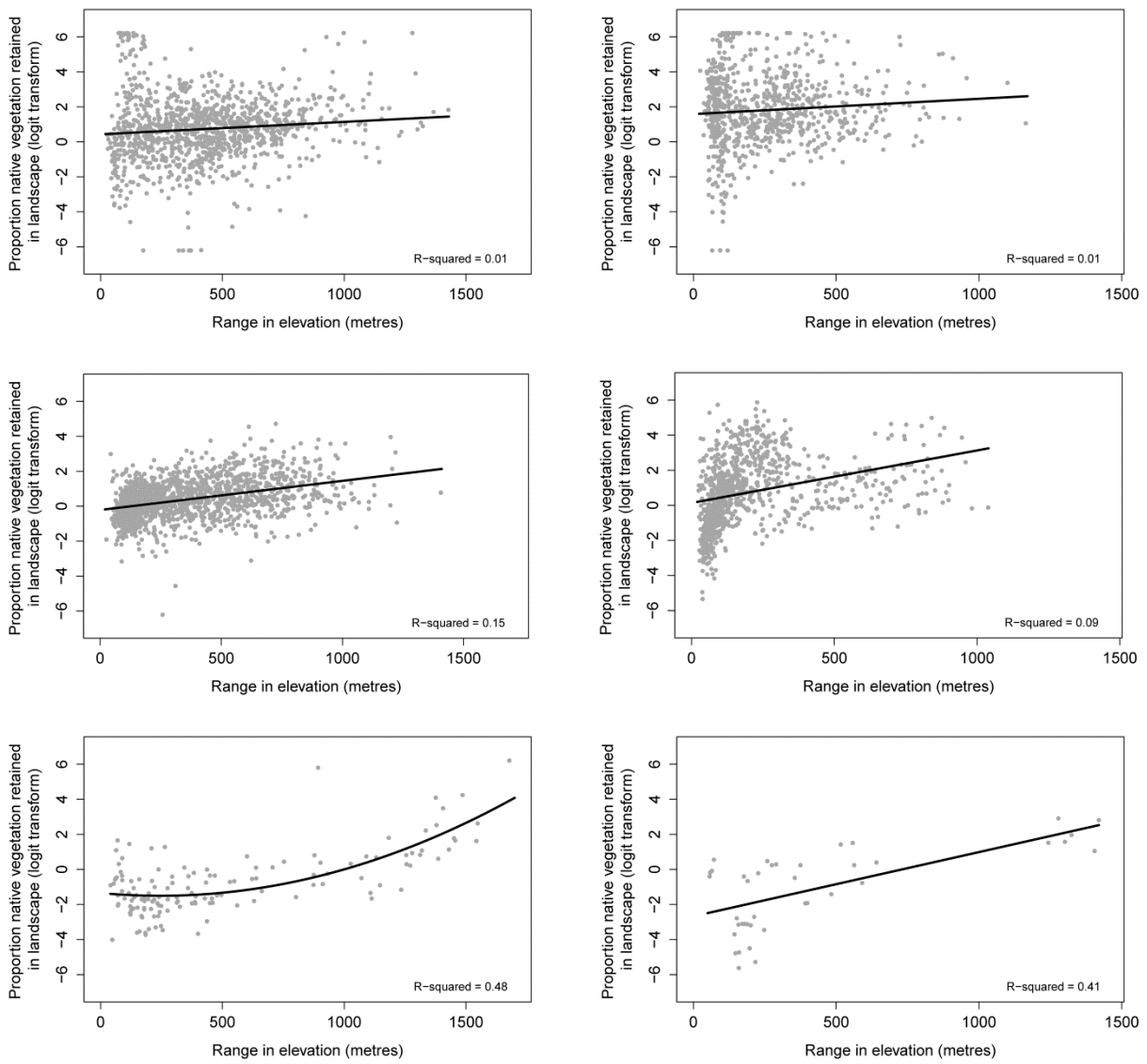


Figure A1.11 Univariate relationship between range in elevation and proportion native vegetation retained in landscape (logit transformed)

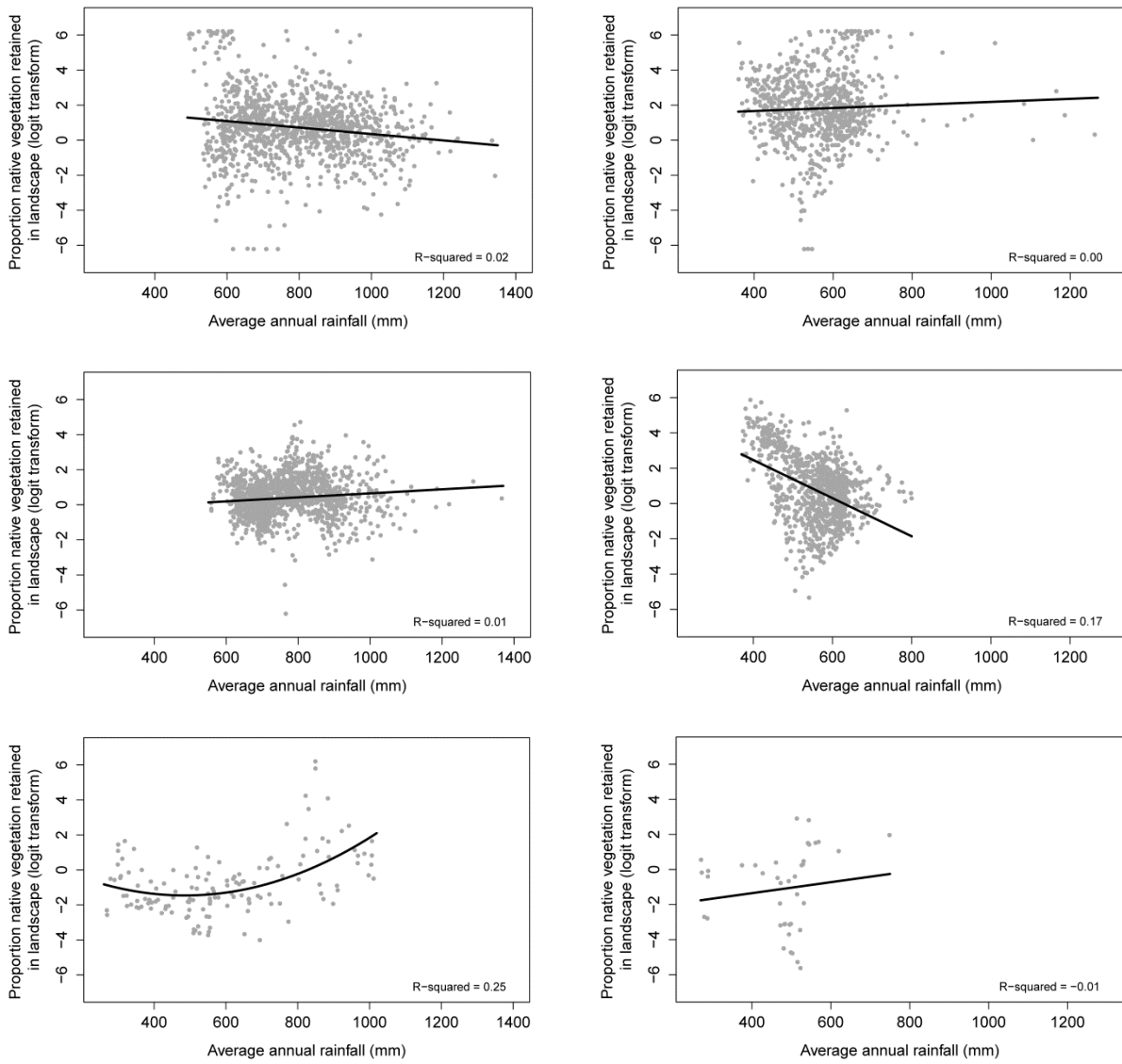


Figure A1.12 Univariate relationship between average annual rainfall and proportion native vegetation retained in landscape (logit transformed)

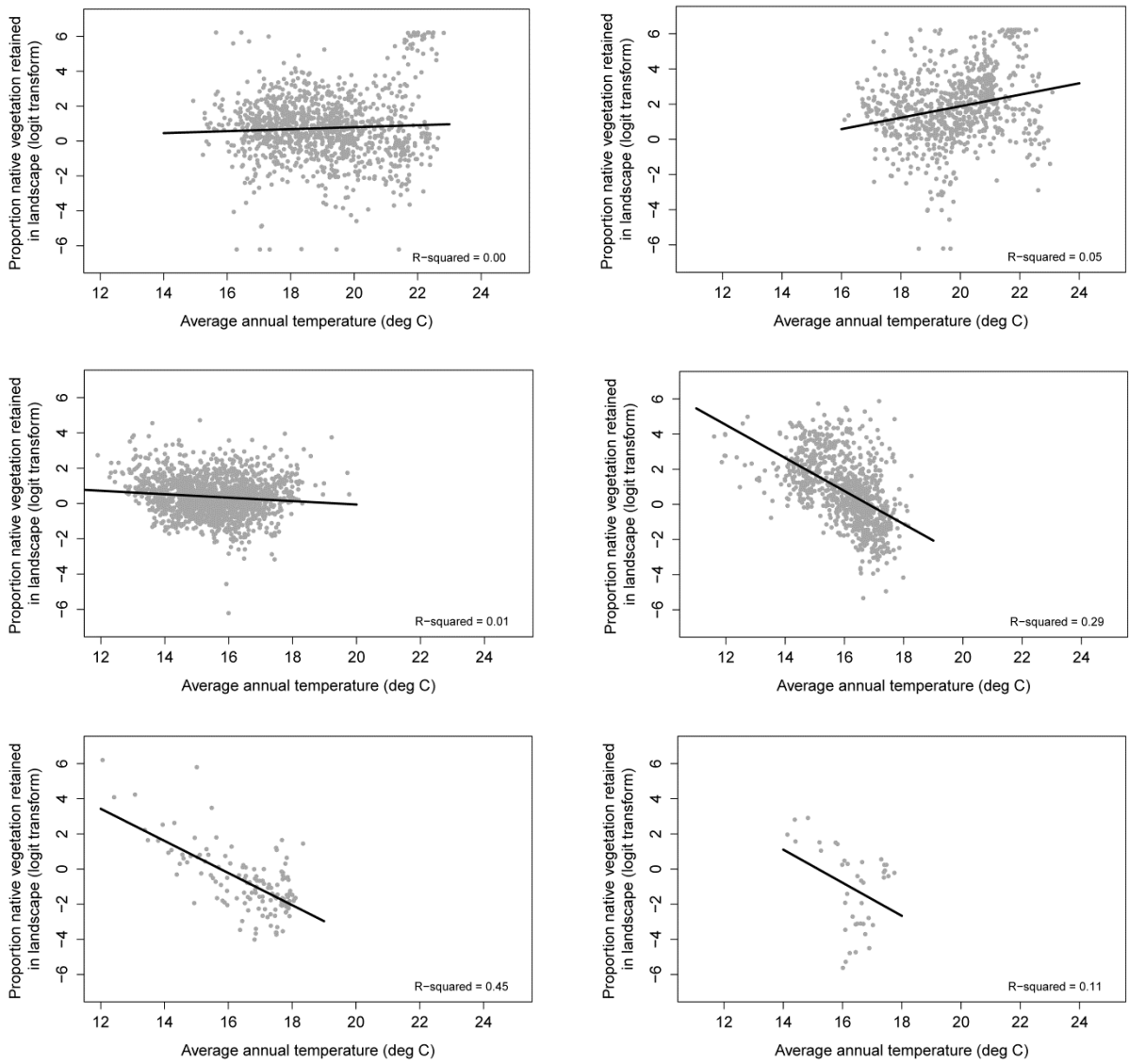


Figure A1.13 Univariate relationship between average annual temperature and proportion native vegetation retained in landscape (logit transformed)

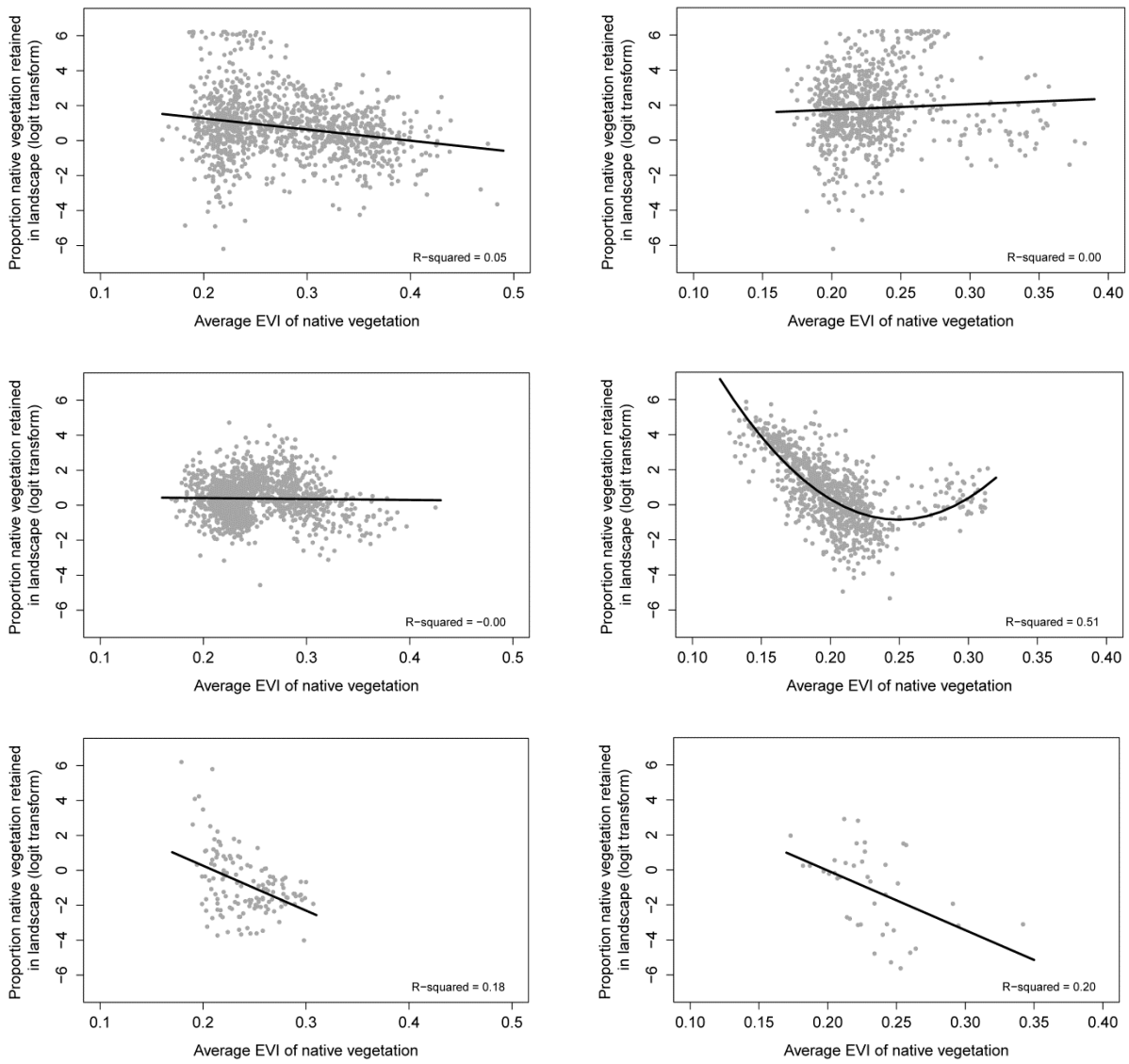


Figure A1.14 Univariate relationship between average EVI of native vegetation and proportion native vegetation retained in landscape (logit transformed)

Appendix B

Chapter 3

Appendix B: Table B1 This list of 232 birds represents those species recorded from surveys (as contained within the New Atlas of Australian Birds database) in the 251 landscape units that were the focus of this analysis.

Scientific name	Common name
<i>Acanthagenys rufogularis</i>	Spiny-cheeked Honeyeater
<i>Acanthiza apicalis</i>	Inland Thornbill
<i>Acanthiza chrysorrhoa</i>	Yellow-rumped Thornbill
<i>Acanthiza iredalei</i>	Slender-billed Thornbill
<i>Acanthiza lineata</i>	Striated Thornbill
<i>Acanthiza nana</i>	Yellow Thornbill
<i>Acanthiza pusilla</i>	Brown Thornbill
<i>Acanthiza reguloides</i>	Buff-rumped Thornbill
<i>Acanthiza uropygialis</i>	Chestnut-rumped Thornbill
<i>Acanthorhynchus tenuirostris</i>	Eastern Spinebill
<i>Accipiter cirrocephalus</i>	Collared Sparrowhawk
<i>Accipiter fasciatus</i>	Brown Goshawk
<i>Accipiter novaehollandiae</i>	Grey Goshawk
<i>Aegotheles cristatus</i>	Australian Owlet-nightjar
<i>Ailuroedus crassirostris</i>	Green Catbird
<i>Alectura lathami</i>	Australian Brush-turkey
<i>Alisterus scapularis</i>	Australian King-Parrot
<i>Anthochaera carunculata</i>	Red Wattlebird
<i>Anthochaera chrysoptera</i>	Little Wattlebird
<i>Anthochaera phrygia</i>	Regent Honeyeater
<i>Aphelocephala leucopsis</i>	Southern Whiteface
<i>Aprosmictus erythropterus</i>	Red-winged Parrot
<i>Aquila audax</i>	Wedge-tailed Eagle
<i>Artamus cyanopterus</i>	Dusky Woodswallow
<i>Artamus leucorhynchus</i>	White-breasted Woodswallow
<i>Artamus minor</i>	Little Woodswallow
<i>Artamus personatus</i>	Masked Woodswallow
<i>Artamus superciliosus</i>	White-browed Woodswallow

Scientific name	Common name
<i>Aviceda subcristata</i>	Pacific Baza
<i>Barnardius zonarius</i>	Australian Ringneck
<i>Burhinus grallarius</i>	Bush Stone-curlew
<i>Cacatua galerita</i>	Sulphur-crested Cockatoo
<i>Cacatua sanguinea</i>	Little Corella
<i>Cacatua tenuirostris</i>	Long-billed Corella
<i>Cacomantis flabelliformis</i>	Fan-tailed Cuckoo
<i>Cacomantis pallidus</i>	Pallid Cuckoo
<i>Cacomantis variolosus</i>	Brush Cuckoo
<i>Calamanthus cautus</i>	Shy Heathwren
<i>Calamanthus pyrrhopygia</i>	Chestnut-rumped Heathwren
<i>Callocephalon fimbriatum</i>	Gang-gang Cockatoo
<i>Calyptorhynchus banksii</i>	Red-tailed Black-Cockatoo
<i>Calyptorhynchus funereus</i>	Yellow-tailed Black-Cockatoo
<i>Calyptorhynchus lathami</i>	Glossy Black-Cockatoo
<i>Carternornis leucotis</i>	White-eared Monarch
<i>Centropus phasianinus</i>	Pheasant Coucal
<i>Certhionyx variegatus</i>	Pied Honeyeater
<i>Ceyx azureus</i>	Azure Kingfisher
<i>Chalcites basalis</i>	Horsfield's Bronze-Cuckoo
<i>Chalcites lucidus</i>	Shining Bronze-Cuckoo
<i>Chalcites minutillus</i>	Little Bronze-Cuckoo
<i>Chalcites osculans</i>	Black-eared Cuckoo
<i>Chalcophaps indica</i>	Emerald Dove
<i>Chthonicola sagittata</i>	Speckled Warbler
<i>Cinclosoma castanotum</i>	Chestnut Quail-thrush
<i>Cinclosoma punctatum</i>	Spotted Quail-thrush
<i>Climacteris affinis</i>	White-browed Treecreeper
<i>Climacteris erythrops</i>	Red-browed Treecreeper
<i>Climacteris picumnus</i>	Brown Treecreeper
<i>Colluricincla harmonica</i>	Grey Shrike-thrush
<i>Colluricincla megarhyncha</i>	Little Shrike-thrush
<i>Columba leucomela</i>	White-headed Pigeon
<i>Coracina lineata</i>	Barred Cuckoo-shrike
<i>Coracina maxima</i>	Ground Cuckoo-shrike
<i>Coracina novaehollandiae</i>	Black-faced Cuckoo-shrike
<i>Coracina papuensis</i>	White-bellied Cuckoo-shrike

Scientific name	Common name
<i>Coracina tenuirostris</i>	Cicadabird
<i>Corcorax melanorhamphos</i>	White-winged Chough
<i>Cormobates leucophaea</i>	White-throated Treecreeper
<i>Corvus tasmanicus</i>	Forest Raven
<i>Coturnix ypsilophora</i>	Brown Quail
<i>Cracticus nigrogularis</i>	Pied Butcherbird
<i>Cracticus torquatus</i>	Grey Butcherbird
<i>Cyclopsitta diophthalma</i>	Double-eyed Fig-Parrot
<i>Dacelo leachii</i>	Blue-winged Kookaburra
<i>Dacelo novaeguineae</i>	Laughing Kookaburra
<i>Daphoenositta chrysoptera</i>	Varied Sittella
<i>Dasyornis broadbenti</i>	Rufous Bristlebird
<i>Dicaeum hirundinaceum</i>	Mistletoebird
<i>Dicrurus bracteatus</i>	Spangled Drongo
<i>Drymodes brunneopygia</i>	Southern Scrub-robin
<i>Entomyzon cyanotis</i>	Blue-faced Honeyeater
<i>Eopsaltria australis</i>	Eastern Yellow Robin
<i>Eudynamis orientalis</i>	Eastern Koel
<i>Eurostopodus argus</i>	Spotted Nightjar
<i>Eurostopodus mystacalis</i>	White-throated Nightjar
<i>Eurystomus orientalis</i>	Dollarbird
<i>Falco longipennis</i>	Australian Hobby
<i>Falcunculus frontatus</i>	Crested Shrike-tit
<i>Geopelia cuneata</i>	Diamond Dove
<i>Geopelia humeralis</i>	Bar-shouldered Dove
<i>Geopelia striata</i>	Peaceful Dove
<i>Gerygone albogularis</i>	White-throated Gerygone
<i>Gerygone fusca</i>	Western Gerygone
<i>Gerygone levigaster</i>	Mangrove Gerygone
<i>Gerygone mouki</i>	Brown Gerygone
<i>Gerygone palpebrosa</i>	Fairy Gerygone
<i>Glossopsitta concinna</i>	Musk Lorikeet
<i>Glossopsitta porphyrocephala</i>	Purple-crowned Lorikeet
<i>Glossopsitta pusilla</i>	Little Lorikeet
<i>Glyciphila melanops</i>	Tawny-crowned Honeyeater
<i>Grantiella picta</i>	Painted Honeyeater
<i>Hieraaetus morphnoides</i>	Little Eagle

Scientific name	Common name
<i>Lalage leucomela</i>	Varied Triller
<i>Lalage sueurii</i>	White-winged Triller
<i>Lathamus discolor</i>	Swift Parrot
<i>Leipoa ocellata</i>	Malleefowl
<i>Leucosarcia picata</i>	Wonga Pigeon
<i>Lichenostomus chrysops</i>	Yellow-faced Honeyeater
<i>Lichenostomus cratitius</i>	Purple-gaped Honeyeater
<i>Lichenostomus fasciocularis</i>	Mangrove Honeyeater
<i>Lichenostomus fuscus</i>	Fuscous Honeyeater
<i>Lichenostomus leucotis</i>	White-eared Honeyeater
<i>Lichenostomus melanops</i>	Yellow-tufted Honeyeater
<i>Lichenostomus ornatus</i>	Yellow-plumed Honeyeater
<i>Lichenostomus penicillatus</i>	White-plumed Honeyeater
<i>Lichenostomus plumulus</i>	Grey-fronted Honeyeater
<i>Lichenostomus virescens</i>	Singing Honeyeater
<i>Lichmera indistincta</i>	Brown Honeyeater
<i>Lophochroa leadbeateri</i>	Major Mitchell's Cockatoo
<i>Lophoictinia isura</i>	Square-tailed Kite
<i>Lopholaimus antarcticus</i>	Topknot Pigeon
<i>Macropygia amboinensis</i>	Brown Cuckoo-Dove
<i>Malurus cyaneus</i>	Superb Fairy-wren
<i>Malurus lamberti</i>	Variiegated Fairy-wren
<i>Malurus melanocephalus</i>	Red-backed Fairy-wren
<i>Malurus splendens</i>	Splendid Fairy-wren
<i>Manorina flavigula</i>	Yellow-throated Miner
<i>Manorina melanocephala</i>	Noisy Miner
<i>Manorina melanophrys</i>	Bell Miner
<i>Manorina melanotis</i>	Black-eared Miner
<i>Melanodryas cucullata</i>	Hooded Robin
<i>Meliphaga lewinii</i>	Lewin's Honeyeater
<i>Melithreptus albogularis</i>	White-throated Honeyeater
<i>Melithreptus brevirostris</i>	Brown-headed Honeyeater
<i>Melithreptus gularis</i>	Black-chinned Honeyeater
<i>Melithreptus lunatus</i>	White-naped Honeyeater
<i>Menura alberti</i>	Albert's Lyrebird
<i>Menura novaehollandiae</i>	Superb Lyrebird
<i>Merops ornatus</i>	Rainbow Bee-eater

Scientific name	Common name
<i>Microeca fascinans</i>	Jacky Winter
<i>Monarcha melanopsis</i>	Black-faced Monarch
<i>Myiagra cyanoleuca</i>	Satin Flycatcher
<i>Myiagra inquieta</i>	Restless Flycatcher
<i>Myiagra rubecula</i>	Leaden Flycatcher
<i>Myzomela obscura</i>	Dusky Honeyeater
<i>Myzomela sanguinolenta</i>	Scarlet Honeyeater
<i>Neochmia modesta</i>	Plum-headed Finch
<i>Neochmia temporalis</i>	Red-browed Finch
<i>Neophema elegans</i>	Elegant Parrot
<i>Neophema pulchella</i>	Turquoise Parrot
<i>Ninox connivens</i>	Barking Owl
<i>Ninox novaeseelandiae</i>	Southern Boobook
<i>Ninox strenua</i>	Powerful Owl
<i>Northiella haematogaster</i>	Blue Bonnet
<i>Nymphicus hollandicus</i>	Cockatiel
<i>Oreoica gutturalis</i>	Crested Bellbird
<i>Origma solitaria</i>	Rockwarbler
<i>Oriolus sagittatus</i>	Olive-backed Oriole
<i>Orthonyx temminckii</i>	Australian Logrunner
<i>Pachycephala inornata</i>	Gilbert's Whistler
<i>Pachycephala olivacea</i>	Olive Whistler
<i>Pachycephala pectoralis</i>	Golden Whistler
<i>Pachycephala rufiventris</i>	Rufous Whistler
<i>Pachycephala rufogularis</i>	Red-lored Whistler
<i>Pardalotus punctatus</i>	Spotted Pardalote
<i>Pardalotus striatus</i>	Striated Pardalote
<i>Petrochelidon nigricans</i>	Tree Martin
<i>Petroica boodang</i>	Scarlet Robin
<i>Petroica goodenovii</i>	Red-capped Robin
<i>Petroica phoenicea</i>	Flame Robin
<i>Petroica rodinogaster</i>	Pink Robin
<i>Petroica rosea</i>	Rose Robin
<i>Phaps chalcoptera</i>	Common Bronzewing
<i>Phaps elegans</i>	Brush Bronzewing
<i>Philemon citreogularis</i>	Little Friarbird
<i>Philemon corniculatus</i>	Noisy Friarbird

Scientific name	Common name
<i>Phylidonyris niger</i>	White-cheeked Honeyeater
<i>Phylidonyris novaehollandiae</i>	New Holland Honeyeater
<i>Phylidonyris pyrrhopterus</i>	Crescent Honeyeater
<i>Pitta versicolor</i>	Noisy Pitta
<i>Platycercus adscitus</i>	Pale-headed Rosella
<i>Platycercus elegans</i>	Crimson Rosella
<i>Platycercus eximius</i>	Eastern Rosella
<i>Plectorhyncha lanceolata</i>	Striped Honeyeater
<i>Podargus ocellatus</i>	Marbled Frogmouth
<i>Podargus strigoides</i>	Tawny Frogmouth
<i>Polytelis anthopeplus</i>	Regent Parrot
<i>Polytelis swainsonii</i>	Superb Parrot
<i>Pomatostomus ruficeps</i>	Chestnut-crowned Babbler
<i>Pomatostomus superciliosus</i>	White-browed Babbler
<i>Pomatostomus temporalis</i>	Grey-crowned Babbler
<i>Psephotus haematonotus</i>	Red-rumped Parrot
<i>Psephotus varius</i>	Mulga Parrot
<i>Psophodes olivaceus</i>	Eastern Whipbird
<i>Ptilinopus magnificus</i>	Wompoo Fruit-Dove
<i>Ptilinopus regina</i>	Rose-crowned Fruit-Dove
<i>Ptilinopus superbus</i>	Superb Fruit-Dove
<i>Ptilonorhynchus maculatus</i>	Spotted Bowerbird
<i>Ptilonorhynchus violaceus</i>	Satin Bowerbird
<i>Ptiloris paradiseus</i>	Paradise Riflebird
<i>Purnella albifrons</i>	White-fronted Honeyeater
<i>Pycnoptilus floccosus</i>	Pilotbird
<i>Pyrrholaemus brunneus</i>	Redthroat
<i>Rhipidura albiscapa</i>	Grey Fantail
<i>Rhipidura rufifrons</i>	Rufous Fantail
<i>Scythrops novaehollandiae</i>	Channel-billed Cuckoo
<i>Sericornis citreogularis</i>	Yellow-throated Scrubwren
<i>Sericornis frontalis</i>	White-browed Scrubwren
<i>Sericornis magnirostra</i>	Large-billed Scrubwren
<i>Sericulus chrysocephalus</i>	Regent Bowerbird
<i>Smicronis brevirostris</i>	Weebill
<i>Sphecotheres vieillotii</i>	Australasian Figbird
<i>Stagonopleura bella</i>	Beautiful Firetail

Scientific name	Common name
<i>Stagonopleura guttata</i>	Diamond Firetail
<i>Stipiturus malachurus</i>	Southern Emu-wren
<i>Strepera graculina</i>	Pied Currawong
<i>Strepera versicolor</i>	Grey Currawong
<i>Struthidea cinerea</i>	Apostlebird
<i>Sugomel niger</i>	Black Honeyeater
<i>Symposiachrus trivirgatus</i>	Spectacled Monarch
<i>Todiramphus macleayii</i>	Forest Kingfisher
<i>Todiramphus pyrrhopygius</i>	Red-backed Kingfisher
<i>Todiramphus sanctus</i>	Sacred Kingfisher
<i>Tregellasia capito</i>	Pale-yellow Robin
<i>Trichoglossus chlorolepidotus</i>	Scaly-breasted Lorikeet
<i>Trichoglossus haematodus</i>	Rainbow Lorikeet
<i>Turnix melanogaster</i>	Black-breasted Button-quail
<i>Turnix varius</i>	Painted Button-quail
<i>Tyto novaehollandiae</i>	Masked Owl
<i>Zoothera heinei</i>	Russet-tailed Thrush
<i>Zoothera lunulata</i>	Bassian Thrush
<i>Zosterops lateralis</i>	Silvereye

Appendix C

Chapter 4

Appendix C: Table C1 This list of birds represents those species recorded from surveys (as contained within the New Atlas of Australian Birds database) in the landscape units that were the focus of this analysis.

Scientific name	Common name	25 km ²	100 km ²	400 km ²
<i>Acanthagenys rufogularis</i>	Spiny-cheeked Honeyeater	x	x	x
<i>Acanthiza apicalis</i>	Inland Thornbill	x	x	x
<i>Acanthiza chrysorrhoa</i>	Yellow-rumped Thornbill	x	x	x
<i>Acanthiza lineata</i>	Striated Thornbill	x	x	x
<i>Acanthiza nana</i>	Yellow Thornbill	x	x	x
<i>Acanthiza pusilla</i>	Brown Thornbill	x	x	x
<i>Acanthiza reguloides</i>	Buff-rumped Thornbill	x	x	x
<i>Acanthiza uropygialis</i>	Chestnut-rumped Thornbill	x	x	x
<i>Acanthorhynchus tenuirostris</i>	Eastern Spinebill	x	x	x
<i>Accipiter cirrocephalus</i>	Collared Sparrowhawk	x	x	x
<i>Accipiter fasciatus</i>	Brown Goshawk	x	x	x
<i>Accipiter novaehollandiae</i>	Grey Goshawk	x	x	x
<i>Aegotheles cristatus</i>	Australian Owlet-nightjar	x	x	x
<i>Ailuroedus crassirostris</i>	Green Catbird	x	x	x
<i>Alectura lathami</i>	Australian Brush-turkey	x	x	x
<i>Alisterus scapularis</i>	Australian King-Parrot	x	x	x
<i>Anthochaera carunculata</i>	Red Wattlebird	x	x	x
<i>Anthochaera chrysoptera</i>	Little Wattlebird	x	x	x
<i>Anthochaera phrygia</i>	Regent Honeyeater	x	x	x
<i>Aphelocephala leucopsis</i>	Southern Whiteface	x	x	x
<i>Aprosmictus erythropterus</i>	Red-winged Parrot	x	x	x
<i>Aquila audax</i>	Wedge-tailed Eagle	x	x	x
<i>Artamus cyanopterus</i>	Dusky Woodswallow	x	x	x
<i>Artamus leucorhynchus</i>	White-breasted Woodswallow	x	x	x
<i>Artamus minor</i>	Little Woodswallow		x	x
<i>Artamus personatus</i>	Masked Woodswallow	x	x	x
<i>Artamus superciliosus</i>	White-browed Woodswallow	x	x	x
<i>Atrichornis rufescens</i>	Rufous Scrub-bird			x

Scientific name	Common name	25 km ²	100 km ²	400 km ²
<i>Aviceda subcristata</i>	Pacific Baza	x	x	x
<i>Barnardius zonarius</i>	Australian Ringneck	x	x	x
<i>Burhinus grallarius</i>	Bush Stone-curlew	x	x	x
<i>Cacatua galerita</i>	Sulphur-crested Cockatoo	x	x	x
<i>Cacatua sanguinea</i>	Little Corella	x	x	x
<i>Cacatua tenuirostris</i>	Long-billed Corella	x	x	x
<i>Cacomantis flabelliformis</i>	Fan-tailed Cuckoo	x	x	x
<i>Cacomantis pallidus</i>	Pallid Cuckoo	x	x	x
<i>Cacomantis variolosus</i>	Brush Cuckoo	x	x	x
<i>Calamanthus cautus</i>	Shy Heathwren	x	x	x
<i>Calamanthus pyrrhopygia</i>	Chestnut-rumped Heathwren	x	x	x
<i>Callocephalon fimbriatum</i>	Gang-gang Cockatoo	x	x	x
<i>Calyptorhynchus banksii</i>	Red-tailed Black-Cockatoo	x	x	x
<i>Calyptorhynchus funereus</i>	Yellow-tailed Black-Cockatoo	x	x	x
<i>Calyptorhynchus lathami</i>	Glossy Black-Cockatoo	x	x	x
<i>Carternornis leucotis</i>	White-eared Monarch	x	x	x
<i>Centropus phasianinus</i>	Pheasant Coucal	x	x	x
<i>Ceyx azureus</i>	Azure Kingfisher	x	x	x
<i>Chalcites basalis</i>	Horsfield's Bronze-Cuckoo	x	x	x
<i>Chalcites lucidus</i>	Shining Bronze-Cuckoo	x	x	x
<i>Chalcites minutillus</i>	Little Bronze-Cuckoo	x	x	x
<i>Chalcites osculans</i>	Black-eared Cuckoo	x	x	x
<i>Chalcophaps indica</i>	Emerald Dove	x	x	x
<i>Chthonicola sagittata</i>	Speckled Warbler	x	x	x
<i>Cinclosoma punctatum</i>	Spotted Quail-thrush	x	x	x
<i>Climacteris affinis</i>	White-browed Treecreeper			x
<i>Climacteris erythrops</i>	Red-browed Treecreeper	x	x	x
<i>Climacteris picumnus</i>	Brown Treecreeper	x	x	x
<i>Colluricincla harmonica</i>	Grey Shrike-thrush	x	x	x
<i>Colluricincla megarhyncha</i>	Little Shrike-thrush	x	x	x
<i>Columba leucomela</i>	White-headed Pigeon	x	x	x
<i>Coracina lineata</i>	Barred Cuckoo-shrike	x	x	x
<i>Coracina maxima</i>	Ground Cuckoo-shrike	x	x	x
<i>Coracina novaehollandiae</i>	Black-faced Cuckoo-shrike	x	x	x
<i>Coracina papuensis</i>	White-bellied Cuckoo-shrike	x	x	x
<i>Coracina tenuirostris</i>	Cicadabird	x	x	x
<i>Corcorax melanorhamphos</i>	White-winged Chough	x	x	x

Scientific name	Common name	25 km ²	100 km ²	400 km ²
<i>Cormobates leucophaea</i>	White-throated Treecreeper	x	x	x
<i>Corvus tasmanicus</i>	Forest Raven	x	x	x
<i>Coturnix ypsilophora</i>	Brown Quail	x	x	x
<i>Cracticus nigrogularis</i>	Pied Butcherbird	x	x	x
<i>Cracticus torquatus</i>	Grey Butcherbird	x	x	x
<i>Cyclopsitta diophthalma</i>	Double-eyed Fig-Parrot		x	x
<i>Dacelo leachii</i>	Blue-winged Kookaburra	x	x	x
<i>Dacelo novaeguineae</i>	Laughing Kookaburra	x	x	x
<i>Daphoenositta chrysoptera</i>	Varied Sittella	x	x	x
<i>Dasyornis broadbenti</i>	Rufous Bristlebird	x	x	x
<i>Dicaeum hirundinaceum</i>	Mistletoebird	x	x	x
<i>Dicrurus bracteatus</i>	Spangled Drongo	x	x	x
<i>Drymodes brunneopygia</i>	Southern Scrub-robin	x		x
<i>Entomyzon cyanotis</i>	Blue-faced Honeyeater	x	x	x
<i>Eopsaltria australis</i>	Eastern Yellow Robin	x	x	x
<i>Eudynamys orientalis</i>	Eastern Koel	x	x	x
<i>Eurostopodus argus</i>	Spotted Nightjar	x	x	x
<i>Eurostopodus mystacalis</i>	White-throated Nightjar	x	x	x
<i>Eurystomus orientalis</i>	Dollarbird	x	x	x
<i>Falco longipennis</i>	Australian Hobby	x	x	x
<i>Falcunculus frontatus</i>	Crested Shrike-tit	x	x	x
<i>Geopelia cuneata</i>	Diamond Dove	x	x	x
<i>Geopelia humeralis</i>	Bar-shouldered Dove	x	x	x
<i>Geopelia striata</i>	Peaceful Dove	x	x	x
<i>Gerygone albogularis</i>	White-throated Gerygone	x	x	x
<i>Gerygone fusca</i>	Western Gerygone	x	x	x
<i>Gerygone levigaster</i>	Mangrove Gerygone	x	x	x
<i>Gerygone mouki</i>	Brown Gerygone	x	x	x
<i>Gerygone palpebrosa</i>	Fairy Gerygone		x	x
<i>Glossopsitta concinna</i>	Musk Lorikeet	x	x	x
<i>Glossopsitta porphyrocephala</i>	Purple-crowned Lorikeet	x	x	x
<i>Glossopsitta pusilla</i>	Little Lorikeet	x	x	x
<i>Glyciphila melanops</i>	Tawny-crowned Honeyeater	x	x	x
<i>Grantiella picta</i>	Painted Honeyeater	x	x	x
<i>Hieraaetus morphnoides</i>	Little Eagle	x	x	x
<i>Lalage leucomela</i>	Varied Triller	x	x	x
<i>Lalage sueurii</i>	White-winged Triller	x	x	x

Scientific name	Common name	25 km ²	100 km ²	400 km ²
<i>Lathamus discolor</i>	Swift Parrot	x	x	x
<i>Leucosarcia picata</i>	Wonga Pigeon	x	x	x
<i>Lichenostomus chrysops</i>	Yellow-faced Honeyeater	x	x	x
<i>Lichenostomus cratitius</i>	Purple-gaped Honeyeater	x	x	x
<i>Lichenostomus fasciogularis</i>	Mangrove Honeyeater		x	
<i>Lichenostomus fuscus</i>	Fuscous Honeyeater	x	x	x
<i>Lichenostomus leucotis</i>	White-eared Honeyeater	x	x	x
<i>Lichenostomus melanops</i>	Yellow-tufted Honeyeater	x	x	x
<i>Lichenostomus ornatus</i>	Yellow-plumed Honeyeater	x	x	x
<i>Lichenostomus penicillatus</i>	White-plumed Honeyeater	x	x	x
<i>Lichenostomus virescens</i>	Singing Honeyeater	x	x	x
<i>Lichmera indistincta</i>	Brown Honeyeater	x	x	x
<i>Lophochroa leadbeateri</i>	Major Mitchell's Cockatoo	x	x	
<i>Lophoictinia isura</i>	Square-tailed Kite	x	x	x
<i>Lopholaimus antarcticus</i>	Topknot Pigeon	x	x	x
<i>Macropygia amboinensis</i>	Brown Cuckoo-Dove	x	x	x
<i>Malurus cyaneus</i>	Superb Fairy-wren	x	x	x
<i>Malurus lamberti</i>	Variegated Fairy-wren	x	x	x
<i>Malurus melanocephalus</i>	Red-backed Fairy-wren	x	x	x
<i>Malurus splendens</i>	Splendid Fairy-wren	x	x	x
<i>Manorina flavigula</i>	Yellow-throated Miner	x	x	x
<i>Manorina melanocephala</i>	Noisy Miner	x	x	x
<i>Manorina melanophrys</i>	Bell Miner	x	x	x
<i>Melanodryas cucullata</i>	Hooded Robin	x	x	x
<i>Meliphaga lewinii</i>	Lewin's Honeyeater	x	x	x
<i>Melithreptus albogularis</i>	White-throated Honeyeater	x	x	x
<i>Melithreptus brevirostris</i>	Brown-headed Honeyeater	x	x	x
<i>Melithreptus gularis</i>	Black-chinned Honeyeater	x	x	x
<i>Melithreptus lunatus</i>	White-naped Honeyeater	x	x	x
<i>Menura alberti</i>	Albert's Lyrebird		x	x
<i>Menura novaehollandiae</i>	Superb Lyrebird	x	x	x
<i>Merops ornatus</i>	Rainbow Bee-eater	x	x	x
<i>Microeca fascinans</i>	Jacky Winter	x	x	x
<i>Monarcha melanopsis</i>	Black-faced Monarch	x	x	x
<i>Myiagra cyanoleuca</i>	Satin Flycatcher	x	x	x
<i>Myiagra inquieta</i>	Restless Flycatcher	x	x	x
<i>Myiagra rubecula</i>	Leaden Flycatcher	x	x	x

Scientific name	Common name	25 km ²	100 km ²	400 km ²
<i>Myzomela obscura</i>	Dusky Honeyeater	x	x	x
<i>Myzomela sanguinolenta</i>	Scarlet Honeyeater	x	x	x
<i>Neochmia modesta</i>	Plum-headed Finch		x	x
<i>Neochmia temporalis</i>	Red-browed Finch	x	x	x
<i>Neophema elegans</i>	Elegant Parrot		x	x
<i>Neophema pulchella</i>	Turquoise Parrot	x	x	x
<i>Ninox connivens</i>	Barking Owl	x	x	x
<i>Ninox novaeseelandiae</i>	Southern Boobook	x	x	x
<i>Ninox strenua</i>	Powerful Owl	x	x	x
<i>Northiella haematogaster</i>	Blue Bonnet	x	x	x
<i>Nymphicus hollandicus</i>	Cockatiel	x	x	x
<i>Oreoica gutturalis</i>	Crested Bellbird	x	x	x
<i>Origma solitaria</i>	Rockwarbler	x	x	x
<i>Oriolus sagittatus</i>	Olive-backed Oriole	x	x	x
<i>Orthonyx temminckii</i>	Australian Logrunner	x	x	x
<i>Pachycephala inornata</i>	Gilbert's Whistler	x	x	x
<i>Pachycephala olivacea</i>	Olive Whistler	x	x	x
<i>Pachycephala pectoralis</i>	Golden Whistler	x	x	x
<i>Pachycephala rufiventris</i>	Rufous Whistler	x	x	x
<i>Pardalotus punctatus</i>	Spotted Pardalote	x	x	x
<i>Pardalotus striatus</i>	Striated Pardalote	x	x	x
<i>Petrochelidon nigricans</i>	Tree Martin	x	x	x
<i>Petroica boodang</i>	Scarlet Robin	x	x	x
<i>Petroica goodenovii</i>	Red-capped Robin	x	x	x
<i>Petroica phoenicea</i>	Flame Robin	x	x	x
<i>Petroica rodinogaster</i>	Pink Robin	x	x	x
<i>Petroica rosea</i>	Rose Robin	x	x	x
<i>Phaps chalcoptera</i>	Common Bronzewing	x	x	x
<i>Phaps elegans</i>	Brush Bronzewing	x	x	x
<i>Philemon citreogularis</i>	Little Friarbird	x	x	x
<i>Philemon corniculatus</i>	Noisy Friarbird	x	x	x
<i>Phylidonyris niger</i>	White-cheeked Honeyeater	x	x	x
<i>Phylidonyris novaehollandiae</i>	New Holland Honeyeater	x	x	x
<i>Phylidonyris pyrrhopterus</i>	Crescent Honeyeater	x	x	x
<i>Pitta versicolor</i>	Noisy Pitta	x	x	x
<i>Platycercus adscitus</i>	Pale-headed Rosella	x	x	x
<i>Platycercus elegans</i>	Crimson Rosella	x	x	x

Scientific name	Common name	25 km ²	100 km ²	400 km ²
<i>Platycercus eximius</i>	Eastern Rosella	x	x	x
<i>Plectorhyncha lanceolata</i>	Striped Honeyeater	x	x	x
<i>Podargus ocellatus</i>	Marbled Frogmouth	x	x	x
<i>Podargus strigoides</i>	Tawny Frogmouth	x	x	x
<i>Polytelis swainsonii</i>	Superb Parrot	x	x	x
<i>Pomatostomus superciliosus</i>	White-browed Babbler	x	x	x
<i>Pomatostomus temporalis</i>	Grey-crowned Babbler	x	x	x
<i>Psephotus haematonotus</i>	Red-rumped Parrot	x	x	x
<i>Psephotus varius</i>	Mulga Parrot			x
<i>Psophodes olivaceus</i>	Eastern Whipbird	x	x	x
<i>Ptilinopus magnificus</i>	Wompoo Fruit-Dove	x	x	x
<i>Ptilinopus regina</i>	Rose-crowned Fruit-Dove	x	x	x
<i>Ptilinopus superbus</i>	Superb Fruit-Dove	x	x	x
<i>Ptilonorhynchus maculatus</i>	Spotted Bowerbird	x	x	x
<i>Ptilonorhynchus violaceus</i>	Satin Bowerbird	x	x	x
<i>Ptiloris paradiseus</i>	Paradise Riflebird	x	x	x
<i>Purnella albifrons</i>	White-fronted Honeyeater	x	x	x
<i>Pycnoptilus floccosus</i>	Pilotbird	x	x	x
<i>Rhipidura albiscapa</i>	Grey Fantail	x	x	x
<i>Rhipidura rufifrons</i>	Rufous Fantail	x	x	x
<i>Scythrops novaehollandiae</i>	Channel-billed Cuckoo	x	x	x
<i>Sericornis citreogularis</i>	Yellow-throated Scrubwren	x	x	x
<i>Sericornis frontalis</i>	White-browed Scrubwren	x	x	x
<i>Sericornis magnirostra</i>	Large-billed Scrubwren	x	x	x
<i>Sericulus chrysocephalus</i>	Regent Bowerbird	x	x	x
<i>Smicromnis brevirostris</i>	Weebill	x	x	x
<i>Sphecotheres vieillotii</i>	Australasian Figbird	x	x	x
<i>Stagonopleura bella</i>	Beautiful Firetail	x	x	x
<i>Stagonopleura guttata</i>	Diamond Firetail	x	x	x
<i>Stipiturus malachurus</i>	Southern Emu-wren	x	x	x
<i>Strepera graculina</i>	Pied Currawong	x	x	x
<i>Strepera versicolor</i>	Grey Currawong	x	x	x
<i>Struthidea cinerea</i>	Apostlebird	x	x	x
<i>Sugomel niger</i>	Black Honeyeater	x	x	x
<i>Symposiarchus trivirgatus</i>	Spectacled Monarch	x	x	x
<i>Todiramphus macleayi</i>	Forest Kingfisher	x	x	x
<i>Todiramphus pyrrhopygius</i>	Red-backed Kingfisher	x	x	x

Scientific name	Common name	25 km²	100 km²	400 km²
<i>Todiramphus sanctus</i>	Sacred Kingfisher	x	x	x
<i>Tregellasia capito</i>	Pale-yellow Robin	x	x	x
<i>Trichoglossus chlorolepidotus</i>	Scaly-breasted Lorikeet	x	x	x
<i>Trichoglossus haematodus</i>	Rainbow Lorikeet	x	x	x
<i>Turnix melanogaster</i>	Black-breasted Button-quail		x	
<i>Turnix varius</i>	Painted Button-quail	x	x	x
<i>Tyto novaehollandiae</i>	Masked Owl	x	x	
<i>Zoothera heinei</i>	Russet-tailed Thrush	x	x	x
<i>Zoothera lunulata</i>	Bassian Thrush	x	x	x
<i>Zosterops lateralis</i>	Silvereeye	x	x	x