Habitat heterogeneity: how it is generated and drives spatial patterns in mammals and birds

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Declaration

This thesis is my own work, except where otherwise acknowledged (see Preface and Acknowledgements).

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"Intuitively, the concept of heterogeneity is clear, but as we scrutinize it our initial impression fractures into complexity"

Kolasa and Rollo 1991

Preface

This thesis is structured as a series of connected manuscripts. With the exception of the Introduction, Paper 1 and the thesis synthesis, these papers have been published, accepted or submitted for publication at the time of the thesis submission. These papers are listed below and are referred to by their Arabic numerals in the text.

1. Stirnemann A.I., Gibbons P., & Lindenmayer D.B. How are we measuring vegetation heterogeneity and when is it biologically relevant? In Prep.
2. Stirnemann A.I., Gibbons P., Blanchard, W., Munro N.T., & Lindenmayer D.B. Effects of topographic variation and fire on habitat heterogeneity. *Landscape Ecology*. In review.
3. Stirnemann A.I., Ikin K., Gibbons P., Blanchard W. & Lindenmayer D.B (2014) Measuring habitat heterogeneity reveals new insights into bird community composition. *Oecologia*. 177: 733-746.
4. Stirnemann, A.I., Mortelliti A., Gibbons P., & Lindenmayer D.B. Fine-scale vegetation heterogeneity influences occupancy in terrestrial mammals. *PloSOne*. (accepted)
5. Stirnemann A.I., Barton P., Gibbons P., Lindenmayer D.B., & Blanchard W. Habitat heterogeneity peaks at intermediate levels of cover. *Ecology*. In review.

All papers were intended as stand-alone pieces of work. For this reason, there is some unavoidable repetition between chapters, for example in the description of study areas and experimental design. In line with The Australian National University's College of Medicine, Biology and Environment guidelines for 'Thesis by Compilation', a Context Statement has been provided at the beginning of this thesis. The Context Statement is not intended to be a complete literature review, but rather a framework for understanding the relationships between all aspects of the research.

I performed the majority of the work for the papers that form this thesis. This included developing the research questions, experimental designs, data collection, statistical analysis, and writing. My supervisors, Philip Gibbons, Wade Blanchard and David Lindenmayer made substantial contributions to the conceptualisation of research and revision of the manuscripts. Additionally, Wade Blanchard provided guidance on the statistical approach used in Papers 2, 3 and 5. Wade Blanchard also developed and ran a simulation model to examine the variables that contribute to the heterogeneity (i.e. deviance) metric (Paper 2, Supplementary Material). The co-authors of each paper also provided comments during the revision of manuscripts. Nicki Munro contributed to the conceptual development of ideas in Paper 2. Karen Ikin contributed to the conceptual development of ideas and guidance with the functional trait analyses used in Paper 3. Alessio Mortelliti provided guidance on the occupancy/detection analysis used in Paper 4. Philip Barton contributed to the conceptual development of ideas in Paper 5. Other assistance for each paper is acknowledged at the end of each paper.

Acknowledgements

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Abstract

Heterogeneity (variation) in vegetation structure is an inherent feature of all terrestrial ecosystems, characterises their structure, and influences the diversity and distribution of biota. Understanding how both the quantity and heterogeneity of a resource shapes the structure and dynamics of ecosystems is of fundamental importance in ecology. The concept of heterogeneity underpins some of the major theories in ecology, including species coexistence theory, source–sink dynamics, fractal theory, and invasion theory, and is important for conservation management. However, our understanding of the spatial distributions of plants and animals is typically underpinned by measures of abundance of the physical environmental (or habitat structural attributes), such as percentage cover, rather than measures of habitat heterogeneity.

In this thesis, I investigated how heterogeneity (variation) and the amount (cover) of habitat features drive spatial distributions in biota, and how spatial heterogeneity in habitat features is generated. First, I tested how heterogeneity of multiple habitat features at different spatial scales is generated by environmental (topography) and disturbance (fire) factors. Second, I tested the effects of both absolute cover and habitat heterogeneity on the spatial distribution of different taxa (birds and mammals). Last, I tested the relationship between heterogeneity of vegetation cover and the absolute amount of vegetation cover for binomial data.

I used a combination of landscape mapping, vegetation surveys, bird point counts and camera trapping within a naturally highly heterogeneous landscape to investigate how cover and heterogeneity of habitat feature influence biota and how it is generated. I found: 1) that heterogeneity of different habitat features is influenced by a variety of different fire and terrain attributes and their interactions, and that their effects can differ depending on the vegetation type and the scale at which variation is measured, 2) that fine-scale heterogeneity can have quite varied effects on biota, depending on the species, life-history traits and community of interest,

3) that both vegetation cover and vegetation heterogeneity contributed to the observed spatial distribution of mammals and birds, and 4) empirical evidence to support our hypothesis that vegetation heterogeneity peaks at intermediate levels of cover, which is consistent with the mean-variance relationship for binomial data

My findings highlighted that landscape ecologists should use a combination of environmental factors as surrogate measures of habitat heterogeneity if they are to develop robust predictive models that accurately describe multiple aspects of faunal habitat. Further, my results suggest that small-scale heterogeneity in terrestrial environments is as important as broad-scale landscape heterogeneity in generating spatial patterns in biota. Different communities and species may be adapted to tolerate different degrees of fine-scale heterogeneity – some may prefer highly heterogeneous environments while others would prefer highly homogenous environments.

My research provides strong quantitative support for the generality of a relationship between vegetation cover and heterogeneity which is potentially transferrable to other studies of ecosystem structure, and the distribution of associated biota. This relationship is likely to have important ramifications for understanding the mechanisms driving both quantity and spatial variation of vegetation and habitat, and the theoretical conceptualisation of ecosystem structure and function, as well as how we measure ecosystems to guide their management.

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Context Statement

Introduction

Spatial variation (heterogeneity) in vegetation structure is an inherent feature of ecosystems that characterises their structure and function (Li & Reynolds 1995; Hutchings, John & Stewart 2000; Ritchie 2010). Understanding how both the quantity and heterogeneity of a resource is formed and influences the structure and dynamics of ecosystems is therefore of fundamental importance in ecology (Benedetti-Cecchi 2003; Stein, Gerstner & Kreft 2014). The concept of heterogeneity underpins some major theories in ecology, including species coexistence theory (Chesson 2000), source–sink dynamics (Johnson 2004), fractal theory (Milne 1997; Ritchie 2010), and invasion theory (Melbourne et al. 2007). However, our understanding of the distributions of plants and animals is typically built upon measures of abundance of the physical environment (or habitat attributes), such as percentage cover (Fahrig et al. 2011), rather than measures of heterogeneity.

Vegetation heterogeneity at the fine-scale is considered to be an important factor affecting the spatial distribution of animals (Benton, Vickery & Wilson 2003; McElhinny et al. 2005). For instance, according to the habitat heterogeneity hypothesis (MacArthur & MacArthur 1961), resources and niches increase with increasing spatial heterogeneity (Pianka 1972; Bazzaz 1975). This is, in turn, believed to structure species richness patterns at a fine-scale by facilitating the co-existence of species (Jeltsch, Moloney & Milton 1999; Palmer 2003) and by providing habitat for species with multiple resource requirements (e.g. Perkins et al. 2000). Understanding how variance (heterogeneity), rather than only the absolute amount, of important habitat features is increasingly recognised as a new avenue for investigating cause-and-effect relationships in ecology (Benedetti-Cecchi 2003). However, few studies have investigated how both variation and absolute cover drive spatial patterning of different biota, despite an understanding of how habitat heterogeneity influences spatial patterns of different taxa being considered to be essential for developing both reserves and landscape management strategies.

If we are to appropriately manage habitat for fauna managers need to know which processes influence heterogeneity of the key habitat features which are important to fauna (Lindenmayer, Franklin & Fischer 2006). However, currently there is a lack of unity between the vegetation dynamics literature and the fauna habitat literature. For example, most studies that have examined how environmental factors (i.e. topography) and disturbance (i.e. fire) influence vegetation heterogeneity have tended to focus on the drivers of plant species diversity, especially plant species richness (e.g. Reynolds et al. 2003; Fraterrigo, Turner & Pearson 2006), or single habitat features (e.g. trees; Lindenmayer et al. 1991). However, from a faunal perspective, it is the heterogeneity of multiple key vegetation features, rather than only plant richness or a single structural feature, which is thought to have a major influence on the distribution and composition of the majority of fauna (Currie 1991; McElhinny et al. 2006). No studies, to our knowledge, have investigated how heterogeneity of multiple key habitat features is generated.

The overarching aim of my PhD research was to understand how habitat heterogeneity influences fauna spatial patterns and how it is generated. Specifically I asked: 1) How does habitat heterogeneity and absolute vegetation cover influence distribution patterns of different taxa (birds and mammals) within the landscape? And 2) What are the drivers of habitat heterogeneity within and between vegetation patches? To determine how habitat heterogeneity is generated and influences fauna, I established field sites within Booderee National Park, in south-eastern Australia. Booderee National Park was an ideal location for examining how heterogeneity of important habitat attributes is generated and its effect on biota. This is because this study area is a naturally heterogeneous environment which is composed of multiple distinct patchily distributed vegetation communities. A diverse range of birds and mammals is also found in relatively high numbers within the area.

Overview of research aims

In Paper 1, I examined current, peer-reviewed knowledge regarding the global effects of habitat heterogeneity on wildlife using a systematic review approach. This enabled me to determine which habitat heterogeneity metrics were most frequently used and how relevant these metrics are for biota. In Paper 2, I tested how heterogeneity of multiple habitat features at different spatial scales is generated by environmental (topography) and disturbance (fire) factors. In Papers 3 and 4, I tested the effects of both absolute cover and habitat heterogeneity on the spatial distribution of different taxa (birds and mammals). Lastly, in Paper 5, I tested the relationship between heterogeneity of vegetation cover and the absolute amount of vegetation cover for binomial data.

Methodology

All field monitoring sites used in my empirical papers were located in Booderee National Park in south-eastern Australia (Figure 1). This is a lowland region (< 170 m ASL) of undulating sandstone overlain by varying depths of deposited sand (Taylor, Abell & Jacobson 1995). Booderee National Park contains a variety of vegetation communities, including heathlands, woodlands and forest – these vegetation communities are patchily distributed within the study area. Booderee National Park has a complex history of repeated natural and prescribed fires. This variation in vegetation, topography and fire history has resulted in an extreme and unique degree of broad- and fine-scale heterogeneity of vegetation attributes (i.e. shrubs and trees). The study area also supports a diverse community of native Australian birds and mammal species.

All empirical research papers utilised the same study sites. To select the location of the sites, I stratified the study area by three variables: vegetation type (heathland, woodland, and forest), fire frequency (< 4 fires since 1937 and 4 to 8 fires since 1987), and slope (low [0.24-3.56 degrees] and high [3.57-15.02 degrees]). This approach allowed me to maximise the range of heterogeneity of habitat attributes across the sites, and also test a range of ecological theories that are associated with habitat heterogeneity (e.g. structural complexity hypothesis, and the habitat heterogeneity hypothesis).

I used a variety of statistical techniques for the analysis in each paper. These techniques included Generalised Linear Modelling (GLM; McCullagh & Nelder 1989), Occupancy modelling while accounting for detection probability (Fiske & Chandler 2011), Generalised Additive Modelling with regression splines (GAM; Wood 2006), and RLQ Analysis (Dolédec et al. 1996). All analysis was conducted using the R statistical package (R Core Team 2012).

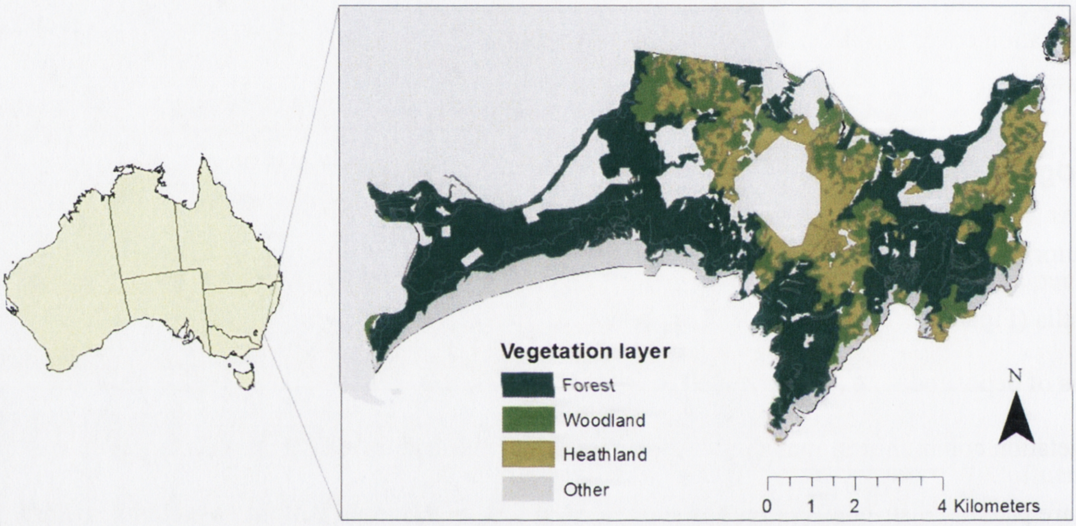

Figure 1. My study area in Booderee National Park is located on the East coast of Australia. It contains a variety of vegetation types, including forest, woodland and heathlands, which are patchily distributed throughout the park.

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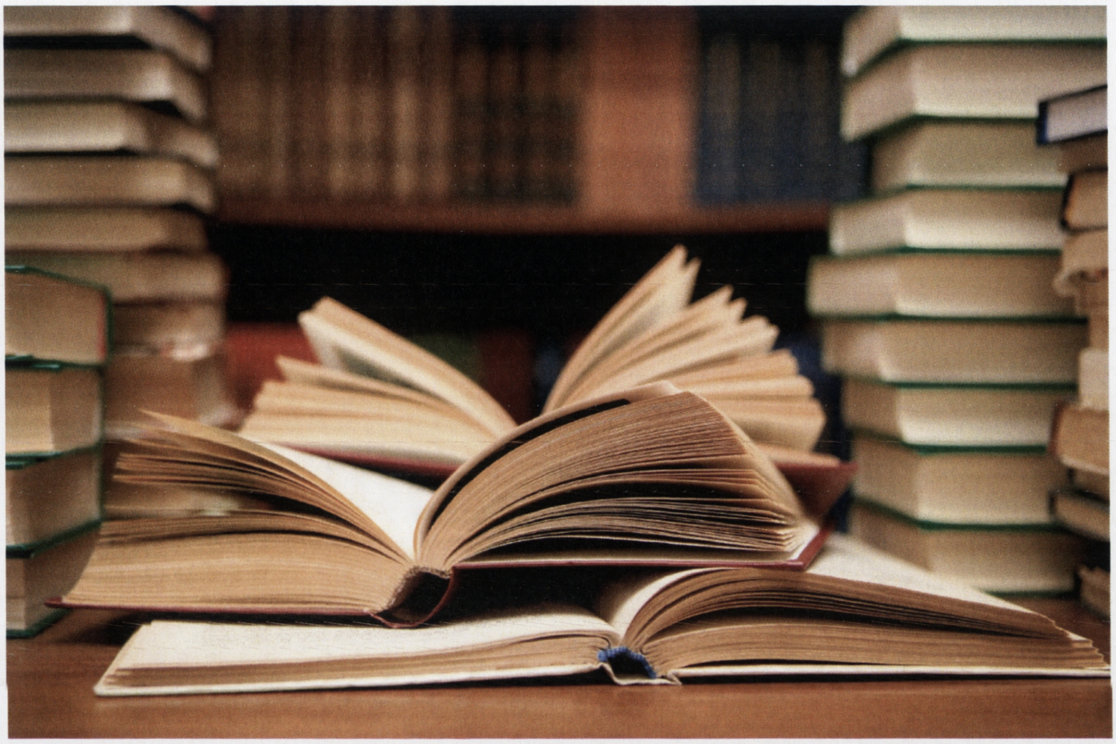
PAPER 1: How are we measuring vegetation heterogeneity and when is it biologically relevant?



We used the Web of Science database to search for articles published in English, between 1993 and December 2014, in which "habitat heterogeneity" appeared in either the abstract or as a keyword. From this database, we extracted 100 articles that included a measure of spatial heterogeneity of vegetation and an independent measure of biota.

Stirnemann A.I., Gibbons P., & Lindenmayer D.B. How are we measuring vegetation heterogeneity and when is it biologically relevant? In Prep.

Abstract

The heterogeneity of vegetation is a key factor influencing the abundance and diversity of biota and thus is an important characteristic of habitat to consider in conservation. Despite this, few articles have investigated how different forms of habitat heterogeneity are being measured and the circumstances regarding when these measures are biologically relevant. Here, we review the most common measurements used within the literature for demonstrating the spatial variation of vegetation within and between sites. Further, we examined the methods used to quantify vegetation heterogeneity (i.e. within and between sites) at different scales using remote-sensing and infield techniques and their biological relevance in association with different biodiversity measures (i.e. abundance and alpha diversity). Our results indicate that within-site measures of vegetation heterogeneity are measured less commonly than between-site heterogeneity measures. However, the probability of a biologically relevant finding was significantly higher when examining the effect of within-site heterogeneity, than between-site heterogeneity, when examining alpha diversity (within site species variation). Conversely, measures of between-site and within-site heterogeneity did not differ when examining species abundance. Thus, the biological relevance of the findings differed depending on the species diversity metrics and heterogeneity metrics utilised within an article. Moreover, we found that the spatial extent of a study area constrains the techniques used to measure habitat heterogeneity. The findings presented here demonstrate that: (1) there should be a focus on measures of habitat heterogeneity that reflect within-site vegetation heterogeneity rather than only measures that reflect between-site vegetation heterogeneity, particularly when examining the effect of heterogeneity on alpha diversity, and (2) we need to develop techniques for measuring fine-scale heterogeneity at broader spatial scales.

Keywords: *habitat heterogeneity hypothesis, review, spatial scale, extent, spatial variation, vegetation metrics*

Introduction

Understanding the spatial variation (heterogeneity) in biodiversity is central to community ecology and conservation biology (Legendre, Borcard & Peres-Neto, 2005; Wiens, Stenseth, Horne *et al.*, 1993). A key idea at the heart of this is the "habitat heterogeneity hypothesis", which predicts that increases in spatial heterogeneity of habitat will increase the amount of environmental resources available for biota, resulting in higher species numbers and community diversity through niche partitioning (Bazzaz, 1975; MacArthur & MacArthur, 1961; Smith, 1972). However, this relationship between habitat heterogeneity and biota is not evident in all studies (Allouche, Kalyuzhny, Moreno-Rueda et al., 2012). The key to being able to better predict and understand what drives the differences in the heterogeneity/diveristy relationship, may emerge from combining sampling theory with an understanding of the factors that influence different measures of biota (i.e. species abundance distributions, diversity metrics).

Habitat heterogeneity can be described using a variety of different measures and sampling procedures (Stein & Kreft, 2014b). A large problem (increasingly) for researchers is how to choose which of the dozens of possible habitat heterogeneity measures are biologically relevant (Stein & Kreft, 2014b), such decisions can be very important when there are limited degrees of freedom available for developing predictive models – as researchers typically need to make choices regarding which measures to include or exclude within a statistical model (Austin 2007, Kearney 2006). Broadly measures of habitat heterogeneity can be grouped into two main categories, within- and between-site heterogeneity (defined in Table 1). It has been proposed that species diversity patterns in a landscape are influenced by both the heterogeneity of habitats within a site (i.e. within-site heterogeneity measures) and by the differentiation among those habitats (i.e. between-site heterogeneity measures) (Whittaker 1960; 1972). However, to our knowledge, nobody has examined the effect of how we sample or measure habitat heterogeneity on the various measures of biodiversity (e.g. abundance, occupancy and diversity [alpha and beta]; defined in Table 1).

Thus, the circumstances in which we should use different heterogeneity and biodiversity measures remains poorly understood.

Frequently, it is heterogeneity in vegetation that is of ecological interest (Brambilla, Guidali & Negri, 2008; Castaño-Villa, Ramos-Valencia & Fontúrbel, 2014; Kerr, 2001), although other abiotic parameters also may be of interest, such as soil moisture or topography (e.g. Burnett, August, Brown *et al.*, 1998; Schlesinger, Raikes, Hartley *et al.*, 1996). Spatial heterogeneity of vegetation can be evaluated at any spatial scale within a landscape, ranging from nanometers to thousands of kilometers (Forman & Gordon, 1981) and in any dimension of space (e.g., horizontally or vertically; Roth, 1976).

There are two common techniques for measuring vegetation heterogeneity at different scales. First, *in-situ* field survey techniques (hereby in-field techniques, defined in Table 1) measure variation at the level of a field site at local scales (Bar-Massada & Wood, 2014; Castaño-Villa *et al.*, 2014; Fischer, Lindenmayer & Cowling, 2004). Second, remote-sensing techniques (defined in Table 1) are used to detect and measure vegetation heterogeneity from local to global scales (Kerr, 2001; López-González, Presley, Lozano *et al.*, 2014; Robinson, Kadlec, Bowers *et al.*, 2014). These two measurement techniques are often complementary (e.g. Katayama, Amano, Naoe *et al.*, 2014; Levin, McAlpine, Phinn *et al.*, 2009; Miyashita, Suzuki, Takada *et al.*, 2007). However, both techniques have limitations. For example, measuring vegetation heterogeneity within a site using in-field techniques is often time consuming and logistically difficult because a single measure of heterogeneity, such as variance in tree heights, may be calculated only by measuring multiple entities or plots (Huang, Swatantran, Dubayah *et al.*, 2014). In contrast, attributes measured using remote-sensing techniques are easily geo-referenced and made spatially explicit. However, remotely sensed images are typically too coarse in resolution to provide a detailed and accurate local assessment of many vegetation attributes (Guisan et al., 2005; but see Huang et al., 2014), although with technological advances this constraint is rapidly becoming less of a problem.

Habitat heterogeneity is scale dependent (Tamme, Hiiesalu, Laanisto *et al.*, 2010; Turner, Gardner, Dale *et al.*, 1989; Wiens, 1989). Different plants and animals are affected by habitat features at different scales depending on their physiology, and life history (e.g. Cole, Pollock, Robertson *et al.*, 2010; Katayama *et al.*, 2014; Kumar, Stihlgren & Chong, 2006; McIntyre, 1997). There are three main spatial scale components which are used when measuring habitat heterogeneity: the spatial extent, the grain and the focal scale (defined in Table 1). Although, the focal size and grain can be identical within a study; the focal size refers to the scale at which data are aggregated for analysis (Whittaker, 2010). It is important to understand the spatial scale at which different habitat heterogeneity measures are quantified and constrains studies, if we are to fully understand species-environmental variation relationships.

If a vegetation heterogeneity measure is biologically relevant at a particular scale, we should be able to detect an effect on biota (Turner, 2005). Furthermore, different methods of measurement, such as within- and between-site heterogeneity, may have different statistical power to effectively describe vegetation heterogeneity at different scales, and associations with different taxa. Previous reviews have shown a taxonomic bias in habitat heterogeneity-diversity studies (Stein *et al.*, 2014b; Tews, Brose, Grimm *et al.*, 2004), but it is not currently known under what circumstances the usage of particular biodiversity species metrics (i.e. abundance, beta diversity or alpha diversity) or measures of vegetation heterogeneity are more appropriate.

Here, we reviewed the usage of different measures of vegetation heterogeneity within the ecological literature. To understand the circumstances in which measures of habitat heterogeneity are biologically relevant, and how spatial scale constrains these different measures, we asked four main questions: (1) How is spatial heterogeneity of vegetation measured in ecological studies? (2) At what scales are these measured and how are measures constrained by the methods used? And (3) What evidence is there that heterogeneity measures are biologically relevant to biota?

Table 1. Key heterogeneity, measurement techniques, spatial scale and biodiversity measure terms

	Meaning
Heterogeneity	
Vegetation heterogeneity	Variation or dissimilarity in vegetation across space
Habitat heterogeneity	Variation or dissimilarity in a suitable features in the environment which has a positive association with a species
Measurement Techniques	
Remote-sensing	Acquisition of information to detect and classify an object or phenomenon using aerial sensor technologies
In-field	Acquisition of information about an object or phenomenon obtained from on-site observation or measurements
Spatial scale	
Extent	Overall geographical area of a study
Grain	Size of the individual units of observation
Focus	Inference space used in the analysis. The focal size and grain can be identical or may refer to the scale at which data are combined for analysis
Biodiversity measures	
Alpha diversity	Species variation between sites - richness, diversity metric (i.e. Simpson's diversity) and evenness of individual biota within a habitat unit
Beta Diversity	
	Species variation within a habitat unit
Abundance	
	Number of a particular species within a habitat unit
Occupancy	
	Presence/absence of species within a habitat unit

Methods

Literature search

We used the Web of Science database to search for articles published in English, between 1993 and April 2015, in which "habitat heterogeneity" appeared in either the abstract or as a keyword. We focused only on the spatial aspects of habitat heterogeneity, and did not examine temporal heterogeneity. From this database, we extracted 100 articles that included a measure of spatial heterogeneity of vegetation and an independent measure of biota.

A measure of spatial vegetation heterogeneity was defined within our study as a measurement that quantified the variation or dissimilarity in a vegetation attribute at a single point in time (Li and Reynolds 1995). We did not collate data on studies that examined temporal vegetation heterogeneity (i.e. studies that examined a measure of variation or dissimilarity in a vegetation attribute at two or more time periods). Abiotic habitat features, such as elevation, slope, water depth, or disturbance effects (e.g. fire), were also not considered in the search, although these would be ecologically relevant for some biota and are sometimes used as surrogate measures or proxies of vegetation heterogeneity (e.g. Brunn et al 2001; Joly & Myers 2001). We discarded all articles that did not contain a measure of vegetation heterogeneity that met our definition.

How is heterogeneity of vegetation measured?

For each measure of spatial heterogeneity of vegetation that we identified, we recorded the measurement technique (i.e. remote-sensing or in-field techniques), and method of calculation (i.e. the way each metric was calculated). Based on the method of calculation, we divided each measure of vegetation heterogeneity into two categories: measures of within-site heterogeneity and measures of between-site heterogeneity. We defined a measure of within-habitat heterogeneity as a measure that quantified the variation within the sampling unit (i.e. a site). Examples of calculation methods for within-site heterogeneity included: the range, standard deviation, and coefficient of variation of vegetation, number of types of vegetation, and diversity of vegetation. We defined a measure of between-site heterogeneity as a measure that quantified the variation between sampling units (i.e. sites). Examples of calculation methods for between-site heterogeneity included: a measure of area, percent/proportion, density, and average height of vegetation. Many studies reported multiple measures of heterogeneity, which we recorded as separate data points for each study.

Scale of measurement

We recorded the extent (total area), focal scale (inference space used in analysis, i.e. a site), and the measurement technique used (remote-sensing or infield) per article. We estimated study extent using maps if it was not reported within a study. We plotted the study extent versus the focal scale per $\log_{10}$ km^2.

Taxonomic groupings

We screened each article for the biota (i.e. protozoa, fungi, plants, invertebrates and vertebrates) which was associated with a particular measure of habitat heterogeneity (i.e. between-site and within-site). Articles were further categorized by the type of vertebrates (i.e. birds, mammals, reptiles, fish and amphibians) and invertebrates within each study. Studies on invertebrates were divided into taxonomic orders and studies that examined multiple orders (i.e. arthropods).

Biological relevance

To determine the biological relevance of within-site and between-sites measures of habitat heterogeneity, we recorded the statistical associations between each measure and an independent measure of biodiversity (e.g. abundance, occupancy, alpha diversity [evenness, richness, Simpson's diversity] and beta diversity) using a 'vote-counting' method (Gates, 2002), with simple counts for respective categories to calculate the proportion of response variables within the different classes. We then divided these associations between those that had empirical support (i.e. was significant [$p \leq 0.05$] or was within 2 delta AIC of the top model; Burnham & Anderson, 1998; Zuur, Ieno, Walker *et al.*, 2009) and those not tested or not reported. The relationships between species occupancy and beta diversity measures were not used in any analysis as samples were either too few or to variable to analysis.

Analysis

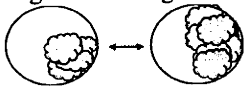
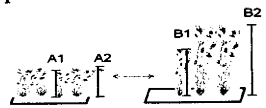
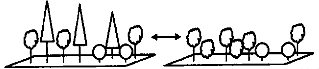
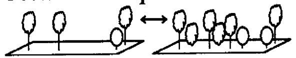
To determine if different measures influenced the probability of having a biologically relevant finding, we converted each categorical biodiversity response into binomial responses. We analysed these with binomial generalized linear mixed models, fitting, as fixed effects, the different taxonomic groups (invertebrates, vertebrates, and other [i.e. plants, fungi, lichen, and protozoa]), the measurement technique (remote-sensing and in-field technique), as well as the biodiversity measure (richness and abundance) and heterogeneity measure (within- and between-site) and their interaction, and article as a random effect (Zuur *et al.*, 2009). We tested if terms should be included in the final model using a likelihood ratio test (Zuur *et al.*, 2009). For our final model we then tested the significance of the different levels within each factor using a Tukey Kramer post hoc test (Tukey, 1949). Analyses were performed using the lme4 library (Bates, Maechler, Bolker *et al.*, 2014) and multcomp library with R (R Core Team, 2012). Articles were given equal weighting in the analyses.

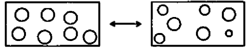
Results

How is heterogeneity of vegetation measured?

We recorded 644 different measures of vegetation heterogeneity from 100 empirical articles. We present the most common measures of within-site and between-site vegetation heterogeneity used within the sampled studies in Table 2. The majority of the measures of heterogeneity consisted of measures of between-site heterogeneity (*n* = 506), which comprised 78% of the total number of measures, whereas within-site heterogeneity measures (*n* = 138) comprised only 21% of the total measures (Table 2). The three most frequently used measurements of between-site vegetation heterogeneity were cover of vegetation, vegetation height and Euclidean distance between vegetation attributes. The three most common measures of within-site vegetation heterogeneity were number of vegetation types, vegetation textual measures and vegetation height. How these metrics were measured and quantified is described in detail below.

Table 2. The ten most common measures used to assess spatial heterogeneity of vegetation and the characteristics (Measure), and the number of types of measures (within-site or between-sites [# of metrics]) and techniques (remote-sensing [R] or in-field [F]) used to quantify each measure (Technique).

Measure	Schematic representation and description	Type of measure	# of metrics	Technique	Example source
Vegetation cover	Variation in the percentage or proportion of vegetation categories  E.g. Variation in the amount of grass cover within or between sites	Between-site	212	R=68 F=145	Cole 2010
		Within-site	3	R=0 F=3	Stirnemann et al 2014
Vegetation height heterogeneity	The variation in vegetation along a vertical plane  E.g. Variation in height of grasses within a sample unit (variation between A1 & A2) or between sample units (variation between A and B)	Between-site	35	R=6 F=29	Cole 2010
		Within-site	17	R=6 F=11	Huang et al 2014
Number of types of vegetation	The number of types of an entity within a sample unit  E.g. Variation in number of different plant species	Within-site	47	R=23 F=24	Baldi 2008
Number within an area (density)	The variation in the number of an entity between sample units  E.g. Variation in density of plant species between areas	Between-site	34	R=6 F=28	Baz & Gracia-Boyero 1995

Distance	Variation in the distance to vegetation attribute between sites E.g. Variation to the distance to closest forest patch in one sampling unit compared to another sampling unit	Between-site	35	R= 26 F=9	Bruun et al 2001
Vegetation textual image	The variation in spectral data in the surrounding designated area (focal scale)	Between-site	10	R=10 F=0	Hurlbert 2004
	E.g. Coefficient of variation calculated from image spectrum data within an area (within-site), or the mean within the area (between-site)	Within-site	21	R=21 F=0	Oindo and Skidmore 2002
Area of vegetation	Area is a variable that expresses the extent of a two-dimensional surface along the horizontal plane	Between-site	23	R=21 F=2	Bruun et al 2001
	 E.g. Variation in area of forest between sites or the std. dev. of forest patches in an area	Within-site	3	R=2 F=1	Levin et al 2009
Stand basal area	Area of a given section of land that is occupied by the cross-section of tree trunks and stems at their base	Between-site	13	R=4 F=9	Wilson et al 1997
	E.g. Live tree basal area (m2/ha) (between-site) or coefficient of variation of tree basal area (within-site)	Within-site	1	R=0 F=1	Castaño-Villa et al 2014
Shape index	Used to calculate the variation in shape between sample units. Can be adjusted for constant to account for a particular patch shape E.g. Ratio of perimeter to area of woodland edge	Between-site	13	R=13 F=0	Sergio et al 2005
Size structure	Used to calculate the variation in size of individual units of vegetation  E.g. Variation in the Diameter at Breast Height (DBH) of trees within an area	Within-site	10	R=0 F=10	Berg 1997

Between-habitat heterogeneity measures

Proportion/percentage vegetation cover

A measure of proportional or percentage vegetation cover was the most common approach used to infer between-site heterogeneity in vegetation (Table 2). When we compiled all measures used within our sample of the literature, measures of vegetation cover comprised 32.9% (*n* = 212) of all the recorded measures. Vegetation cover was measured using either remote-sensing techniques (*n* = 68) or in-field techniques (*n* = 145). Studies using remote-sensing techniques included measures of the cover of a dominant vegetation class (Janssen, Fortin & Hebert, 2009), and the vegetation cover of areas under different land uses (Bellis, Pidgeon, Radeloff *et al.*, 2008). Studies using in-field techniques to quantify the vegetation cover included measures of the proportion of an area covered by a particular plant species (Cole *et al.*, 2010) or group of plants (e.g. annual grass; Price, Edwards, Connors *et al.*, 2005). Of the 153 measures of between-site heterogeneity of vegetation cover that were tested for empirical support, 47.7% (*n* = 73) were associated with an independent measure of biodiversity. A measure of within-site heterogeneity of the proportion or percentage of vegetation cover was rarely measured (0.4% of total measures; *n* = 3) within the sampled studies.

Vegetation height heterogeneity

A measure of between-site height heterogeneity quantifies the difference in vegetation structure between sample units along a vertical plane. Vegetation height was the second most common measure used to quantify between-site vegetation heterogeneity (Table 2), used in 5.4% (*n* = 35) of all measurements of between-site vegetation heterogeneity. Studies used both remote-sensing (*n* = 6) and in-field techniques (*n* = 29) to quantify between-site height heterogeneity. Between-site height heterogeneity was calculated from the mean height of plant categories (i.e. grasses) within a sample unit. In both remote-sensing and in-field studies, vegetation categories were often further divided into height classes based on the height frequency clusters of the vegetation. For example, trees were divided into a mid-story and upper-story (Baz & Garcia-Boyero, 1995).

Distance

A measure of the Euclidean distance between vegetation variables (distance) was the third most common approach used to infer between-site heterogeneity in vegetation, used in 4.9% (*n* = 32) of all measurements of between-site vegetation heterogeneity (Table 2). Distance was measured using remote-sensing techniques (*n* = 23) and in-field techniques (*n* = 9). For example, remote-sensing techniques were used to measure the distance to the closest forest patch (Brosi, 2009), linear habitat (Wretenberg, Pärt & Berg, 2010), and to the forest edge (Miyashita *et al.*, 2007). In-field techniques were used to measure between different types of vegetation, such as grasses, herbs, shrubs, and trees (Dennis, Young & Gordon, 1998; Venkataraman, Shanker & Sukumar, 2005).

Within-habitat heterogeneity measures

Number of types of vegetation

A measure of the number of types of vegetation within a site is the most common approach used to infer within-site heterogeneity in vegetation (Table 2). A measure of the number of vegetation types comprised 7.2% (*n* = 47) of all measures recorded in the sampled articles, and was quantified using either remote-sensing techniques (*n* = 23) or in-field techniques (*n* = 24). For example, measures using remote-sensing techniques included the number of biomes (Kerr, 2001), land uses (Jeanneret, Schüpbach & Luka, 2003) and habitat types (Herzon & O'Hara, 2007) within an area. Examples of in-field measures included a count of the number of species of plants, (González-Megías, Gómez & Sánchez-Piñero, 2011), trees (Pinkus-Rendón, León-Cortés & Ibarra-Núñez, 2006), and macrophyte species (Choi, Jeong, Kim *et al.*, 2014) within a site.

Vegetation image texture

Vegetation image texture quantifies variation in vegetation spectral data within a designated area. Vegetation image texture was the second most common measure used to quantify vegetation within-site heterogeneity (Table 2) used in 5.2% (*n* = 19) of the sampled measures. A metric of within-site image texture heterogeneity can be calculated by measuring the variation (i.e. variance, homogeneity, contrast, entropy, dissimilarity or angular-second moment) among neighbouring pixels in the intensity or grey-scale values to measure the texture of a vegetation image. Currently, vegetation image texture is only measured using remote-sensing techniques (Oindo & Skidmore, 2002).

Vegetation height heterogeneity

A measure of within-site height heterogeneity quantifies the variation (e.g. standard deviation, coefficient of variation) in vegetation structure along a vertical plane within a given site. Height (i.e. vertical) heterogeneity was the third most common measure used to quantify within-site vegetation heterogeneity within the selected literature (Table 2), used in 2.6% ($n = 17$) of all measurements of vegetation heterogeneity. A measure of within-site height heterogeneity can be quantified using remote-sensing ($n = 6$) or in-field ($n = 11$) techniques. For example, remote-sensing techniques, such as Light detection and Ranging (LiDAR), can be used to directly characterise within-site heterogeneity in vegetation heights (Seavy, Viers & Wood, 2009).

Scale of measurement

Of the 100 articles examined, 10% ($n = 10$) did not document the spatial extent at which the study was undertaken. Where the spatial extent was documented, studies using remote-sensing techniques covered a scale between 10 to 100,000,000 km^2 ($n = 28$). In-field studies encompassed study areas with spatial scales at 1 to 10,000 km^2 ($n = 40$). A combination of techniques (in-field and remote sensing) was used on study sites of a spatial scale between 100 to 10,000 km^2 ($n = 22$). Therefore, only remote sensing techniques were used, for all studies reviewed with a spatial extent greater than 10,000 km^2 (Fig. 1). In studies using in-field techniques, the focal scale range covered a scale between 3650 m^2 to 2.25 km^2 ($n = 40$). In studies using remote-sensing techniques, the focal scale range covered a scale between 2 m^2 to 3136 km^2 ($n = 28$). In studies using a combination of techniques (in-field and remote-sensing) the focal scale range covered a scale between 2.5 cm^2 to 1357170 km^2 ($n = 22$).

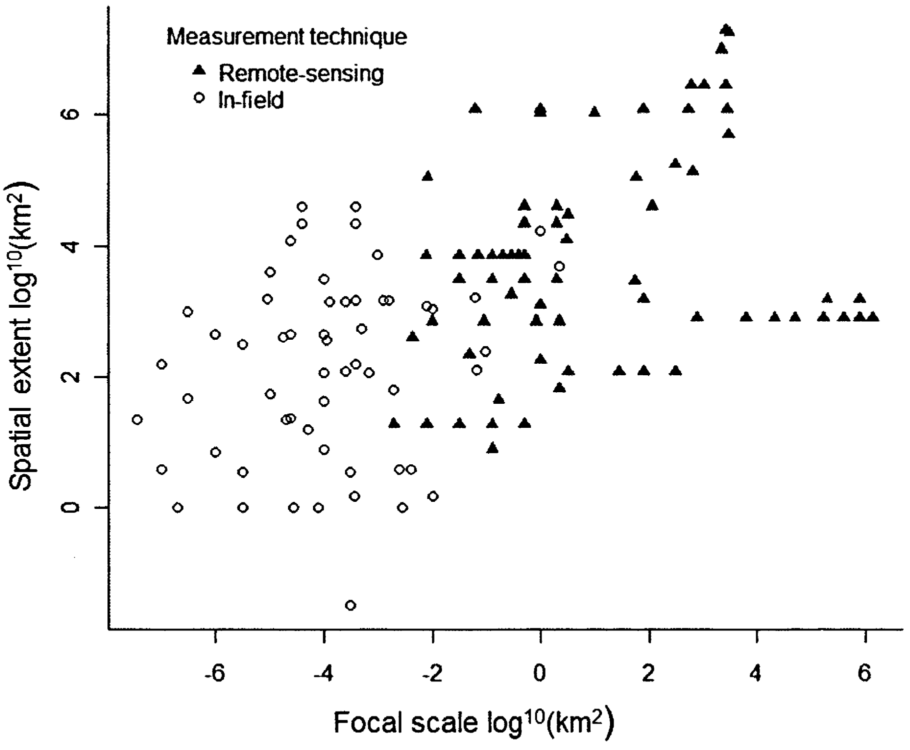


Figure 1. The extent (total area of each study) and focal (size of the individual units of observation) scale at which habitat heterogeneity is measured using remote-sensing and in-field techniques.

Taxonomic groupings

Of the 100 articles we examined, studies on vertebrates were the most commonly represented group (66%). Invertebrates comprised 30% of all publications, while the response of fungi, lichens and plants to vegetation heterogeneity was examined in only 4% of articles surveyed (Fig. 2). In the vertebrate grouping, birds were examined in 40% of studies, followed by 17% for mammals; reptiles (5%), fish (3%) and amphibians (3%). The frequency of publications that focused on different orders of invertebrates was more evenly distributed, with 5% of articles on butterflies and moths (Lepidoptera), 4% of articles on beetles (Coleoptera), 3% on bees and wasps (Hymenoptera), 3% of articles examined spiders (Araneae), and 1% on crickets and grasshoppers (Orthopteran). The majority of studies on invertebrates examined multiple orders (14%).

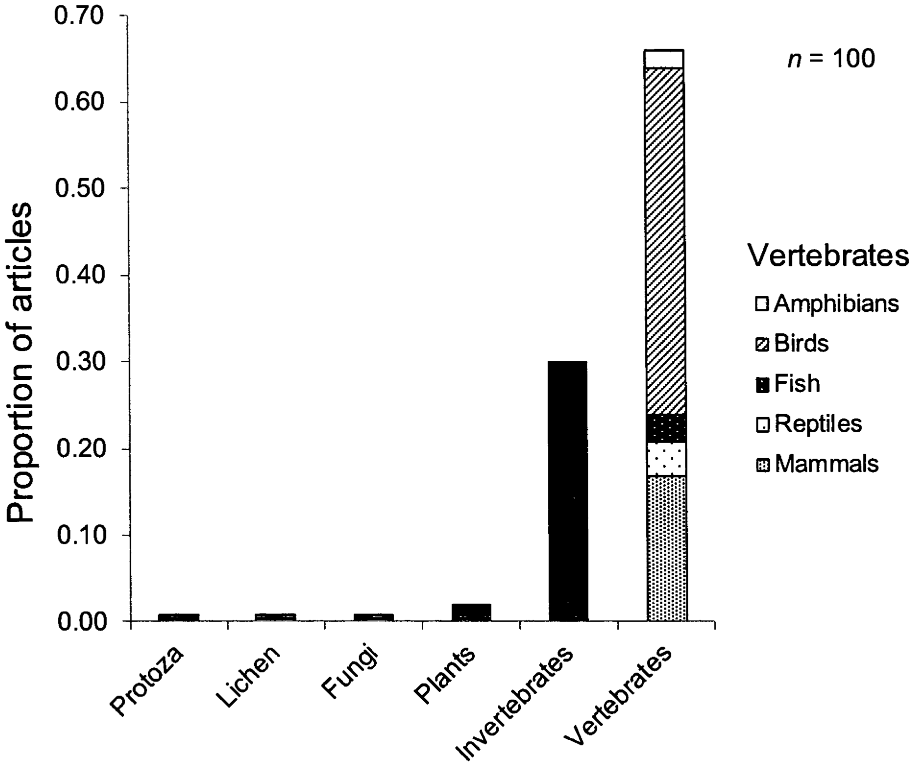


Figure 2. The proportion of articles between 1993 and 2015 that examined the influence of habitat heterogeneity on biota (protozoa, lichen, fungi, plants, invertebrates and vertebrates).

Biological relevance

We tested if the probability of a biologically relevant response was affected by the type of biodiversity measure used as a response variable (abundance and alpha diversity), measurement technique (remote-sensing and in-field), measure of heterogeneity (within- and between-site), and broad taxonomic grouping (invertebrates, vertebrate and others). We found that the probability of having a biologically relevant finding was explained by an interaction between the measures of heterogeneity and the biodiversity measures (Table 3). The probability of a biologically relevant finding was significantly higher when examining the effect of within-site heterogeneity, than between-site heterogeneity, when examining alpha diversity (Tukey HSD; p<0.05; Fig 3a). However, there was no significant difference in the probability of having a biologically relevant finding between heterogeneity measures when examining species abundance. Further, we found that the probability of a biologically relevant result was significantly higher for vertebrates than for invertebrates (Tukey HSD; p<0.05), and there was no significant difference between invertebrates and vertebrates with other taxa (Fig 3b). There was no evidence that measurement technique had any influence on the probability of a biological relevance response.

Table 3. a) Coefficient estimates (± SEs) and p values for the final model of the probability of biologically relevant findings. b) Coefficient estimates (± SEs) and p values for the pairwise Tukey comparisons of the each of factor levels for the measures of heterogeneity and measures of biodiversity, and c) taxonomic groupings. Significant values (p<0.05) in bold.

a)	Terms in final model	Coefficient ± SE	P
	(Intercept)	0.096 ± 0.407	0.812
	TAXA vertebrate	1.036 ± 0.408	**0.021**
	TAXA other	1.734 ± 0.757	0.011
	MH within-site	-0.575 ± 0.508	0.257
	MB richness	-0.521 ± 0.375	0.164
	MH within-site × MB alpha diversity	1.504 ± 0.583	**0.009**
b)	Pairwise Tukey comparisons	Coefficient ± SE	p
	within-site abundance vs. between-site abundance	-0.575 ± 0.508	0.663
	between-site alpha diversity vs. between-site abundance	-0.521 ± 0.375	0.498
	within-site alpha diversity vs. between-site abundance	0.407 ± 0.430	0.774
	between-site alpha diversity vs. within-site abundance	0.054 ± 0.482	0.999
	within-site alpha diversity s vs. within-site abundance	0.983 ± 0.498	0.193
	within-site alpha diversity vs. between-site alpha diversity	0.928 ± 0.330	**0.024**
		Coefficient ± SE	P
c)	other vs. invertebrates	1.734 ± 0.757	0.053
	vertebrates vs. invertebrates	1.036 ± 0.408	**0.027**
	vertebrates vs. other	-0.698 ± 0.733	0.597

The terms in the final model included three factors: broad taxonomic groupings (TAXA; invertebrates, vertebrate and other), measures of species biodiversity (MB; alpha diversity and abundance) and measures of heterogeneity (MH; within-site and between-site). Terms in the full model included four main effects and an interaction (between the measures of species biodiversity and measures of heterogeneity) represented by × and a random effect (article; *n* = 57).

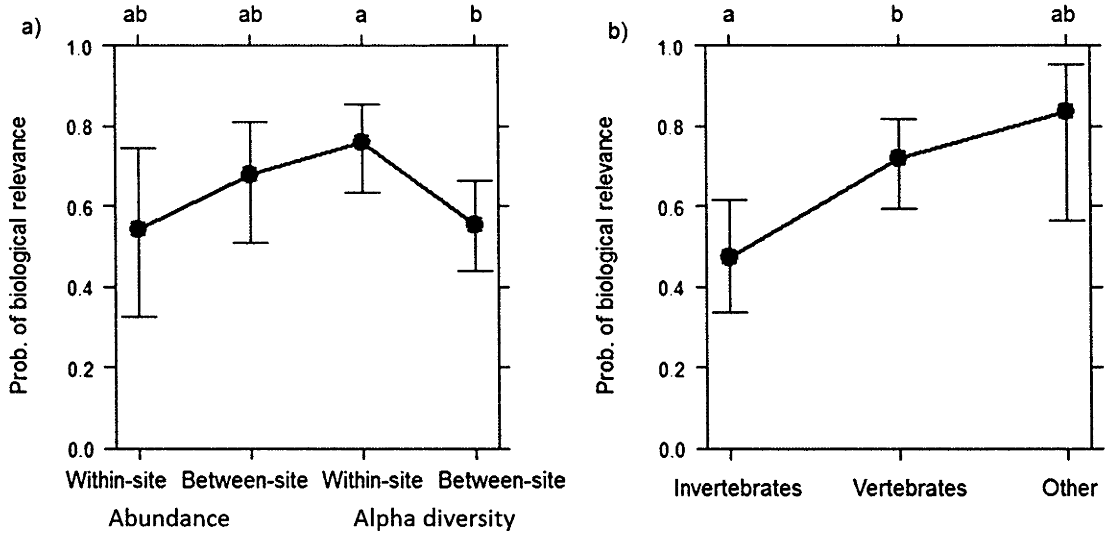


Figure 3. a) The probability of having a biologically relevant findings (± 95% CI) in relation: a) to an interaction between types of heterogeneity measurement (within-site and between-site) and the types of species diversity measures (abundance and alpha diversity), and b) to taxonomic groups (invertebrates, vertebrates and other (protozoa, lichen, fungi, and plants). The letters above each plot represent statistically similar pairwise Tukey comparisons of the each of factor levels. Model coefficient estimates (± SEs), and significance levels (p<0.05) are shown in Table 3.

Discussion

We examined the most common measures and types of habitat heterogeneity, the methods used to measure them, their biological relevance, and the scale at which habitat heterogeneity was examined in the literature. We found that: (1) within-site measures of vegetation heterogeneity are measured less commonly than between-site measures, (2) the proportion of biologically relevant results differed depending on both the species diversity metrics and heterogeneity metrics utilised within an article, and (3) the techniques used to measure heterogeneity can constrain the spatial extent of a study area or vice versa.

How is vegetation heterogeneity measured?

Our results indicated that while measures of between-site vegetation heterogeneity (i.e. the quantity of vegetation within a site) are routinely used as a response variable, comparatively, within-site measures of vegetation heterogeneity are seldom measured. Quantifying within-site vegetation heterogeneity is important because the underlying causal processes that influence vegetation, as well as the response of biota to vegetation can be obscured by measuring only the absolute quantity of a habitat feature (i.e. between–site measures) (Fraterrigo & Rusak, 2008). Therefore, by ignoring within-site vegetation variability, we risk overlooking key information about ecosystem function (Benedetti-Cecchi, 2005; Stirnemann, Ikin, Gibbons *et al.*, 2014).

We also found that some of the most common measures of between-site vegetation heterogeneity rarely quantified within-site vegetation heterogeneity (Table 2). For example, within our sampled studies, proportion/percentage of cover was the most commonly used measure of between-site vegetation heterogeneity (i.e. 32.9% of total measures). However, in contrast, we found that within-site heterogeneity was rarely explicitly measured (i.e. 3% of total measures). Accurately estimating the heterogeneity within an area can be more time consuming than estimating cover, particularly when using in-field techniques. For instance, a number of sub-plots are needed to accurately estimate the true heterogeneity of cover attributes within a plot, whereas the overall cover can be estimated fairly precisely with a smaller number of sample points. In contrast, the reason why within-site measures of proportion/percentage cover using remote-sensing techniques are rarely measured may relate to authors making a choice regarding what to include. For instance, when not everything can be included in a statistical model (due to limited degrees of freedom), they seem to choose measures of between-site heterogeneity. However, our findings suggest measures of within-site heterogeneity may deserve more attention in the future. Studies focusing on the effect of within-site measures, such as vegetation cover, on the spatial distribution of biota, as well as between-site measures may provide useful insights into how variation in vegetation attributes influences ecosystem dynamics.

Biological relevance

Our study is the first to show empirically, that the proportion of biologically relevant results is affected by the heterogeneity metrics and species biodiversity measures utilised (Fig 3 and Table 3). For instance, we found the probability of having a biologically relevant finding was significantly higher when examining the effect of within-site heterogeneity, than between-site heterogeneity, when examining alpha diversity. Conversely, the effect of heterogeneity measures on the biological relevance of either measure was not significantly different when examining species abundance. This finding may be because different biodiversity metrics represent fundamentally different features of a biological assemblage (Chiarucci, Bacaro & Scheiner, 2011), and are influenced by the availability of different resources and factors in the environment. For instance, according to the habitat heterogeneity theory, alpha diversity is proportional to the amount of niches available (Bazzaz, 1975; MacArthur *et al.*, 1961; Smith, 1972). Hence, the relative effect of a measure of heterogeneity on alpha diversity is likely to depend on how well a heterogeneity measures characterises niche availability. Thus, our results indicate that within-heterogeneity measures characterise niche availability better than between-site measures. This finding suggests that it is worthwhile to include with-site heterogeneity measures more routinely in studies of diversity and distribution.

In past studies species biodiversity metrics have been combined within meta-analyses (e.g. Tews et al., 2004). Our findings indicate, as advocated by Whittaker (2010; 2001) and Stein, Gerstner and Kreft (2014a), the importance of distinguishing between the different types of biodiversity response measure used within a meta-analysis, especially when examining habitat heterogeneity. Future studies should investigate the relationship between between-site heterogeneity and beta diversity, as it could be that between-site heterogeneity is very important when it comes to explaining beta diversity (species variation between sites), or even gamma diversity (total diversity within a study system). we were unable to investigate this is our study due to a small sample size.

Scale and measurement technique

Our results indicated that when in-field techniques are used to measure vegetation heterogeneity, a relatively smaller spatial area (extent) is used than studies using only remote-sensing techniques (Fig 1). A synthesis of work on the spatial grain of in-field studies by Kareiva and Anderson (1988) illustrated that the grain of studies can be constrained by the duration of a study. Our investigation demonstrates how the extent and focal scale of a study is also constrained by the measurement techniques or vice versa. A constraint of scale (extent, focal or grain) can affect what measures can be used, the types of heterogeneity that can be measured (Tews *et al.*, 2004), and the interpretation of spatial patterns (e.g. see Van Horn, 2002). Our results also show a tendency for studies to examine heterogeneity at particular scales (Fig. 1). Understanding that the extent of a study sets the upper and lower limits of the focal scale (inference space used in analysis) is important, as a bias for particular spatial scales or a constraint of the study extent also can limit what questions and theories can be examined (Barton, Cunningham, Manning *et al.*, 2013).

The findings presented here demonstrate that (1) there should be a focus on measures of habitat heterogeneity that reflect within-site vegetation heterogeneity rather than only measures that reflect between-site vegetation heterogeneity, particularly if alpha diversity is of interest, and (2) we need to develop techniques for measuring fine-scale heterogeneity at broader spatial scales. This would allow researchers to derive more accurate associations between vegetation spatial heterogeneity and the diversity of a range of different taxa.

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Supplementary material

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PAPER 2: Effects of environmental variation and disturbance on habitat heterogeneity

Booderee National Park in south-eastern Australia is a naturally heterogeneous environment with several distinct vegetation types and has over 70 years of spatially explicit fire records.

Stirnemann A.I., Gibbons P., Blanchard, W., Munro N.T., & Lindenmayer D.B. Effects of topographic variation and fire on habitat heterogeneity. Landscape Ecology. In review.

Abstract

Habitat heterogeneity is of critical importance for many fauna. Identifying the scales at which the physical environment (e.g. topography) and disturbance (e.g. fire regime) affects habitat heterogeneity is critical for quantifying and predicting the distribution of fauna and is necessary to appropriately manage habitat for fauna. We asked: 1) Which topographic features and fire variables influence habitat heterogeneity? And, 2) Do the associations between topographic features and fire variables and habitat heterogeneity change with spatial scale? Using a stratified random design we examined how the heterogeneity of nine habitat variables derived from vegetation (i.e. leaf litter, grasses, sedges, ferns, grass trees, shrubs, medium sized trees and tall trees) is affected by topography (slope, aspect, elevation) and fire regime (interval and severity) at a landscape-scale (i.e. between patches) and at a fine-scale (i.e. within patches) within a naturally heterogeneous environment in south-eastern Australia. Seven of nine habitat variables were significantly associated with at least one of the fire and topographic variables we measured. The direction and significance of these associations differed depending on the scale at which we measured heterogeneity. Our study showed that habitat heterogeneity cannot be described by a single environmental or disturbance variable. Our results indicate that landscape ecologists should use a combination of environmental factors as surrogate measures of habitat heterogeneity, if they are to develop robust predictive models that accurately describe multiple aspects of fauna habitat. Our findings provide a guide for using fire and topography to restore and manage heterogeneity of key habitat features at different spatial scales.

Keywords: *spatial heterogeneity; vegetation cover; variation; fire; topography; scale; surrogate*

Introduction

All ecosystems are variable across space (Levin 1992) and the term heterogeneity is used in ecology to describe this spatial patchiness and variability (Benton et al. 2003). The physical structure of most ecosystems is determined by soil type, geology, climate and vegetation (Grime 2001). Heterogeneity in vegetation also influences the occurrence, abundance and richness of fauna (e.g. Berg 1997; Levin et al. 2009; Schooley and Branch 2007). For instance, an increase in the degree of heterogeneity of vegetation results in greater niche diversity and an increase in the numbers of coexisting species in a landscape (Bazzaz 1975; MacArthur and MacArthur 1961; Smith 1972). The spatial patterning of vegetation heterogeneity in the landscape is also an important driver of the spatial patterns in biodiversity (Tews et al. 2004). Understanding the mechanisms influencing heterogeneity of habitat variables derived from vegetation is therefore of crucial concern when managing biodiversity (Hobbs 1997; Wiens et al. 1993).

Topographic features (e.g. slope, aspect, elevation) and fire regimes (e.g. fire interval and frequency) are recognized as key drivers of vegetation heterogeneity (Fraterrigo and Rusak 2008; Turner 1989). For example, fire interval can influence the proportion of cover of vegetation across the spatial extent of a disturbance (e.g. Wanthongchai et al. 2011; Watson et al. 2009). Topographic features can affect spatial heterogeneity of vegetation indirectly through their impacts on abiotic conditions (e.g. Huggett and Cheesman 2002; Neilson and Wullstein 1986; Oleksyn et al. 1998), as well as by interacting with disturbance processes such as fire (e.g. Alexander et al. 2006; Kushla and Ripple 1997). However, the majority of studies examining the factors influencing vegetation heterogeneity have tended to focus on the drivers of plant species diversity, especially plant species richness (e.g. Fraterrigo et al. 2006; Reynolds et al. 2003), or single habitat features (e.g. trees; Lindenmayer et al. 1991). However, from a faunal perspective, it is the heterogeneity of multiple key vegetation features, rather than only plant richness or a single structural feature that is thought to have a major influence on the distribution and composition of the majority of fauna (Currie 1991; McElhinny et al. 2006). Determining how multiple environmental features and their interactions drive spatial heterogeneity of key vegetation features is vital for: 1) providing a basis for management decisions, such as prescribed burning (Lindenmayer et al. 2006), and 2) building robust predictive models of species distributions (Austin 2007).

Identifying the scales at which the physical environment affects vegetation heterogeneity is necessary to predict and manage habitat for fauna because different biota function at different scales (Allen and Hoekstra 1992; Bar-Massada and Wood 2014). For instance, vegetation heterogeneity at fine scales (10's of metres) is important for animals that are not very mobile or occupy a small home range. Whereas, vegetation heterogeneity at broader scales (100's of metres to kilometres) can be important for animals that are very mobile or occupy a large home range (Wiens 1989). Many studies have examined how environmental surrogates (such as elevation) and disturbance regimes influence vegetation heterogeneity at broad scales, but we have little understanding of how vegetation heterogeneity varies among different spatial scales. For instance, most studies focus on understanding the influence of ecological processes on vegetation heterogeneity at the landscape-scale, or between vegetation patches (i.e. different classes of habitat) (Gustafson 1998; Turner 2005). These studies either consider each patch as a homogenous entity in terms of within-patch resources and structure (Forman 1995) or focus on homogenous areas deliberately avoiding highly heterogeneous areas (Lookingbill et al. 2011). There are few studies that have explicitly examined heterogeneity, as a measure of variation of vegetation cover (as opposed to the number of habitat types), at multiple scales (i.e. within and between patches).

We conducted a landscape-scale study to answer two key questions. First, we asked, which topographic features and fire variables influence habitat heterogeneity? We hypothesised that slope and aspect are important drivers of habitat heterogeneity as these features influence moisture or nutrient-limited vegetation (Specht and Specht 2002), whereas elevation will not because our study area has a low elevation range (0-105 m asl) (Huggett and Cheesman 2002; Neilson and Wullstein 1986; Oleksyn et al. 1998). We also hypothesised that fire interval and fire severity is important drivers of habitat heterogeneity because they can influence the cover of vegetation (Sousa 1984; Wanthongchai et al. 2011; Watson et al. 2009). We expected a combination of both fire **and** topographic features to be important because they interact and are drivers of vegetation heterogeneity in other systems (e.g. Alexander et al. 2006; Kushla and Ripple 1997). Second, we asked if associations between topographic features and fire variables and habitat heterogeneity change with spatial scale. We expected to see a greater effect of different topographic features and fire variables on habitat features at a landscape-scale (between patches) than at the fine-scale (within patches), as broad-scale mechanisms (such as fire and topography) can mask local-scale mechanisms (Hutchings et al. 2000; Lookingbill et al. 2011).

Our study landscape within Booderee National Park in south-eastern Australia was ideal for this study because this area is a naturally heterogeneous environment with several distinct vegetation types and has over 70 years of spatially explicit fire records. Our findings have strongest applicability to ecosystems with high spatial heterogeneity (i.e. ecosystems that contain multiple small patches, and different vegetation types), and which are influenced by frequent fire events. This includes areas in Australia, South Africa, the Mediterranean, Canada and the USA which are highly bio-diverse and subject to fire.

Methods

Study area

We conducted this study within Booderee National Park in the Jervis Bay Territory on the south coast of New South Wales, south-eastern Australia (approximate coordinates 35°10' S 150°40' E; Fig. 1). This is a lowland region (< 170 m ASL) of undulating sandstone overlain by varying depths of deposited sand (Taylor et al. 1995). This area is characterised by a temperate maritime climate, with average rainfall of approximately 1200 mm that is largely consistent over the year. Mean monthly temperature ranges from 17 °C to 26 °C. Our study area is dominated by contrasting vegetation types that differ in terms of their tree cover, including heathlands (no tree cover), woodlands (sparse tree cover) and forest (dense tree cover), which are patchily distributed within the park (Ingwersen 1977). The majority of the forest areas are dominated by eucalypt species (*Eucalyptus botryoides* and *E. pilularis*). The dominant crown cover in the woodland consisted of banksia (*Banksia integrifolia, B. serrata*) and eucalypt or *Corymbia* species (*Corymbia gummifera, E. sclerophylla,* and *E. sieberi*). The understorey of forest and woodland contains a range of shrubs, grass trees (*Xanthorrhoea* spp.), forbs, sedges, grasses and Austral Bracken (*Pteridium esculentum).* Heathlands are dominated by shrubs (*Baeckea imbricata, Allocasuarina distyla, B. ericifolia, Sprengelia incarnata* and *A. distyla*) and clumps of mallee-form (multi-stemmed) trees (*E. obstans*, *C. gummifera* and *E. sieberi*) (Taws 1997).

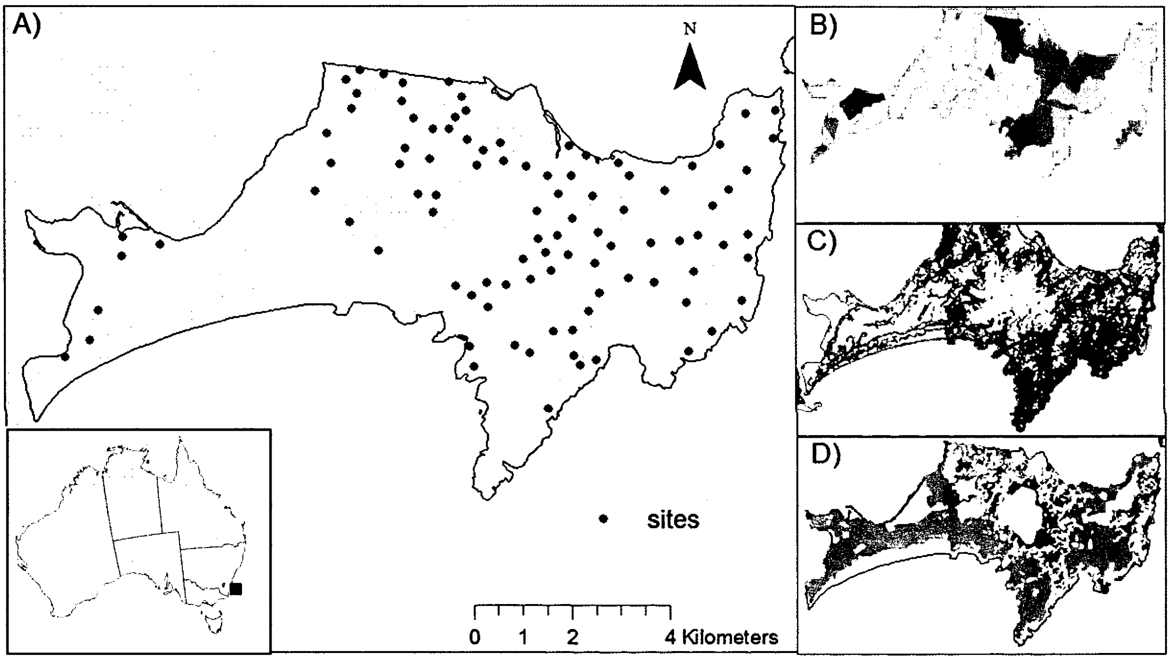

Figure 1. A) The location of each field site (*n* sites = 96) within Booderee National Park in south-eastern Australia was determined by randomly selecting an equal number of sites (*n*=8) within a stratified study area (12 levels). The study area was created by combining three spatial layers: B) fire frequency (two levels: 0 - 3 fire events [light greys] and 4-8 fire events [dark greys]), C) slope (two levels: high [dark grey] and low [light grey]) and D) vegetation type (3 levels: forest [medium grey], woodland [light grey] and heath [dark grey]). White areas indicate built up areas, prohibited land and other vegetation types.

Booderee National Park has a complex history of both natural and prescribed fires. Spatially-explicit records of the fire history of the Jervis Bay Territory date back to 1937 (DSEWPaC 2013). At the time of this study (2011), the number of fires recorded for any given area in the park varied from zero to eight fires between 1937 and 2010. The severity of the fires also has been variable, ranging from low-severity fires to high-severity events.

Study design

We stratified our study area by three variables: 1) fire frequency (representing a disturbance variable), 2) slope (representing a topographic variable), and 3) vegetation type. We converted fire frequency and slope to categorical variables to assist site selection. Fire frequency consisted of two categories (< 4 fires since 1937 and 4 to 8 fires since 1987), as did slope angle (low [0.24-3.56 degrees] and high [3.57-15.02 degrees]). Vegetation type consisted of three categories (forest, woodland and heath). These three factors are known to influence both the degree of vegetation heterogeneity and amount of vegetation cover within the landscape (e.g. Gandiwa 2011; Gould et al. 2006; Jin et al. 2008; Specht and Specht 2002). Our stratified approach enabled us to maximise the maximum possible range (i.e. very low and very high values) of both heterogeneity and cover of different vegetation variables across our sites. We randomly selected 96 sites (eight sites in each fire/slope/vegetation stratification treatment; Fig. 1) using random points in ArcGis (ESRI 2006).

Each site consisted of a circular plot with a 25 metre radius. Within each site, we established nine subplots, three on each of three radial lines (Fig. 2). Subplots also were evenly located 90, 210, or 330 cardinal degrees from the central point. Subplots (six meters long) were evenly distributed from the centre: 1) 4 to 9 m, 2) 12 to 17 m, and 3) 20 to 25 m. There was a four meter distance between subplots to minimise spatial dependence. Each subplot consisted of six sampling points each spaced one metre apart.

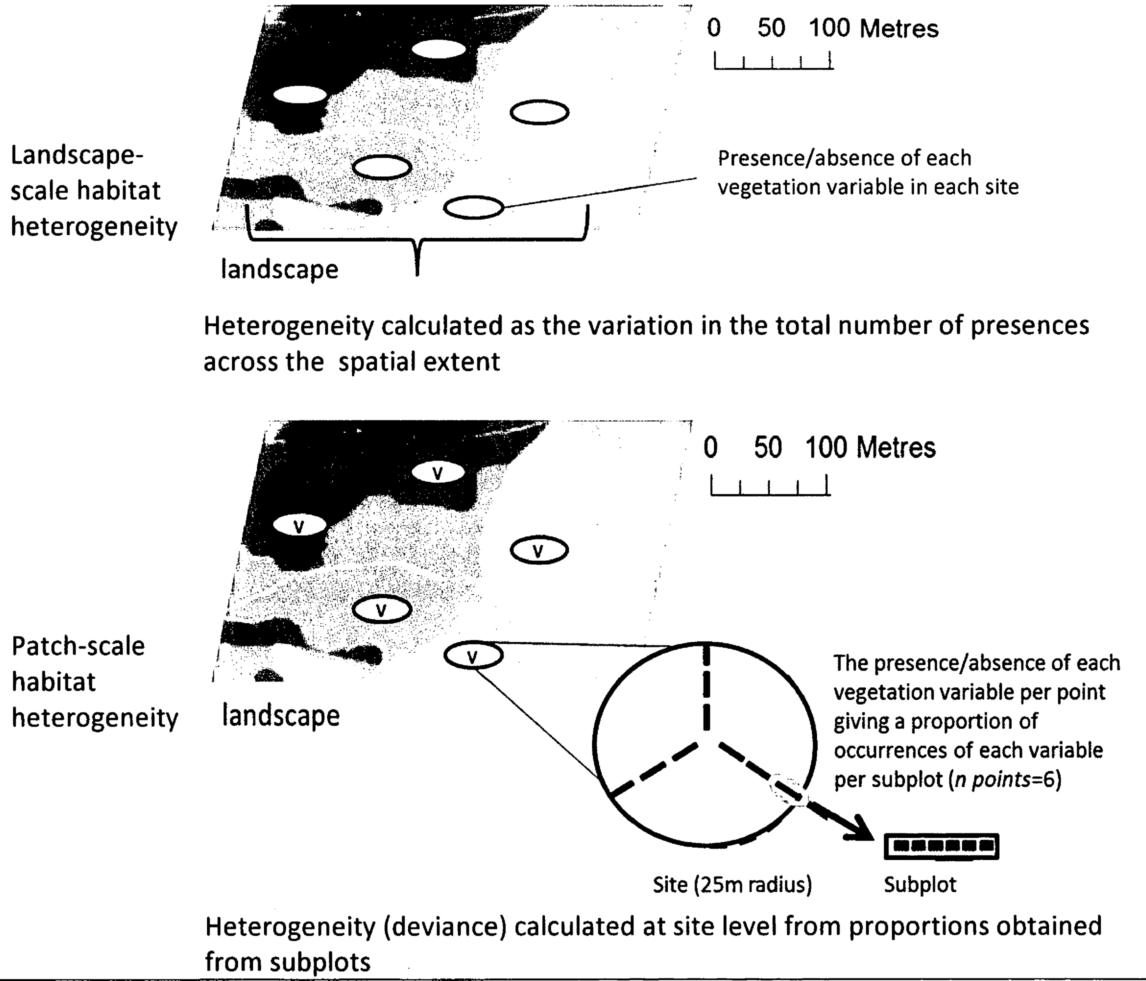

Figure 2. Diagram depicting the methods utilised for calculating: 1) landscape-scale habitat heterogeneity, and 2) patch-scale habitat heterogeneity. These measures represent two different spatial scales at which habitat heterogeneity is quantified within the landscape e.g. the patch scale and the landscape scale. Differences in habitat heterogeneity can be driven by variation in physical features which can be continuous (i.e. slope) or categorical (i.e. fire frequency). Variation in a physical feature within this diagram is represented by fire frequency which varies from light to dark patches with increased frequency. To quantify each measure of landscape-scale vegetation heterogeneity, we calculated the proportion of presences out of the total (n_{points} = 54) of each of the nine habitat parameters across the entire site. This value was then compared between sites (patches) as a measure of between sites variation across the landscape (*n* sites = 96). To quantify the measure of patch-scale habitat heterogeneity we established nine subplots, three on each of three radial lines, within each site. Each subplot consisted of six sampling points each spaced one metre apart. The measure of patch-scale habitat heterogeneity was calculated based on the proportions obtained from the subplots.

Vegetation measures

We measured the presence/absence of nine habitat (response) features at each of the 54 sampling points within each of the 96 sites, using the point intercept method (Elzinga et al. 1998), during July 2011. Our habitat features were: leaf litter (dead leaf material directly covering the ground), fine woody debris (woody debris <5 cm in circumference), grasses, sedges/rushes, ferns (fern spp. including Austral Bracken), grass trees (*Xanthorrhoea* spp; a large grass-like tussock life form), shrubs (vegetation with a woody stem between 0-4 m in height), medium-sized trees (vegetation with a woody stem between 4-10 m in height) and tall trees (vegetation with a woody stem > 10 m in height). More than one habitat feature could occur at a sampling point. We selected these nine habitat features because they strongly influence the composition of birds, mammals and reptiles in Australia (McElhinny et al. 2006; Swinburn et al. 2007).

Heterogeneity measures

We calculated two measures of heterogeneity: 1) a landscape-scale heterogeneity measure, and 2) a patch-scale heterogeneity measure for each of the nine habitat features (Fig. 2). Landscape-scale vegetation heterogeneity measures the variation of cover of habitat features between vegetation patches along a gradient. To quantify each measure of landscape-scale vegetation heterogeneity, we calculated the proportion of presences out of the total ($n_{points} = 54$) of each of the nine habitat parameters across the entire site. This value was then compared between sites (patches) as a measure of between sites variation across the landscape.

Patch-scale vegetation heterogeneity measures the variation of vegetation cover within a patch. In this study, we defined patch-scale vegetation heterogeneity as a measure of the differences in the: (1) cover and/or (2) spatial dependency of habitat features among the nine sub-plots within each site (see supplementary material, Fig. S1). Heterogeneity is greater when there is increased spatial dependence and/or increased difference between sub-samples within a site. Our measure of patch-scale heterogeneity was derived by fitting a logistic regression model (a generalised linear model with a binomial distribution) to the cover data for each site. The response variable was the number of times (out of six) each feature was present, for each of the nine sub-plots for each site. We did not include any predictor variables in the model, as the goal was to assess the adequacy of the model constant in describing the percent cover across the nine-subplots. We assessed the adequacy of the model by dividing the residual deviance by the degrees of freedom (in this case, d.f. = 8) which can be interpreted as a measure of over-dispersion. We used this measure of over-dispersion as our measure of heterogeneity at the site level (see Crawley 2002; McCullagh and Nelder 1989; Zuur et al. 2009 for additional technical details). Our justification for using this measure of over dispersion (residual deviance divided by the degrees of freedom) as our measure of patch-scale vegetation heterogeneity was that it captures the differences in proportions between the nine subplots and the spatial dependency within a site (see the simulation model illustrating this in the supplementary table, Fig. S1 & S2). This approach was preferred to the usual measures of heterogeneity (such as the coefficient of variation) because it respects the underlying binomial structure of the data (Crawley 2002).

Explanatory variables

We used seven explanatory variables in our analysis: three fire variables, three topographic variables, and a measure of the proportion of tall tree cover within each site. We calculated the three fire metrics (mean fire interval, maximum fire interval and severity of the most recent fire) from the fire history map of Booderee National Park (Department of the Environment, unpublished data). We also calculated three topographic metrics (slope, aspect and elevation) from a 10 m resolution digital elevation model (DEM) of the study site. Tall tree cover was used as a continuous proxy for vegetation type, as the three dominant vegetation types (heath, woodland and forest) have contrasting amounts of tree cover. Summary values and descriptions for how we derived all variables are provided in Table 1. We also considered using the topographic wetness index (TWI), fire frequency and, the standard deviation of slope within our analysis, but excluded these variables after preliminary analysis (see below). We calculated all the fire and topographic metrics from Geographic Information System (GIS) layers of the study site, using Arc Info in conjunction with ArcMap v.9 (ESRI 2006).

Table 1. List of examined variables, variable description, and summary statistics.

Variable	*Variable description*	*Mean (minimum -maximum) (±SD)*
Slope angle (degrees)	Steepness of the slope. Predicted from a 10m digital elevation model.	4.70 (0.24 - 15.02) (±*3.28*)
Elevation (m)	Predicted heights interpolated from contour data with drainage enforcement from stream data.	57.08 (2.04 - 154) (±*35.05*)
Aspect (cosine of aspect)	Northern component of aspect scaled from 1 to -1. Negative is more northerly and positive more southerly.	0.11 (-0.99 - 1) (±*0.65*)
Maximum fire interval (years)	Maximum fire interval between recorded fires. Only calculated if more than one fire, otherwise recorded as a 0 fire interval.	17.51 (0 - 37) (±8.56)
Mean fire interval (events)	Number of fires events per site divided by 74 years (since 1937)	13.34 (0 - 37) (±*7.88*)
Fire severity (high or low)	Fire severity in the last 10 years (0 = no severe fires in last 10 years; 1 = severe fire in last ten years).	Categorical (0, 1)

Data analysis

Our goal was to investigate which measures of habitat heterogeneity at the landscape-scale and patch-scale (Table 1) were significantly associated with potential explanatory variables representing environmental variation (topographic variables), disturbance (fire variables) and vegetation type (tall tree cover). Prior to analysis, we assessed collinearity in the explanatory variables using pairwise scatterplots, and Variance Inflation Factors (Bjornstad and Falck 2001; Cliff and Ord 1981). Variance Inflation Factors for the fire variables (mean fire interval, maximum fire interval, and fire severity) and topographic variables (elevation, aspect and slope) were all below the preselected threshold of three, suggesting our explanatory variables were not collinear (Zuur et al. 2009). However, fire frequency and mean fire interval were correlated. We also found the standard deviation of slope and the TWI were correlated with the mean slope value per site. For these reasons, we elected not to include the TWI, standard deviation of slope and fire frequency in further analysis, as collinearity among covariates may result in type II errors (Zuur et al. 2010). We retained mean fire interval, maximum fire interval, fire severity, elevation, aspect and slope in the full model.

We constructed binomial generalised linear models (GLMs) (number of presences out of 54 for each vegetation variable) to investigate the role of topographic and fire variables as predictors of landscape-scale vegetation heterogeneity. We used a binomial distribution in our model because this distribution is most appropriate for binary data (Zuur et al. 2009). All models included six main effects (three topographic and three fire variables) and four interactions. To control for tall tree cover, we included this variable as a main effect in most models (excluding the models where tall tree cover was the predictor). We tested all possible subsets (i.e. combinations of the explanatory variables) and ranked all models using the Akaike Information Criterion (AIC; Burnham and Anderson 2002) within the MuMIn package in R (R Core Team 2012). Models with the lowest AIC, and thus highest Akaike weight, were considered to have the best fit with the data. We tested both the full and best ranked models for over dispersion by dividing the residual deviance by the degrees of freedom (Zuur et al. 2009). We detected over-dispersion in one of these models (tall tree cover) so we corrected the standard errors using a quasi-GLM model. In this model, the variance is given by $\phi \times n \times p \times (1 - p)$, where the mean is $n \times p$ (n is the number of trials and p is the proportion of successes [presence of a habitat feature]) and ϕ is the dispersion parameter (Zuur et al. 2009). The quasi-GLM model does not produce an Akaike Information Criterion (AIC) value, so we identified the best fitting model by applying a backward stepwise approach using the F-test of significance (p>0.05) to remove non-significant variables. We repeated the process using a generalised linear mixed model (GLMM) which included site as a random effect (to handle the over dispersion of the data) and used AIC for model selection, as this approach used the same selection procedure (the log likelihood) as our other eight variables. We obtained consistent results for the tall tree cover model using both methods.

We constructed Gaussian GLMs to investigate the role of topographic and fire variables as predictors of patch-scale vegetation heterogeneity while controlling for the proportion of tall tree cover. As in the binomial GLMs for landscape-scale vegetation heterogeneity, we tested all possible subsets (i.e. combinations of the explanatory variables) and ranked all models using the Akaike Information Criterion (AIC; Burnham and Anderson 2002) within the MuMIn package in R (R Core Team 2012). Models with the lowest AIC, and thus highest Akaike weight, were considered to have the best fit with the data.

We validated each of the 18 models after analysis by inspecting the residual plots to confirm that model assumptions were met. We confirmed sites were independent and that there was no spatial autocorrelation between explanatory variables using correlograms to plot the level of correlation between sites (Bjornstad and Falck 2001). We then confirmed that both the Pearson and deviance residuals of the models contained no dependence structure (McCullagh and Nelder 1989). All statistical analyses were performed using the software package R (R Development Core Team 2012).

Results

Seven of the nine habitat variables were associated with at least one of the fire and topographic variables we measured at either the landscape-scale (i.e. between patches and/or the patch scale (i.e. within patches) (Table 2). The direction and effect of these associations differed depending on the scale at which we measured vegetation heterogeneity. In most cases, the effect of an interaction between fire and topographic variables on vegetation features at one scale did not correspond to significant interaction at the other scale.

Effect of fire on vegetation heterogeneity

At the landscape-scale, after controlling for vegetation type (measured by tall tree cover), maximum fire interval was a significant predictor for heterogeneity of fern cover only (Table 2 & 3). That is, heterogeneity of fern cover between patches increased with the time since the last fire. Fire severity had a negative effect on heterogeneity of leaf litter at this scale. Mean fire interval did not affect heterogeneity of cover of habitat features at the landscape-scale.

At the patch-scale, after controlling for tall tree cover, fire severity was a significant predictor of heterogeneity of medium-sized trees and tall trees (Table 2 & 4). Within patches, higher severity fires was correlated with tall trees becoming more homogeneous and medium-sized trees more heterogeneous in comparison to patches subjected to lower severity fires. At the patch-scale, the heterogeneity of grass cover decreased (i.e., grass cover became more uniform) with longer mean fire intervals. Maximum fire interval did not affect any habitat features at the patch-scale.

Table 2. Summary of the response of 18 best ranked models of two different measures of habitat heterogeneity: landscape-scale heterogeneity (cover of each habitat feature) and patch-scale heterogeneity (residual deviance of the cover of each habitat feature) as predicted by three topographic variables (slope angle, aspect and elevation), three fire variables (maximum fire interval, mean fire interval and fire severity) and the proportion of tall tree cover. It should be remembered that the response variables are the heterogeneity of the vegetation feature. Therefore a positive relationship indicates an increase in heterogeneity of that habitat feature, while a negative relationship indicates a decrease in heterogeneity (or an increase in homogeneity). Response variables indicated with a plus sign (+) have a positive relationship with a predictor. Response variables indicated with a dash (—) have a negative relationship with a predictor. Blank cells indicate predictor variables that were not considered important using AIC.

	Predictor variables						
Response variables	Cover of tall trees	Slope	Elevation	Aspect	Mean fire interval	Maximum fire interval	Fire severity
Landscape-scale heterogeneity of 9 habitat features							
Leaf litter	—	—		—			—
Fine woody debris	—	+					
Grasses	—	—	+				
Sedges	+						
Ferns	—					+	
Grass trees	—						
Shrubs	+						
Medium trees	—	—		—			
Tall trees	NA						
Patch-scale heterogeneity of 9 habitat features							
Leaf litter							
Fine woody debris			+				
Grasses	+			Interaction with severity	—		Interaction with aspect
Sedges							
Ferns							
Grass trees	—						
Shrubs				Interaction with mean fire interval	Interaction with aspect		
Medium-sized trees	+	—					+
Tall trees	NA	—	+				—

Effect of topography on vegetation heterogeneity

At the landscape-scale, after controlling for tall tree cover, slope was a significant predictor for heterogeneity of leaf litter, fine woody debris, grasses, and medium-sized trees (Table 2). The direction of the response to slope differed between habitat features: heterogeneity of leaf litter, grasses, and medium-sized trees were negatively associated with slope; while fine woody debris was positively associated with slope. Aspect was an important predictor for both leaf litter and medium-sized tree heterogeneity at the landscape scale. More southerly aspects had a negative association with both leaf litter and medium-sized tree heterogeneity at this scale. Elevation had a positive effect on grass heterogeneity at the landscape-scale.

At the patch-scale, slope was a significant predictor for medium-sized trees and tall trees. Slope had a negative effect on medium-sized tree heterogeneity and tall tree heterogeneity. Elevation influenced both the heterogeneity of fine-woody debris and tall trees. There was an increase in heterogeneity for both fine woody debris and tall trees with increasing elevation.

Effect of an interaction between fire and topography on vegetation heterogeneity

At the landscape-scale, we found no effect of an interaction between topography and fire variables on any of the nine habitat features. At the patch-scale, after controlling for tall tree cover, the heterogeneity of shrub cover was best explained by an interaction between mean fire interval and aspect (Table 2). For example, on northern aspects, heterogeneity in shrub cover increased with mean fire interval (Fig. 3a). In contrast, as mean fire interval increased, shrub cover became more uniform on southern aspects. Fire severity interacted with aspect to influence the heterogeneity of grasses within a patch. For example, a low fire severity resulted in an increase in the degree of heterogeneity of grasses on southerly aspects. In contrast, a high severity fire resulted in the heterogeneity of grasses declining on southerly aspects (Fig 3b).

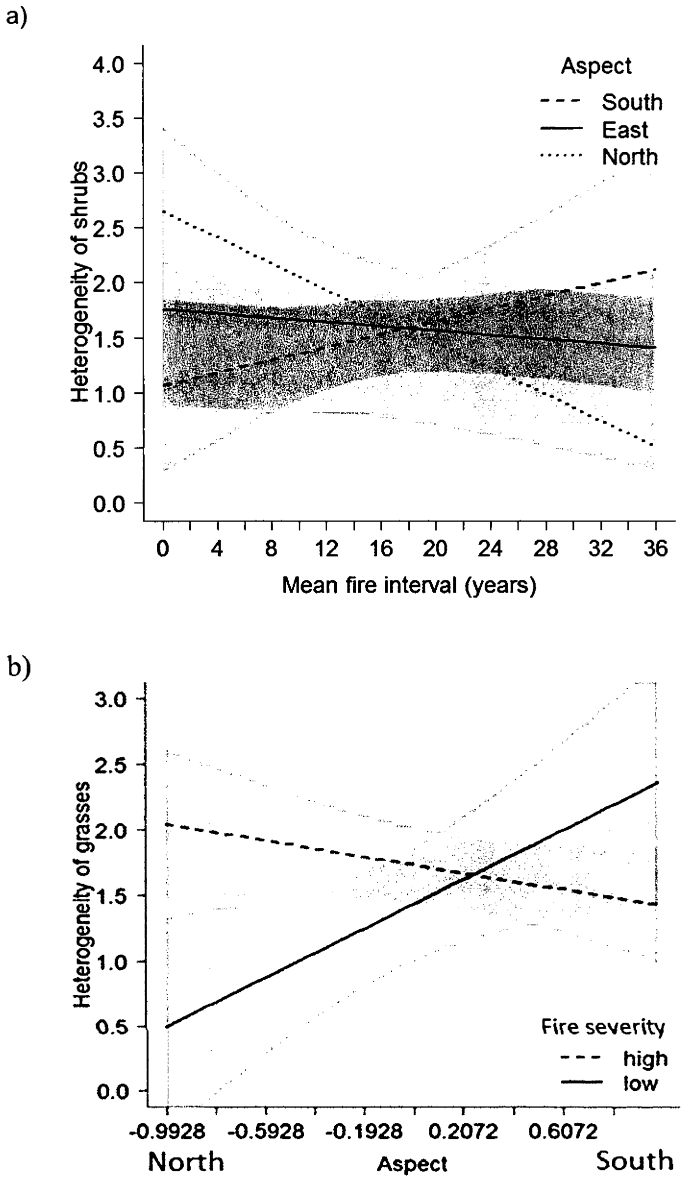

Figure 3. Response at the patch-scale of: a) heterogeneity of shrubs to an interaction between mean fire interval and aspect, and b) heterogeneity of grasses to an interaction between fire severity and aspect. The heterogeneity measure displayed on in the y-axis is a measure of over dispersion (see supplemental materials for details).

Tall tree cover

Tall tree cover was an important driver of heterogeneity at the landscape and the patch-scales (Table 2). At the landscape scale, it influenced heterogeneity in all eight vegetation variables, whereas it influenced heterogeneity at the patch-scale of three of the eight vegetation variables.

Table 3. Coefficient estimates (± standard error) for the best-ranked generalised linear models (GLMs) investigating the role of topography (slope, elevation and aspect) and fire (mean fire interval, maximum fire interval and fire severity) as predictors of landscape-scale heterogeneity of the nine habitat features (leaf litter, fine woody debris, grasses, sedge, fern, grass trees, shrubs, and medium trees [all n = 96]) controlling for vegetation type. Null models are excluded (tall trees).

Habitat features	*Variables in final optimal models*	*Coefficient ± S.E.*	*t-value*
Litter	Intercept	1.728 ± 0.124	13.89
	Tall trees cover	-0.732 ± 0.300	-2.44
	Aspect	-0.115 ± 0.053	-2.15
	Slope	-0.025 ± 0.010	-2.48
	Fire severity	-0.117 ± 0.076	-1.53
Fine wood debris	Intercept	0.749 ± 0.093	8.03
	Tall trees cover	-5.123 ± 0.256	-19.94
	Slope	0.021 ± 0.009	2.34
Grasses	Intercept	0.246 ± 0.098	2.49
	Tall trees cover	-2.465 ±0.245	-10.05
	Slope	-0.018 ± 0.008	-2.07
	Elevation	0.001 ± 0.00082	1.51
Sedges	Intercept	-1.670 ± 0.086	-19.33
	Tall trees cover	6.668 ± 0.268	24.84
Ferns	Intercept	0.076 ±0.130	0.58
	Tall trees cover	-8.672 ± 0.374	-23.14
	Maximum fire interval	0.009 ± 0.005	1.82
Grass trees	Intercept	-2.149 ± 0.070	-30.69
	Tall trees cover	-0.025 ± 0.012	-2.02
Shrubs	Intercept	-0.922 ± 0.080	-11.51
	Tall trees cover	3.035 ± 0.244	12.40
Medium-sized trees	Intercept	1.296 ± 0.336	6.76
	Tall trees cover	0.260 ± 0.073	-17.81
	Slope	-0.574 ± 0.285	-2.01
	Severity	0.086 ± 0.039	2.19

Table 4. Coefficient estimates (± standard error) for the best-ranked generalised linear models (GLMs) investigating the role of topography (slope, elevation and aspect), fire (mean fire interval, maximum fire interval and fire severity) and tall tree cover as predictors of patch-scale heterogeneity of the nine habitat features (leaf litter, fine woody debris, grasses, sedge, fern, grass trees, shrubs, medium-sized trees, and tall trees [all *n* = 96]) controlling for vegetation type. Null models are excluded (litter, sedges, ferns).

Habitat features	*Variables in final optimal models*	*Coefficient ± S.E.*	*t-value*
Fine woody debris	Intercept	1.841 ± 0.26	7.05
	Elevation	0.007 ± 0.004	1.86
Grasses	Intercept	1.390 ± 0.33	4.17
	Tall trees cover	0.259 ± 0.069	3.73
	Mean fire Interval	-0.030 ± 0.016	-1.87
	Severity	0.311 ± 0.27	1.12
	Aspect	0.935 ± 0.39	2.37
	Severity x Aspect	-1.247 ± 0.452	-2.76
Grass trees	Intercept	1.252 ± 0.124	10.081
	Tall trees cover	-0.227 ± 0.05	-4.542
Shrubs	Intercept	1.859 ± 0.217	8.53
	Mean fire interval	-0.015 ± 0.014	-1.06
	Aspect	-0.796 ± 0.33	-2.39
	Mean fire interval x aspect	0.044 ± 0.022	2.04
Medium-sized trees	Intercept	1.296 ± 0.33	3.86
	Tall trees cover	0.260 ± 0.073	3.55
	Slope	-0.574 ± 0.28	-2.02
	Severity	0.086 ± 0.03	2.20
Tall trees	Intercept	2.646 ± 0.49	5.395
	Elevation	-0.013 ± 0.005	-2.679
	Slope	0.081 ± 0.05	1.529
	Severity	-0.806± 0.38	-2.118

Discussion

Despite its established importance for biodiversity, habitat heterogeneity is rarely measured directly in the field (Tews et al. 2004). Our results demonstrated that the drivers of habitat heterogeneity (topography and fire) can operate at different scales on different habitat features. Our findings have implications for field survey design, predicting the occurrence of fauna and habitat management and restoration.

Which topographic features and fire variables influence habitat heterogeneity?

Vegetation responses to fire

Our results indicate that different aspects of the fire regime, such as fire interval (maximum and mean) and fire severity, can influence heterogeneity of different habitat features (Table 2). For example, at the patch-scale, an increase in the mean fire interval resulted in a lower degree of grass heterogeneity, whereas the degree of heterogeneity of medium-sized trees was higher following a high severity fire rather than a low severity fire. A large fire interval may reduce the heterogeneity of grasses by allowing the growth of shrubs that may shade out grasses uniformly across a site (Specht and Specht 1989; Vlok and Yeaton 2000).

The relationship we observed in our study area between fire severity and medium-sized tree heterogeneity occurs in other ecosystems. For example, in North American ecosystems, such as those dominated by pine forest, mixed conifer forest and sequoia groves, high severity fires result in small patches of intense surface burning which, in turn, result in small openings in the tree canopy leading to fine-grained heterogeneity within the landscape (Chang 1996). Similarly, in tropical savannah in northern Australia, high severity fires result in increased mortality of large trees (Williams et al. 1999), and hence increased heterogeneity in tree cover at the fine-scale. That different habitat features exhibit different responses to various fire components is likely to be because different plants have different adaptations and response times to fire (Bradstock et al. 2012).

Vegetation responses to topography

Our study revealed that the three topographic features (slope, elevation, and aspect) influenced habitat features at the landscape-scale and patch-scale (Table 2). We also found that each of these topographic variables had a different effect on the heterogeneity of different habitat variables and that the relationship mostly varied with spatial scale. For example, slope influenced the heterogeneity of leaf litter, fine-woody debris, grasses and medium-sized trees at the landscape-scale, and the heterogeneity of medium-sized trees and tall trees at the patch-scale. In our study, slope variation and terrain steepness are highly correlated, so the underlying processes driving the associations is difficult to unravel. However, it is well established that differences in larger units of slope (e.g. steep slopes versus plateaus) can influence soil moisture and soil depth, which has been found to drive dissimilarities in occupancy of different vegetation at the landscape-scale (Specht and Specht 2002). Prior studies have also found that variation in small units of slope (i.e. alternating hummocks and hollows) can result in variation in micro-environmental and climatic variables, (Greig-Smith 1979; Peterson and Pickett 1990; Specht and Specht 2002), which can drive the establishment and spatial patterning of tree seedlings (Smith et al. 2014). Thus, some of the heterogeneity in the spatial patterning at the fine scale of large life forms, such as trees, may be driven by earlier life stages in these larger life forms.

Despite our study area having a low elevation range (0-105 m asl), we found that elevation influenced different habitat features at both the patch-scale and landscape-scale. For example, elevation influenced grasses at the landscape-scale and the heterogeneity of tall trees and fine woody debris at the patch-scale. Tall tree canopy heterogeneity at the fine-scale may be associated with an increase in grass cover with elevation at the landscape-scale. Heterogeneity in the canopy foliage (canopy gap size) influences the plant communities on the ground by influencing the light environment, resulting in an increase in small plants with low shade tolerance (Kern et al. 2012), such as grasses. The influence of elevation on canopy heterogeneity of tall trees may be specific to our study area. Further investigation is required to determine if canopy heterogeneity increases with elevation in other landscapes.

We found that aspect influenced the heterogeneity of medium-sized trees and leaf litter at the landscape-scale. Aspect clearly alters vegetation patterns. For example, Specht and Specht (2002) found on northern aspects in Australia, greater direct-beam solar radiation and lower soil moisture content resulted in lower stand biomass and stand density.

Interaction between topography and fire as drivers of vegetation heterogeneity

At the patch-scale, we found that a longer mean fire interval resulted in: 1) additional heterogeneity of shrubs on southern-facing aspects; and 2) lowered heterogeneity of shrubs on northern-facing aspects. We also found that lower fire severity within a patch resulted in: 1) additional heterogeneity of grasses on southern-facing aspects, and 2) lowered heterogeneity of grasses on northern-facing aspects. In contrast, high severity fires resulted in the opposite effect. Potentially, the lower soil-moisture content on northern compared to southern aspects, such as occurs in the Southern Hemisphere (Specht and Specht 2002) may alter both the fire behaviour and conditions (Lindenmayer et al. 1999) as well as change the recovery potential of vegetation within a site (Badano et al. 2005; Cerdà and Doerr 2005; Díaz-Delgado and Pons 2001). Our finding that landscape-scale fire components (such as mean fire interval and severity) can influence vegetation heterogeneity when interacting with aspect at the scale of the patch may go some way to explaining the high levels of fine-scale variation in vegetation that is present within some study sites (e.g. Lydersen and North 2012).

Does the influence of topography and fire on vegetation heterogeneity change with spatial scales?

We found that seven of the nine habitat variables we measured in our study responded to either topographic and/or fire variables at least at one scale (Table 2). However, different topographic and fire variables and their interactions influenced the heterogeneity of habitat features at different spatial scales (i.e. landscape-scale and patch-scale). For example, there were strong associations between habitat heterogeneity and slope at the landscape scale (controlling for vegetation type), whereas a variety of environmental and disturbance variables (i.e. fire severity, mean fire interval, slope, aspect and elevation) were strongly associated with heterogeneity at the patch scale (Table 2). These results support previous findings that broad-scale topographical features (e.g., slope) can mask local-scale mechanisms (i.e. interspecific competition, edaphic and micro-topographic features) which influence vegetation heterogeneity (Hutchings et al. 2000; Lookingbill et al. 2011). These findings clearly indicate that measures of vegetation heterogeneity are scale-dependent.

How well does a single indirect environmental feature describe vegetation heterogeneity?

Our findings indicate that using a single topographic feature or disturbance variable cannot capture the heterogeneity of multiple habitat features within a single scale, let alone across multiple spatial scales. In our study topography variables (slope, aspect, and elevation) and fire variables (maximum fire interval, mean fire interval, and fire severity) influenced heterogeneity of different habitat features, at different scales. This finding is important because in many studies only one or two environmental variables are used as surrogates of habitat heterogeneity (e.g. Koh et al. 2006; Moreno-Rueda and Pizarro 2009). For example, elevation is frequently used as a lone surrogate for habitat heterogeneity (e.g. Huggett and Cheesman 2002). Environmental variables are a useful surrogate for habitat heterogeneity in locations where there is limited vegetation mapping over large areas (Franklin 1995) and may provide extra details about local floristics and associated species (e.g. McMullan-Fisher et al. 2009). However, our findings indicate that if ecologists are to develop robust predictive models that accurately predict multiple aspects of faunal habitat it is important that they use a combination of variables as surrogate measures of habitat heterogeneity.

Implications for management

Our results demonstrated that vegetation heterogeneity is influenced in a dissimilar fashion by topography and fire at different spatial scales. Our findings imply that we need to manage the various components of fire across different spatial and temporal scales. For example, variation in the maximum fire interval is important for influencing heterogeneity of ferns at the landscape-scale, whereas variation in the mean fire interval is important for influencing grass heterogeneity at the patch-scale. Our also findings suggested that fire severity might be a particularly important agent for creating or maintaining heterogeneity of some habitat features (i.e. medium-sized trees and tall trees) within a patch where there is little variation in topography. Further, when managing other habitat features (i.e. shrubs and grasses) it is important that the topographic features in the landscape are considered when determining the fire regime. At a fine-scale, as part of restoration practices, we can modify topographic features to increase vegetation heterogeneity. For instance, in agricultural areas where the landscape structure has been altered (i.e. slope variation is homogenised by earthworks and land clearing) fine-scale topographic variation may be restored or artificially changed to promote plant species adapted to specific micro-climates. Overall, our results highlighted that within-patch heterogeneity, as well as landscape scale heterogeneity, deserves further consideration in management planning (Knapp and Keeley 2006; Lookingbill et al. 2011; Rocca 2009).

Conclusion

A better understanding of the variables that influence the heterogeneity of habitat features at different spatial scales is important for providing insights into how best to conserve and manage biodiversity. Our study explicitly examine how multiple environmental surrogates and disturbance variables and their interactions, influence the heterogeneity of nine key habitat features at two different spatial scales (i.e. landscape-scale and patch-scale). While the specific relationships between environmental drivers and habitat features may be most pertinent to similar ecosystems, an understanding of how to build robust predictive models that accurately reflect key vegetation heterogeneity features can be applied to most terrestrial ecosystems.

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Supporting information

Title: Simulation model illustrates how patch-scale vegetation heterogeneity captures the differences in proportions between the nine subplots and the spatial dependency within a site

Methods:

We carried out a simulation study to examine the effects of: a) variability in the proportion of cover over the site; and b) the amount of spatial dependence in the cover has on our measure of site level heterogeneity. We measured heterogeneity by calculating the residual deviance divided by residual degrees of freedom of a model that assumes a constant cover (see the Methods section for more details). We considered three levels of variability in the proportion of cover: none – all of the nine subplots had the same proportion of cover, set at 0.5; moderate – the cover in each subplot was sampled from a Beta distribution with parameters 10 and 10, which corresponds to a standard deviation of 0.109; and large – was sampled from a Beta distribution with parameters 1 and 1, which has a standard deviation of 0.289. Note the Beta (1, 1) distribution is also known as the Uniform (0, 1) distribution. Three levels of spatial dependence were also used, as measured by the parameter (r) in the spatial exponential model (Sherman 2011): r = 0, corresponding to independent observations, r = 0.4 corresponding to a moderate level of spatial dependence; and r = 0.8, corresponding to a large level of spatial dependence. The functional form for the spatial dependence (Sherman 2011) is given by:

$$C(d) = exp(-r\ d),$$

where d is the distance between the two points, r is the degree of dependence and C denotes the covariance between the two points. For each of the 9 combinations of variation in cover and spatial dependence we generate 10,000 sets of data consisting of 54 point counts. Note that each subplot consists of six individual point counts (see the Methods section for more details). For each of the simulated data sets we computed the residual deviance/df, the variance in the 9 estimated subplot proportions and Pearson goodness of fit statistic/df. For details on the method of simulating binary data with spatial dependence we used the method of O'Brien and Dunson (2004).

Results:

The results of our simulation study are summarized in Figures S1-S2. The same general pattern can be seen in each of the figures, that is, as spatial dependence increases and/or variation in subplot proportions increases the amount of observed heterogeneity increases. We also plotted each of the three measures versus each other and all behave in a similar fashion, however, we feel that the residual deviance/df has slightly more desirable statistical properties.

Figure S1. Simulation model illustrating with large differences in the (1) sub-plot proportions (props) and/or (2) spatial dependence (spat dep) among the nine sub-plots have larger residual deviances/df and hence are more heterogeneous. When values are greater than one there is over-dispersion (residual deviance divided by the degrees of freedom) (heterogeneity). Abbreviations correspond to: Constant (const), B (10,10) refers to a Beta distribution with parameters 10 and 10, Beta (1,1) refers to a Beta distribution with parameters 1 and 1 and r is the spatial dependence parameter (see Supplementary methods).

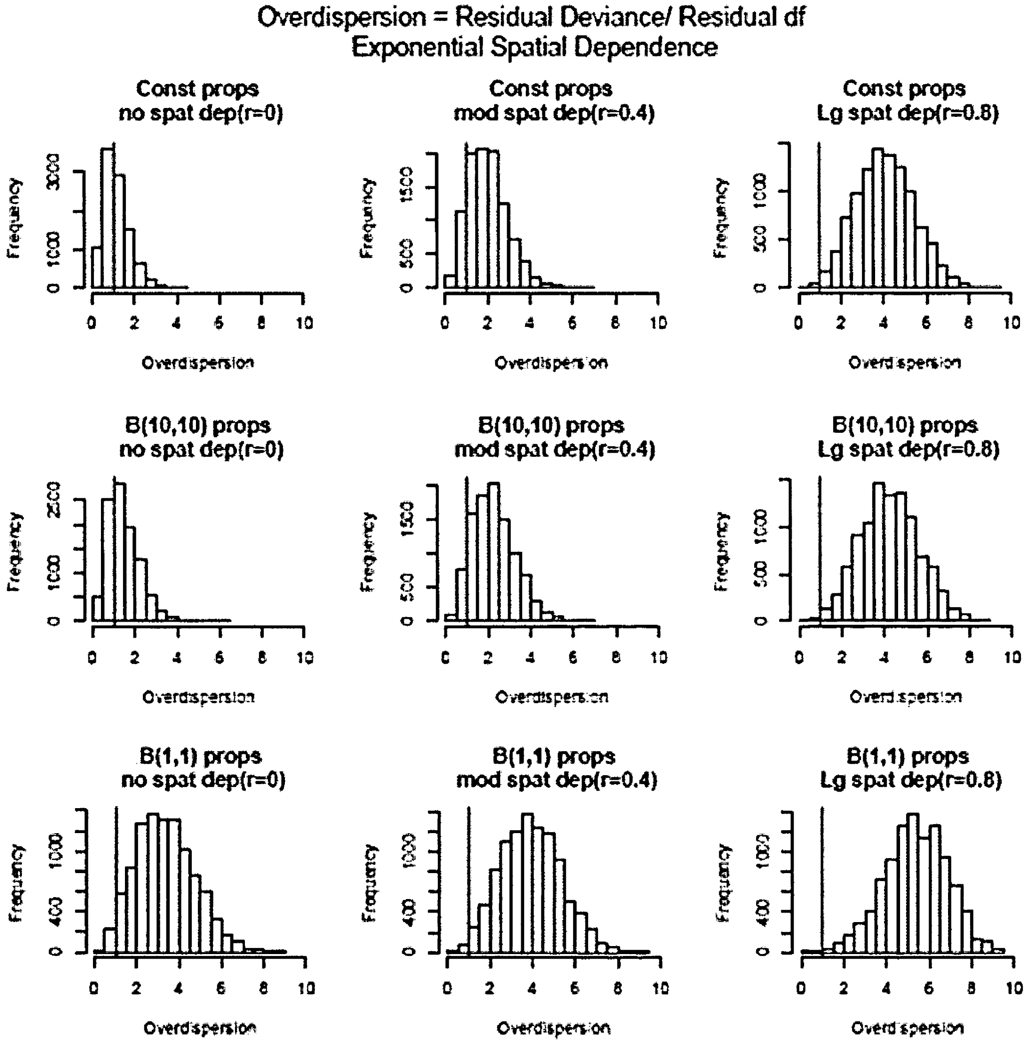
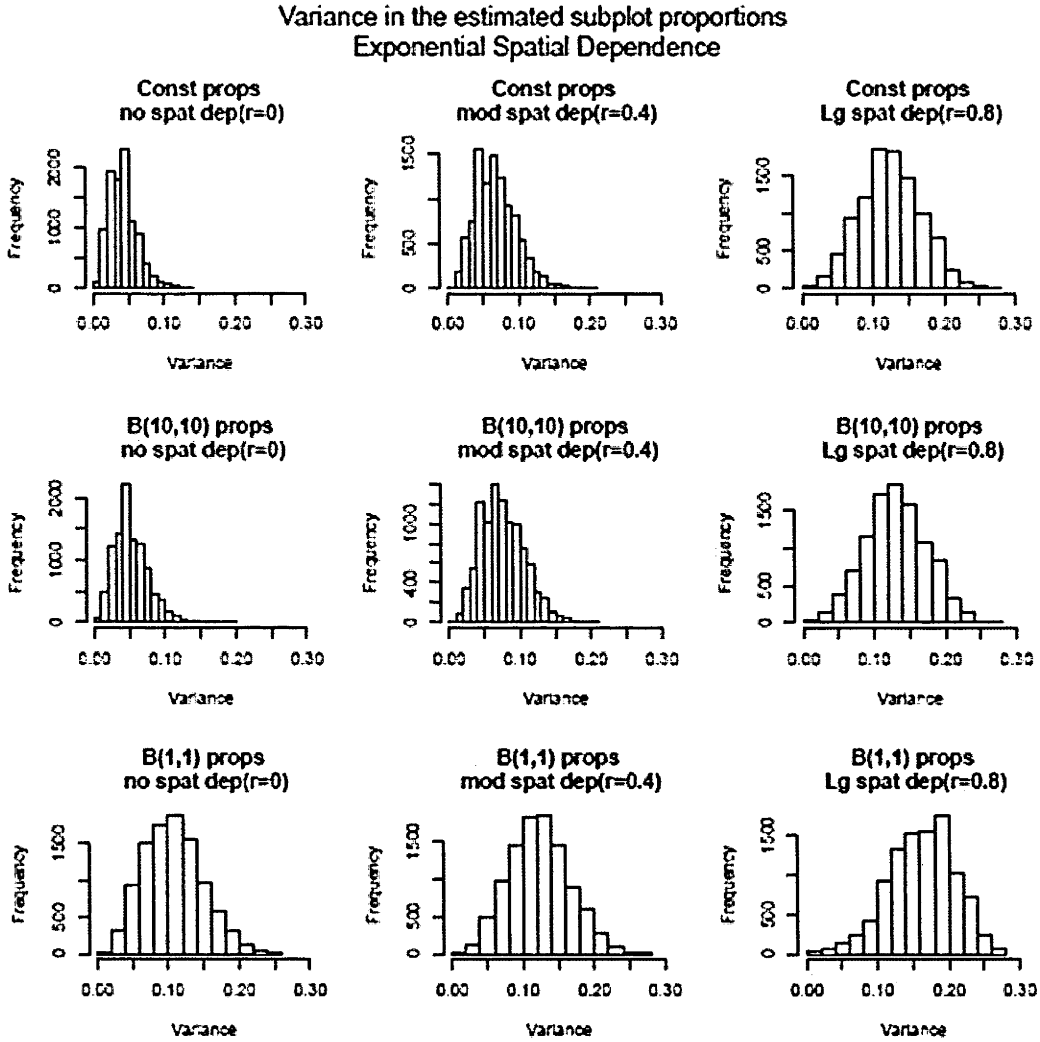


Figure S2. Simulation model illustrating with large differences in the (1) sub-plot proportions (props) and/or (2) spatial dependence (spat dep) among the nine sub-plots have larger variances and hence are more heterogeneous. Abbreviations correspond to: Constant (const), B(10,10) refers to a Beta distribution with parameters 10 and 10, Beta(1,1) refers to a Beta distribution with parameters 1 and 1 and r is the spatial dependence parameter (see Supplementary methods) .



PAPER 3: Measuring habitat heterogeneity reveals new insights into bird community composition

A diverse array of bird species with different life history traits is present in Booderee National Park.

Stirnemann A.I., Ikin K., Gibbons P., Blanchard W. & Lindenmayer D.B (2014) Measuring habitat heterogeneity reveals new insights into bird community composition. Oecologia.177(3):733-746 DOI 10.1007/s00442-014-3134-0

Abstract

Fine-scale vegetation cover is a common variable used to explain animal occurrence, but we know less about the effects of fine-scale vegetation heterogeneity. Theoretically, fine-scale vegetation heterogeneity is an important driver of biodiversity because it captures the range of resources available in a given area. In this study we investigated how bird species richness and birds grouped by various ecological traits responded to vegetation cover and heterogeneity. We found that both fine-scale vegetation cover (of tall trees, medium-sized trees and shrubs) and heterogeneity (of tall trees, and shrubs) were important predictors of bird richness, but the direction of the response of bird richness to shrub heterogeneity differed between sites with different proportions of tall tree cover. For example, bird richness increased with shrub heterogeneity in sites with high levels of tall tree cover, but declined in sites with low levels of tall tree cover. Our findings indicated that an increase in vegetation heterogeneity will not always result in an increase in resources and niches, and associated higher species richness. We also found birds grouped by traits responded in a predictable way to vegetation heterogeneity. For example, we found small birds benefited from increased shrub heterogeneity supporting the textual discontinuity hypothesis and non-arboreal (ground or shrub) nesting species were associated with high vegetation cover (low heterogeneity). Our results indicated that focusing solely on increasing vegetation cover (e.g. through restoration) may be detrimental to particular animal groups. Findings from this investigation can help guide habitat management for different functional groups of birds.

Keywords: *Spatial heterogeneity, Variation, Ecological traits, Fine scale, Habitat management*

Introduction

In the face of rapid, global loss of biodiversity, knowledge of the underlying environmental processes that control species distributions is vital for their conservation (Lindenmayer and Hobbs 2007). A detailed understanding of habitat-fauna associations is fundamental for informing the way we manage habitat for animals (Jacobsen 2012; 2011), and restore habitats (Lindenmayer et al. 2010), and underpins conservation theory and practice (Lindenmayer and Hobbs 2007; Zeng et al. 2013).

Most studies examining relationships between the habitat provided by the physical structure of vegetation and the presence and abundance of animals focus on the amount (e.g. cover) rather than the heterogeneity of habitat (Morrison et al. 2006). However, fine-scale structural vegetation heterogeneity (i.e. variation in vegetation at a scale of tens of metres) is considered to be an important factor affecting animal occurrence and composition (Benton et al. 2003; McElhinny et al. 2005). For instance, according to the habitat heterogeneity hypothesis (MacArthur and MacArthur 1961), resources and niches increase with increasing spatial heterogeneity (Bazzaz 1975; Pianka 1972). This is, in turn, believed to structure species richness patterns at a fine scale by facilitating the co-existence of species (Jeltsch et al. 1999; Palmer 2003) and by providing habitat for species with multiple resource requirements (e.g. Perkins et al. 2000).

The importance of environmental heterogeneity to fauna is determined partly by the spatial scale at which heterogeneity is measured and partly by the ecological traits of animals (Allouche et al. 2012; González-Megías et al. 2011; Wood et al. 2013). For instance, fauna-heterogeneity associations can depend on the spatial scale observed (Bar-Massada et al. 2012; Benton et al. 2003; Morelli et al. 2013). By contrast, although research is accumulating on the interaction between vegetation heterogeneity, spatial scale, and biodiversity (e.g. Brosi 2009), little is known about how fauna with different ecological traits respond to vegetation heterogeneity. It has been postulated that fine-scale heterogeneity of vegetation structure is important for small species and those with limited mobility because they perceive and interact with their environment at a fine spatial scale (Fischer et al. 2008; Vanbergen et al. 2007; Wiens 1989). The ecological traits of such species mean that their requirements can be met over a small spatial scale, whereas by contrast, large and mobile fauna utilise a larger area (Holland et al. 2005). However, fauna simultaneously interact with their environment at multiple scales (e.g. Leyequién et al. 2010; Lindenmayer 2000; Steffan-Dewenter et al. 2002), so large or mobile species also may respond to fine-scale structural vegetation heterogeneity.

The potential importance of fine-scale structural vegetation to species occurrence raises the general question: do current explanatory models best describe the factors by which birds are responding to the environment? As with many species, birds are sensitive to the total cover of important habitat features like vegetation (Karr and Roth 1971) and it follows that the cover, or amount, of habitat features like vegetation inform most models of habitat use by birds. But birds may also be sensitive to heterogeneity in the configuration of those features, and respond differently to canopy, mid-storey and ground cover characteristics (McElhinny et al. 2006). It is well known that animals respond to vertical vegetation heterogeneity [i.e. the number of vegetation strata, sometime referred to as structural complexity or structural diversity (MacArthur and Horn 1969)], but few studies examine how the fine-scale heterogeneity of different habitat features influences birds. This is despite varying combinations of different amounts of vegetation cover and structural heterogeneity existing in nature (Figure. 1). Consequently, there is limited understanding of how to manage fine-scale horizontal vegetation heterogeneity to improve habitat for birds.

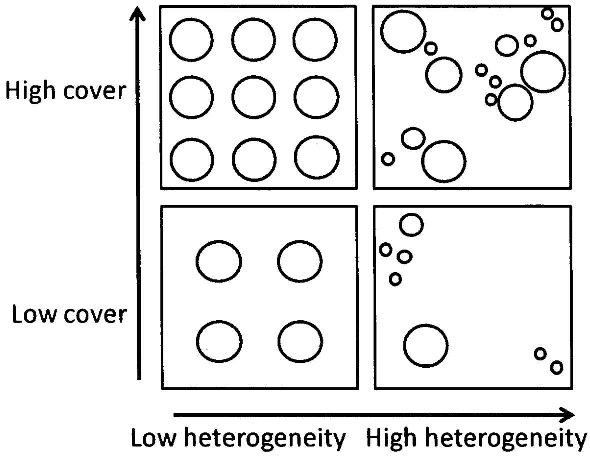


Figure. 1 A conceptual figure showing four scenarios of vegetation within a site, separating the amount of vegetation cover from the spatial heterogeneity of vegetation per se. Each *square* represents a site within which the *circles* (*grey*) represent vegetation cover. The figure illustrates that given a certain amount of vegetation within an area, vegetation can be distributed uniformly or heterogeneously distributed.

In this study we asked: does measuring vegetation heterogeneity in addition to vegetation cover improve our ability to explain bird richness and bird species trait associations? To answer this question, we investigated how bird species richness and birds grouped by various ecological traits responded to structural vegetation cover and vegetation heterogeneity at a fine spatial scale, i.e. within a 25-m radius. We expected to find strong responses in bird species richness to structural vegetation heterogeneity because of increased niche availability in heterogeneous vegetation (Bazzaz 1975). We also predicted that responses of bird species to vegetation heterogeneity would differ with the proportion of tall tree cover (a proxy for vegetation type) because previous studies have postulated that variable heterogeneity–richness responses occur in different environments (Allouche et al. 2012). Lastly, we predicted that the response of species to vegetation cover and heterogeneity would be related to their body masses, mobility, foraging and nesting traits (Table 1).

Table 1. A list of traits that may be associated with the total cover and/or heterogeneity of vegetation, the trait categories used in our study, predicted response and justification.

Trait	Categories	Prediction	Reference
Body mass	Small (< 25 gr), large (>25 gr)	Smaller-bodied species are associated with complex heterogeneous fine-grained habitats, because (i) small birds utilise shrubs: (iii) the movement of large birds may be restricted in dense vegetation and (iii) an increase in the number of niches.	(Holling 1992) (Fischer et al. 2008)
Mobility index	Low (<-0.9), medium (0.61-0.45) and high (>0.47)	Species with limited mobility are associated with more heterogeneous areas (which provide more diverse foraging and nesting opportunities) because their requirements need to be met within a small area.	(Hutchings et al. 2000)
Foraging method	Pounce, wood searcher, foliage, ground, aerial and various	Species that use multiple substrates for foraging are associated with more heterogeneous habitat.	(Gorini et al. 2012)
Nest type	Hollow, cup, and dome	Species with cup and dome nests are associated with high vegetation cover (low heterogeneity) because it can impede the ability of predators to find nests.	(Martin 1993)
Nest location	Arboreal , non-arboreal and varied (nest in both)	Non-arboreal (ground or shrub) nesting species are associated with high vegetation cover (low heterogeneity) because it can impede the ability of predators to access nests.	(Vikery and Arlettaz 2012)
Nest height range	Minimum nest height/maximum nest height	Species with a large nest range are associated with increased flexibility in nest placement. Therefore, these species may favour highly heterogeneous habitat	(Khoury et al. 2009)

Materials and methods

Study area

Our study was located within Booderee National Park in the Jervis Bay Territory on the south coast of New South Wales, south-eastern Australia (approximate coordinates 35°10′ S 150°40′ E; see Figure 4.2). This is a lowland region (<170 m a.s.l.) of undulating sandstone overlain by varying depths of deposited sand (Taylor et al. 1995). This area is characterised by a temperate maritime climate, with average rainfall of approximately 1,200 mm that is largely consistent over the year. Mean annual temperature ranges from 17 to 26 °C. The study area is dominated by contrasting vegetation types that differ in terms of their tree cover, including heathlands (no tree cover), woodlands (sparse tree cover) and forest (dense tree cover), which are patchily distributed within the park (Ingwersen 1977). The majority of the forest areas are dominated by eucalypt species (*Eucalyptus botryoides* and *Eucalyptus pilularis*). The woodland areas are dominated by banksia (*Banksia integrifolia*, *Banksia serrata*) and eucalypt or Corymbia species (*Corymbia gummifera*, *Eucalyptus sclerophylla*, and *Eucalyptus sieberi*). Heathlands are dominated by shrubs (*Baeckea imbricata, Allocasuarina distyla, Baeckea ericifolia*, *Sprengelia incarnata* and *A. distyla*) and clumps of mallee-form (multi-stemmed) trees (*Eucalyptus obstans, C. gummifera* and *E. sieberi*) (Taws 1997).

Booderee National Park has a complex history of both natural and prescribed fires. Spatially explicit records of the fire history of the territory have been kept since 1937 (DSEWPaC 2013). For example, the records indicate 230 separate fire events of various sizes within the boundary of the Park between 1937 and 2011.

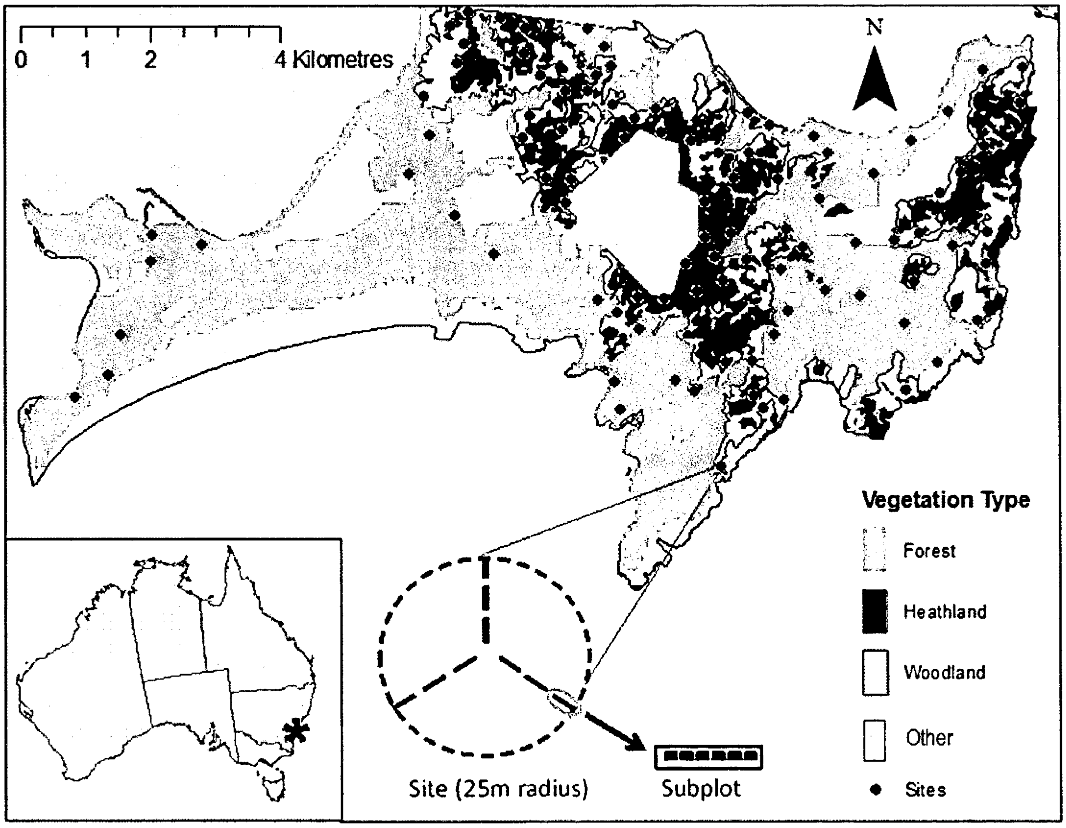


Figure 2. Our study was located within Booderee National Park on the south coast of New South Wales, south-eastern Australia. The study area supports a variety of vegetation types including heathland, woodland, and forest. *Black points* are the sites (*n*=96). Within each site we had nine subplots. Each subplot consisted of six sampling points, each spaced 3 m apart. At each of the 54 sampling points per site, we measured the presence/absence of the three vegetation features.

Study design

We stratified the study area into three broad vegetation types (forest, woodland and heathland), two fire frequency categories (0–3 years; 4–8 years), and two slope categories [low (0.24–3.56°) and high (3.57–15.02°)]. These factors influence both the degree of vegetation heterogeneity and amount of vegetation cover within the landscape (e.g. Gandiwa 2011; Gould et al. 2006; Jin et al. 2008; Specht and Specht 2002). We randomly selected eight sites within each of our 12 different category combinations for a total of 96 sites. Our stratified approach enabled us to maximise the maximum possible range (i.e. very low and very high values) of both heterogeneity and cover of different vegetation variables across our sites.

Vegetation surveys

At each of our 96 sites, we collected data on structural vegetation features that are known to influence bird community composition: shrubs (0–4 m), medium-sized trees (4–10 m), and tall trees (>10 m) (McElhinny et al. 2006). Each site consisted of a circular plot with a 25-m radius (Fig. 2). Within each site, we had nine subplots. Subplots were evenly distributed into three distance categories from the centre: (1) 4–9 m, (2) 12–17 m, and (3) 20–25 m. Subplots also were evenly located 90, 210, or 330 cardinal degrees from the central point. Each subplot consisted of six sampling points, each spaced 3 m apart. At each of the 54 sampling points per site, we measured the presence/ absence of the three vegetation features using the point intercept method (Elzinga et al. 1998).

We calculated two measures for each of these vegetation features: a measure of the percent cover, and a measure of heterogeneity. The total percent cover (hereafter called 'cover') was calculated at each site as the proportion of presences out of the total number of points measured at each site ($n = 54$).

A measure of heterogeneity

Vegetation heterogeneity measures the patchiness of vegetation cover at a site (see Fig. 1). Our measure of heterogeneity was derived by fitting a logistic regression model (a generalised linear model with a binomial distribution) to the cover data for each site. The response variable was the number of times (out of six) each feature was present, for each of the nine sub-plots (see above) for each site. We did not include any predictor variables in the model, as the goal was to assess the adequacy of the model constant in describing the percent cover across the nine subplots. We assessed the adequacy of the model by dividing the residual deviance by the df (in this case, $df = 8$) which can be interpreted as a measure of over-dispersion. We used this measure of over-dispersion as our measure of heterogeneity at the site level (see Crawley 2002; McCullagh and Nelder 1989; Zuur et al. 2009 for additional technical details). This approach was preferred to the usual measures of heterogeneity (such as the coefficient of variation) as it respects the underlying binomial structure of the data (Crawley 2002).

Bird surveys

We surveyed the presence of birds at each of our 96 sites using 5-min fixed-radius point counts (Sutherland et al. 2004). One of us (I. A. S.) recorded all birds heard or seen within a 25-m radius of the centroid of all 96 sites, excluding fly-over observations. We recorded birds within a small sampling (25-m radius) to minimise detection differences between sites. It is highly likely that if a species is present at a site, it would be detected within the cause of the six surveys (Montague-Drake et al. 2009; Tyre et al. 2003). Three surveys, between dawn and 10 a.m., were completed at each site on different days during the bird breeding season (October–November) in 2010 and again in 2011. That is, each site was surveyed six times over 2 years. Surveys were not undertaken during rain or high wind to minimise bias caused by weather. For all analyses we considered a species to be present at the site if it was recorded at least once over the six surveys.

Analysis of bird species richness

Prior to analysis, we assessed our explanatory variables for collinearity, the presence of extreme outliers, and leverage effects in the explanatory variables using pairwise scatterplots, correlation coefficients and boxplots (Bjornstad and Falck 2001; Cliff and Ord 1981). We found the explanatory variables were not strongly collinear ($r > 0.5$), contained no extreme outliers, and had no strong multi-collinearity. Therefore, all variables were initially included in the regression models.

We modelled the response of total bird species richness as a function of the six main effects (three total cover variables and three structural heterogeneity variables) and one interaction using a Poisson generalised linear model within the R statistical software (R Core Team 2012). We used a Poisson distribution in our model because this distribution is most appropriate for count data (Zuur et al. 2009). To test if predictors have different effects in different levels of tall tree cover (a proxy for vegetation type), we quantified the effects of interactions between shrub heterogeneity and tall tree cover within each global (fully parameterised) model. We tested all possible subsets (i.e. combinations of the explanatory variables) and ranked all models in the 95 % confidence set using the Akaike information criterion (AIC) within the MuMIn package in R (R Core Team 2012). Models with the lowest AIC, and thus highest Akaike weight (interpreted as the relative likelihood of the model being the best), were considered to have the best fit with the data. We considered any models that had AIC differences ≤2 of the final model to have comparable support (Burnham and Anderson 2002). To calculate the relative importance of each variable we summed the Akaike weight of all comparative models that included that variable (Zuur et al. 2009).

The final model (model 1) that we preferred involved all candidate terms except medium-sized tree heterogeneity, which had a negligible effect. Although simpler models had similar values for AIC we did not feel justified in disregarding any more terms. We tested the final model for overdispersion by inspecting both the Pearson and deviance residuals (McCullagh and Nelder 1989). Our models also showed no spatial auto-correlation in the model residuals once the spatial auto-correlation explained by the explanatory variables had been accounted for (Bjornstad and Falck 2001) and we found no evidence for over-dispersion. Therefore, we did not further consider over-dispersion and spatial auto-correlation in the estimation of parameters.

Analysis of bird species traits

We used RLQ analysis (Dolédec et al. 1996) to relate bird species traits to our vegetation data. RLQ analysis was used to provide simultaneous ordination, and to analyse the joint structure of three data sets: R (bird species traits), L (bird species presence/absence data), and Q (vegetation data) (Dolédec et al. 1996). We performed two separate RLQ analyses: one using vegetation heterogeneity measures (i.e. tall tree heterogeneity, medium-sized tree heterogeneity and shrub heterogeneity) and the second using total cover measures (i.e. tall tree cover, medium-sized tree cover and shrub cover). This approach allowed us to maximise the covariance between site and species trait scores along biological meaningful axes that were directly relevant to our aims.

To obtain our data set of bird species traits (Q), we modified a selection of bird traits based on life history and morphological attributes derived from Lindenmayer and Cunningham (2011). These data included body mass (small <25 g, large >25 g), foraging method (pounce, wood searcher, foliage, ground, aerial and various), nest type (hollow, cup, and dome), nest location (arboreal, non-arboreal and varied), and nest height range (minimum nest height/maximum nest height) (Supplementary material, Table S1). We also calculated a mobility index based on the residual wing loading of each bird species [i.e. the residual after the linear regression of log body mass against log wing length per bird is fitted (Warton et al. 2006)]. We subsequently categorised bird mobility into three categories (low < −0.9, medium −0.61 to 0.45, and high >0.47).

We used a Hill–Smith principal components analysis for qualitative and quantitative data to relate the species matrix (L) to the vegetation matrix (Q). We used canonical correspondence analysis to relate the bird trait matrix (R) to the vegetation matrix (Q) (ter Braak 1986). Subsequently, RLQ analysis was used to combine the independent analyses in a simultaneous ordination. We tested the significance of the marginal effects of the individual variables (significance level at $\alpha = 0.05$) using a Monte-Carlo test (999 permutations) (Dolédec et al. 1996). We then tested the significance of the first two axes of the ordination (significance level at $\alpha = 0.05$). The RLQ analyses were performed within the ade4 package (Chessel et al. 2004) in the R statistical environment (R Core Team 2012).

Results

We detected a total of 47 bird species at our 96 sites. Mean species richness (pooled over six surveys) recorded at each site was 8.6 (range 2–17; SD 3.23). We observed 40 bird species in forest, 37 bird species in woodland, and 33 bird species in heathland.

Bird species richness

Five models predicting total bird richness had comparable support (i.e. were within two delta AIC of our top model; Table 2). The best five models formed a hierarchal sequence from complex to simple models. These included: (1) the top model containing cover of tall trees, medium trees and shrubs, and heterogeneity of tall trees and shrubs; (2) a model containing cover of tall trees, medium trees and shrubs, and heterogeneity of shrubs; (3) a model containing heterogeneity of tall trees, and cover of tall trees, medium trees and shrubs; (4) a model containing heterogeneity of tall trees, and cover of medium trees and shrubs; and (5) our global model which included all terms. That is, all best ranked models contained a combination of variables representing vegetation cover and heterogeneity. All five top-ranking models performed better than the null model. Across the five best ranked models the relative importance of the cover parameters was greater than that of the three heterogeneity parameters (Table 2b).

A similar directional response of heterogeneity and cover to bird species richness was observed across all five models. Of the cover variables, shrub cover and medium-sized tree cover were negatively associated with total bird richness (Table 2). Of the heterogeneity variables, tall tree heterogeneity were positively associated with total bird richness, whereas medium-sized tree heterogeneity and shrub heterogeneity was negatively associated.

The final preferred top model (model 1) predicting bird species richness contained all candidate terms, except medium-sized tree cover which had a negligible effect (Table 2c). Although simpler models had similar values for AIC we did not feel justified in disregarding anymore terms. The response of total bird richness to shrub heterogeneity differed with different levels of tall tree cover (Table 2; Figure 3). At sites with high amounts of tall tree cover, increasing shrub heterogeneity was associated with increasing total bird richness. However, at sites with low amounts of tall tree cover, increasing shrub heterogeneity was associated with declining total bird richness. Of the cover variables, shrub cover and medium-sized tree cover were negatively associated with total bird richness, whereas tall tree heterogeneity was positively associated with total bird richness (Table 2c).

Table 2. Summary and outcomes of model selection process for bird species richness

a)
95 % Confidence set $_a$

Models		Log(L)	K	AIC	Wi
1	SC + MTC + TTC + SH +TTH + SH × TTC	−240.306	7	494.6	0.306
2	SC + MTC + TTC + SH + SH × TTC	−241.598	6	495.2	0.229
3	SC + MTC + TTC + TTH	−242.808	5	495.6	0.185
4	SC + MTC + TTH	−243.921	4	495.8	0.166
5	5 SC + MTC + TTC + SH + TTH +MTH + SH × TTC	−240.295	8	496.6	0.114
6	Null	−261.346	1	524.7	0

b)
Relative importance $_b$

Terms	W
SC	1
MTC	1
TTC	0.834
TTH	0.771
MTH	0.649
SH × TTC	0.649
SH	0.114

c)
Models with substantial support $_c$

Models	Terms	Coefficient ± SE
1	(Intercept)	2.610 ± 0.151
	SC	−0.384 ± 0.151
	MTC	−0.336 ± 0.156
	TTC	−0.239 ± 0.249
	TTH	0.029 ± 0.018
	SH	−0.042 ± 0.038
	SH × TTC	0.214 ± 0.099
2	(Intercept)	2.674 ± 0.143
	SC	−0.449 ± 0.14
	MTC	−0.353 ± 0.154
	TTC	−0.171 ± 0.243
	SH	−0.037 ± 0.037
	SH × TTC	0.226 ± 0.098
3	(Intercept)	2.405 ± 0.122
	SC	−0.291 ± 0.145
	MTC	−0.328 ± 0.156
	TTC	0.205 ± 0.136
	TTH	0.034 ± 0.017

4	(Intercept)	2.545 ± 0.07
	SC	-0.382 ± 0.131
	MTC	-0.354 ± 0.155
	TTH	0.046 ± 0.015
5	(Intercept)	2.612 ± 0.151
	SC	-0.385 ± 0.151
	MTC	-0.322 ± 0.178
	TTC	-0.231 ± 0.255
	TTH	0.029 ± 0.018

TTC Tall trees cover, *MTC* medium-sized trees cover, *SC* shrubs cover, *TTH* tall trees heterogeneity, *MTH* medium-sized tree heterogeneity, *SH* shrub heterogeneity

[a] The 95 % confidence set of models, showing for each model the maximised log-likelihood [*Log*(*L*)], number of estimable parameters (*K*), Akaike's information criterion (*AIC*), difference in AIC compared with the best ranked model (Δ_i), and the Akaike weights (w_i); models are ordered by decreasing w_i. Terms in the full model (model 5) included six main effects and an interaction (between shrub heterogeneity and tall tree cover) represented by ×

[b] The relative importance of each term in the 95 % confidence set, ordered by decreasing importance

[c] Model coefficients ± SEs) and 95 % confidence intervals for models with substantial support ($\Delta_i \leq 2$), ordered by decreasing effect size

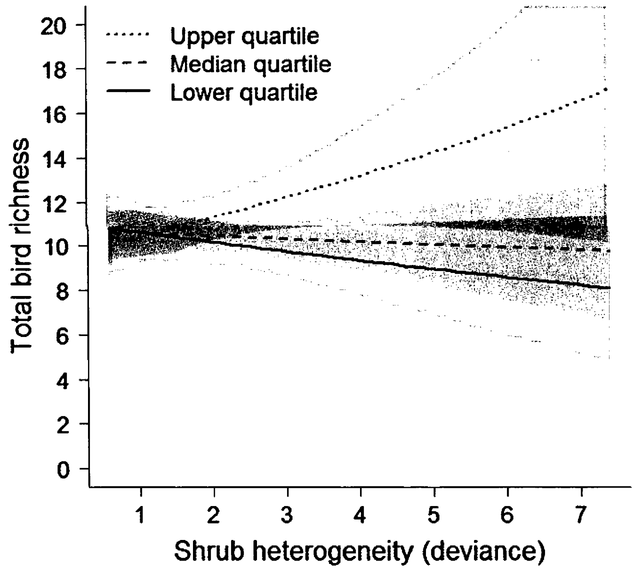


Figure 3. Predicted changes in total bird species richness (mean ± 95 % confidence intervals) with shrub heterogeneity interacting with different amounts of tall tree cover [upper quartile (56 %), median quartile (14 %) and lower quartile (0 %)] of the top ranked model.

Differences between birds grouped by traits

Vegetation

The RLQ analyses of vegetation cover revealed a significant relationship between the bird species traits and vegetation variables (permutation test p-value < 0.001). The first two axes of this RLQ ordination together explained 99.3 % of the total variance (Table 3). The RLQ analysis of vegetation cover arranged sites and trait characteristics along a gradient from high shrub cover to high levels of tall tree cover on axis 1, and a gradient from high shrub/tall tree cover to high cover of medium-sized trees on axis 2 (Fig. 4.4a). That is, the main gradient for changes in bird traits with vegetation cover appeared to be from heath to forest, with a secondary gradient from layered forest to woodland. The RLQ analyses of vegetation heterogeneity also revealed a significant relationship between the species traits and vegetation variables (permutation test p-value < 0.001). The first two axes of the RLQ ordination together explained 97.5 % of the total variance (Table 3). The RLQ analysis of heterogeneity arranged sites and trait characteristics along a gradient from low to high levels of heterogeneity of tall trees on axis 1, and a gradient ranging from low heterogeneity of shrubs and medium-sized trees to high heterogeneity of shrubs and tall trees on axis 2 (Fig. 4.4b).

Body mass traits

Small birds had a positive relationship with the cover of medium-sized trees and with the heterogeneity of shrubs and medium-sized trees. Large birds exhibited the opposite relationship to small birds, that is, a positive relationship with tall tree heterogeneity.

Mobility traits

Species with low mobility were positively related to shrub cover and medium-sized tree heterogeneity, and negatively related to shrub heterogeneity. Species with high mobility were positively related to both shrub cover and heterogeneity of shrub cover.

Foraging traits

Pouncing species were negatively associated with the cover of medium-sized trees but had a positive association with large trees and the heterogeneity of shrubs and medium-sized trees. Ground-feeding species were positively associated with shrub cover and negatively associated with medium-sized tree cover and the vegetation heterogeneity of all strata. Wood-searching species were negatively associated with medium-sized trees and had a positive relationship with vegetation heterogeneity of all strata. Foliage feeders had a positive relationship with large and medium-sized tree cover as well as vegetation heterogeneity of all strata. Aerial feeders were positively associated with both the cover of medium-sized trees and heterogeneity of all strata. Species with various feeding methods were positively associated with shrub cover but were negatively associated with vegetation heterogeneity of all strata.

Nest traits

Of the nest traits, cup nesters were positively associated with both the cover and heterogeneity of tall trees and shrubs. Dome nesters were positively associated with shrub cover, negatively associated with medium-sized trees cover, and negatively associated with the heterogeneity of tall trees. Hollow nesters were positively associated with the cover and heterogeneity of tall trees and negatively associated with the cover and heterogeneity of medium-sized trees. Species with varied nesting methods (i.e. the composite group various nesters) were negatively associated with both the cover and heterogeneity of medium-sized trees and shrubs. Arboreal nesters were positively associated with medium and tall tree cover, as well as the heterogeneity of all strata. Non-arboreal nesters were positively associated with cover of shrubs but negatively associated with vegetation heterogeneity of all strata. Species associated with a wide range of nest heights had a positive relationship with both the cover of tall and medium trees and the heterogeneity of tall trees, but were negatively associated with the heterogeneity of medium-sized trees and shrubs.

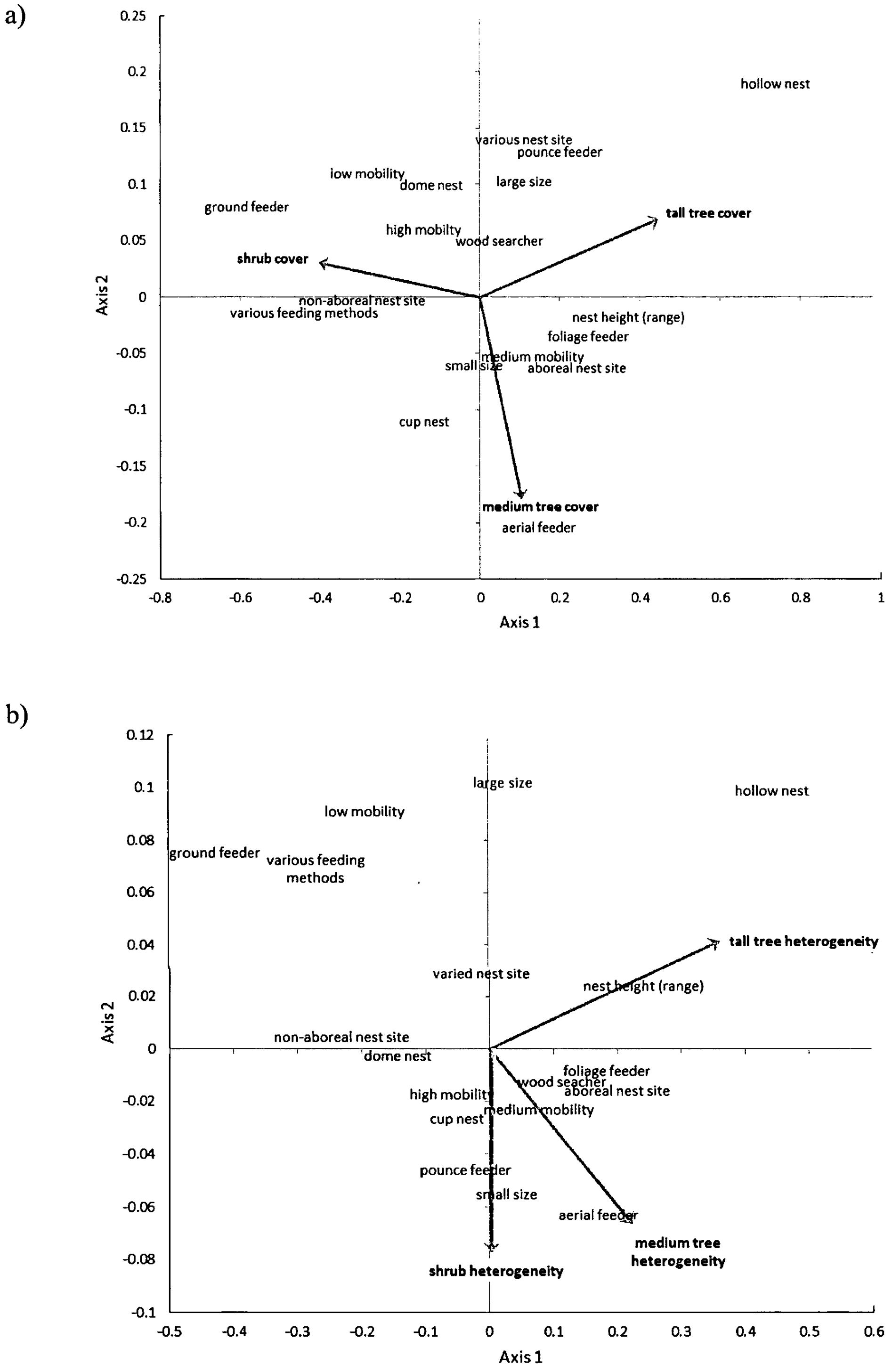


Figure 4. RLQ scores along the first two axes relating characteristics of species (traits) to vegetation characteristics: a) total cover of tall trees, medium-sized trees and shrubs and b) the heterogeneity of tall trees, medium-sized trees and shrubs. Positions of species traits relative to the vegetation characteristics indicate close associations.

Table 3. Results of the RLQ analysis of the vegetation (R), the species present (L), and their life-history traits (Q) for vegetation cover and vegetation heterogeneity.

	Vegetation cover		Vegetation heterogeneity	
	Axis 1 (%)	Axis 2 (%)	Axis 1 (%)	Axis 2 (%)
Separate ordinations				
R (PCA)	1.71 (57.08)	0.99 (33.24)	1.41 (46.89)	0.99 (33.07)
L (CA)	0.40 (9.33)	0.23 (5.38)	0.40 (9.33)	0.23 (5.38)
Q (Hill-Smith PCA)	3.26 (25.12)	1.85 (14.23)	3.27 (25.12)	1.85 (14.26)
RLQ analysis				
Simulated p-value	0.00099		0.00099	
RLQ axis eigenvalues	0.38 (90.12)	0.04 (9.15)	0.18 (91.42)	0.01 (6.15)
Covariance	0.61	0.19	0.24	0.11
Projected variance: R	1.69 (98.81)	2.70 (83.46)	1.36 (96.31)	2.15 (89.96)
Correlation: L	0.30 (48.48)	0.13 (29.05)	0.22 (35.75)	0.09 (20.67)
Projected variance: Q	2.34 (71.76)	4.26 (0.83)	2.6 (79.7)	4.13(80.9)

Separate ordinations: eigenvalues (and percent variance explained) for the first two axes from the ordinations of the R (Hill–Smith principal components analysis), L (correspondence analysis) and Q (Hill–Smith principal components analysis) tables. RLQ analysis: simulated *p*-value, eigenvalues (and percent variance explained), covariance and correlation (and percent variance) with the correspondence analysis of the L matrix, and projected variance (and percent variance) with the R and Q matrices

Discussion

Our findings demonstrated that heterogeneity of vegetation structure at a fine spatial scale is an important predictor of bird species richness in addition to the cover of vegetation variables. Our study is the first to show that bird species with particular traits respond not only to the amount of cover, but also had a preference for, or were restricted by, different degrees of vegetation heterogeneity. Our results indicated that by taking into account not only the amount of vegetation (i.e. cover), but also how the heterogeneity of different vegetation structures influences fauna, we will be more effective in managing and restoring habitats.

Why does a combination of vegetation heterogeneity and cover influence bird richness?

A combination of both vegetation heterogeneity and total cover of different vegetation structures at the fine scale (as demonstrated by our study within a 25-m radius), had an important influence on species richness (Table 2). Combinations of vegetation heterogeneity and vegetation cover reflect different requirements for birds. Vegetation cover may fulfil needs based on the amount of resources, whereas vegetation heterogeneity may fulfil needs based on how varied the spatial arrangements of these resources are. For example, some species of passerine require shrub cover to provide a refuge from predators (Perkins et al. 2000), but they also require access to varying amounts of both vegetation structure and open ground within a site for foraging (Benton et al. 2003; Gorini et al. 2012). Hence, a measure of cover may ultimately prove most useful when considered in combination with information on structural heterogeneity.

We found that vegetation cover parameters were stronger determinants of total bird species richness than the vegetation heterogeneity parameters, as indicated by the relative variable importance metric (Table 2b). Heterogeneity is more complex to measure and quantify then cover, as numerous subplots are required to calculate a robust measure of variation. Thus, our findings suggested that cover should remain a principal metric for measuring vegetation variables. However, we should be cautious regarding our interpretation of these results, as these findings may differ depending on the measure of heterogeneity and the scale at which heterogeneity is measured (Bar-Massada and Wood 2014; Bar-Massada et al. 2012).

Why is there a difference in bird richness in response to heterogeneity in different amounts of tall tree cover?

In contrast to the habitat heterogeneity hypothesis (Mac Arthur and MacArthur 1961), our results suggested that an increase in heterogeneity does not always result in an increase in species richness. We found that, at a fine-scale (within a 25 m radius), the strength of the response of species richness to heterogeneity of shrub cover varied with the proportion of tall tree cover. Total bird richness increased with shrub heterogeneity in vegetation with high levels of tall tree cover (55 % cover), whereas there was a decline in bird richness in vegetation with low levels of tall tree cover (>14 % cover; Fig. 3). In previous studies conducted across multiple spatial scales [i.e. concentric circles of different sizes centred on a site (Leyequién et al. 2010)], variation in richness–heterogeneity responses at different scales has generally been attributed to species turnover (Levin 1992; Zamora et al. 2007). Similarly, in our study, variation in the responses of bird species richness to shrub heterogeneity may be because our bird communities vary across areas with different levels of tall tree cover—the latter corresponding to changes in contrasting vegetation communities (i.e. heath, woodland and forest). Likewise, Bar-Massada and Wood (2014) found that the response of bird richness to fine-scale vegetation height heterogeneity varied in both strength and direction with habitat type. González-Megías et al. (2011) found a similar habitat specific response in arthropods. Hence, our findings and those of others (Bar-Massada and Wood 2014; González-Megías et al. 2011) support the suggestion by Allouche et al. (2012) that fine-scale heterogeneity-richness relationships vary between variable environments.

One possible explanation for the varied response of bird richness to shrub heterogeneity with different proportions of tall tree cover is competition between species. For instance, an increase in fine-scale heterogeneity in shrubs in the presence of tall trees may provide more niches or resources for one bird community (e.g. forest birds), which may, in turn compete for resources with other communities (e.g. woodland and heathland birds) thus leading to a turnover in species rather than opportunities for more species. Previous studies have found that the effects of vegetation heterogeneity may vary considerably depending on what is perceived as a habitat by the taxonomic group (reviewed in Tews et al. 2004) and community being studied. Overall, this suggests that we should not assume that an increase in vegetation heterogeneity will always result in an increase in resources and niches, and in turn higher species richness.

What is the association between bird traits, vegetation heterogeneity and vegetation cover?

We found, as predicted (Table 1), that certain key ecological traits of organisms strongly affect how species respond to both the amount of vegetation cover and heterogeneity of vegetation (Fig. 4a, b). It has previously been demonstrated that species with different traits have a preference for various amounts of cover of different structural vegetation at the fine scale (e.g. Hanspach et al. 2012; Ikin et al. 2012). This is the first study to demonstrate empirically, as previously hypothesised (González-Megías et al. 2011; Patthey et al. 2012), that species with different ecological traits also vary in their response to different degrees of vegetation heterogeneity at a fine scale. For example, pounce feeders showed a preference for high vegetation heterogeneity at the scale we measured (i.e. within a 25 m radius), while ground-feeding species preferred uniformly dense vegetation cover. Our results provide support for the postulate by Hutchings et al. (2000) and Katayama et al. (2014), that particular functional groups may have developed evolutionary adaptions to the degree of heterogeneity or homogeneity of vegetation in the landscape. Thus, birds with particular traits may be ecologically restricted or have a preference for areas with particular levels of heterogeneity of different vegetation structures, just as some bird species are restricted by the amount of cover of particular vegetation structures (e.g. Ikin et al. 2012). Previous studies have found that the constancy of associations between functional groups and vegetation cover varies over space (Bonthoux et al. 2013). Similarly, the response of functional groups to vegetation heterogeneity is also likely to be spatially dependent. For example, modifying the plot design (i.e. extent and grain) has the potential to reveal different responses of the various functional bird groups to vegetation heterogeneity (Barton et al. 2013). In our study, we only examined the heterogeneity-trait associations at a single spatial scale. Further research is needed to test if the effect of vegetation heterogeneity on functional trait associations holds across multiple spatial scales.

Body mass traits

Our findings lend support for the textual discontinuity hypothesis (Holling 1992), that small-bodied birds are associated with habitat with high structural complexity and fine-grained heterogeneity (Table 1). We found small birds were positively associated with shrub heterogeneity, and medium-sized tree heterogeneity. By contrast, large birds were positively associated with tall tree heterogeneity (Fig. 4). A relationship between the amount of habitat structure and bird body mass has been demonstrated elsewhere (e.g. Allen and Holling 2002; De la Montana et al. 2006). For example, in Australia, Fischer et al. (2008) found a higher number of small bird species in landscapes with dense, complex vegetation, than in landscapes with a less dense, simple vegetation. Our study suggested that the fine-scale heterogeneity of structural vegetation, as well as vegetation cover, can also contribute to the body mass distribution of birds.

Mobility traits

Species with limited mobility are thought to be associated with more heterogeneous areas because their resource requirements need to be met within a small area (Hutchings et al. 2000). In support of this suggestion, we found that species with low mobility were associated with medium-sized tree heterogeneity. However, we also found species with low mobility were associated with dense uniform cover of shrubs. For species with low mobility, high levels of dense, uniform shrub cover may be important for protection against predation (Gorini et al. 2012), whereas the high degree of medium-sized tree heterogeneity may increase the abundance and diversity of insect prey in the local area (González-Megías et al. 2011). Hence, species with low mobility may be capitalizing on both the heterogeneity and cover of different vegetation structures.

Foraging traits

Species that used multiple substrates, such as aerial feeders and pounce feeding species, were associated with heterogeneous habitats at the fine scale. For example, we found that pounce and aerial feeders showed a preference for sites with a high degree of medium-sized tree and shrub heterogeneity. These results make ecological sense because both pounce and aerial feeders require access to varying amounts of both vegetation structure for perch sites (Holmes and Recher 1986) and either open ground for the former, or open aerial space for the latter, to access prey (Benton et al. 2003; Gorini et al. 2012). For example, the grey fantail (*Rhipidura* *albiscapa*), an aerial feeder, perches in dense understorey vegetation and uses aerial foraging methods, such as hawking and sallying, to capture invertebrates flying in spaces between stems. In contrast, we found ground-feeding species were associated with habitat with high cover and low heterogeneity, potentially as protection against predation (Gorini et al. 2012).

Nest traits

We found, as predicted, that dome-nesting species, and non-arboreal-nesting species were associated with uniform, high cover of tall trees and shrubs, whereas species with a wide nesting height range were associated with high heterogeneity of tall trees. In contrast to our initial hypothesis, we found cup nesters responded to medium-sized tree heterogeneity. This finding may be because many of the cup-nesting species in our study, such as the rufous whistler (*Pachycephala rufiventris*), conceal their nests through crypsis, rather than by using vegetation, as an anti-predator strategy (Weidinger 2001). Our results suggested that some functional groups of birds may have evolved strategies for capitalizing on vegetation heterogeneity, whereas others capitalize on homogeneous environments.

What are the key implications of our results for management?

It is generally believed that maintaining or promoting vegetation heterogeneity at all scales is vital to improve conservation outcomes (McGranahan et al. 2013). However, while this may be mostly true at the landscape scale [i.e. more than tens of kilometres (but see Allouche et al. 2012)], our results suggested that vegetation heterogeneity may selectively disadvantage particular animal groups. For certain species assemblages and environmental combinations, manipulating habitats to produce high levels of vegetation cover can have negative consequences, while for other species, managing for high levels of vegetation heterogeneity can have negative consequences (see Figs. 3, 4). Moreover, different combinations of the amount of cover and heterogeneity of different habitat features may be needed by species with different traits. For example, pounce-feeding species, such as the eastern yellow robin *(Eopsaltria australis)*, preferred sites with high quantities of large tree cover and a high degree of shrub heterogeneity (Fig. 4; Supplementary Material Appendix, Fig. A1). In comparison, relatively large ground-foraging species, like the threatened eastern bristlebird (*Dasyornis brachypterus*), preferred sites with high cover and low heterogeneity of shrubs.

Our results suggest that focusing solely on increasing vegetation cover (e.g. through restoration and fire management) may be detrimental to particular animal groups. Management strategies may be most effective in improving or restoring habitat for different functional groups of birds if managers not only taken into account the amount of vegetation, but also focus on varying levels of vegetation heterogeneity. For instance, a widely applied management intervention for restoring forest and woodland ecosystems in agricultural landscapes worldwide, is to actively revegetate areas to increase native vegetation cover (Munro and Lindenmayer 2011; Benayas et al. 2008). This involves planting blocks of densely and sparse planted native shrubs and trees in a landscape (Rey Benayas and Bullock 2012). However, our findings suggested that to improve habitat for birds, management also needs to consider how the placement of shrubs and trees influences the degree of vegetation heterogeneity in a planted block. For example, planting heterogeneous clusters of shrubs and medium-sized trees may encourage the presence of declining pounce-feeding species in agricultural areas, such as the eastern yellow robin (Reid 1999). In natural landscapes, such as our study site, fire management is an important tool used to influence the amount of cover of structural vegetation, and in turn biodiversity (Barton et al. 2014). Similarly, the degree of vegetation heterogeneity at the fine-scale also can be influenced by different aspects of the fire regime and past fire management actions. For example, in natural landscapes, at the fine-scale (within a 25-m radius), the different aspects of the fire regime (i.e. mean fire interval and intensity) can influence the heterogeneity of different-habitat structures that are important to birds (Alexander et al. 2006; Kushla and Ripple 1997; Schoennagel et al. 2003). Which fire regime would be most appropriate would be dependent on the environment and past management actions (Bradstock et al. 2005). Depending on what species or groups are given the highest priority in conservation planning, our findings can be used to guide how areas within a landscape can be manipulated to preferentially benefit species of concern or particular functional groups of birds.

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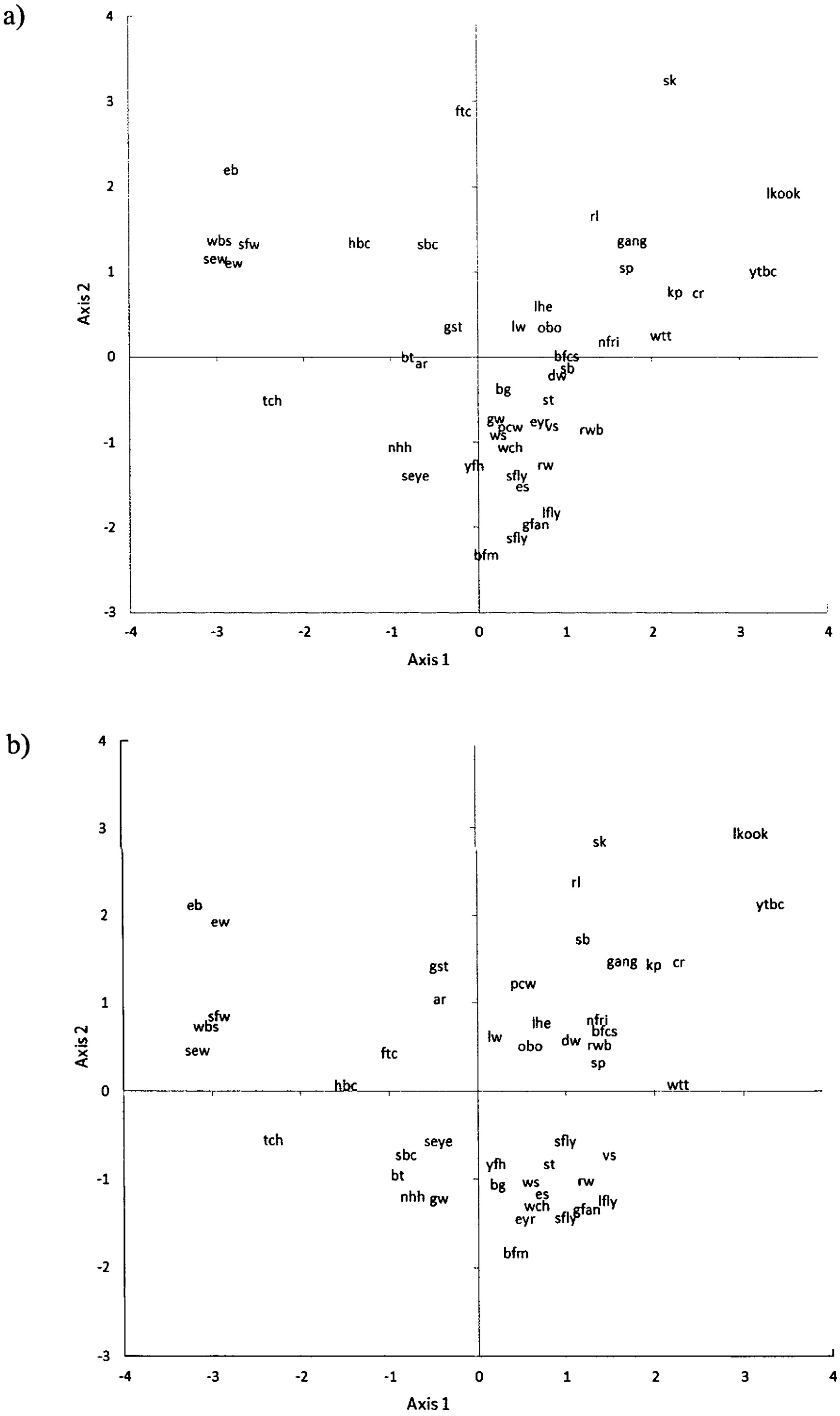
Supplementary material

Table A.1. Bird species, species abbreviations and qualitative variables (traits) used in the RLQ analyses.

Species code	Common name	Scientific name	Feeding method	Nest type	Nest location	Nest height (range)	Body size	Mobilty
ar	Australian Raven	*Corvus coronoides*	various	cup	aboreal	18.3	large	high
bfcs	Black-faced Cuckoo-shrike	*Coracina novaehollandiae*	wood searcher	cup	aboreal	36.5	large	high
bfm	Black-faced Monarch	*Monarcha melanopsis*	aerial	cup	aboreal	8.7	small	medium
bg	Brown Gerygone	*Gerygone mouki*	foliage	dome	aboreal	11.8	small	medium
bt	Brown Thornbill	*Acanthiza pusilla*	foliage	dome	non-aboreal	8	small	medium
cr	Crimson Rosella	*Platycercus elegans*	foliage	hollow	aboreal	20.6	large	medium
dw	Dusky Woodswallow	*Artamus cyanopterus*	aerial	cup	varied	34.6	large	high
eb	Eastern Bristlebird	*Dasyornis brachypterus*	ground	dome	non-aboreal	0.8	large	low
es	Eastern Spinebill	*Acanthorhynchus tenuirostris*	foliage	cup	aboreal	17.1	small	medium
ew	Eastern Whipbird	*Psophodes olivaceus*	ground	cup	non-aboreal	2.1	large	low
eyr	Eastern Yellow Robin	*Eopsaltria australis*	pounce	cup	aboreal	19.8	small	medium
ftc	Fan-tailed Cuckoo	*Cacomantis flabelliformis*	pounce	dome	varied	9	large	high
gang	Gang-Gang Cockatoo	*Callocephalon fimbriatum*	foliage	hollow	aboreal	18.5	large	high
gfan	Grey Fantail	*Rhipidura albiscapa*	aerial	cup	aboreal	30	small	high
gst	Grey Shrike-thrush	*Colluricincla harmonica*	various	cup	varied	20	large	medium
gw	Golden Whistler	*Pachycephala pectoralis*	wood searcher	cup	non-aboreal	7.5	small	medium
hbc	Horsfield's Bronze-cuckoo	*Chalcites baslis*	various	dome	varied	10	small	high
kp	Australian King-parrot	*Alisterus scapularis*	foliage	hollow	aboreal	19.2	large	medium
lfly	Leaden Flycatcher	*Myiagra rubecula*	aerial	cup	aboreal	34.5	small	high
lhe	Lewin's Honeyeater	*Meliphaga lewinii*	wood searcher	cup	varied	24.8	large	medium
lkook	Laughing Kookaburra	*Dacelo novaeguineae*	pounce	hollow	aboreal	58.8	large	low
lw	Little Wattlebird	*Anthochaera chrysoptera*	foliage	cup	varied	14.9	large	medium
nfri	Noisy Friarbird	*Philemon corniculatus*	foliage	dome	aboreal	33.2	large	medium
nhh	New Holland Honeyeater	*Phylidonyris novaehollandiae*	foliage	cup	non-aboreal	6.9	small	medium
obo	Olive-backed Oriole	*Oriolus sagittatus*	foliage	dome	aboreal	18.9	large	medium
pcw	Pied Currawong	*Strepera graculina*	variedious	cup	aboreal	30	large	medium
rl	Rainbow Lorikeet	*Trichoglossus haematodus*	foliage	hollow	aboreal	14.5	large	low
rw	Rufous Whistler	*Pachycephala rufiventris*	wood searcher	cup	aboreal	26.2	small	medium
rwb	Red Wattlebird	*Anthochaera carunculata*	foliage	cup	aboreal	29.67	large	medium
sb	Satin Bowerbird	*Ptilonorhynchus violaceus*	foliage	cup	aboreal	38	large	low
sbc	Shining Bronze-cuckoo	*Chalcites lucidus*	foliage	dome	varied	6	small	high
sew	Southern Emu-wren	*Stipiturus malachurus*	ground	dome	non-aboreal	1.14	small	low
seye	Silvereye	*Zosterops lateralis*	various	cup	aboreal	11.75	small	medium
sfly	Satin Flycatcher	*Myiagra cyanoleuca*	aerial	cup	aboreal	25.5	small	high
sfw	Superb Fairy-wren	*Malurus cyaneus*	ground	dome	non-aboreal	5.6	small	low
sk	Sacred Kingfisher	*Todiramphus sanctus*	pounce	hollow	varied	34.5	large	low
sp	Spotted Pardalote	*Pardalotus punctatus*	foliage	hollow	varied	15	small	medium
st	Striated Thornbill	*Acanthiza lineata*	foliage	dome	aboreal	22.9	small	medium
tch	Tawny-crowned Honeyeater	*Glyciphila melanops*	ground	cup	non-aboreal	1.2	small	medium
vfw	Variegated Fairy-wren	*Malurus lamberti*	ground	dome	non-aboreal	3	small	low
vs	Varied Sittella	*Daphoenositta chrysoptera*	wood searcher	cup	aboreal	37.5	small	high
wbs	White-browed Scrubwren	*Sericornis frontalis*	ground	dome	non-aboreal	2.9	small	low
wch	White-cheeked Honeyeater	*Phylidonyris niger*	foliage	cup	non-aboreal	3.4	small	medium
ws	Welcome Swallow	*Hirundo neoxena*	aerial	cup	varied	26	small	high
wtt	White-throated Treecreeper	*Cormobates leucophaea*	wood searcher	hollow	aboreal	24	small	medium
yfh	Yellow-faced Honeyeater	*Lichenostomus chrysops*	foliage	cup	non-aboreal	24.8	small	medium
ytbc	Yellow-tailed Black-Cockatoo	*Calyptorhynchus funereus*	foliage	hollow	aboreal	50	large	high

Figure S1. RLQ scores along the first two axes of bird species grouped by habitat-association in relation to the: a) proportion cover of tall trees, medium-sized trees and shrubs, **and** b) heterogeneity of tall trees, medium-sized trees and shrubs. Bird species abbreviations given in Supplementary material Table S1.



PAPER 4: Fine-scale habitat heterogeneity influences occupancy in terrestrial mammals

Images of black wallabies [*Wallabia bicolor*], long-nosed bandicoots [*Perameles nasuta*], and bush rats [*Rattus fuscipes*]) that were captured with camera traps.

Stirnemann, A.I., Mortelliti A., Gibbons P., & Lindenmayer D.B. Fine-scale vegetation heterogeneity influences occupancy in terrestrial mammals. PLosOne. (accepted)

Abstract

Vegetation heterogeneity is an inherent feature of most ecosystems, characterises the structure of habitat, and is considered an important driver of species distribution patterns. However, quantifying fine-scale heterogeneity of vegetation cover can be time consuming, and therefore it is seldom measured. Here, we determine if heterogeneity is worthwhile measuring, in addition to the amount of cover, when examining species distribution patterns. Further, we investigated the effect of the surrounding landscape heterogeneity on species occupancy. We tested the effect of cover and heterogeneity of trees and shrubs, and the context of the surrounding landscape (number of habitats and distance to an ecotone) on site occupancy of three mammal species (the black wallaby [*Wallabia bicolor*], the long-nosed bandicoot [*Perameles nasuta*], and the bush rat [*Rattus fuscipes*]) within a naturally heterogeneous landscape in a temperate region of Australia. We found that fine-scale heterogeneity of vegetation attributes is an important driver of mammal occurrence of two of these species. Further, we found that, although all three species responded positively to vegetation heterogeneity, different mammals vary in their response to different types of vegetation heterogeneity measurement. For example, the black wallaby responded to the proximity of an ecotone, and the bush rat and the long-nosed bandicoot responded to fine-scale heterogeneity of small tree cover, whereas none of the mammals responded to broad scale heterogeneity (i.e. the number of habitat types). Our results highlight the influence of methodological decisions, such as how heterogeneity vegetation is measured, in quantifying species responses to habitat structures. The findings confirm the importance of choosing meaningful heterogeneity measures when modelling the factors influencing occupancy of the species of interest.

Key words: *Australia, fine-scale, habitat heterogeneity, habitat management, marsupials, small-medium-sized mammals, spatial heterogeneity, variation.*

Introduction

Heterogeneity (defined here as dissimilarity or variation in a given attribute of vegetation across space) characterises the habitat structure of most ecosystems, and influences the distribution of biota [1-3]. For example, according to habitat heterogeneity theory [4], biota are more likely to occupy highly heterogeneous habitats as these habitats provide greater fitness benefits and resources [5, 6]. The study of heterogeneity in ecology and biogeography is a diverse topic that has received considerable attention and motivated the quantification of many different measures of vegetation heterogeneity (e.g. number of habitats, variation in habitat features [7]). An understanding of how vegetation heterogeneity influences biota is needed to identify the factors that drive species-habitat relationships [8]. While knowledge of association between some measures of vegetation heterogeneity (e.g. number of habitats and foliage height diversity) and biota have be recognised for decades [4, 9], there is still only a limited understanding of the effect of different types of heterogeneity on the spatial distribution of different fauna.

At the fine-scale (10's of meters), vegetation is typically measured in terms of its amount or cover [10, 11]. Fine-scale variation in vegetation cover (hereafter habitat heterogeneity) is rarely explicitly measured, despite being regarded as critical for explaining the distribution of biota [12, 13]. An understanding of habitat heterogeneity is important since variation in the configuration of vegetation at the fine-scale is thought to influence species patterns through their response to risks, such as predation [14], and access to resources [5, 6]. Therefore, quantifying vegetation heterogeneity, as well as the amount of vegetation cover is believed to be essential for understanding animal distribution patterns and for informing management decisions [15-17]. However, studies rarely quantify fine-scale habitat heterogeneity, possibly because robust measures of habitat heterogeneity are time consuming to gather in the field (i.e. requires multiple samples per plot). Therefore, the influence of habitat heterogeneity, as well as the amount of vegetation cover, on species occupancy is not well understood. Knowing if and how habitat heterogeneity and cover influences species occupancy is important for informing management decisions on how to manage understory and over-storey vegetation to make it more suitable for species.

The context and surrounding heterogeneity of a landscape also plays an important role in driving species distribution patterns [18-20]. For instance, the proximity of a site to an ecotone (a highly heterogeneous and diverse area where different vegetation communities coincide; [21]) has been found to influence small mammal occupancy (e.g. [22]). Moreover, the context of the embedded habitats (e.g. the surrounding number of habitat types, hereafter landscape heterogeneity) also can influence species richness [23]. The response of biota to ecotones has been studied under various levels of anthropogenic influence (natural, semi-natural; e.g. [22, 24]). In contrast, the majority of studies that have investigated the influence of landscape heterogeneity on biota have been restricted to landscapes under intense anthropogenic influence [25, 26].

Small- to medium-sized terrestrial mammals are an ideal group for investigating the influence of habitat heterogeneity and landscape heterogeneity. This is because mammals of this size have relatively low mobility (comparatively to other taxonomic groups [i.e. birds]) and thus have more restricted home range and habitat requirements [27]. Most small- to medium-sized terrestrial mammals also perceive the environment at small spatial scales [28, 29], which should make them particularly sensitive to both fine-scale vegetation structure and the surrounding landscape heterogeneity.

We conducted a multi-scale study to answer two questions: 1) What is the influence of the amount and heterogeneity of habitat on mammal occupancy? And 2) What is the influence of different forms of vegetation heterogeneity (fine-scale vegetation heterogeneity, landscape heterogeneity and distance to ecotones) on mammal occupancy?

To answer these questions, we investigated the factors influencing occupancy patterns of three small- to medium-sized mammals, which have different environmental needs. Our study environment within

Booderee National Park in south-eastern Australia was ideal for this investigation because this area is a naturally heterogeneous, patchy and characterised by many distinct vegetation types. Geological and fire disturbance processes in this landscape are also spatially variable, resulting in varied amounts of fine- to broad-scale habitat heterogeneity within the study area [30].

Here we test the hypothesis by Louys et al. [12] and McElhinny et al. [13], that some habitat attributes influence the occupancy of biota in terms of their variance, or heterogeneity, in addition to the more common measure of amount of cover. Furthermore, based on the habitat heterogeneity theory [4], we hypothesise that species occupancy will exhibit a positive response to habitat heterogeneity, landscape heterogeneity and proximity to ecotones. Theoretically, vegetation heterogeneity is an important driver of biodiversity because it captures the range of resources available in a given area [31].

Materials and Methods

Study area

Our study was located within Booderee National Park (35°10′ S latitude, 150°40′ E longitude) in the Jervis Bay Territory in south-eastern Australia (Fig 1). Booderee National Park is a lowland region (< 170 m ASL) of sandstone bedrock overlain by varying depths of deposited sand [32]. This area is characterised by a temperate maritime climate, with average rainfall of approximately 1200 mm that is largely consistent over the year. Mean annual temperature ranges from 17 °C to 26 °C. Booderee National Park is characterised by an extreme and unique degree of broad- and fine-scale vegetation heterogeneity within a fairly small area (~6500 ha). Therefore, potential confounding influences on mammal presence associated with climate and topography are minimised. Booderee National Park contains a variety of vegetation types, from dry heathlands to wet rainforest, which are patchily distributed within the park [33, 34]. At the fine-scale, the varied terrain, topography and fire history of the park has resulted in a high degree of variation in the different types of structural vegetation (e.g. trees and shrubs) within vegetation patches. For our study, we recognised four broad categories of vegetation (forest, woodland, shrubland, and heathland) and 29 vegetation sub-formation classes (S1

Table). The 29 vegetation sub-formation classes cover a wide range of natural vegetation, including: littoral rainforest, *Eucalyptus paniculata* dry sclerophyll forest, *Backhousia myrtifolia* dry rainforest, *Eucalyptus gummifera* dry woodland, *Avicennia marina* mangrove woodland, *Baeckea imbricata* coastal heath, and *Allocasuarina* dry shrubland. There are 12 forest groups, 7 woodland groups, 5 heathland groups and 5 shrubland groups. Full profiles of each of the 29 vegetation sub-formation classes are provided in Taws [34].

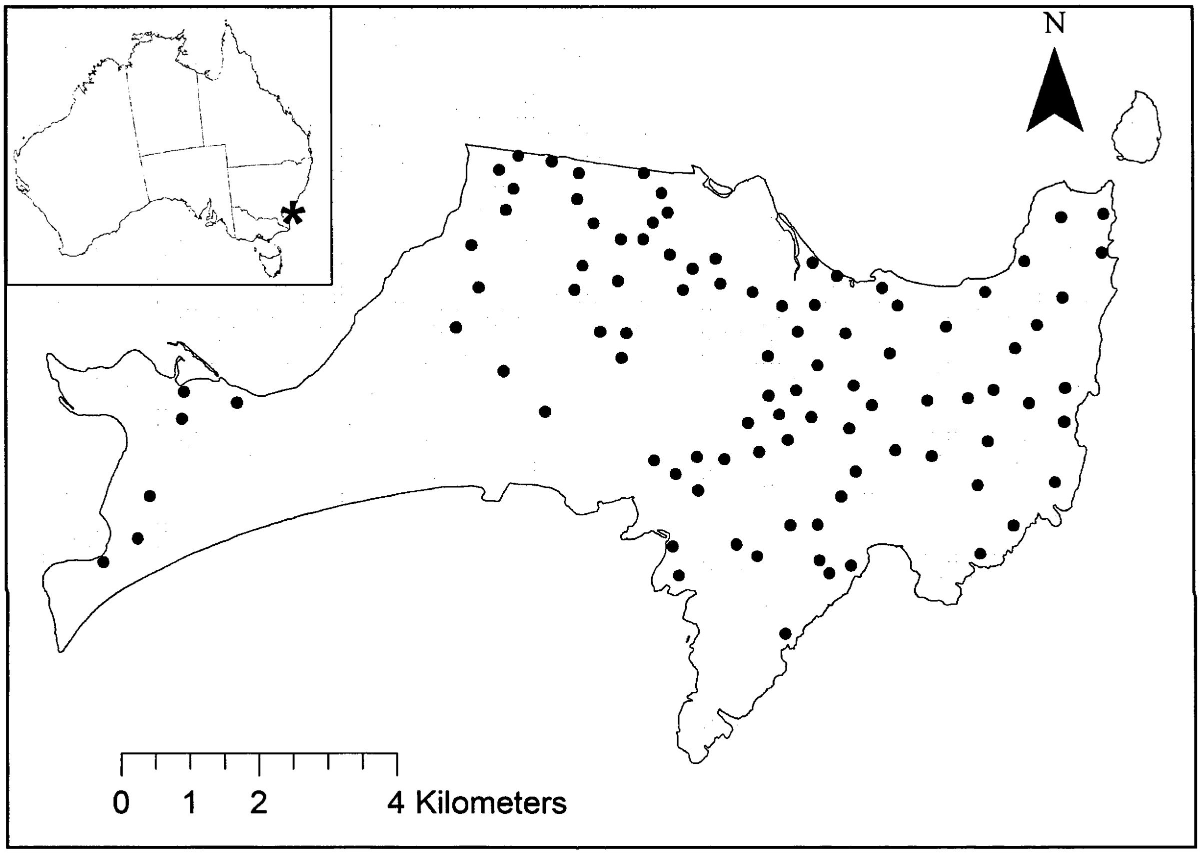


Fig 1. Our study was located within Booderee National Park on the south coast of New South Wales, south-eastern Australia. Black points are the study sites (*n*=96).

Booderee National Park has a complex history of both natural and prescribed fires. Spatially-explicit records of the fire history of the Jervis Bay Territory date back to 1937 [35].

Study design

We used a stratified design to investigate the occurrence of small mammals in relation to fine-scale differences in the amounts of vegetation heterogeneity and vegetation cover. We stratified the study area into three of the vegetation types (forest, woodland and heathland), two fire frequency categories (0-3 years; 4-8 years), and two slope categories (low [0.24-3.56 degrees] and high [3.57-15.02 degrees]) (S2 Table). These three factors are known to influence both the degree of vegetation heterogeneity and amount of vegetation cover within the landscape (e.g. [36-39]). We selected eight (25m radius) sites within each of the 12 stratification treatments giving 96 sites within the study area. Our stratified approach enabled us to maximise the range (i.e. very low to very high values) of both heterogeneity and cover of different vegetation variables across our sites.

Study species

We focused on three target species in our study the: black wallaby (*Wallabia bicolor*), long-nosed bandicoot (*Perameles nasuta*), and bush rat (*Rattus fuscipes*). All species are currently classified as least concern by IUCN red data list [40] and are distributed widely along the east coast of Australia [41]. The black wallaby is a macropod marsupial that weighs about 10.3-20.5 kg [41]. It is predominantly a browser and consumes a wide variety of plant and fungus species [42]. The long-nosed bandicoot is an omnivorous marsupial that weight ranges from 85–1100 g [41]. Its diet is primarily invertebrates, succulent plant material, and fungi [43]. The bush rat is an omnivorous mammal that weighs about 200 g [44] and eats plant material, fungi and invertebrates [45].

Habitat data

We selected 10 fine- and broad-scale explanatory variables that that are considered to influence the distribution of small- and medium-sized mammals [13, 46, 47]. We divided these explanatory variables into two categories, those characterising structural habitat at a fine-scale (within a 25 m radius), and those characterising broader context of the surrounding landscape (within a 50 m, 100 m and 150 m radius) .

Fine-scale habitat variables

Our fine-scale habitat variables were measures of the amount and variation of important structural habitat attributes at this scale [13]. To obtain these variables at each of our 96 sites, we collected data on three habitat attributes: shrubs (0-4 m); small trees (4-10 m) and tall trees (>10m). Each site consisted of a circular plot with a 25 metre radius. Within each site, we established nine subplots. Subplots were evenly distributed into three distance categories from the centre: 1) 4 to 9 m, 2) 12 to 17 m, and 3) 20 to 25 m. Subplots also were evenly located at 90, 210, or 330 cardinal degrees from the central point. Each subplot consisted of six sampling points, each spaced one metre apart. At each of the 54 sampling points per site, we measured the presence/absence of the three habitat attributes using the point intercept method [48].

We calculated two fine-scale measurements for each of the three habitat attributes: 1) a measure of the total percent cover and, 2) a measure of heterogeneity. To quantify each measure of total percent cover (hereafter called 'cover'), we calculated the proportion of presences out of the total ($n_{points} = 54$) of each of the three habitat attributes.

Habitat heterogeneity is a measure of the variation of vegetation cover within a patch. In this study, we defined habitat heterogeneity as a measure of the differences in the: (1) proportion cover and/or (2) spatial dependency of habitat attributes, among the nine sub-plots within each site. Higher spatial dependence and/or increased difference between sub-samples within a site denote higher vegetation heterogeneity.

Our measure of fine-scale vegetation heterogeneity was derived by fitting a logistic regression model (a generalised linear model with a binomial distribution) to the cover data for each site. The response variable was the number of times (out of six) each feature was present, for each of the nine sub-plots (see above) for each site. We did not include any predictor variables in the model as the goal was to assess the adequacy of the model constant in describing the percent cover across the nine-subplots. We assessed the adequacy of the model by dividing the residual deviance by the degrees of freedom (in this case, d.f. = 8) which can be interpreted as a measure of over-dispersion. We used this measure of over-dispersion as our measure of heterogeneity at the site level. This approach was preferred to the usual measures of heterogeneity (such as the coefficient of variation) as it respects the underlying binomial structure of the data [49].

Broad-scale habitat variables

To calculate broad-scale heterogeneity measures, we created a radius around each of the central points of each site at 50 m, 100 m, and 150 m (hereafter referred to as buffers). Within each buffer, we calculated the number of vegetation types from a detailed vegetation layer of the study site [see 34] using Arc GIS [50]. This measure of landscape heterogeneity represents the degree of landscape fragmentation surrounding each site (i.e. as the number of habitats increase the habitat fragmentation in the area will also increase) [8]. To retain the nested structure between each buffer, but reduce collinearity between buffers, we recast each variable as a linear combination of the variable (i.e. the 150m extent remains the same, while the 100 m and 50 m extents are recalculated as the difference between the original variable and the one it is nested within; [51]).

To calculate the distance to the ecotone, we measured the Euclidean distance from each site to the closest ecotone (transition zone between vegetation communities) using Arc GIS. The nearest ecotone was deemed to be the closest habitat sub-formation based on detailed vegetation maps of the study area (see [34]). Arc GIS operations were calculated in Arc-View GIS version 9.2 [50].

Camera trapping protocol

We used remote trail camera models with passive infrared sensors (either Scoutguard SG550® or Reconyx PC90®) to detect small- to medium-mammals at each of our 96 sites. Each camera was mounted approximately 50 cm above the ground at the centre of each site. A bait station was placed approximately 2.5 m in front of each camera. A small amount of peanut butter mixed with oats was secured to the ground under a vent cowl, as a lure at each site [52]. We sampled twenty-four sites continuously for eight consecutive nights. Twelve sites were sampled with Reconyx cameras and 12 sites were sampled with Scoutguard cameras. The twenty-four cameras (12 Scoutguard and 12 Reconyx) were rotated between sites until all sites had been surveyed with both cameras. All camera monitoring occurring within April-May 2011.

Statistical analysis

We used occupancy models to determine the factors influencing species occupancy as these models can correct for imperfect detection due to false absences (i.e. failure to detect a species that is present at the site; [53]). False absences are common in fauna studies, with detection probability typically being less than one in field conditions (e.g. [54]).

In our models, a site (*sensu* [55]) was defined as a camera-trap station. In our study a "visit" to a site was any record of each species within a 24-hour time period (i.e. from midday to midday). The response variable in our analysis was the detection history of each mammal species per site, which is the sequence of visits (1's and 0's) over the complete survey period (eight days per site).

Detection covariates

We identified four detection covariates (three continuous and one categorical variable) that we hypothesised could cause variation in species detection probability (*p*): type of remote camera (camera type), vegetation type (e.g. tall tree cover), heterogeneity of shrub cover and the total shrub cover (S3 Table). Previous studies have suggested that different camera models differ in their ability to detect mammals [56, 57]. The amount of understorey (e.g. cover of shrubs) also affects the intensity of use of an area by small mammals [58, 59] and thus may influence detection probability. Spatial heterogeneity in the environment (i.e. shrub heterogeneity) also may influence detection probability, as it can influence the movement patterns of small mammals [60]. Detection probability may also be lower within particular vegetation types. In our study, we used tall tree cover as a continous proxy of vegetation type. To account for a detection bias, we incorporated these four variables (camera type, shrub cover, shrub heterogeneity, and vegetation type) into the detection component of our models for each species.

Occupancy covariates

We measured ten site variables that we hypothesized could affect occupancy of our three target mammal species: three cover variables (shrub, small trees and larger trees), three heterogeneity variables (shrub, small trees and larger trees), the distance to an ecotone, and the number of habitats surrounding our sites (within 50 m, 100 m and 150 m buffers; S3 Table). These ten covariates were chosen to represent key habitat types or limiting factors for these species.

Prior to analysis, we assessed collinearity in the all explanatory variables using pairwise scatterplots, and Variance Inflation Factors [61, 62] with the R software [63]. Variance Inflation Factors were all below three, suggesting our explanatory variables were not strongly collinear [51] and we therefore considered all variables in our occupancy models

We used single-season models to model the probability of occupancy (ψ) of each mammal species per site, while accounting for detection probability (p) [55], within the software package unmarked [64]. We used single-season models as we assume the populations of all three of our study species were closed to any changes with respect to occupancy of the sampling sites during our sampling period [55]. Due to convergence issues within our full models, we also were unable to use a backward stepwise approach [65]. Thus, we used a multi-step process with a forward stepwise selection approach to determine the best ranked model [66]. First, we used forward stepwise selection to consider the effect of all single variables on species detection probability. We then tested all combinations of all single predictor variables that were ranked above the null model. We retained the top ranked parameterisation for detection probability and repeated the process with the occupancy predictor variables to determine the best occupancy model for each species. The ranking of each of the models were compared using Akaike's Information Criteria adjusted for sample size (AICc) [67]. To account for uncertainty in model selection, we used a model averaging approach (i.e. we averaged all models within two delta AICc of our top model) to predict site occupancy [67].

Results

We detected the bush rat at 13 of the 96 sites (14%); the long-nosed bandicoot was detected at 17 of the 96 sites (18%); and the black wallaby at 35 of the 96 sites (36%).

Black wallaby

The top ranked model predicting the probability of black wallaby occupancy contained distance from an ecotone in the occupancy component of the model and camera type in the detection component (Table 1).The probability of occupancy of the black wallaby had a strong negative association with distance from an ecotone (Fig 2). We found no evidence to suggest that either heterogeneity or cover of any of the fine-scale habitat attributes (shrubs, small trees or tall trees) influenced the probability of occupancy of the black wallaby. The probability of detecting black wallaby was affected by camera type, and was higher for Reconyx cameras, than for Scoutguard cameras (Fig 2). Two models predicting the probability of black wallaby occupancy had comparable support (i.e. were within two delta AIC of our top model; Table 2). The second ranked model predicting black wallaby occupancy contained all candidate terms contained in the top ranked model, except tall tree cover.

Table 1. Estimated parameters (β) and standard error (S.E.) of the top ranked occupancy models for black wallaby, long-nosed bandicoot, and bush rat.

Species	Parameter	Variable	β	S.E
Black wallaby	Ψ	Intercept	1.03	0.58
	Ψ	Distance to an ecotone	-16.13	7.62
	P	Intercept	-1.84	0.30
	P	Camera type	1.20	0.39
Long-nosed bandicoot	Ψ	Intercept	-1.04	0.72
	Ψ	Small tree heterogeneity	0.75	0.36
	Ψ	Small tree cover	-8.09	4.50
	P	Intercept	-1.86	0.40
Bush rat	Ψ	Intercept	-2.13	0.68
	Ψ	Small tree heterogeneity	0.44	0.19
	P	Intercept	-3.14	0.87
	P	Shrub cover	2.45	1.26

Table 2. Summary of the top ranked occupancy models (Δ AICc <2) and relative weights (*W*) for: black wallaby, long-nosed bandicoot, and bush rat. The terms in the parentheses represent the detection (*p*) and occupancy (ψ) covariates found in the models: camera type (cam), distance to an ecotone (E), small tree heterogeneity (STH), shrub cover (SC), small tree cover (STC) and tall tree cover (TTC). Absence of the ψ parameter in the model notation implies a constant model.

Species	Model	Δ AICc	*W*
Black wallaby	ψ(E,), p(CAM)	0	0.47
	ψ(E, TTC), p(CAM)	1.74	0.19
Long-nosed bandicoot	Ψ(STH, STC), p()	0	0.40
Bush rat	ψ(STH), p(SC)	0	0.52
	ψ(STH, TTC), p(SC)	1.60	0.23
	ψ(STH, STC), p(SC)	1.83	0.21

Long-nosed bandicoot

The top ranked model predicting the probability of long-nosed bandicoot occupancy contained small tree heterogeneity and small tree cover in the occupancy component of the model, with the detection component held constant (Table 1). The probability of occupancy of the long-nosed bandicoot was highest in areas with a high degree of small tree heterogeneity and low amounts of small tree cover (Table 1 and Fig 2). None of the other models we tested had comparable support (i.e. were within 2 delta AIC of the best ranked long-nosed bandicoot model; Table 2).

Bush rat

The top ranked model predicting the probability of bush rat occupancy contained small tree heterogeneity within the occupancy component of the model, and shrub cover within the detection component (Table 1). The probability of occupancy of the bush rat was highest in areas with high levels of small tree heterogeneity (Fig 2). The detection probability of the bush rat was highest in areas with high levels of shrub cover (Fig 2).

Two models predicting the probability of bush rat occupancy had comparable support (i.e. were within two delta AIC of our top model; Table 2). The second ranked model contained the same variables as the top ranking model, but also included an effect of tall tree cover. The third ranked model also contained same variables as the top model, but also included an effect of small tree cover.

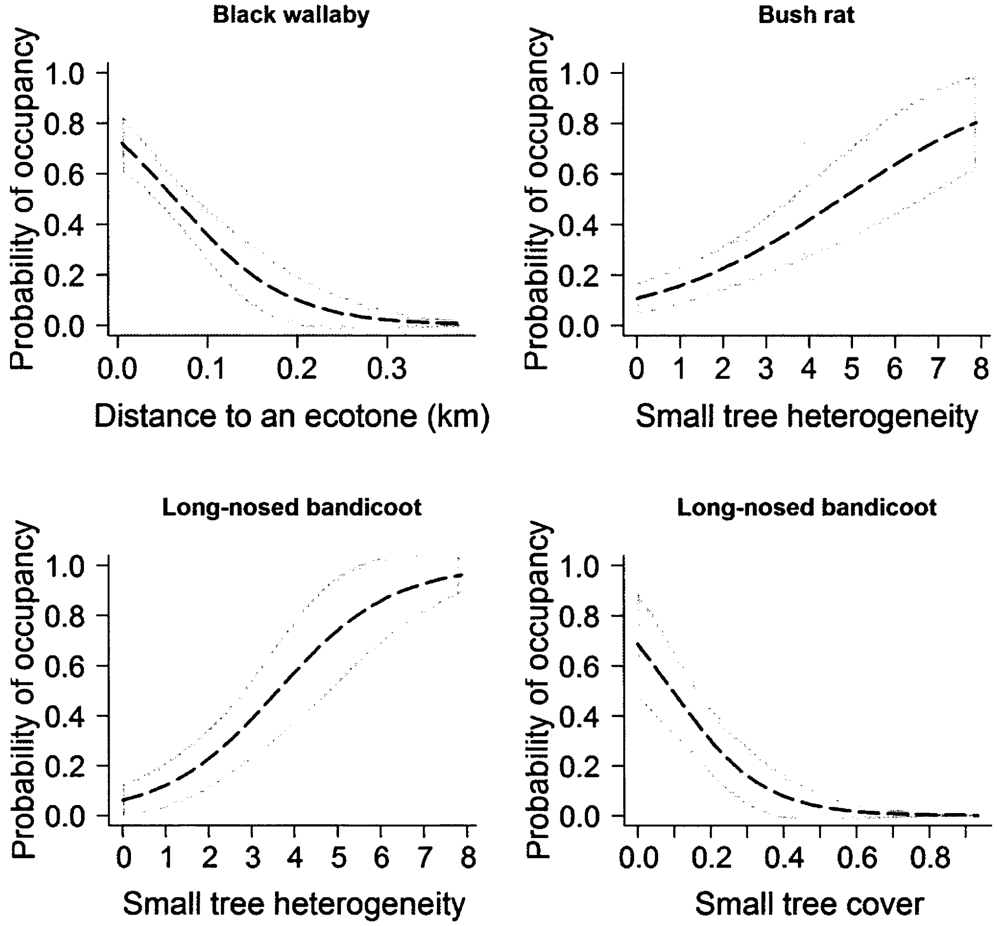


Fig 2. Probability of occupancy (± S.E.) of three mammals: black wallaby, bush rat, and long-nosed bandicoot in response to cover of small trees and heterogeneity of small trees, and distance to an ecotone.

Discussion

We found empirical evidence to support our hypothesis that fine-scale heterogeneity of vegetation cover can influence mammal occupancy. To the best of our knowledge, no other study has explicitly tested for and established this relationship. Furthermore, we found different species varied in their response to different types of vegetation heterogeneity. For example, the black wallaby responded to proximity of ecotones, and the long-nosed bandicoot and bush rat responded to fine-scale habitat heterogeneity, whereas landscape heterogeneity appeared to have no effect on the probability of occupancy of our three study species. Our results highlighted the impact of methodological decisions such as how heterogeneity in vegetation is measured, in influencing species responses and the importance of choosing meaningful, heterogeneity measures for the species and study system of interest.

What are the effects of fine-scale habitat heterogeneity and cover on occupancy?

We found, as hypothesised (but not explicitly tested) by Louys et al. [12] and McElhinny et al. [13], that some habitat attributes may influence the occupancy of biota in terms of their variance or heterogeneity rather than the more commonly used measure, absolute cover. For example, we found that small tree heterogeneity was included in the final model for the long-nosed bandicoot, and both heterogeneity and cover of small trees were included in the final model for the bush rat (Table 2). Understanding how variance (heterogeneity) of important features of habitat, rather than the average value, influence a response variable is increasingly recognised as a new avenue for investigating cause-and-effect relationships in ecology [68] and for deepening our understanding of species spatial patterns. Indeed, our results demonstrate that our measure of fine-scale habitat heterogeneity may be useful for categorising suitability of habitat for the bush rat and long-nosed bandicoot, and other potentially heterogeneity-sensitive species (e.g. Long-nosed Potoroo [*Potorous tridactylus*]; [15]).

How does fine-scale habitat heterogeneity influence occupancy?

As expected and based on the habitat heterogeneity hypothesis [4, 5], we found a positive effect of fine-scale habitat heterogeneity on species occupancy. We found that the long-nosed bandicoot and the bush rat were more likely to occur at sites with high levels of fine-scale small tree heterogeneity, and that the long-nosed bandicoot may be less likely to occur at sites with high levels of cover of small trees (4-10 m high; Fig 2). Our findings suggest that just as some species are adapted to dense habitats or to more open habitats, other species have adapted to take advantage of heterogeneity in the cover of habitat attributes [10].

Although a relationship between fine-scale habitat heterogeneity and species occupancy has not been previously explicitly tested for and established, past studies suggested such a relationship existed. For example, our findings for the long-nosed bandicoot concur with the observation of Bennett [69] that higher numbers of this species appear to occur in locally heterogeneous areas (i.e. sites with both dense understorey and open areas). In contrast, no previous studies have suggested that the bush rat is adapted to heterogeneous habitat. However, a study by Spencer et al. [70] found that the density of the bush rat was greatest at intermediate levels of mid-story cover. At intermediate levels of vegetation cover, the potential for high levels of heterogeneity of vegetation cover is highest [49]. Thus bush rat density in the study by Spencer et al. [70] also may be influenced by heterogeneity in mid-story cover or a correlated environmental attribute that these heterogeneous places offer, rather than cover *per se*.

At first glance, the influence of heterogeneity of cover of small trees seems unlikely to provide any direct benefit to ground-dwelling, terrestrial vertebrates, such as bush rats and long-nosed bandicoots. It therefore seems likely that this vegetation attribute was correlated with some other environmental factor that is of greater direct relevance to ground-dwelling animals. Occupying these highly heterogeneous areas would be advantageous to these species, if areas which are highly heterogeneous in terms of small tree cover provide higher abundance and greater variety of foraging resources (e.g. fungi, plants, fruit and invertebrates) than homogenous areas. Alternatively, the relationship with small tree heterogeneity and occupancy could reflect an adaptive trade-off between foraging needs and the need to avoid aerial predatiors (e.g. raptors) [14, 69, 71].

How does ecotone proximity influence occupancy?

As we hypothesised on the outset of this investigation, we found that the probability of black wallaby occupancy was higher near to an ecotone (Fig 2). We suggest that the black wallaby is likely to be utilising the contrasting habitats surrounding an ecotone to meet their daily resource requirements and/or exhibiting behavioural trade-offs between predator avoidance (e.g. foxes [*Vulpes vulpes*]) and foraging behaviour. In the context of our study, an ecotone provides both dense habitat for shelter and predator avoidance, as well as feeding habitat [72, 73]. Other small macropod species have been shown to trade-off increased foraging benefits to remain close to protective vegetation cover [74]. Foraging resources for the black wallaby (plants and fungi; [73]) also may be higher closer to an ecotone. For instance, a higher density and diversity of plants (i.e. shrubs and herbs) and fungi can occur at ecotones, because different vegetation communities can co-occur in this transition zone [31, 75, 76]. A preference for ecotones has been reported for a number of other small to medium-sized macropod species, including the red-necked pademelon (*Thylogale thetis*), rufous hare-wallaby (*Lagorchestes hirsutus*), the red-necked wallaby (*Macropus rufogriseus*), and the bridled nail-tail wallaby (*Onychogalea fraenata*) [47]. These findings, and our own results, suggest that ecotones are an important habitat resource for small to medium-sized macropods.

Surprisingly, we found no effect of the distance from an ecotone for either the bush rat or long-nosed bandicoot. This suggests that these species have a preference for particular types of heterogeneous habitat (i.e. small tree heterogeneity) rather than heterogeneous edge habitat *per se*. Many studies have difficulty teasing apart habitat and edge effects [77]. However, our study emphasises how these two different factors can have different effects on different species.

How does broad-scale habitat heterogeneity influence occupancy?

Despite a body of literature demonstrating the role of landscape heterogeneity (defined as the number of habitat types in our study) as a key determinant of species diversity responses [78-80], and in contrast to our hypothesis, we found no evidence of a relationship (negative or positive) between landscape heterogeneity and species occupancy, regardless of the spatial scales measured (i.e. within a 50, 100 and 150m radius of each site; Table 2). Our findings indicate that our study species were resilient to variation in landscape heterogeneity within our naturally heterogeneous landscape. For our study species, the majority of native habitats are neither inhabitable nor a barrier to movement, and an increase in the number of habitat types does not necessarily result in an increase in resources. Our findings highlight how similar to different aspects of fire mosaics [81], not all landscape heterogeneity elements may have functional roles for the various animal species [82].

Implications of our results for management

While the maintenance of homogenous habitat is important for conserving some biota and communities [7, 10], we found that some small mammals, such as the long-nosed bandicoot and the bush rat, preferred fine-scale heterogeneous habitat. Our findings highlight the importance of fine-scale habitat heterogeneity to facilitate the persistence of these and other heterogeneity sensitive species. Our findings of a positive relationship between mammal occupancy and vegetation heterogeneity may be extended to threatened species and therefore indicate the vegetation heterogeneity should be considered when assessing the habitat requirements of threatened species. Promoting vegetation heterogeneity would be important in areas which have demonstrated a loss of fine-scale heterogeneity over time (e.g. associated with changing fire regimes) and an associated decline in fauna or for a threatened species that has identified heterogeneity as an important feature and where managers want to increase its area of occupancy. Furthermore, we found that different mammal species responded to different forms of vegetation heterogeneity. These findings suggest that management strategies that focus solely on managing only a single form of vegetation heterogeneity may disadvantage particular mammal species. For example, vegetation thinning to reduce vegetation cover homogeneity, may benefit heterogeneity-sensitive mammal species by increasing tree canopy heterogeneity at the fine-scale [83], but may have no beneficial effects for species that respond to other forms of heterogeneity, such as the black wallaby that was associated with ecotones. Other management actions, such as prescribed burning, can influence many forms of heterogeneity. For example, prescribed burning can result in both an increase in edge habitat [84], and an increase in vegetation heterogeneity in areas with topographically variable terrain [85, 86]. An understanding of the different ecosystem processes driving the different forms of vegetation heterogeneity can be used to determine which management strategies to use to benefit or disadvantage different species.

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Supplementary material

S1 Table. The four broad categories of vegetation (forest, woodland, shrubland, and heathland) and 29 vegetation sub-formation classes used in our study

We identified four broad categories of vegetation (forest, woodland, shrubland, and heathland) and 29 vegetation sub-formation made up of different vegetation communities in our study. Full profiles of each of the 29 vegetation sub-formation classes are provided in Taws (1997).

Vegetation sub-formation	Broad vegetation categories
Acacia sophorae, *Leptospermum laevigatum* coastal shrubland	Shrublands
Allocasuarina distyla dry heath	Heathland
Allocasuarina distyla rocky heath	Heathland
Allocasuarina distyla, *Melaleuca capitata* rocky shrubland	Shrublands
Allocasuarina dry shrubland	Shrublands
Allocasuarina verticillata dry shrubland	Shrublands
Avicennia marina mangrove woodland	Woodlands
Backhousia myrtifolia dry rainforest	Forest
Baeckea imbricata coastal heath	Heathland
Banksia ericifolia intermediate heath	Heathland
Banksia integrifolia dry sclerophyll forest	Forest
Banksia integrifolia dry woodland	Woodlands
Banksia serrata dry woodland	Woodlands
Casuarina glauca swamp forest	Forest
Ceratopetalum apetalum warm temperate rainforest	Forest
Dry rainforest	Forest
E.botryoides swamp forest	Forest
E.sclerophylla, *E.gummifera* dry woodland	Woodlands
Eucalyptus botryoides dry sclerophyll forest	Forest
Eucalyptus botryoides swamp forest	Forest
Eucalyptus botryoides wet sclerophyll forest	Forest
Eucalyptus gummifera dry woodland	Woodlands
Eucalyptus paniculata dry sclerophyll forest	Forest
Eucalyptus pilularis dry schlerophyll forest	Forest
Eucalyptus sclerophylla, *E.gummifera* dry woodland	Woodlands
Eucalyptus sieberi , *E. gummifera* dry woodland	Woodlands
Leptospermum laevigatum coastal scrub	Shrublands
Littoral rainforest	Forest
Sprengelia incarnata intermediate heath	Heathland

S2 Table. The stratified design

Sampling was stratified by fire frequency (0-3years; 4-8 years), slope angle (low [0.24-3.56 degrees]) and vegetation type (forest, woodland and heathland). We randomly selected 96 sites (eight replicates per treatment).

	Fire frequency (<3 years)		Fire frequency (4-8 years)	
	Low slope	High slope	Low slope	High slope
Forest	8	8	8	8
Woodland	8	8	8	8
Heath	8	8	8	8
				Total = 96 sites

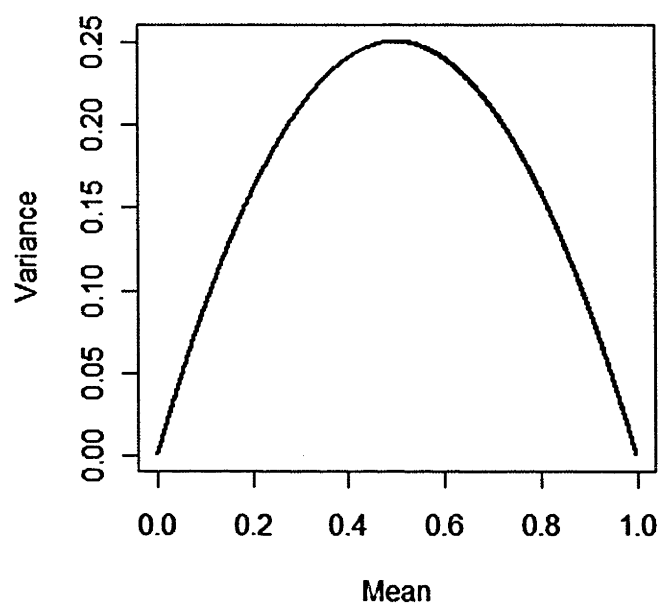
S3 Table. The explanatory variables, model-covariate, spatial scale of measurement, and a description of the measures used in the analysis. **The explanatory variables in the generalised linear models consisted of detection and occupancy covariates.**

a)

b)

c)

PAPER 5: Vegetation heterogeneity peaks at intermediate levels of cover



The relationship between mean (proportion of successes of the true distribution) and variance of binomial distribution can be described with a quadratic equation, with a single peak at 0.5. In this relationship the variance of a binomial distribution changes with the mean. That is, the variance is low when the mean is very high or very low, and the variance is greatest when the mean is equal to 0.5 (Crawley 2002)

Stirnemann A.I., Barton P., Gibbons P., Lindenmayer D.B., & Blanchard W. Habitat heterogeneity peaks at intermediate levels of cover. Ecology. In review.

Abstract

Heterogeneity in vegetation structure is an inherent feature of all terrestrial ecosystems, characterises their structure, and influences the diversity and distribution of biota. The relationship between vegetation cover and heterogeneity can be thought of in conceptually similar terms as the mean-variance relationship for binomial data, which indicates that heterogeneity peaks at intermediate levels of cover. Here, we use the mean/variance relationship for binomial data as a conceptual model for testing the relationship between vegetation cover and heterogeneity. We then extend this idea and test for associations between vegetation heterogeneity and cover, and bird occupancy. We confirmed that a quadratic relationship between cover and heterogeneity existed for all vegetation attributes that we measured, and that heterogeneity peaked at intermediate levels of cover. Four out of five bird species support our hypothesis that species with positive linear associations with vegetation heterogeneity are more likely to occur at intermediate levels of vegetation cover. Our results demonstrate that the mean/variance relationship of binomial data is a useful approach for conceptualising the relationship between vegetation cover and heterogeneity. This has important implications for how we should be analysing and interpreting vegetation heterogeneity, and is potentially transferrable to all studies examining ecosystem structure and the distribution of associated biota.

Key words: *binomial, conceptual model, ecosystem structure, occupancy, measures, mean/variance relationship, spatial scale, variation.*

Introduction

Spatial variation (heterogeneity) in vegetation structure is an inherent feature of ecosystems that characterises their structure and function (Li & Reynolds 1995; Hutchings *et al.* 2000; Ritchie 2010). Understanding how both the quantity and heterogeneity of a resource shapes the structure and dynamics of ecosystems is therefore of fundamental importance in ecology (Benedetti-Cecchi 2003; Stein *et al.* 2014). The concept of heterogeneity underpins some major theories in ecology, including species coexistence theory (Chesson 2000), source–sink dynamics (Johnson 2004), fractal theory (Milne 1997), and invasion theory (Melbourne *et al.* 2007). However, our understanding of the distributions of plants and animals is typically built upon measures of abundance of the physical environment (or habitat attributes), such as percentage cover (Fahrig *et al.* 2011), rather than measures of habitat heterogeneity, possibly because measures of heterogeneity are more time consuming to gather (i.e. requires multiple samples per plot) than other measures.

The variability (or heterogeneity) of a measure of cover and the amount of cover can be thought of in conceptually similar terms as the mean-variance relationship of binomial data, and represented by the binomial probability distribution (Fig. 1a; Morris 1982; Crawley 2002). We can use this mean-variance relationship as a conceptual model for testing the relationship between vegetation cover and heterogeneity, calculated from the number of successes/failures out of *n* trials. This relationship is relevant to ecology because many vegetation attributes are measured as cover, yet mechanistically they often influence biota in terms of their variance, or heterogeneity. The relevance of this binomial mean-variance relationship has not been previously interpreted in the field of ecology in relation to heterogeneity and cover, and represents a promising new way to describe a general pattern in ecosystems.

Based on the binomial mean-variance relationship (Fig. 1a), we hypothesised that vegetation heterogeneity across sites has a quadratic relationship with vegetation cover. That is, heterogeneity values will tend towards zero when cover is at the extremes (minimum and maximum, Crawley 2002). Conceptually, if the cover/heterogeneity relationship is empirically supported, then we predict that plant and animal species exhibiting a positive linear response to heterogeneity on the logit scale will demonstrate a quadratic relationship with cover on the same scale (Fig. 6.3a). We investigated this hypothesis by: (1) testing the relationship between heterogeneity and cover of four different vegetation attributes, and (2) examining the relationship between the site occupancy of bird species that are positively linearly associated with tall tree heterogeneity and tall tree cover.

If the relationship between heterogeneity and cover is supported by empirical data, it has important implications for how we contemplate both vegetation cover and vegetation heterogeneity in ecology. For example, we should be able to make broad inferences about heterogeneity from simple cover estimates without having to measure vegetation heterogeneity directly. Moreover, this relationship may have significant implications for how we should be analysing and interpreting the relationship between the cover of vegetation attributes and the habitat preferences of biota. This relationship has deeper implications, therefore, for both the theoretical conceptualisation of ecosystem structure and function, as well as how we examine ecosystems to guide their management.

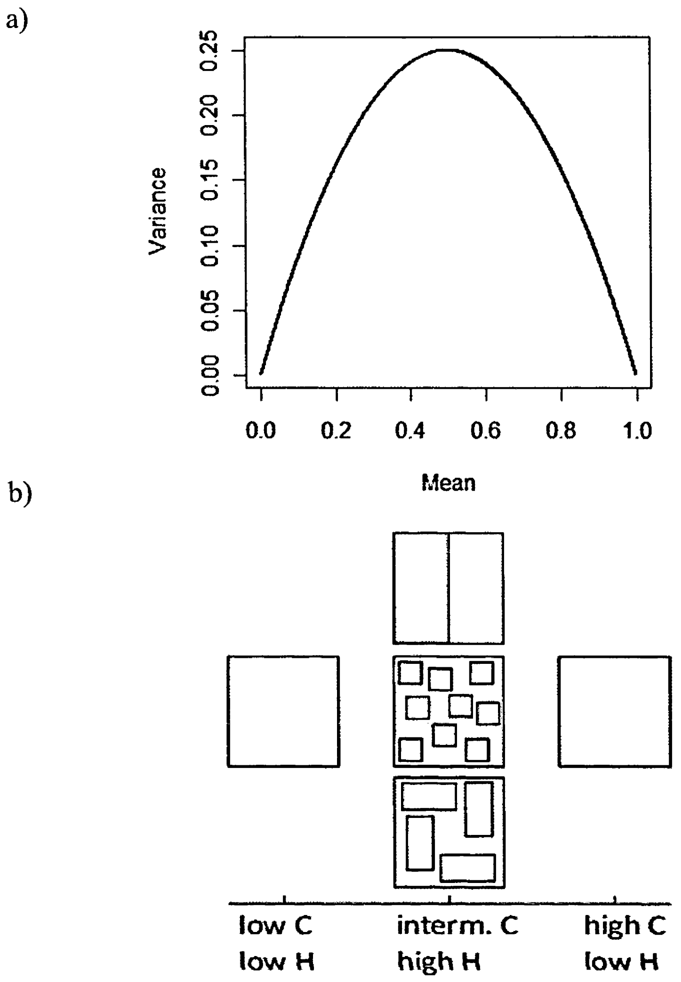


Figure 1. (a) The relationship between mean (proportion of successes of the true distribution) and variance of binomial distribution can be described with a quadratic equation, with a single peak at 0.5. In this relationship the variance of a binomial distribution changes with the mean. That is, the variance is low when the mean is very high or very low, and the variance is greatest when the mean is equal to 0.5 (Crawley 2002). (b) Simplified diagram depicting the relationship between cover (C) and heterogeneity (H) on the ground. Each square represents a site within which the grey areas represent vegetation cover. A greater range of heterogeneity values are possible at intermediate (interm.) levels of cover where there are more options for different configurations of cover, whereas at the extreme ends (where cover is very high or very low) there are fewer possible configurations, and thus variation in vegetation heterogeneity.

Materials and methods

Study area

Our study was located within Booderee National Park on the south coast of New South Wales, south-eastern Australia (approximate coordinates 35°10' S 150°40' E). Booderee National Park provides an ideal environment for our study because the area is characterised by a wide range in cover and heterogeneity for several vegetation attributes within a fairly small area (~7,500 ha) due to the varied geology, topography and fire history (Ingwersen 1977; Taylor *et al.* 1995; Taws 1997). More details on the study area can be found in Stirnemann *et al.* (2014).

Vegetation attributes

We stratified the study area into three broad vegetation types (forest, woodland and heathland), two fire frequency categories (0-3 fires since 1987; 4-8 fires since 1987), and two slope categories (low [0.24-3.56 degrees] and high [3.57-15.02 degrees]). We selected these three factors as they are known to influence both the degree of vegetation heterogeneity and the amount of vegetation cover within the landscape (e.g. Specht & Specht 2002; Gould *et al.* 2006; Jin *et al.* 2008; Gandiwa 2011). Hence, our stratified approach enabled us to sample the full range of both heterogeneity and cover of different vegetation attributes across our sites (i.e. from very low to very high values). We randomly positioned 96 sites within the study area, eight (25m radius) sites within each of the 12 strata.

Each site consisted of a circular plot with a 25 metre radius. Within each site, we established nine subplots, three on each of three radial lines located 90, 210, and 330 cardinal degrees from the central point. Subplots (six meters long) were evenly distributed from the centre: 1) 4 to 9 m, 2) 12 to 17 m, and 3) 20 to 25 m. There was a minimum of three meters between each of the subplots to minimise spatial dependence. Each subplot consisted of six sampling points each spaced one metre apart.

We measured the presence/absence of four habitat attributes at each of the 54 sampling points within each of the 96 sites, using the point intercept method (Elzinga *et al.* 1998). Our vegetation attributes were: (1) leaf litter (dead leaf material directly covering the ground), (2) shrubs (vegetation with a woody stem between 0-4 m in height), (3) small trees (vegetation with a woody stem between 4-10 m in height) and (4) tall trees (vegetation with a woody stem > 10 m in height). We completed all measurements between April and May 2011.

Quantifying cover and heterogeneity

We calculated a measure of mean cover and heterogeneity for each of the four vegetation attributes at each of the 96 plots. To quantify cover, we calculated the proportion of presences out of the total (n_{points}=54) of each of the vegetation attributes. To quantify heterogeneity, we used a measure of over-dispersion at the site-level, derived from a logistic regression model (McCullagh & Nelder 1989; Crawley 2002; Zuur *et al.* 2009). We used this measure of over-dispersion as our measure of heterogeneity rather than a traditional measure of heterogeneity (e.g. coefficient of variation) because our approach recognises the underlying binomial structure of our data (Crawley 2002). To quantify the measure of over-dispersion (our measure of vegetation heterogeneity), we fitted a logistic regression model (a generalised linear model with a binomial distribution) to the cover data for each site. The response variable was the number of times (out of six) each habitat attribute was present, for each of the nine sub-plots for each site. We did not include any predictor variables in the model. For each model, to quantified the amount of over-dispersion per site we divided the residual deviance by the degrees of freedom (d.f. = 8).

Bird surveys

We surveyed the presence/absence of bird species at each of our 96 sites at Booderee National Park, using five-minute fixed-radius point counts (Sutherland 2004). One observer (IAS) recorded the presence of all birds heard or seen within a 25 m radius of the centroid of all 96 sites. Three surveys, between dawn and 10 am, were completed at each site during the bird breeding season (October-November) in 2010 and again in 2011.

Data analysis

We fitted Gaussian Generalised Additive Models (GAMs) with integrated smoothness estimation to investigate relationships between cover and heterogeneity for each of our four habitat attributes. We selected GAMs to explore these relationships as they are sufficiently flexible to allow the underlying pattern to emerge from our data (Wood 2006), rather than imposing a pre-determined distribution on our data (Austin 2007). To select and check the choice of the smoothing parameters (the regression splines) in each of our four models, we fitted each model and extracted the deviance residuals. We then fitted an equivalent, single, smooth to the residuals, using a substantially increased smooth function to see if there was pattern in the residuals that could potentially be explained by increasing the smooth function (Wood 2006).

We used binomial GAMs to investigate if we could predict whether the probability of bird occupancy (p) exhibiting a significant positive linear response to heterogeneity on the logit scale would show an approximate quadratic relationship with cover on the same scale. Each GAM was fitted with presence/absence bird species data as the response variable. Bird presence/absence data were obtained from pooling presence data from six surveys at each of our 96 study sites. We used the cover and heterogeneity of tall tree cover as our explanatory variable. We used a two-step process to examine the predicted relationship between bird occupancy (logit (p)) and, heterogeneity and cover. First, we used GAMs to model the response of bird occupancy of each species to heterogeneity of tall tree cover. Next, for each species that exhibited a significant, positive linear response to heterogeneity of tall tree cover, we modelled the response of species occupancy to tall tree cover. As above, we selected and checked the smoothing parameters using the protocol established by Wood (2006).

To validate each model, we plotted the residuals of the GAM against each of the explanatory variables (Zuur *et al.* 2009). To verify that sites were independent from each other, we plotted the residuals against the spatial coordinates for each site (Zuur *et al.* 2009). In all plots, the patterns were not strong enough to be of concern. All GAMs were constructed within the mgcv package in R (R Core Team 2012).

Results

Is there a quadratic relationship between vegetation heterogeneity and cover?

We found evidence that each of the habitat variables has a quadratic relationship between heterogeneity and cover (Table 2 & Fig. 2). That is, heterogeneity was highest at intermediate levels of cover and lowest at extreme levels of minimum and maximum cover. However, it is worth noting that the habitat attributes litter and small trees have three degrees of freedom, suggesting that the models are not simple quadratic models (Table 2). The peak of the curve varied depending on the vegetation attribute. For example, leaf litter had the highest level of predicted heterogeneity, followed by small trees, tall trees, and shrubs. The relationship between heterogeneity and cover was not perfectly quadratic (i.e. there were a number of outliers) (Fig. 2). The residual deviance for all four vegetation attributes was highest at intermediate levels of cover and lowest at the extreme levels of cover.

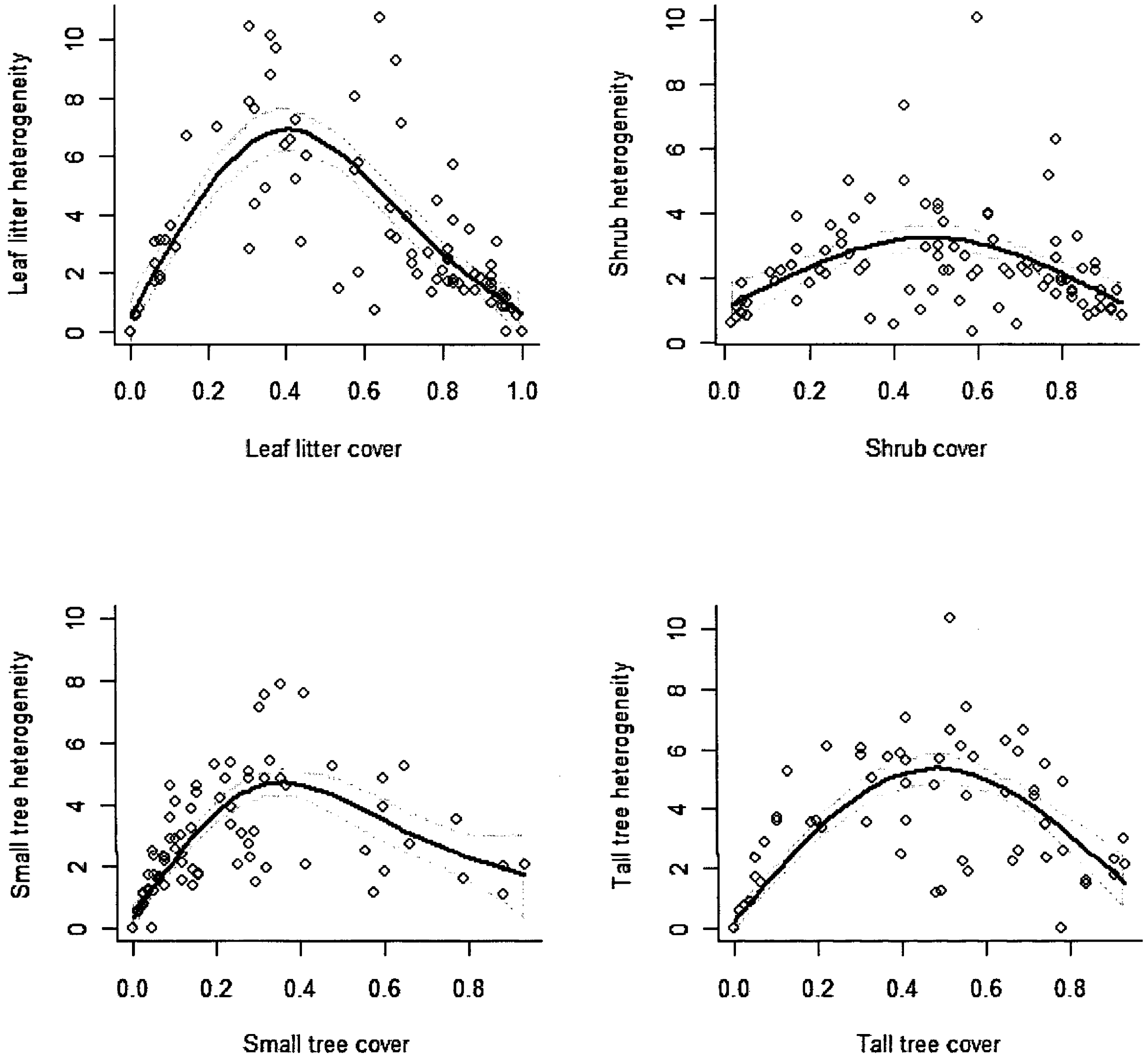


Figure 2. Empirical evidence of a quadratic relationship between cover and heterogeneity of four different vegetation attributes (leaf litter, shrubs, small trees and tall trees). The bold line represents that fitted values from each Generalised Additive Model (± 95% confidence intervals) and the dots represent the actual empirical data (*n*=96).

How does the mean-variance relationship influence animal occupancy?

Of the 32 bird species that we recorded at more than 20% of the sites, five bird species exhibited a significant positive linear relationship with heterogeneity of tall tree cover. We found that 80 percent (*n* = 4 out of 5) of the bird species, exhibiting a positive linear relationship with tall tree heterogeneity, also exhibited evidence of a quadratic relationship with tall tree cover. These species were the satin bowerbird (*Ptilonorhynchus violaceu*), dusky woodswallow (*Artamus cyanopterus*), eastern spinebill (*Acanthorhynchus tenuirostris*) and sacred kingfisher (*Todiramphus sanctus*) (Fig. 3). The olive-backed oriole (*Oriolus sagittatus*) also exhibited a positive linear effect with tall tree heterogeneity, but exhibited no evidence of a quadratic relationship with tall tree cover.

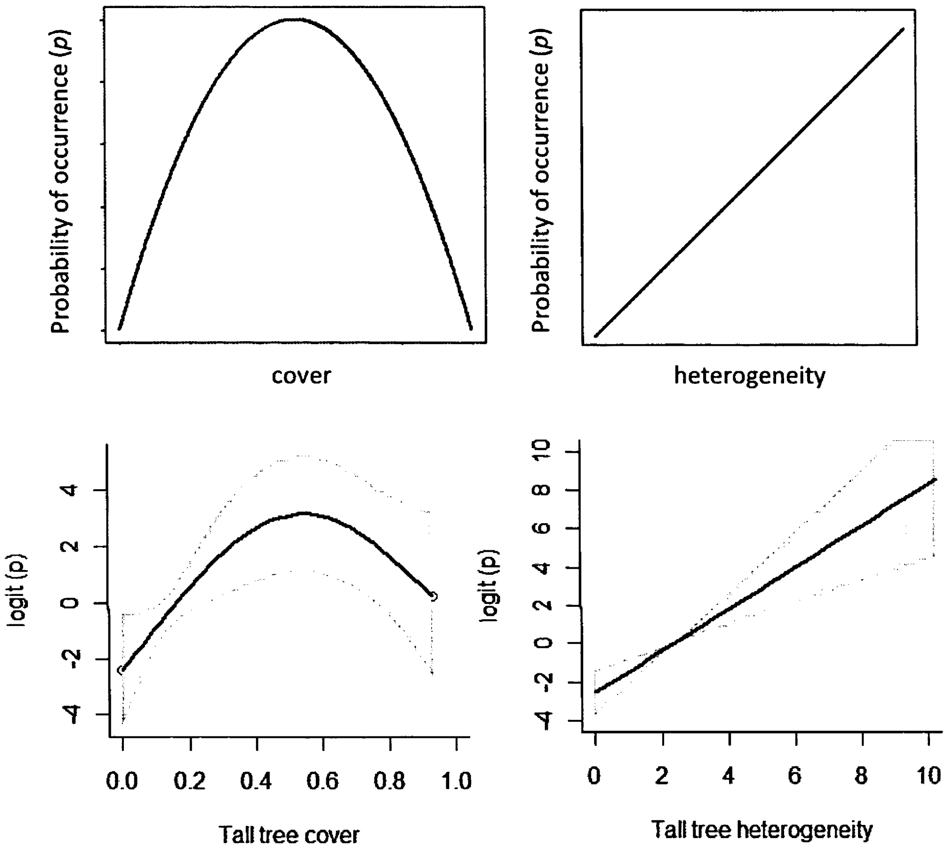


Figure 3. Hypothesised relationships between the probability of occurrence (logit (p)) of a species and (a) the cover and (b) heterogeneity of a habitat attribute. An example of the pattern we observed between the probability of occurrence (logit (p)) of satin bowerbird and (c) tall tree cover, given this species had (d) a positive linear relationship with heterogeneity. The bold line represents that fitted values (± SE).

Table 2. Results from Generalized Additive Models predicting the relationship between: (a) heterogeneity and cover for each vegetation attribute (leaf litter, shrubs, small trees and large trees) and (b) Satin bower bird (*Ptilonorhynchus violaceus*) occupancy and tall tree cover, and tall tree heterogeneity. A summary of the smoothing terms (estimated degrees of freedom [edf], and the chi-squared test [F]) for each model are included.

a)

Response variable	Explanatory variable	edf	F
Heterogeneity of leaf litter	Litter cover	2.92	53.65
Heterogeneity of shrub cover	Shrub cover	1.96	12.91
Heterogeneity of small trees	Small tree cover	2.74	49.67
Heterogeneity of tall trees	Tall tree cover	1.99	107.7

b)

Response variable	Explanatory variable	edf	F
Satin bower bird occupancy	Tall tree cover	2.07	3.46
Satin bower bird occupancy	Tall tree heterogeneity	1	4.52

Discussion

We found empirical evidence from our vegetation data (Fig. 2) to support our hypothesis that vegetation heterogeneity peaks at intermediate levels of cover, consistent with the mean-variance relationship for binomial data (Fig. 1a; Crawley 2002). To the best of our knowledge, no other study has explicitly tested for and established this relationship. Furthermore, we found that bird species with a positive linear association with vegetation heterogeneity were more likely to occur at intermediate levels of cover (Fig. 3). Below we discuss the implications of the relationship between heterogeneity and cover for the way we collect, analyse and interpret vegetation and habitat data in ecology.

Why heterogeneity is under-utilised in ecology

Understanding how ecological processes influence heterogeneity (variance) and how heterogeneity influences assemblage structure is increasingly recognised as important in ecology (Benedetti-Cecchi 2005; Stirnemann *et al.* 2014). However, actual variation within a habitat is rarely explicitly measured (McElhinny *et al.* 2006). In contrast, absolute cover is routinely quantified and is one of the dominant ways of quantifying vegetation structure and animal habitat (Morrison *et al.* 2006; Stirnemann *et al.* 2014). This is probably because accurately estimating the heterogeneity within an area can be more time consuming than estimating cover. For instance, a number of sub-plots are needed to accurately estimate the true heterogeneity of cover attributes within a plot, whereas the overall cover can be estimated fairly precisely with a smaller number of sample points. However, our findings imply that we can make broad inferences from our cover measures about the level of heterogeneity in an area, using the heterogeneity/cover relationship. For example, we can infer that sites with high cover or low cover would tend to have low levels of vegetation heterogeneity, whereas sites with intermediate cover would have a higher likelihood of high levels of heterogeneity (Fig. 1b). Hence, vegetation cover is a resource that can be broadly indicative of its heterogeneity.

How widely applicable are our results?

It is plausible that any vegetation attribute measured in terms of its cover could similarly exhibit a quadratic relationship with heterogeneity. Indeed, this relationship has been used to describe and quantify spatial patterns and dynamics in plant diseases (i.e. dispersal, disease incidence etc; Madden & Hughes 1995; Yang 1995). Similarly, we could use the heterogeneity/cover relationship to better understand the mechanisms determining spatial habitat dynamics and to help explain the persistence and stability of plants and animals in biological communities. Moreover, studies have found that new properties can emerge because different components or metrics interact (Palmer *et al.* 1997; Suweis *et al.* 2013). Hence, from a theoretical point of view, we can also use this relationship to develop theory that integrates both cover and heterogeneity, and also examine the synergistic role of these two interacting factors in pattern formation.

We found that the heterogeneity/cover relationship for all four vegetation attributes was strongly supported at the local scale (10's of meters; Fig 2). However, we propose that the cover/heterogeneity relationship should be spatially independent, regardless of the scale of measurement (i.e. grain [minimum resolution of the data] and extent [size of landscape or study area under consideration]; Turner 1989) within a study, given that both the mathematical relationship (Fig. 1) and the mechanism underlying the relationship will remain constant (Table 1). Generally, in most other statistical relationships in ecology, a constant change in the spatial scale of measurement between two metrics results in a change in the statistical relationship (Wu *et al.* 2002). For instance, most interacting metrics exhibit either a predictable linear change, such as shown by Taylor's power law (the relationship between-sample variance in density and the overall mean density of a sample of organisms in a study area on the log scale; Taylor 1961; Kilpatrick & Ives 2003), change in a step-like fashion as the scale changes, or exhibit erratic and unpredictable behaviour (Wu *et al.* 2002). Few relationships between metrics, to our knowledge, exhibit a constant relationship across scales.

We suggest that future empirical studies focusing on the cover/heterogeneity relationship should test the validity of the heterogeneity/cover relationship across vegetation attributes, ecosystems, and spatial scales. To determine if this pattern is prevalent in different systems, it is important that cover and heterogeneity metrics are: (i) based on binomial data (number of successes out of a number of trials; Crawley 2002), and that (ii) cover is measured across the entire range of the proportional scale (i.e. across the extremes, from 0 to 1). This last point is important because if the heterogeneity/cover relationship is not measured across the entire cover range the relationship can be masked.

Table 1. Definitions of terms used in this paper

Terms	Definitions
Binomial data	Data that have been generated by observing the number of successes out of *n* number of trials.
Heterogeneity	We defined heterogeneity in this study as a measure of variation or dissimilarity. Our measure of heterogeneity quantifies the differences in the: (1) proportion cover and/or (2) spatial dependency of habitat features, among the nine sub-plots within each site. Heterogeneity is greater when there is increased spatial dependence and/or increased difference between sub-samples within a site.
Cover	The proportion of presences out of the total (*n* points = 54) of each of the four vegetation features
Scale of variation	25m radius – scale at which heterogeneity was measured within
Grain	Subplot (6m transect) – smallest unit of analysis
Extent	Approximately 7,500 ha – extent of study area

Implications for the way vegetation and habitat data are analysed

The relationship between vegetation cover and heterogeneity has important implications for how we assess and interpret responses by species to habitat cover. Many studies assume a linear relationship between the presence/absence of animals and cover (Catling & Burt 1995; Morrison *et al.* 2006), and tend to not test, (or at least don't state they have tested), for a non-linear response during analysis (Austin 2002; Austin 2007). However, just as Austin *et al.* (2002) states that plant community structure may exhibit non-linear relationships along an environmental gradient, our results indicate that (due to the cover/heterogeneity relationship), a linear response to a measure of cover will not necessarily apply to species which are responding to heterogeneity (Fig. 3). This finding has important implications for how we assess cover/occupancy relationships as it indicates that when inferences based on straight-line relationships are fitted without justification, the findings can be erroneous (Austin 2007), particularly for species with a preference for high habitat heterogeneity. These results highlight that it is vital that researchers establish whether there is any evidence of non-linearity between the response variable (e.g. probability of occupancy of a species) in relation to the cover of vegetation and habitat attributes in all studies.

Our findings suggest that extrapolation of a linear model beyond the range of cover data measured may not be appropriate, as the relationship between cover and occupancy may not be consistent across the data set, particularly for heterogeneity-sensitive species. Such an assumption could result in the resulting conclusions being false and consequently, if used for conservation planning purposes, could lead to misdirected management decisions. For example, Lunney (1987) conducted a study on the influence of shrub cover on the probability of occupancy by the bush rat (*Rattus fuscipes*). Using a generalised linear modelling approach, they found that *R. fuscipes* prefer areas with 40% shrub cover. Lunney (1987) interpreted this to mean *R. fuscipes* preferred dense shrub cover. However, the relationship between cover and rat occupancy is not necessarily linear beyond 40% cover, as *R. fuscipes* could be a heterogeneity-sensitive species, although this has not been tested. The optimal amount of cover for *R. fuscipes* may be at intermediate levels (with high vegetation heterogeneity) rather than maximum levels of vegetation cover (i.e. 100%). Thus, managing for dense shrub cover may be detrimental for this species.

We found that of the five bird species that showed a positive relation with heterogeneity of tree cover and only four of these display the expected relation with plant cover. This finding indicates that we should be somewhat cautious when inferring the importance of plant heterogeneity on bird occupancy in all cases. That one species may not behaved as expected may have be due to a mathematical explanation or due to heterogeneity not being the causal mechanism beneath all occupancy relationships. For instance, although we assume that heterogeneity is the causal mechanism underpinning bird distribution, whereas the percentage cover is only a proxy. But since the two variables are correlated, it may be that percentage cover is the causal mechanism, while heterogeneity is only a proxy. Alternatively, sampling error might simply have precluded the identification of an otherwise statistically necessary relation.

Implications of the heterogeneity/cover relationship on management

We argue that understanding the heterogeneity/cover relationship is crucial for integrating ecology theory and practice. Although research indicates that vegetation heterogeneity is an important factor to consider when managing habitat for fauna (e.g. Stirnemann *et al.* 2014), historically management actions are mostly interested in actively increasing the amount (cover) of native vegetation when rehabilitating or vegetating an area (Benayas *et al.* 2008; Munro & Lindenmayer 2011; Cunningham *et al.* 2014). The abstract nature of heterogeneity (Kolasa & Pickett 1991) makes it a difficult for managers to contemplate how to best manage variation in vegetation structure. We suggest that the cover/heterogeneity relationship could be used to bridge the gap between ecological theory and practice.

Our study provides some firm evidence that the cover/heterogeneity relationship can be used to broaden our fundamental understanding of the structure of ecosystems, as well as broaden resistance of ecosystems to disturbance. For example, one potential application is to use this relationship to gain insights into the susceptibility of plant communities to exotic plant species invasions under different vegetation cover conditions. For instance, studies suggest that homogeneous environments have higher resistance to the invasion of many exotic plant species, whereas conversely heterogeneous environments, with higher niche availability, are more susceptible to invasion (Davis *et al.* 2000; Byers & Noonburg 2003; Melbourne *et al.* 2007). Thus, increased resistance, such as obtained in areas with low levels of habitat heterogeneity, could be achieved by aiming for high levels of cover. In contrast, the silver-spotted skipper butterfly (*Hesperia comma*), requires the maintenance of high levels of heterogeneity of cover of short turf and patches of bare ground with suitable clumps of the host plant (*Festica ovina*) (Pullin 2002). In this situation, high levels of habitat heterogeneity could be achieved by aiming for intermediate levels of cover of turf habitat, which is tractable management goal.

Is heterogeneity still worth measuring?

Our results demonstrated that, at intermediate levels of cover, the pattern of the deviations in the residuals were higher than at extreme (i.e. the maximum and minimum) levels of cover (Fig 2). These findings suggest that although we can make broad inference about heterogeneity in relation to cover, explicitly measuring heterogeneity is still important, particularly at intermediate levels of cover where, due to greater number of options for different configurations of cover, heterogeneity is most variable (Fig 1b).

Measuring heterogeneity in habitat cover is important as this metric provides information on variation in the configuration of habitat, additional information not provided by a measure of absolute cover (McElhinny *et al.* 2006; Fraterrigo & Rusak 2008). Additionally, mechanistically biota may be influenced by the variance, or heterogeneity of habitat attributes rather than the amount or there may be a synergistic effect of both metrics. This can only be determined by actually measuring both variables.

Conclusion

Our study provides strong quantitative support for the generality of a relationship between vegetation cover and heterogeneity, similar to that for binomial data, and which is potentially transferrable to all studies of ecosystem structure, and the distribution of associated biota. This relationship has important implications for understanding the mechanisms driving both quantity and spatial variation of vegetation and habitat, and the theoretical conceptualisation of ecosystem structure and function, as well as how we measure ecosystems to guide their management. Moreover, our findings confirmed that the heterogeneity/cover relationship can result in occupancy of animals which have a positive linear response to heterogeneity, having a quadratic response to cover. These findings indicate that, to prevent erroneous management decisions testing for non-linear responses between species and cover should be a routine procedure, and that we should not extrapolate beyond our data range.

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SYNTHESIS

Overview

Understanding how ecological processes influence heterogeneity (variance) of habitat attributes, and how habitat heterogeneity influences biota, is increasingly recognised as important in both terrestrial and marine ecology (Benedetti-Cecchi 2005; Fraschetti et al. 2006; Fraterrigo and Rusak 2008). However, the variation in vegetation cover within a habitat is rarely explicitly measured (Paper 1) and is seldom used as a response variable for describing the effect of disturbance (e.g. fire) or as predictor variable for describing species richness or occupancy (Fraterrigo and Rusak 2008). In contrast, the quantity of vegetation cover is routinely estimated and is one of the dominant ways of quantifying vegetation structure and animal habitat (Morrison et al. 2006; Paper 1). However, the underlying causal processes that influence vegetation, as well as the response of biota to vegetation can be obscured by measuring only the absolute quantity of a habitat feature. Thus, we risk overlooking key information about ecosystem function by ignoring variability in vegetation cover (Fraterrigo and Rusak 2008). In the following paragraphs, I draw together the key findings of my empirical research chapters, and discussed their implications for theory and management.

This thesis has added to the knowledge on the mechanisms driving spatial patterning of vegetation and biota by presenting an in-depth investigation into how multiple taxa responded to both the amount (cover) and spatial heterogeneity of vegetation features (Papers 3 & 4), as well as how different terrain and fire components and their interactions are driving these observed patterns in vegetation (Paper 2). I found that heterogeneity of vegetation structure at a fine spatial scale, in addition to the cover of vegetation variables, is an important predictor of bird species richness and mammal occupancy (Papers 3 & 4). Furthermore, my research has shown that fine-scale heterogeneity can have quite varied effects on biota, depending on the species, life-history traits and community of interest (Papers 3 & 4). Different communities and species may be adapted to tolerate different degrees of fine-scale heterogeneity – some may prefer highly heterogeneous environments while others would prefer highly homogenous environments. The overall finding emerging from these two studies suggests that, just as in marine ecology (Fraschetti et al. 2013; Fraschetti et al. 2006), small-scale heterogeneity in terrestrial environments is as important as broad-scale landscape heterogeneity in generating spatial patterns in biota. Many studies try to limit the heterogeneity within a dataset. However, our results suggest that measures of small-scale spatial variance should not be considered merely as a statistical nuisance (Avois et al. 2000; Fraschetti et al. 2005), and should be included as a covariate within statistical models.

An understanding of the processes generating spatial pattern in vegetation is considered essential for quantifying and predicting the distribution of fauna and is necessary to appropriately manage habitat for fauna (Kirkpatrick et al. 2011; Lindenmayer et al. 2006). The effects of fire and topography on plant species richness and single habitat features (e.g. trees; Lindenmayer et al. 1991) is well known among plant ecologists (e.g. Alexander et al. 2006; Huggett and Cheesman 2002; Kushla and Ripple 1997; Neilson and Wullstein 1986; Oleksyn et al. 1998). My study built on this previous work by investigating some of the processes driving heterogeneity of multiple key vegetation features that are important to biota (Paper 2). My research showed that heterogeneity of different habitat features is influenced by a variety of different fire and terrain attributes and their interactions and that their effects can differ depending on the vegetation type and the scale at which variation is measured. My findings highlighted that landscape ecologists should use a combination of environmental factors as surrogate measures of habitat heterogeneity if they are to develop robust predictive models that accurately describe multiple aspects of faunal habitat.

An understanding of how different metrics interact is considered essential for investigating, evaluating, and monitoring landscape structure and change (Gökyer 2013; Walz 2011). In Paper 5, I found empirical evidence based on my vegetation data to support the hypothesis that vegetation heterogeneity peaks at intermediate levels of cover, which is consistent with the mean-variance relationship for binomial data (Crawley 2002). The mean/variance relationship of binomial data may be a useful approach for conceptualising the relationship between vegetation cover and heterogeneity. For instance, the abstract nature of heterogeneity (Kolasa and Pickett 1991) makes it a difficult for managers to contemplate how to best manage variation in vegetation structure. The cover/heterogeneity relationship can be used to broaden our fundamental understanding of the structure of ecosystems, as well as broaden resistance of ecosystems to disturbance. For instance, studies suggest that homogeneous environments have higher resistance to the invasion of many exotic plant species (Davis *et al.* 2000; Byers & Noonburg 2003; Melbourne *et al.* 2007). Therefore, one potential application is to use this relationship to gain insights into the susceptibility of plant communities to exotic plant species invasions under different vegetation cover conditions. Thus, increased resistance, such as obtained in areas with low levels of habitat heterogeneity, could be achieved by aiming for high levels of cover. However, I caution that inferring the effects of variation indirectly from non-linear functions is imprecise, and is not the same as examining these effects directly.

Management implications

My empirical research on vegetation heterogeneity, in Booderee National Park, provides an evidence base on which to manage biota and key habitat features. This is because my research suggests that:

1) Different animal species respond to different forms of vegetation heterogeneity, (i.e., ecotones, fine-scale heterogeneity in vegetation cover, Paper 4). Therefore, different management strategies (i.e. fire, vegetation thinning) can be used to benefit or disadvantage different species by modifying these different forms of vegetation heterogeneity.
2) The maintenance of homogenous habitat is important for conserving some biota and communities (Paper 3). Conversely, birds with particular traits and some

species of mammal preferred fine-scale heterogeneous habitats (Papers 3 & 4). Therefore, we need to manage for both homogeneous and heterogeneous patches within the landscape when undertaking vegetation restoration aimed at increased biodiversity.

3) Specific management strategies can be used to increase or decrease heterogeneity of different vegetation features both within and between patches (Paper 2). Therefore, specific management actions can be used to promote fine-scale heterogeneous habitat features for heterogeneity-sensitive species, or conversely, promote homogeneous habitat. For example, prescribed burning in some habitats can be used to increase small tree heterogeneity in areas with topographically variable terrain (Paper 2) and this will benefit species such as the Long-nosed Bandicoot and the Bush Rat (Paper 4).

Future research and limitations of study

In suggesting the three management actions above, I acknowledge that further research is required to improve our understanding of how managing vegetation heterogeneity influences bird and mammal distribution patterns. An investigation is needed into the efficacy of the management strategies I recommended – particularly when conducting management actions such as restoration and re-vegetation activities. This would require the implementation of experimental monitoring of target species in restored or re-vegetated sites where different levels of fine-scale vegetation heterogeneity have been manipulated (e.g. by vegetation thinning, or when planting seedlings) while holding the vegetation amount (the mean effect) constant. The success of the management actions could be measured by determining the probability of presence of target species in restored and re-vegetated stands/patches characterised by different levels of vegetation heterogeneity.

Another important avenue of research arising from this thesis will be to investigate the transferability and validity of the heterogeneity/cover relationship (as discussed in Paper 5) across vegetation attributes, ecosystems, and spatial scales. To determine if this pattern is prevalent in different systems, it is important that cover and heterogeneity metrics are: **(i)** based on binomial data (number of successes out of a number of trials; Crawley 2002), and **(ii)** that cover is measured across the entire range of the proportional scale (i.e. across the extremes, from sites which contain 0% cover to sites with 100% cover). This last point is important because if the heterogeneity/cover relationship is not measured across the entire cover range, the relationship can be masked (i.e. hump shaped heterogeneity/cover relationship would not be apparent).

In summary, this thesis added to knowledge of the spatial patterning of biota by presenting an in-depth investigation into: **1)** how heterogeneity (variation) and the amount (cover) of habitat features influence the distribution of biota and **2)** the how fire and terrain attributes may be driving the observed patterns in vegetation. Furthermore, our research provides strong quantitative support for the generality of a relationship between vegetation cover and heterogeneity which is potentially transferrable to other studies of ecosystem structure, and the distribution of associated biota (Paper 5). This relationship is likely to have important ramifications for understanding the mechanisms driving both quantity and spatial variation of vegetation and habitat, and the theoretical conceptualisation of ecosystem structure and function, as well as how we measure ecosystems to guide their management.

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Eastern yellow robin (*Eopsaltria australis*)