

Using atlas data for large scale conservation strategies: a case study of NSW s mammals

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PhD Thesis

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13th September 2011

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Global threatening processes such as habitat loss, overexploitation, invasive species, and climate change are driving many species to extinction at an alarming rate. This has particularly affected mammal populations across Australia where mammal extinctions over the past two centuries have been the highest in the world. Setting aside areas for protection is the principle strategy for safeguarding against biodiversity and maintaining ecosystem processes. Identifying areas for protection requires comprehensive knowledge of species' distributions, where relative comparisons can be made over large scales. Spatially explicit datasets, such as atlases, harbour the greatest potential of large-scale information of biodiversity. These however, are seldom fully utilised for large-scale conservation initiatives and management. This thesis provides concepts, methods, and operational guidelines for conservation efforts using large data over extensive scales. To achieve this, I utilised NSW's atlas data and focused on records of native terrestrial mammals. Chapter 1 provides an overview of global threats, conservation strategies, and specifically the state of Australia's mammals. In chapter 2, I demonstrated how atlas data, collated at multiple spatial scales can be used to rank survey methods best suited for the detection of each mammal species. This approach provides a methodological process used to identify efficient monitoring strategies tailored for unique species' inventories at regional and bioregional scales. Chapter 3 tests the efficacy of the existing Australian bioregional framework for representing mammal species within protected areas. The bioregional framework, which primarily relies on vegetation communities, is used to measure representation of biodiversity and prioritise new inclusions to the national protected area network. The chapter presents an alternative approach for prioritisation driven by mammal assemblages, using patterns co-occurring species. Results and performance for mammal representation are then assessed against the bioregional framework. Chapter 4 builds upon identified mammal assemblages to model anticipated effects of climate change on whole assemblages simultaneously and identify climate-resilient faunal communities. Identified areas are then used within to prioritise land for additions to the existing protected area network, given impacts of climate change on mammalian distributions. Chapter 5 examines the ecological and evolutionary mechanisms shaping Australia's mammal community assemblages. By exploring trait interactions across spatial scales, a more precise scaling for evolving determinants of niche overlap are made. This provides unique insight into the evolutionary pathways and their rates, allowing identification of the scales in which these operate in shaping present-day communities. Finally, in Chapter 6, I summarise the research presented in the thesis and discuss directions for future work.

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Acknowledgments

With all my heart I would like to thank my beloved wife for endeavouring with me on this long journey. Thank you for your support, love, and understanding and I hope it was a fun ride for you as well!

To my amazing son Oz, your arrival into our family during my studies was perfect timing. I am grateful for the time I could spend with you. To our recent addition to the family, Taito you are the best graduation present I could wish for!

To my two supervisors, I truly appreciate the time and effort you made. I have learned a great deal from you both.

I dedicated the thesis to my mom, who patiently waited for her turn, thank you for the lot.

Finally, farewell to my student concession card, you have been a great companion in movies, planes, buses, and trains for nine whole years.

Preface



This thesis consists of five research papers (Chapters 2-5, appendix), an introductory chapter (Chapter 1) and a concluding chapter (Chapter 6). Chapters 2-5 have either been published, accepted, or are currently in review. As each chapter is an individual paper, some repetition occurs. In addition, tables and figures are not numbered sequentially throughout the thesis but are specific to the chapter/paper in which they appear. References are located at the end of the paper in which they are referred to. This thesis is a compilation of my own work with guidance from my supervisors Richard Kingsford and Daniel Ramp. I conceptualised my research, conducted all data analysis and wrote and illustrated the manuscripts. My co-authors proof-read and edited the final manuscript versions. The contributions of my co-authors are detailed below.

Chapter 2: Bino, G., Ramp, D., Kingsford, R.T. Learning from the past: using historical occurrence data and species distribution modelling to inform fauna surveys at landscape-scales. Both D. Ramp and R.T. Kingsford provided conceptual guidance and advice in their function as my supervisors.

Chapter 3: Bino, G., Ramp, D., and Kingsford, R.T. Improving bioregional frameworks for conservation by including mammal distributions. Both D. Ramp and R.T. Kingsford provided conceptual guidance and advice in their function as my supervisors.

Chapter 4: Bino, G., Ramp, D., and Kingsford, R.T. Are protected areas adequate for conserving climate refugia for fauna? Both D. Ramp and R.T. Kingsford provided conceptual guidance and advice in their function as my supervisors.

Chapter 5: Bino, G., Ramp, D., and Kingsford, R.T. Niche evolution in terrestrial mammals: clarifying scale-dependencies in phylogenetic and functional drivers of assemblages. Both D. Ramp and R.T. Kingsford provided conceptual guidance and advice in their function as my supervisors.

Appendix: E. Roger, **G. Bino**, D. Ramp, Linking habitat suitability and road mortalities across geographic ranges. The appendix is a collaborative research between G. Bino and E. Roger as part of E. Rogers' thesis. Both G. Bino and E. Roger contributed equally to the analysis. As lead author, E. Roger wrote the first draft of manuscript. D. Ramp provided conceptual guidance and advice in his function as E. Roger's supervisor.

Abstract

Global threatening processes such as habitat loss, overexploitation, invasive species, and climate change are driving many species to extinction at an alarming rate. This has particularly affected mammal populations across Australia where mammal extinctions over the past two centuries have been the highest in the world. Setting aside areas for protection is the principle strategy for safeguarding against biodiversity and maintaining ecosystem processes. Identifying areas for protection requires comprehensive knowledge of species' distributions, where relative comparisons can be made over large scales. Spatially explicit datasets, such as atlases, harbour the greatest potential of large-scale information of biodiversity. These however, are seldom fully utilised for large-scale conservation initiatives and management. This thesis provides concepts, methods, and operational guidelines for conservation efforts using large data over extensive scales. To achieve this, I utilised NSW's atlas data and focused on records of native terrestrial mammals. Chapter 1 provides an overview of global threats, conservation strategies, and specifically the state of Australia's mammals. In chapter 2, I demonstrated how atlas data, collated at multiple spatial scales can be used to rank survey methods best suited for the detection of each mammal species. This approach provides a methodological process used to identify efficient monitoring strategies tailored for unique species' inventories at regional and bioregional scales. Chapter 3 tests the efficacy of the existing Australian bioregional framework for representing mammal species within protected areas. The bioregional framework, which primarily relies on vegetation communities, is used to measure representation of biodiversity and prioritise new inclusions to the national protected area network. The chapter presents an alternative approach for prioritisation driven by mammal assemblages, using patterns co-occurring species. Results and performance for mammal representation are then assessed against the bioregional framework. Chapter 4 builds upon identified mammal assemblages to model anticipated

effects of climate change on whole assemblages simultaneously and identify climate-resilient faunal communities. Identified areas are then used within to prioritise land for additions to the existing protected area network, given impacts of climate change on mammalian distributions. Chapter 5 examines the ecological and evolutionary mechanisms shaping Australia's mammal community assemblages. By exploring trait interactions across spatial scales, a more precise scaling for evolving determinants of niche overlap are made. This provides unique insight into the evolutionary pathways and their rates, allowing identification of the scales in which these operate in shaping present-day communities. Finally, in Chapter 6, I summarise the research presented in the thesis and discuss directions for future work.

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Chapter 1: Introduction

Biodiversity loss and its scale

Biodiversity underpins ecosystem functioning, providing services essential for human wellbeing such as food security, human health, clean air and water, economic development, and poverty reduction (CBD COP10 2010). Biodiversity is under threat worldwide. Many scientists consider that the Earth has now entered a global biodiversity extinction crisis (UNEP 2007). Human population growth and socio-economic developments are overexploiting natural resources, driving the loss of natural habitats, promoting species' invasion, and global climate change, all of which are leading to biodiversity loss and ecosystem breakdown (Pimm and Raven 2000, Thomas et al. 2004, Wake and Vredenburg 2008). Recent assessments reveal that although wide-spread mitigation measures have been taken, population sizes, extent, condition, and habitat connectivity continue to decline in wild, all accelerating rates of extinction (Butchart et al. 2010). Economic and demographic growth of human population, coupled with globalisation, has shifted threats to biodiversity from small and localised to a global concern (Millennium Ecosystem Assessment 2005). Demand for resources (e.g., timber, livestock, water, or agricultural products) in developed countries is affecting wilderness areas across the globe.

In Australia, since European colonisation, approximately 200 years ago, rates of environmental change, and the loss of biodiversity have dramatically increased. At present, Australia's per capita ecological footprint (a measure of our individual impacts on the environment through our consumption of natural resources) is one of the largest in the world. Nearly 60% of Australia's land mass has been transformed for the production of livestock based on native pastures (DEWA 2009). Through predation and competition, invasive species have caused catastrophic declines in Australia's biodiversity (DEWA 2009). Predation by the

red foxes (*Vulpes vulpes*) and feral cats (*Felis catus*) may be a dominant driver of Australia's extensive mammal extinctions (Dickman 1996, Smith and Quinn 1996, Abbott 2002, Letnic et al. 2009, Kutt 2012). The pressures affecting Australia's biodiversity now operate at large regional and national scales. In turn, this is necessitating a reciprocal increase in the scale of conservation efforts, coordinated at multiple spatial scales with the scale of action tailored to the scale of the threat (Lindenmayer and Franklin 2002).

Conserving biodiversity

Establishing protected areas has been a key strategy to counter biodiversity loss. Currently, protected areas are one of the largest planned changes of land use, covering 12.9% of the Earth's land surface (WCMC 2011). Ideally, protected areas need to meet two core objectives: (a) the representation of all species within the protected area network, and (b) their long term viability under current and future conditions (Margules and Pressey 2000). In recent decades, prioritising areas for conservation has shifted from opportunistic selection to a more quantitative and systematic process, attempting to capture the full patterns of biodiversity (Brooks et al. 2006, Wilson et al. 2009). Pioneered by Myers *et al.* (2000), identification of global biodiversity hotspots are a focus for considerable efforts in developing strategies for allocating global conservation resources. At regional scales, systematic conservation planning, using software algorithms such as MARXAN (Ball et al. 2009), can identify cost-effective and efficient land units while achieving conservation targets. Wide adoption of these methods has significantly increased the demand for spatially explicit information for mapping species, ecosystems, as well as threats. Species' distribution data are of critical importance to any attempt at documenting and conserving biodiversity.

Atlas Data

Increasingly, conservation managers are collecting data sets into large compilations of biodiversity data. These data sets are broadly defined as biodiversity Atlas data (Dunn and Weston 2008). Availability of data for estimating the distributions of species is a critical constraint on prioritising conservation efforts (Whittaker et al. 2005). Atlas projects gather and manage spatially-explicit species' occurrence distributional data, with increasing applicability in confronting different conservation issues (Underhill et al. 2008, Robertson et al. 2010). Although these datasets can accumulate considerable biases (Robertson et al. 2010), correct use of data stored in atlases can support a wide range of conservation initiatives, including describing species distribution, conservation management and planning, monitoring disease transmission, and movement patterns (Dunn and Weston 2008). This is attributed to their breadth of coverage as the largest source of occurrence data, collected from monitoring of multiple species (Pomeroy et al. 2008). Compilation of multiple datasets, providing greater spatial and temporal coverage, has provided considerable improvements for establishing conservation status and detecting population trends of many species (Baillie et al. 2004). To compensate for incomplete species' spatial coverage, one of the more important applications of atlas data is generation of distribution estimates for species or species' distribution models (Elith et al. 2006, Elith and Leathwick 2007).

Species distribution models

Species' distribution models (SDM) are empirical models relating occurrence data to a selected set of environmental predictors (Guisan and Zimmermann 2000). Early uses of SDMs focused on the ecological insights of causal drivers governing the distributions of species (Mac Nally 2000). Recently, developments in computational power, new statistical models, Geographic Information Systems (GIS), and availability of remotely sensed data have resulted in proliferation of SDM research and application (Elith and Leathwick 2009).

SDMs can be grouped:(1) interpolated predictions, those made within the range of predictors, used for example in global analyses of species' distributions, regional conservation planning, and species recovery and reintroduction (Guisan and Thuiller 2005); and (2) extrapolated predictions, used for example, to forecast impacts of projected climate change and potential species' invasions (Guisan and Thuiller 2005).

Atlas of NSW

First founded in 1980, the Atlas of NSW Wildlife is the NSW environment agency (Office of Environment and Heritage) database of fauna and flora records. Since, it has accumulated over four million recorded sightings, covering the entire state of NSW. Atlas records include data from multiple survey sources, collected by government staff, researchers, naturalists, environmental consultants, land management officers, and the public. In this thesis, presence-absence data were derived for NSW's native terrestrial mammals. Chapters 2 & 5 use records of 53 mammal species (14 families), up to 2008, comprising approximately 40,000 point locations. Chapters 3 & 4 are grounded on records of 61 mammal species (14 families), up to 2009, comprising approximately 76,000 point locations (Figure 1).

Figure 1

Records of native terrestrial mammals, 1990 – 2009, obtained from the Atlas of NSW Wildlife (OEH 2009).



Mammals as a case study

Global processes such as habitat loss (e.g., agricultural expansion, water resource development), landscape fragmentation (e.g., roads), invasive species, and climate change are driving many species, especially mammals, to extinction at increasing rates (Cardillo et al. 2006, Morrison et al. 2007). With 25% of all mammal species at risk of extinction and 52% of all known populations in decline, the global conservation status of mammals is likely to continue to deteriorate (Schipper et al. 2008).

In Australia, recorded mammal extinctions over the past two centuries have been the highest in the world (Baillie 1996), while the country ranks also highly in number of threatened species, with 57 species listed on the IUCN Red List (IUCN 2009). Rapid extinctions in Australian mammals are results of a range factors including: disease, competition with introduced herbivores, loss of habitat, and introduced predators (Johnson 2006). A range of environmental and species' attributes have been investigated as possible determinants of susceptibility to extinction, including: body mass, geographic range, diet, phylogeny, habitat use, environmental productivity, and change (Johnson et al. 2002, Fisher et al. 2003, Brook et al. 2008, Davidson et al. 2009).

Setting aside areas for conservation reduces extinction risk to mammals (Karanth et al. 2010), and is a vital conservation strategy for species' protection (CBD COP10 2010). Prioritisation should be informed by the specific condition of each species and the distribution of threats across the landscape, both of which vary considerable across the landscape (McKenzie et al. 2007, Fritz et al. 2009). Consequently, an explicit basis for setting conservation priorities among different spatial regions within Australia is required (McKenzie et al. 2007). If mammal conservation is to succeed, strategies must be driven by

comprehensive information of species distributions, coordinated across appropriate scales (Watson et al., 2011).

Thesis structure

In this thesis, I employ the use of the NSW atlas dataset to tackle several key large-scale conservation concerns, implemented at a large scale across NSW, Australia. I explore methods for identifying efficient combinations of survey methods for predicting the distribution of species (chapter 2), tested the existing large scale prioritisation framework in Australia and proposed an alternative approach driven by mammal assemblages (chapter 3). I further build on identified NSW's mammal assemblages to systematically prioritise land for additions to existing protected areas under present and future conditions (chapter 4). Finally, I explore the ecological and evolutionary mechanisms and their scales in shaping present-day mammal community assemblages (chapter 5).

Chapter 2: Prioritising optimal combinations of survey methods for predicting fauna distributions at regional scales

In chapter 2, I identify how survey method, used to detect mammals in NSW, contributed to the efficacy of predictive distribution models for different species. Using all mammal records from NSW wildlife atlas (1990-2008), I model and predict the distributions of 53 mammals across NSW. By incorporating the survey technique used to detect each species, I rank the contribution of each technique to the model. When all predictive models were considered simultaneously, optimal combinations could be identified for NSW's mammals. To increase efficiency, I identify optimal combinations for each of the 18 bioregions found within NSW.

Chapter 3: Demarcating bioregions: how best to represent mammal distributions at regional scales

In chapter 3, I examine the existing framework used to prioritise acquisition of land for the Australian national reserve system within NSW. As this framework is primarily driven by distinct vegetation formations, its efficacy in representing fauna diversity remains largely untested. I examine the representation of 61 mammal species within NSW's protected area network, using their predicted distributions. Additionally, I project future representation outcomes if this framework was perpetuated. As an alternative, I employ a statistical approach to cluster predictive distributions into 11 reoccurring mammal assemblages. I then compare the efficacy of the bioregional and mammal assemblage frameworks for prioritising land and representing mammal diversity within the protected area network.

Chapter 4: Incorporating climate refugia for faunal assemblages in assessments of protected area adequacy

In chapter 4, I provide explicit land prioritisation using the mammal assemblage framework, aiming to achieve adequate representation of mammal diversity in NSW and increase likelihood of maintaining ecosystem function. Conserving biodiversity under accelerated climate change requires our understanding and capacity to predict ecological response. Importantly we should safeguard areas of high resilience, such as climate refugia, and ensure our conservation initiatives are well adapted to climate change. By quantifying each assemblage's current climatic envelope, I identify areas of climate stability (i.e., climate refugia) and quantify anticipated changes to biodiversity representation within NSW's protected areas network. Using a systematic process under current and projected climate change for 2050, I provide spatially explicit recommendations for prioritising land for protection. By relying on climate-resilient faunal communities to guide conservation priorities, outcomes are more robust, ensuring the long term representation of biodiversity.

Chapter 5: Evolutionary pathways in Australia's terrestrial mammals: scaling phylogenetic and phenotypic drivers of communities

In chapter 5, I explore the contribution of several functional traits (i.e., diet, weight, and habitat) and phylogenetic relatedness in shaping present day community assembly. It is currently postulated that interactive forces between functional traits and phylogenetic relatedness drive many biogeographic patterns over evolutionary time scales. However, determining which traits contribute to formation of ecological niches currently remains subjective and ambiguous. Using predictive models, I examine the levels of sympatry exhibited among mammal species across NSW and tested for phylogenetic clustering. By repeating these analyses across several spatial scales, I examine scale dependencies and interactions of functional traits and phylogenetic relatedness in determining niche overlap. This novel approach provided unique insight into the evolutionary pathways, their rates, and scales shaping present-day communities.

Chapter 6: Conclusions

In chapter 6, I summarise my findings and their implications to improving large scale conservation efforts applied nationally and globally. Using NSW's atlas data to model and predict the distributions of mammal species, I argue that considerable opportunity exists when utilising multispecies datasets to improve conservation outcomes. Still, substantial improvements remain both in data collection and ecological theory which I discuss, as well as suggest potential avenues for future research.

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Chapter 2: Learning from the past: using historical occurrence data and species distribution modelling to inform fauna surveys at landscape-scales

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Ecography (in review)

Prioritising optimal combinations of survey methods for predicting fauna distributions at regional scales

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Abstract

Monitoring for species occupancy is often carried out at local scales, reflecting specific targets, available logistics, and funding. Problematically, conservation planning and management operate at larger scales and use information inventories with large-scale coverage. Translating information between local and landscape scales is commonly treated in an ad-hoc manner, but conservation decision-making can benefit from quantifying spatialknowledge relationships. Fauna occupancy monitoring, in particular, suffers from this issue of scale, as there are many different survey methods employed for different purposes. Rather than ignoring how informative these methods are when predicting regional distributions, we describe a statistical approach that identifies survey combinations that provide the greatest additive value in mammal detection across different scales. We identified minimal sets of survey methods for 53 terrestrial mammal species across a large area in Australia (New South Wales, 800,642 km²) and for the 18 bioregions it encompasses. Utility of survey methods varied considerably at a landscape-scale. Unplanned opportunistic sightings were the single largest source of species information (35%). The utility of other survey methods varied spatially; some were retained in optimal combinations for many bioregions, while others were spatially restricted or unimportant. Predator scats, Elliot and pitfall trapping, spotlighting and diurnal Herpetofauna surveys were the most frequently required systematic methods at a landscape-scale. Use of our approach enables the identification of efficient combinations of survey methods, maximising returns for predicting the distribution of species. Given survey costs and limited budgets, our analytical approach could guide monitoring objectives by prioritising minimal sets of survey methods for regional and bioregional monitoring.

Chapter 2

Introduction

Regional biodiversity conservation is reliant upon coordinated monitoring programs that are suitable in landscape and global-scale planning (Lindenmayer et al. 2008, Pereira and Cooper 2006). Problematically, monitoring is frequently driven by management goals specific to local scales, despite the fact that conservation outcomes can be improved when landscapescale inferences are made (Radford and Bennett 2007). Translating information between local and landscape scales is commonly treated in an ad-hoc manner, but conservation decisionmaking can benefit from quantifying spatial-knowledge relationships. Fauna occupancy monitoring, in particular, suffers from this issue of scale, as there are many different survey methods employed for different purposes. Identifying species regional distributions presents a considerable challenge to conservation practitioners, particularly with regard to costeffectiveness, accuracy, reliability, and spatial variability in detection (Jones 2011). Finescale spatial and temporal information on species' locations are needed for reporting on representation and for detecting change at landscape-scales (Nielsen et al. 2009); information that is vital for landscape-scale conservation practice (Nichols and Williams 2006). This integration has, to date, been difficult for fauna as there is often a paucity and sparseness of data (Pressey 2004). To overcome this, the quantity, quality, and utility of faunal distribution data need to be increased (Brooks et al. 2004) through appropriate and effective monitoring programs. In the meantime, statistical approaches can be used to extract scaled information from past surveys that harbour information on multiple species obtained from a variety of survey methods, which can be used for planning future monitoring programs.

Monitoring usually uses expert knowledge to select methods best suited for the targeted species, trading-off costs, detection probability, and suitability to the local habitat. Accordingly, the actual techniques chosen (i.e., survey methods) and their intensity and scale are often targeted towards capturing individuals or identifying behaviour, movement patterns,

and habitat associations. Inevitably, the deployment of survey methods is spatially variable across landscapes, reflecting species' distributions, cost-effectiveness, suitability of survey methods, detection effectiveness, and management targets (Garden et al. 2007, Gardner et al. 2008, Msoffe et al. 2007). Unlike vegetation surveys, fauna monitoring often utilises surveys targeting one or only a few species sharing similar activity patterns or similar traits (Doan 2003, Garden et al. 2007). These locational fauna data are usually collated from multiple and spatially dependent sources of information including: systematic surveys methods, historical reports, environmental consultancies, naturalist reports, and the general public (Dunn and Weston 2008). Available landscape-scale data for species form a spatially varying pattern of location points. A key question is whether survey method and species' distribution modelling can inform and prioritise monitoring efforts.

Local-scale survey data are often compiled into regional atlases (Robertson et al. 2010). These extensive datasets harbour considerable benefit for conservation, primarily through their ability to build species⁴ distribution models (SDMs) from their spatially-referenced records (Elith et al. 2006, Fisher et al. 2004). SDMs can be used to predict species⁴ invasions (Richardson and Thuiller 2007), manage species⁴ recoveries and reintroductions (Hirzel et al. 2004, Pearce and Lindenmayer 1998), predict the impacts of climate change on species⁴ distributions (Araújo et al. 2006), and improve understanding of complex biogeographic systems (Franklin 2010). Data for SDMs are typically amalgamated without regard to the survey method despite the varying frequencies of surveys methods and detection effectiveness being critical when inferring robust distributions. This appears to be particularly remiss, as explicitly incorporating the effectiveness of surveys should improve SDMs and inform future surveys by quantifying the spatially-explicit contribution of different survey methods to species distributions. Such analyses could then identify minimal sets of survey methods that maximise regional representation of species through local-scale monitoring.

Here, we quantified the relative contribution of species' occurrence points, collected using different survey methods, by incorporating survey method as an independent categorical variable within an SDM framework. We analysed two occurrence data collected over the past two decades for 53 terrestrial mammal species across New South Wales (NSW), Australia. Specifically, we used SDMs for each species to examine the effectiveness of each survey method and its relative contribution in the detection of each mammal species. We also aimed to identify complementary combinations of survey methods that maximised effective _capture' of species at various scales. This could improve detection of terrestrial mammal species across NSW and within bioregions. Our approach aimed to provide a valuable basis for assessing cost-effectiveness of monitoring programs for regional biodiversity assessments across different scales, survey methodologies and species.

Materials and methods

Survey method ranking

As mammal species can be detected using a range of survey methods, we examined the overall contribution of different survey methods across several biomes to SDMs. To consider the effects of survey method alone, other confounding spatial variables should be eliminated. Ideally, a rigorous research design would be required to determine the effect of survey method but this is rarely possible for large areas and multiple sources of data and designs. However, using analysis of covariance it is possible to isolate the effects of environmental and geographic variables across species ranges (McNeil et al. 1996). To control the effects of environmental and geographic covariates across the species⁴ range, we incorporated survey method as a categorical independent variable within an SDM framework. This statistically controlled for the effects of continuous environmental and geographic variables that were not our primary interest. We used records for 53 native terrestrial mammal species from the NSW Atlas dataset (DECCW 2009) between 1990 and 2009 (minimising temporal changes in distributions) and with a spatial accuracy finer than 500m, comprising about 40,000 point locations across NSW (800,642km²).

Sampling bias frequently affects occurrence records (Araújo and Guisan 2006) but incorporating background data (i.e., absence data) with similar spatial biases can substantially improve model performance (Phillips et al. 2009). As we have previously reported (Bino et al. 2012), we generated informed pseudo-absences for each species using location points for other terrestrial mammal species in the database. We assumed that failure to detect a species, when a suitable method was employed, was a plausible pseudo-absence. This indirectly accounted for spatial sampling biases found in each survey method as both presence and absence data were derived from the same dataset and contained identical spatial biases. For transect survey methods, we considered the exact point locations rather than the beginning or

end of a transect survey. To minimise potential false pseudo-absences, we eliminated pseudoabsence points within the home-range of each species recorded to be present. Home-ranges were obtained from the literature, conservatively using the largest value reported (Appendix 1).

We selected six environmental and climate variables previously shown to provide reasonable representation of mammalian niche envelopes at landscape-scales (Boitani et al. 2008, Guisan and Thuiller 2005). Variables selected included: (1) elevation; (2) average tenyear (2000-2009) Enhanced Vegetation Index (EVI) (Justice et al. 1998); (3) annual mean temperature; (4) annual precipitation; (5) annual mean moisture index, all three derived from ANUCLIM 5.1 (Nix 1986); and (6) distance to the nearest water body (Kingsford et al. 2004). Finally, survey method for each record was included as a factor. We also had to assume that minimal vegetation change occurred, 1990-2009 at the 250m scale. Although some land clearing has occurred over this period, most of the land clearing was before 1990 (OEH 2011, SoE 2011). To avoid over-parameterisation of our models, we did not include interaction among variables (Araujo and Rahbek 2006, Thuiller et al. 2008). We employed Generalised Additive Models (GAMs) to predict distributions of species (package gam, R Development Core Team 2010). We used a boot-strapping model selection process for each species with all 63 unique combinations (obtained from the six identified predictor variables: 2^{n} - 1) (Steverberg et al. 2001). For each variable combination, we bootstrapped the data 1,000 times, randomly selecting 63.2% of the data (Hastie et al. 2009) and validating our models on the remainding 36.8%. The .632+ estimator provides good overall model performance, combining low variance with only moderate bias compared to other crossvalidation methods (Efron and Tibshirani 1997, Leathwick et al. 2006). We evaluated model performance by examining the Akaike's Information Criterion (AIC), trading-off explained variation against model complexity, and the area under the receiver operating characteristic
curve (AUC). We selected the most parsimonious model from a trade-off between the fewest numbers of predictor variables and the lowest average AIC +2 (Burnham and Anderson 2002). Using the final model, sighting probabilities (0-1) were predicted across NSW for each species at a resolution of 250 meters. Model performances were good, with most AUC values above 0.85 [0.75-0.85 (n=1), 0.85-0.95 (n=25), and 0.95-1 (n=27)].

To gauge the overall contribution of each survey method to SDMs (effect size), we parameterised our models without an intercept (means parameterisation or cell means model) (Rutherford 2001, Searle 2006). Specifically, the GAM model is:

$$logit(p) = \beta_1(sm_1) + \dots + \beta_j(sm_j) + S_1(x_1) + \dots + S_n(x_n)$$

where p_i is the species' probability of sighting (occurrence) for cell (i); sm₁,...,sm_j are the survey methods able to detect the species; β_j the associated coefficient; $x_1,...,x_n$ are the environmental explanatory variables; and S_i the nonparametric smooth function.

Subsequently, for each model we extracted all survey method coefficients: $sm_i = \begin{pmatrix} \beta_1 \\ \vdots \\ \beta_j \end{pmatrix}$, for

species i. In a given model, larger coefficient values for each survey method reflected a larger probability of occurrence (i.e., detection) for the survey method, given all other variables are constant (e.g., elevation, precipitation) (Hastie et al. 2009). For each species' SDM, we standardised coefficient values (0-1), with zero values assigned to survey methods that detected no species. We developed standardised coefficients by calculating:

$$std.\,\beta_i = \frac{\beta_i + \left|\min\left\{\begin{pmatrix}\beta_1\\ \vdots\\ \beta_j\end{pmatrix}\right\}\right|}{\max\left\{\begin{pmatrix}\beta_1\\ \vdots\\ \beta_j\end{pmatrix}\right\} + \left|\min\left\{\begin{pmatrix}\beta_1\\ \vdots\\ \beta_j\end{pmatrix}\right\}\right|}$$

Standardising coefficient ratios in the final GAM model, enabled us to create a within-species survey method ranking of detection (Wood 2006), (Appendix 2), and create a between-species comparable scaling for subsequent analysis.

Optimal combinations of survey methods

We investigated efficiency of survey method for mammal species, across NSW. To do this, we identified the smallest set survey methods, while maximising contribution to SDMs (e.g., GAM). We used the Marxan software (Ball and Possingham 2000, Ball et al. 2009) to incorporate obtained coefficients of each survey method for each species. Designed to provide solutions for site selection and reserve design, Marxan uses a simulated annealing algorithm to select a set of planning units that captures biodiversity targets for minimum total cost (Ball et al. 2009). Here, we replaced planning units in the Marxan platform with survey methods and set the corresponding coefficient as the biodiversity targets. In effect, this produced a predefined coefficient value at a minimum set of survey methods. As each species' survey method coefficients were standardised (0-1), we set the biodiversity target to one (i.e., the best survey methods used to detect that species). To minimise the number of survey methods selected, we allowed Marxan to select a combination of methods which summed to one. This allowed for either the selection of single best survey method or an additive combination of less efficient methods whose sum was equivalent to the best method. The coefficient values do not necessarily indicate detection probability per se, but their relative scaling does. Species were assumed to be undetected if the target was unattained. We used the ichness heuristic algorithm', iterated 1,000 times to find an optimal solution (Ball et al. 2009). We then summed the sets of survey methods selected, providing us with a ranking for each method in detecting each species. We also searched for combinations of optimal systematic survey methods by excluding all unplanned opportunistic sightings. This

excluded black-striped wallabies (*Macropus dorsalis*) and platypus (*Ornithorhynchus anatinus*) whose records were opportunistic.

As species composition varied across habitats, we repeated our analyses at the fine scale of 18 Bioregions across NSW (Thackway and Cresswell 1995). Bioregions are routinely used as the planning framework for the national reserve system of Australia. Species' inventories for each bioregion can be compiled using different methods (e.g., examining atlas occurrence data) but we chose to use our SDMs. To minimise misclassifications (Type I error), we identified a threshold, maximising agreement between observed and predicted distribution of each species, within each bioregion (Liu et al. 2005). We also adopted a conservative approach to our species' distribution modelling, incorporating one standard deviation from the average probability across a species' range to its core distribution (Merrill and Mattson 2003). This core distribution did not prevent occurrence in in adjoining cells but increased certainty.

We also investigated the relationship between body mass and survey method by collating species' average body mass from the literature (Jackson 2003, Menkhorst and Knight 2004, Strahan et al. 1983) and investigating potential detection biases of different survey methods, providing coefficient value as a predictor of survey method. Coefficient values of each survey techniques were the response variable and the species' body mass the predictor in a linear regression. We predicted that large species (i.e., body mass) would be easily detected using visual methods, whereas small species would be more readily detected by trapping.

Finally, we gauged the effects of sampling effort on the number of species detected using each survey method and species' rarefaction curves (EstimateS version 8.2.0, (Colwell 2006). We then extrapolated the expected number of species detected at 10,000 records by

fitting the Chapman-Richards exponential model (Flather 1996). We constrained the model $(S_x = a(1 - e^{-bx})^c)$, where S is the predicted number of species at x records), by limiting the asymptotic number of species (a) to 53 species, representing the overall recorded number of species. We grouped spotlight data for transect and site locations and separately grouped all opportunistic and incidental sightings, whether on route or from a designated survey site (i.e. _off-site' or _on-site' respectively). We ran separate analyses for these grouped survey methodologies.

complimentarity

Results

Efficacy of survey methods

Some survey methods reliably detected a wide range of species (maximum 43), but others were highly specific (minimum 3) (Figure 2). Opportunistic sightings (off' and on-site') detected the largest number of species (43 and 39, respectively). Predator scat' surveys and _transect spotlighting' were next best, detecting 34 and 31 species respectively. At the opposite extreme, _cage trapping', _nocturnal streamside', and _walking spotlight transects' detected the least number of species (three, 11, 11, respectively). Separate grouping of all opportunistic and spotlighting sightings preserved the dominance of opportunistic sightings, detecting 45 species (Figure 2). Spotlighting techniques (transect', walking', and site') detected almost as large a number of species (43 species), highlighting this method's overall efficiency. Species accumulation curves showed sampling effort considerably increased the number of species detected for most survey methodologies, after 10,000 observations (Figure 2), but the overall hierarchy of methods was maintained. Playback methods, noturnal streamside' surveys, and cage trapping methods substantially increased the number of species detected, as sample size increased. Opportunistic sightings (off^{*} and on-site^{*}) and predator scat' surveys were estimated to detect 44 ± 1.9 , 43 ± 0.5 , and 40 ± 4.5 species respectively, while walking spotlight transect' and pitfall trapping' were estimated to detect 15 ± 0.2 and 18 ± 0.7 species respectively.

Species body mass was significantly related to coefficient values for five survey methods (Figure 3 & Appendix 4). Body mass had the strongest positive relationship with sighting probability for opportunistic sightings, but was also positively correlated with _transect spotlighting' (but not _site spotlighting') and _predator scats'. Conversely, body mass had the strongest negative relationship with sighting probability when recorders

engaged in trapping (_pitfall' and _Elliot'). Body mass was not correlated to detectability from _hair tubes' and _cage trapping'.

Identifying optimal combinations of survey methods

Only four survey methods were needed to provide good landscape-scale detection coverage for all 53 mammal species (Table 2). These included _opportunistic records off-site', _pitfal' and _Eliot trapping', and _predator scat', each recording 27, 10, 10, and 6 species respectively. _Hair sampling tubes' and _cage trapping' were included in half of the simulated solutions, suggesting some contribution to detection of species. Excluding opportunistic records from the analysis reduced efficiency, as six survey methods were required to achieve full detection coverage of all mammal species (Table 2): _predator scats', _Eliot' and _pitfall trapping', transect and walking spotlighting, and _diumal Herpetofauna' surveys, each detecting 12, 11, 10, 10, 7, and one species respectively.

Terrestrial mammalian species richness ranged from eight to 37 across NSW's Bioregions, generally increasing towards the east coast (Appendix 3). NSW's North Coast, the Sydney Basin, and New England Tablelands Bioregions had the largest number of species with 37, 35, 35 species respectively (Appendix 3). As NSW covers a large number of regions and habitats, we identified the optimal combination of survey methods for each bioregion. Optimal survey methods in most bioregions included: _pitfall trapping', _transect spotlighting', _Elliot trapping', _walking spotlighting', _diurnal Herpetofauna', and _predator scats' (Table 3). When selecting for a combination of survey methods, _Nocturnal streamside' surveys added no value for modelling the distribution of examined species at landscapescales. The number of survey methods needed to attain efficient distribution models in each bioregion ranged from two in the Nandewar Bioregion to six in the Australian Alps Bioregion (Table 3). Across NSW's bioregions, full detection coverage of species was achieved using an average of 3.5 survey methods. While some methods were efficient across the entire area of NSW (e.g., _pitfall traps', _transect spotlighting'), others were more spatially confined (_cage trapping') (Figure 4).

Discussion

Conservation management and planning decisions need to be made at broad, landscape-scales utilising all available biotic data (Jones 2011, Nielsen et al. 2009). Many decisions are highly dependent on good monitoring at a similar scale (Radford and Bennett 2007), but fauna monitoring is rarely coordinated at landscape-scales, primarily driven by unique local management targets, available logistics, and funding (Nichols and Williams 2006). Often, rigour of data available at broad scales is considerably poorer than from targeted surveys but failure to use landscape-scale data is a poor use of resources to help mitigate biodiversity loss. Consequently, large-scale biodiversity and conservation analyses have to rely on disparate localised data (Gladstone and Davis 2003, Grand et al. 2007, Lozier et al. 2009, Polasky et al. 2000, Yoccoz et al. 2001). Across the state of NSW (800,642km²), roughly the size of France and United Kingdom combined, terrestrial mammals were recorded using 15 different survey methods, which had highly variable detection of species (Figure 2). The plethora and uneven spread of methods, over a period of three decades, reflects their relative success across different habitats and species (Figures 3 & 4); over prolonged periods, it is unlikely that surveys methods persist if they do not detect target species. Our examination of survey methods showed three interrelated factors operated, spatial deployment (Figure 1), sampling effort (Figure 2), and specificity of detection (Figure 3) but, we identified clear opportunities for improving and optimising landscape-scale monitoring.

There were four survey methods or six without opportunistic surveys, in combination, which produced good bioregional assessments of mammal species across NSW's 18 bioregions (Tables 2&3). A focus on just these methods could considerably improve

monitoring and decision effectiveness and would be obvious candidates for detecting species' population trends (Nielsen et al. 2009) and biodiversity responses to rapid global change (Pereira and Cooper 2006). Further, it was possible to improve survey detections at finer scales (i.e., targeted monitoring) or landscape-scale surveillance monitoring (Nichols and Williams 2006) without compromising the landscape-scale monitoring (~12,000 - ~225,000 km²) by implementing the best set of methods for each bioregion (Table 3). Further, costeffectiveness should be improved for successful conservation programs (Cleary 2006). Survey costs (e.g. time, equipment) vary considerably among taxa (Gardner et al. 2008), driven by the specific survey methods. For example, costs for cage trapping (traps, setting, checking) are considerably higher than transect spotlighting. Monitoring costs could be reduced through effective multi-species sampling designs (Manley et al. 2004, Nichols et al. 2008). Only a few studies at local scales have linked the probability of sighting a species with associated costs (Garden et al. 2007, Gardner et al. 2008). We did not incorporate costs because these were not available but integrated ranking of survey methods into conservation planning software (i.e., Marxan) could easily provide cost estimations if available. Another approach, which can significantly reduce costs and increase landscape-scale monitoring effectiveness is to combine multiple survey methods, including those not initially intended for the detection of mammals (Figure 2 and Table 2). For example, we found that diurnal herpetofauna surveys, not designed for mammal detection, were important for assessment of mammal distribution (Figure 2 and Table 2). Time of survey was also important with nocturnal and diurnal surveys increasing detection probabilities and numbers of mammal species (Figures 2, 3 and Table 2), as with frog surveys (de Solla et al. 2005). Multi-taxa surveys covering the full daily cycle (Table 3 & Figure 4) can significantly increase the total detection of species across a range of taxonomic classes. Our overall approach provides can

improve representation of biodiversity (Manley et al. 2004), simultaneously increasing costeffectiveness and sensitivity of monitoring to detection of threatening processes.

The importance of opportunistic surveys for providing effective monitoring was surprising because usually such surveys are not valued (Dormann et al. 2007, Elith and Leathwick 2009). Opportunistic sightings provided the largest source of presence data, spanning large spatial extents at a fraction of the cost of systematic surveys (Figure 2). Ideally systematic surveys should be implemented across landscapes but this is probably idealistic over large regions and so opportunistic surveys should be valued and encouraged. In the NSW's Atlas, opportunistic sightings of terrestrial mammals formed the largest source of occurrence records (35%) and covered the highest number of species (85%). For 51% of species, opportunistic sightings ranked the most effective for detection and regional-scale monitoring (Table 2). Opportunistic sightings could be increased by encouraging the general public to report observations through dedicated websites, assessed for quality (e.g. fauna identification), before importation into an atlas. To increase spatial resolution, visitors to national parks could use GPS units (most current mobile phones provide location coordinates) and record observations. More importantly, professional staff and researchers should record and report as many opportunistic sightings as possible during systematic surveys. Addressing and designing programmes that may use volunteer data can be greatly improved by considering these types of issues, structuring programmes where volunteers report both presence' and absence' records.

There were inevitable challenges in use of a large data (e.g. NSW Atlas). These formed two general deficiency categories: (1) spatial bias in use opportunistic sightings compared to systematic surveys and (2) variation in species detection across habitats. Atlases frequently have the largest source of occurrence data, consisting of systematic and opportunistic records (Robertson et al. 2010). Systematic surveys, controlled for effort and detection, provide the most reliable estimates of the distribution and density of species (Grantham et al. 2008) but, opportunistic sightings are inexpensive and plentiful although heavily affected by detection and spatial bias (Grand et al. 2007), such as proximity to roads (Austin et al. 1994). Opportunistic sightings are characteristically spatially auto-correlated (Dormann et al. 2007, Elith and Leathwick 2009) and favour _presence' records, inaccurately measuring species' distribution (Hernandez et al. 2006). Effects of spatial bias can be reduced by incorporating background data (i.e., absence data) with similar spatial biases, substantially improving model performance (Phillips et al. 2009). So, we generated informed pseudo-absences for each species, using location points from other terrestrial mammal species in the database for each survey method. We assumed failure to detect a species at a locality, when survey method detected the species in question elsewhere, could be defined as an absence. This analysis probably provided some reduction in spatial bias.

Problematically, changes in detection probability of a species, vary with species' life history traits, weather conditions, surveyor's skill, and the specific method employed (Tyre et al. 2003). Consequently, species' absence in any given locality may not be a true absence (MacKenzie et al. 2002, MacKenzie et al. 2006). We explored this for species' body mass, showing a correlation with detection efficacy of five survey methods employed across NSW (Figure 3). False absences have significant ramifications, affecting conservation measures, which if incorrect may increase local extinction risk (Narain et al. 2005, Wintle et al. 2005). Minimising the likelihood of false absences depends on the knowledge relating to the detection probability, usually achieved by repeated-measures approach (Fiske and Chandler 2011). These are exacerbated when dealing with many species at large scales, spanning several biomes. We developed a novel approach to this problem by employing species' distribution modelling to rank the ability of survey methods to detect mammal species. By doing so, we reduced the confounding effects of environmental and geographic covariates across a species' range, thus isolating the effects of survey methods to detection (McNeil et al. 1996). Our approach simultaneously scaled detection for each species, accounting for variable deployment across a range of habitats and bioregions, based on accumulated occurrence data. Estimated species' distributions, using atlas data, have provided valuable information at coarse scales elsewhere (Leitão et al. 2011, Phillips et al. 2009). The problem of spatial bias is also inevitably affected by the modelling approach, potentially affecting inference more than the method used to control inherit spatial biases (Barbet-Massin et al. 2012). Clearly, a key objective for data collection in atlases is to minimise biases and provide high quality biological data.

Conclusions

The contribution of local surveys to regional monitoring and assessment could be significantly improved by selecting appropriate survey methods and maximising cost-effectiveness. We showed the value of a mammal species' distribution modelling framework in ranking the contribution of multiple survey methods, consolidated from multiple data sources (e.g. atlas data), where survey method reflected historical deployment (i.e., survey methods, localised targets, logistics, and expert knowledge). We concluded that implementing a few survey methods could maximise information on mammalian biodiversity distribution across large landscapes. The methodology could be applied to other landscapes of the world with similar data and expanded in taxonomic range. There remains considerable value in large datasets collected using many different survey methods but use of collected data also needs to be maximised to underpin effective conservation decision-making.

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Tables

Table 1

List of the 11 survey methodologies investigated in this study along with an example of employed protocol and target species in NSW, Australia.

Method	Protocol	Target species
Cage trapping	This technique involved setting large cage traps at 200 m intervals	Medium-sized mammals.
	along a two km transect.	
Diurnal Herpetofauna	Half-hectare area (50 x 100 m) is actively searched.	Reptile and frogs.
Elliott trapping	Setting ten Elliott B traps at 20 m intervals along a 200 m transect.	Small-sized mammals.
Hair sampling tubes	Large hair-sampling tubes are placed at 20-100 m intervals along a	Small and medium-sized
	200 m - 2 km transect.	mammals
Nocturnal playbacks	On arrival at a site, the surrounding area is searched by spotlight for	Nocturnal birds and
	five minutes to detect any fauna in the immediate vicinity, followed by	mammals.
	10 minutes of broadcasting and listening. The surroundings are then	
	searched again.	
Nocturnal streamside	A 200 m stretch is searched; at standing water bodies a half hectare	Frogs
	(50 x 100 m) area is surveyed.	
Pitfall trapping	Five dry pitfall traps (e.g., 20 litter plastic buckets) are set along a 100	Invertebrates, small
	m transect.	mammals, frogs and

	reptiles.
Predator scats are collected opportunistically during targeted surveys	Mammal and avian
and away from standard sites during systematic surveys.	predators.
A 200 m transect is walked. Surveyors also listen intently for fauna	Arboreal mammals
calls during the survey period.	
A team of two surveyors drive along an eight km transect.	Arboreal mammals
Walking along a 300m- 2 km transect. All fauna seen or heard within	Arboreal mammals
50 m are recorded.	
Sightings made when travelling to/from survey sites and during times	Any
not committed to sampling period.	
	Predator scats are collected opportunistically during targeted surveys and away from standard sites during systematic surveys. A 200 m transect is walked. Surveyors also listen intently for fauna calls during the survey period. A team of two surveyors drive along an eight km transect. Walking along a 300m- 2 km transect. All fauna seen or heard within 50 m are recorded. Sightings made when travelling to/from survey sites and during times not committed to sampling period.

Table 2

The proportion of each survey method has been selected by Marxan to achieve target detection when considering only systematic

Scenario	Survey method	Selection proportion ±SD	Number of species
	Cage Trapping	0.50±0.06	
X	Hair Sampling Tubes	0.50 ± 0.06	
onl	Diurnal Herpetofauna	1	1
tic	Walking Spotlight Transect	1	7
ama	Transect Spotlighting	1	10
yste	Pitfall Trapping	1	10
S	Elliott Trapping	1	11
	Predator Scat	1	12
	Transect Spotlighting	0.03±0.02	
lgs	Nocturnal Playbacks	0.04±0.02	
htii	Diurnal Herpetofauna	0.14±0.03	
SIg.	Site Spotlighting	0.27±0.05	
ntal	Incidental Fauna Sighting	0.20 ± 0.04	
ider	Opp. Rec. at Standard Sites	0.34 ± 0.09	
inci	Walking Spotlight Transect	0.52 ± 0.06	
ng	Predator Scat	1	6
ipn	Pitfall Trapping	1	10
Incl	Elliott Trapping	1	10
	Opp. Rec. Off Site	1	27

surveys and when considering opportunistic sightings¹.

¹Survey methods which were not selected have been omitted. Optimal solutions were selected unanimously (i.e., proportion of 1). The number of species each survey method, in the best single solution, contributes to achieve the total number of species is provided.

Table 3

The proportion of each survey method has been selected by Marxan to achieve target detection in each one of the 18 bioregions.

Bioregion	Walking Spotlight Transect	Transect Spotlighting	Site Spotlighting	Predator Scat	Pitfall Trapping	Nocturnal Streamside	Nocturnal Playbacks	Hair Sampling Tubes	Elliott Trapping	Diurnal Herpetofauna	Cage Trapping
Australian Alps	1	1	0	1	1	0	0	0.57	1	1	0.43
Brigalow Belt South	0.33	1	0.38	0.43	1	0	0.37	0.22	1	1	0.49
Broken Hill Complex	1	0.46	0.49	0.05	1	0	0.05	0	0	1	0
Channel Country	1	0.21	0.22	0.2	1	0	0	0.14	0	1	0.23
Cobar Peneplain	1	0.47	0.4	0.28	1	0	0.13	0.41	0.44	1	0
Darling Riverine Plains	1	0.56	0.34	0.1	1	0	0.1	0	1	1	0
Mulga Lands	1	0.54	0.42	0.28	1	0	0.04	0.4	0.36	1	0
Murray Darling Depression	1	0.5	0.43	0.07	1	0	0.07	0	0	1	0
NSW North Coast	0.43	1	0.29	1	1	0	0.28	0.54	1	0	0.46
NSW South Western Slopes	0.24	1	0.21	1	1	0	0.55	0.22	1	1	0.23
Nandewar	0.22	1	0.41	0.68	0.51	1	0.0.46	0.53	1	0.09	0.28
New England Tablelands	0.31	1	0.34	1	0.31	0	0.0.35	0.69	1	0	0.31
Riverina	1	0.28	0.29	0.6	1	0	0	0	0	1	0.23
Simpson Strzelecki Dunefields	1	0.27	0.2	0.16	1	0	0	0.22	0	1	0.15
South East Corner	0.22	1	0.17	1	1	0	0.61	0.22	1	0	0.17
South Eastern Highlands	0.25	1	0.23	1	0.39	0	0.52	0.61	1	0	0.07
South Eastern Queensland	0.26	1	0.41	1	0.22	0	0.33	0.78	1	0	0.22
Sydney Basin	0.24	1	0.2	1	1	0	0.56	0.3	1	0	0.14

Figures

Figure 1: The distribution of occurrence records from NSW's ATLAS dataset of native terrestrial mammals.

Figure 2: The number of species recorded in NSW ATLAS dataset for each of the survey methods (including when all opportunistic and spotlighting techniques are grouped into single categories) (shaded box). Estimated number of species detected at 10,000 records based on the fitted accumulation curve (black circle).

Figure 3: Coefficient values of each survey techniques extracted from the selected model, plotted against log body mass (g) of species (linear regression significance values *<0.05, **<0.01).

Figure 4: Spatial representation of the frequency [%] each survey method has been selected by Marxan to achieve target detection in each one of the 18 bioregions. Detailed results can be seen in Table 3.

Figure 1











Figure 4



Appendix

Appendix 1

Average home-range of the 53 terrestrial mammal species modelled across NSW. Corresponding literary sources are provided in the table followed by the full reference. Minimum home range radius set at 100m. Due to lack of information, home range was estimated for three species (labelled accordingly under source).

Order	Family	Scientific name	Common Name	Home range [m]	Source
Dasyuromorphia	Dasyuridae	Antechinus agilis	Agile antechinus	100	(Lazenbycohen & Cockburn 1991)
		Antechinus flavipes	Yellow-footed antechinus	720	(Marchesan & Carthew 2008)
		Antechinus stuartii	Brown antechinus	126	(Lazenbycohen & Cockburn 1991)
		Antechinus swainsonii	Dusky antechinus	100	(Sanecki et al. 2006)
		Dasyurus maculatus	Spotted-tailed quoll	3000	(Belcher & Darrant 2004)
		Ningaui yvonneae	Southern ningaui	150	(Darren & Canhew 2007)
		Phascogale tapoatafa	Brush-tailed phascogale	668	(Soderquist 1994)
		Planigale gilesi	Paucident planigale	205	(Read 1984)
		Planigale tenuirostris	Narrow-nosed planigale	395	(Read 1984)
		Sminthopsis crassicaudata	Fat-tailed dunnart	350	(Read 1984)
		Sminthopsis leucopus	White-footed dunnart	1000	(Lunney & Leary 1989)
		Sminthopsis macroura	Stripe-faced dunnart	300	(Anke & Soderquist 2005)

		Sminthopsis murina	Common dunnart	550	Estimated
Diprotodontia	Acrobatidae	Acrobates pygmaeus	Feather-tail glider	100	(Lindenmayer 1997)
	Burramyidae	Cercartetus nanus	Eastern pygmy possum	100	(Harris et al. 2007)
	Macropodidae	Macropus dorsalis	Black-striped wallaby	540	(Evans 1996)
		Macropus fuliginosus	Western grey kangaroo	1200	(Priddel et al. 1988)
		Macropus giganteus	Eastern grey kangaroo	700	(Moore et al. 2002)
		Macropus parma	Parma wallaby	160	(Lentle et al. 2004)
		Macropus parryi	Whiptail wallaby	460	(Kaufmann 1974)
		Macropus robustus	Common wallaroo	495	(Clancy & Croft 1990)
		Macropus rufogriseus	Red-necked wallaby	480	(Mar et al. 2003)
		Macropus rufus	Red kangaroo	1500	(Priddel et al. 1988)
		Petrogale penicillata	Brush-tailed rock wallaby	220	(Short 1980)
		Thylogale stigmatica	Red-legged pademelon	110	(Vernes et al. 1995b)
		Thylogale thetis	Red-necked pademelon	130	(Vernes et al. 1995a)
		Wallabia bicolor	Swamp wallaby	290	(Troy & Coulson 1993)
	Phalangeridae	Trichosurus caninus	Short-eared possum	125	(McCarthy & Lindenmayer 1998)
		Trichosurus vulpecula	Common brush-tail possum	400	(Mar et al. 2003)
	Phascolarctidae	Phascolarctos cinereus	Koala	970	(Ellis et al. 2002)
	Potoroidae	Aepyprymnus rufescens	Rufous bettong	440	(Tyndale-Biscoe 2005)
		Potorous tridactylus	Long-nosed potoroo	180	(Tyndale-Biscoe 2005)

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	Pseudocheiridae	Petauroides volans	Greater glider	115	(Pope et al. 2004)
		Pseudocheirus peregrinus	Common ring-tail possum	100	(Jones et al. 1994)
	Vombatidae	Vombatus ursinus	Common wombat	320	(Murray 2008)
Monotremata	Ornithorhynchidae	Ornithorhynchus anatinus	Platypus	222	(Gust & Handasyde 1995)
	Tachyglossidae	Tachyglossus aculeatus	Short-beaked echidna	565	(Wilkinson et al. 1998)
Peramelemorphia	Peramelidae	Isoodon macrourus	Northern brown bandicoot	130	(Gordon 1974)
		Perameles nasuta	Long-nosed bandicoot	150	(Scott et al. 1999)
		Petaurus australis	Yellow-bellied glider	520	(Goldingay & Kavanagh 1993)
		Petaurus breviceps	Sugar glider	165	(Quin 1995)
		Petaurus norfolcensis	Squirrel glider	165	(Quin 1995)
Rodentia	Muridae	Hydromys chrysogaster	Water rat	180	(DEC. 2009)
		Mastacomys fuscus	Broad-toothed rat	100	(Bubela et al. 1991)
		Melomys burtoni	Grassland melomys	100	(Begg et al. 1983)
		Melomys cervinipes	Fawn-footed melomys	100	(Rader & Krockenberger 2006)
		Pseudomys bolami	Bolam's mouse	100	Estimated
		Pseudomys gracilicaudatus	Eastern chestnut mouse	100	(Strahan et al. 1983)
		Pseudomys novaehollandiae	New holland mouse	100	(Lock & Wilson 1999)
		Pseudomys pilligaensis	Pilliga mouse	100	(Tokushima & Jarman 2008)
		Rattus fuscipes	Bush rat	100	(Maitz & Dickman 2001)
		Rattus lutreolus	Swamp rat	100	(Maitz & Dickman 2001)

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Appendix 2

Survey method coefficients and additional GAM statistics extracted from each of the 53 species distribution models.

Common name	Survey Method	Coef. Estimate	Std. Error	z value	Pr(> z)	presence	absence	Comments
Agile Antechinus	Elliott Trapping	0.57	1.29	0.45	0.66	46	9811	single
Black-striped Wallaby	Opportunistic Records Off Site	-23.11	16.34	-1.41	0.16	10	8766	single
Bolam's Mouse	Pitfall Trapping	40.57	61.06	0.66	0.51	14	1182	single
Broad-toothed Rat	Opportunistic Records at Standard Sites	56.38	47.8	1.18	0.24	5	9630	
	Predator Scat	57.38	0.73	1.9	0.05	6	6063	
Brown Antechinus	Diurnal Herpetofauna	-6.31	0.52	-12.12	0	5	5155	
	Elliott Trapping	0.81	0.45	15.85	0	2798	6683	
	Hair Sampling Tubes	-3.03	0.45	7.24	0	215	7066	
	Nocturnal Playbacks	-7.26	0.73	-1.3	0.19	3	6916	
	Opportunistic Records at Standard Sites	-5.15	0.49	2.37	0.02	27	8747	
	Opportunistic Records Off Site	-5.67	0.5	1.27	0.2	20	8544	
	Pitfall Trapping	-0.93	0.48	11.16	0	45	1029	
	Predator Scat	-4.53	0.48	3.74	0	39	5625	
	Site Spotlighting	-6.2	0.59	0.18	0.85	7	6022	
	Transect Spotlighting	-7.44	0.73	-1.55	0.12	3	6698	
Brush-tailed Phascogale	Elliott Trapping	-18.01	4.24	-4.24	0	3	9808	
	Opportunistic Records at Standard Sites	-17.33	0.82	0.83	0.4	3	9617	
	Opportunistic Records Off Site	-15.39	0.61	4.29	0	31	8693	
	Transect Spotlighting	-17.03	0.73	1.33	0.18	5	6897	
Brush-tailed Rock Wallaby	Diurnal Herpetofauna	-9.15	3.31	-2.76	0.01	2	5646	
	Nocturnal Playbacks	-18.33	1	-0.03	0.97	2	7500	
	Opportunistic Records at Standard Sites	-16.67	0.74	2.2	0.03	24	9552	
	Opportunistic Records Off Site	-15.1	0.72	4.45	0	94	8674	
	Transect Spotlighting	-16.87	0.78	1.84	0.07	10	6923	
Bush Rat	Cage Trapping	-5.45	0.66	-8.22	0	68	2922	

	Elliott Trapping	-7.55	0.13	26	0	2034	7152	
	Hair Sampling Tubes	-10.04	0.14	6.26	0	336	6852	
	Nocturnal Streamside	-12.87	0.59	-3.33	0	3	1074	
	Opportunistic Records at Standard Sites	-11.8	0.19	-4.81	0	53	8759	
	Opportunistic Records Off Site	-12.24	0.21	-6.52	0	38	8605	
	Pitfall Trapping	-9.3	0.23	7.05	0	34	860	
	Predator Scat	-10.51	0.15	2.64	0.01	166	5109	
	Site Spotlighting	-13.46	0.4	-6.42	0	7	6167	
	Transect Spotlighting	-13.73	0.36	-7.93	0	9	6715	
	Walking Spotlight Transect	-9.23	0.76	2.19	0.03	2	53	
	Wet Pitfall Trapping	-11.44	0.52	-1.02	0.31	4	222	
Common Brush-tail Possum	Cage Trapping	-3.69	0.44	-8.33	0	40	2604	
	Diurnal Herpetofauna	-8.95	0.25	-6.32	0	29	4230	
	Elliott Trapping	-9.4	0.27	-7.41	0	21	7800	
	Hair Sampling Tubes	-5.2	0.17	12.94	0	630	5671	
	Incidental Fauna Sighting	-8.16	0.21	-3.68	0	60	1845	
	Nocturnal Playbacks	-6.35	0.17	5.98	0	346	5731	
	Nocturnal Streamside	-8.46	0.39	-2.75	0.01	8	995	
	Opportunistic Records at Standard Sites	-7.07	0.17	1.79	0.07	329	7040	
	Opportunistic Records Off Site	-6.67	0.17	4.16	0	468	7704	
	Predator Scat	-5.76	0.17	9.37	0	353	4396	
	Site Spotlighting	-5.65	0.17	10.27	0	696	4911	
	Transect Spotlighting	-5.71	0.17	9.79	0	491	5887	
	Walking Spotlight Transect	-5.79	0.38	4.13	0	11	82	
Common Dunnart	Diurnal Herpetofauna	-4.25	2.25	-1.89	0.06	6	5494	
	Elliott Trapping	-6.7	0.43	4.15	0	50	9383	
	Hair Sampling Tubes	-9.06	0.71	-0.79	0.43	3	7561	
	Nocturnal Streamside	-7.73	0.82	0.94	0.35	2	1221	
	Opportunistic Records at Standard Sites	-7.9	0.48	1.25	0.21	16	9491	
	Opportunistic Records Off Site	-7.92	0.5	1.17	0.24	13	8674	
	Pitfall Trapping	-4.93	0.45	7.86	0	50	1012	

	Predator Scat	-7.97	0.56	0.96	0.34	7	5944	
	Site Spotlighting	-8.84	0.61	-0.57	0.57	5	6716	
	Wet Pitfall Trapping	-3.7	0.51	9.48	0	14	250	
Common Ring-tail Possum	Diurnal Herpetofauna	9.25	0.98	9.43	0	13	5104	
-	Elliott Trapping	15.93	0.76	-3.38	0	2	8515	
	Hair Sampling Tubes	18.92	0.35	1.18	0.24	22	6931	
	Incidental Fauna Sighting	20.91	0.31	7.73	0	69	1960	
	Nocturnal Playbacks	20.98	0.29	8.6	0	200	6353	
	Nocturnal Streamside	19.28	0.47	1.66	0.1	7	1120	
	Opportunistic Records at Standard Sites	20.38	0.29	6.51	0	163	8492	
	Opportunistic Records Off Site	21.11	0.28	9.15	0	281	8297	
	Predator Scat	21.35	0.29	9.89	0	214	4982	
	Site Spotlighting	22.05	0.28	12.58	0	486	5549	
	Transect Spotlighting	22.23	0.28	13.21	0	572	6353	
	Walking Spotlight Transect	22.27	0.42	8.88	0	12	89	
Common Wallaroo	Diurnal Herpetofauna	-2.69	0.75	-3.57	0	2	5441	
	Incidental Fauna Sighting	-1.91	0.73	4.73	0	31	1942	
	Nocturnal Playbacks	-5.47	1	-0.09	0.93	2	7270	
	Opportunistic Records at Standard Sites	-1.48	0.71	5.48	0	171	8985	
	Opportunistic Records Off Site	-0.68	0.71	6.61	0	285	8179	
	Predator Scat	-4.09	0.84	1.54	0.12	5	5903	
	Site Spotlighting	-2.89	0.73	3.41	0	29	6435	
	Transect Spotlighting	-2.79	0.74	3.5	0	22	6658	
Common Wombat	Diurnal Herpetofauna	-0.25	0.43	-0.57	0.57	76	4698	
	Hair Sampling Tubes	-2.97	0.43	-5.79	0	6	7320	
	Incidental Fauna Sighting	-1.58	0.4	-2.7	0.01	7	2064	
	Nocturnal Playbacks	-1.69	0.22	-5.53	0	31	6599	
	Nocturnal Streamside	-2.74	0.72	-3.12	0	2	1059	
	Opportunistic Records at Standard Sites	1.54	0.12	16.57	0	967	7146	
	Opportunistic Records Off Site	1.02	0.13	12.16	0	627	7550	
	Predator Scat	-0.25	0.17	1.52	0.13	79	5188	

	Site Spotlighting	-0.44	0.15	0.42	0.68	125	5290	
	Transect Spotlighting	-1.58	0.22	-4.93	0	30	6359	
Dusky Antechinus	Elliott Trapping	-0.32	1.33	-0.24	0.81	47	9592	
	Hair Sampling Tubes	-1.49	0.47	-1.82	0.07	6	7662	
	Opportunistic Records at Standard Sites	-3.23	0.61	-4.25	0	3	9584	
	Predator Scat	-1.13	0.38	-1.3	0.19	11	5966	
Eastern Chestnut Mouse	Elliott Trapping	-3.73	11.83	-0.32	0.75	6	9834	
	Opportunistic Records Off Site	-6.09	0.58	2.36	0.02	40	8757	
Eastern Grey Kangaroo	Diurnal Herpetofauna	3.84	1.75	2.19	0.03	17	4826	
	Hair Sampling Tubes	5.78	0.75	-2.54	0.01	2	6358	
	Incidental Fauna Sighting	10.13	0.26	9.3	0	174	1470	
	Nocturnal Playbacks	7.77	0.34	0.26	0.79	19	6671	
	Nocturnal Streamside	7.19	0.75	-0.65	0.51	2	1053	
	Opportunistic Records at Standard Sites	10.37	0.25	10.69	0	339	8191	
	Opportunistic Records Off Site	11.56	0.25	15.62	0	788	7473	
	Predator Scat	9.86	0.27	8.16	0	97	5149	
	Site Spotlighting	9.36	0.26	6.39	0	114	5638	
	Transect Spotlighting	9.75	0.27	7.8	0	102	5900	
	Walking Spotlight Transect	8.88	0.77	1.56	0.12	2	97	
Eastern Pygmy Possum	Diurnal Herpetofauna	-0.35	2.49	-0.14	0.89	2	5645	
	Elliott Trapping	1.36	0.75	2.75	0.01	17	9618	
	Opportunistic Records Off Site	0.31	0.78	1.29	0.2	9	8754	
	Pitfall Trapping	4.94	0.75	7.53	0	26	1175	
	Predator Scat	1.96	0.74	3.59	0	21	5996	
	Site Spotlighting	-0.21	0.84	0.58	0.56	5	6782	
	Transect Spotlighting	0.32	0.87	1.17	0.24	4	6939	
Fat-tailed Dunnart	Elliott Trapping	-62.22	12.36	-5.03	0	6	9829	
	Incidental Fauna Sighting	-126.39	0.6	-3.25	0	9	2055	
	Opportunistic Records Off Site	-125.78	0.9	-1.48	0.14	3	8764	
	Pitfall Trapping	-123.87	0.54	1.06	0.29	39	1166	
Fawn-footed Melomys	Elliott Trapping	-10.44	1.58	-6.63	0	118	9297	

	Hair Sampling Tubes	-25.53	0.72	-6.5	0	2	7666	
	Opportunistic Records at Standard Sites	-24.37	0.72	-4.87	0	2	9606	
	Opportunistic Records Off Site	-22.84	0.27	-7.33	0	17	8732	
	Predator Scat	-22.56	0.23	-7.32	0	25	5887	
	Site Spotlighting	-23.81	0.72	-4.08	0	2	6715	
	Transect Spotlighting	-24.1	0.42	-7.59	0	6	6938	
Feather-tail Glider	Incidental Fauna Sighting	-9.03	0.7	-12.81	0	7	2065	
	Nocturnal Playbacks	-8.91	0.47	0.26	0.79	18	7311	
	Opportunistic Records at Standard Sites	-9.59	0.49	-1.13	0.26	12	9442	
	Opportunistic Records Off Site	-8.52	0.45	1.15	0.25	29	8690	
	Predator Scat	-9.15	0.51	-0.23	0.82	11	5959	
	Site Spotlighting	-6.85	0.41	5.35	0	131	6312	
	Transect Spotlighting	-7.67	0.43	3.14	0	53	6896	
	Walking Spotlight Transect	-5.77	0.58	5.59	0	6	106	
Grassland Melomys	Elliott Trapping	-48.21	8.31	-5.8	0	56	9728	
	Opportunistic Records Off Site	-50.61	0.61	-3.95	0	3	8762	
	Predator Scat	-51.83	0.75	-4.84	0	2	6040	
	Transect Spotlighting	-51.89	0.75	-4.89	0	2	6948	
Greater Glider	Diurnal Herpetofauna	-8.77	1	-8.74	0	2	4869	
	Nocturnal Playbacks	-3.22	0.71	7.82	0	655	5829	
	Nocturnal Streamside	-5.6	0.76	4.16	0	13	1079	
	Opportunistic Records at Standard Sites	-5.23	0.71	4.96	0	119	8349	
	Opportunistic Records Off Site	-4.04	0.71	6.66	0	567	8084	
	Predator Scat	-5.61	0.72	4.4	0	75	4770	
	Site Spotlighting	-2.66	0.71	8.62	0	687	5520	
	Transect Spotlighting	-1.91	0.71	9.69	0	2314	6036	
	Walking Spotlight Transect	-1.69	0.84	8.47	0	6	100	
Koala	Call Playback	-10.73	0.75	-2.61	0.01	8	37	
	Diurnal Herpetofauna	-13.39	0.5	-9.15	0	15	5267	
	Incidental Fauna Sighting	-10.28	0.46	-3.3	0	40	1946	
	Koala Scat Analysis	7.58	109.59	0.15	0.88	62	62	
	Nocturnal Playbacks	-12.9	0.47	-8.72	0	31	6959	
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	Opportunistic Records at Standard Sites	-12.12	0.45	-7.5	0	85	8937	
	Opportunistic Records Off Site	-11.01	0.44	-5.09	0	221	8011	
	Predator Scat	-13.82	0.53	-9.49	0	11	5439	
	Site Spotlighting	-12.13	0.45	-7.43	0	56	6426	
	Transect Spotlighting	-11.53	0.45	-6.13	0	97	6229	
	Walking Spotlight Transect	-11.51	0.83	-3.3	0	2	118	
Long-nosed Bandicoot	Cage Trapping	-0.9	0.94	-0.95	0.34	23	3139	
	Elliott Trapping	-3.09	0.41	-5.32	0	8	9217	
	Hair Sampling Tubes	-1.04	0.26	-0.53	0.6	46	7289	
	Nocturnal Playbacks	-0.93	0.27	-0.12	0.9	37	7189	
	Nocturnal Streamside	-1.82	0.62	-1.49	0.14	3	1181	
	Opportunistic Records at Standard Sites	0.02	0.24	3.89	0	95	9191	
	Opportunistic Records Off Site	0.11	0.23	4.35	0	109	8627	
	Predator Scat	-0.18	0.24	2.97	0	68	5608	
	Site Spotlighting	-0.22	0.25	2.69	0.01	57	6501	
	Transect Spotlighting	0.14	0.23	4.46	0	106	6716	
Long-nosed Potoroo	Cage Trapping	-17.52	3.95	-4.44	0	20	3207	
	Elliott Trapping	-20.31	0.63	-4.44	0	3	9693	
	Hair Sampling Tubes	-19.33	0.64	-2.85	0	3	7718	
	Nocturnal Playbacks	-18.96	0.56	-2.55	0.01	4	7481	
	Opportunistic Records at Standard Sites	-18.38	0.5	-1.7	0.09	6	9633	
	Opportunistic Records Off Site	-18.07	0.4	-1.39	0.17	11	8756	
	Predator Scat	-18.98	0.56	-2.61	0.01	4	6040	
Narrow-nosed Planigale	Pitfall Trapping	2.59	1.16	2.22	0.03	17	1221	Single
New Holland Mouse	Elliott Trapping	-34.28	2.73	-12.54	0	348	9462	
	Hair Sampling Tubes	-38.21	0.72	-5.48	0	2	7717	
	Opportunistic Records at Standard Sites	-37.96	0.52	-7.08	0	4	9615	
	Opportunistic Records Off Site	-37.71	0.52	-6.59	0	4	8759	
	Pitfall Trapping	-33.48	0.23	3.46	0	32	1209	
Northern Brown Bandicoot	Cage Trapping	-39.77	0.7	-7.86	0	19	3075	

	Elliott Trapping	-36.21	0.47	-4.11	0	6	9493	
	Hair Sampling Tubes	-33.24	0.25	4.13	0	104	7384	
	Opportunistic Records at Standard Sites	-34.42	0.32	-0.43	0.67	20	9468	
	Opportunistic Records Off Site	-34.09	0.29	0.66	0.51	33	8713	
	Predator Scat	-32.61	0.25	6.73	0	142	5510	
	Site Spotlighting	-35.69	0.62	-2.25	0.02	3	6721	
	Transect Spotlighting	-36.17	0.5	-3.75	0	5	6818	
Pale Field Rat	Elliott Trapping	-18.32	3.61	-5.07	0	100	9705	
	Hair Sampling Tubes	-20.46	0.26	-8.07	0	22	7663	
	Opportunistic Records Off Site	-21.22	0.36	-8.14	0	10	8761	
	Pitfall Trapping	-20.05	0.49	-3.5	0	5	1208	
	Predator Scat	-21.59	0.42	-7.86	0	7	6037	
	Transect Spotlighting	-21.87	0.53	-6.75	0	4	6941	
Parma Wallaby	Hair Sampling Tubes	-12.34	4.48	-2.75	0.01	2	7690	
	Nocturnal Playbacks	-12.05	0.92	0.32	0.75	3	7447	
	Opportunistic Records at Standard Sites	-11.25	1	1.09	0.28	2	9638	
	Opportunistic Records Off Site	-7.88	0.71	6.25	0	154	8662	
	Predator Scat	-11.33	0.87	1.17	0.24	4	6049	
	Transect Spotlighting	-10.79	0.78	1.98	0.05	9	6906	
Paucident Planigale	Pitfall Trapping	0.74	0.8	0.93	0.35	20	1179	single
Pilliga Mouse	Elliott Trapping	47.5	63.81	0.74	0.46	28	9732	single
Platypus	Opportunistic Records at Standard Sites	-11.96	2.33	-5.14	0	9	9628	
	Opportunistic Records Off Site	-22.82	2.31	-4.71	0	23	8729	
Red Kangaroo	Diurnal Herpetofauna	-7.09	6.48	-1.09	0.27	2	5513	
	Incidental Fauna Sighting	-3.74	0.74	4.56	0	87	1490	
	Opportunistic Records at Standard Sites	-4.53	0.76	3.37	0	23	9504	
	Opportunistic Records Off Site	-3.6	0.85	4.11	0	7	8742	
Red-legged Pademelon	Opportunistic Records at Standard Sites	-6.89	3.03	-2.27	0.02	4	9647	
	Opportunistic Records Off Site	-5.21	0.53	3.16	0	41	8758	
	Predator Scat	-6.53	0.6	0.61	0.54	10	5920	
	Transect Spotlighting	-8.25	0.87	-1.56	0.12	2	6924	

Red-necked Pademelon	Hair Sampling Tubes	-19 79	1 51	-13.06	0	5	7339	
Red neeked i ddemeion	Opportunistic Records at Standard Sites	-17.19	0.49	5 27	0	24	9540	
	Opportunistic Records Off Site	-15.06	0.45	10.48	0	359	8547	
	Predator Scat	-16.93	0.47	6 11	ů 0	58	5581	
	Site Spotlighting	-18 46	0.63	2.09	0.04	5	6661	
	Transect Spotlighting	-17 91	0.49	3.85	0	27	6655	
Red-necked Wallaby	Diurnal Herpetofauna	-7.06	0.45	-15.71	0	-7	5175	
	Hair Sampling Tubes	-8.09	0.63	-1.65	0.1	4	6899	
	Incidental Fauna Sighting	-2.11	0.4	12.48	0	136	1684	
	Nocturnal Playbacks	-7.49	0.54	-0.8	0.42	7	6951	
	Opportunistic Records at Standard Sites	-4.04	0.38	7.84	0	221	8696	
	Opportunistic Records Off Site	-2.54	0.38	11.9	0	983	7759	
	Predator Scat	-5.69	0.42	3.27	0	33	5307	
	Site Spotlighting	-5.73	0.42	3.2	0	34	6345	
	Transect Spotlighting	-5.45	0.4	4.03	0	61	6037	
Rufous Bettong	Cage Trapping	-25.03	8.01	-3.12	0	2	3145	
C	Hair Sampling Tubes	-23.18	0.73	2.53	0.01	31	7557	
	Opportunistic Records at Standard Sites	-23.45	0.79	2.02	0.04	9	9584	
	Opportunistic Records Off Site	-22.79	0.73	3.06	0	32	8708	
	Predator Scat	-23.86	0.78	1.49	0.14	9	5891	
Short-beaked Echidna	Cage Trapping	-5.37	0.75	-7.14	0	4	3079	
	Diurnal Herpetofauna	-4.59	0.54	1.44	0.15	28	5060	
	Hair Sampling Tubes	-5.08	0.56	0.51	0.61	15	7167	
	Incidental Fauna Sighting	-3.84	0.53	2.9	0	58	1846	
	Opportunistic Records at Standard Sites	-2.76	0.51	5.16	0	276	8371	
	Opportunistic Records Off Site	-2.61	0.51	5.46	0	246	8079	
	Predator Scat	-3.89	0.53	2.81	0	39	5362	
	Site Spotlighting	-5.21	0.55	0.29	0.77	19	6096	
	Transect Spotlighting	-5.45	0.59	-0.14	0.89	10	6443	
Short-eared Possum	Cage Trapping	-9	0.72	-12.58	0	6	3079	
	Elliott Trapping	-10.22	0.65	-1.88	0.06	4	9344	

	Hair Sampling Tubes	-9.75	0.58	-1.31	0.19	6	7278	
	Nocturnal Playbacks	-6.99	0.42	4.74	0	83	7068	
	Nocturnal Streamside	-8.69	0.82	0.38	0.7	2	1187	
	Opportunistic Records at Standard Sites	-7.76	0.46	2.72	0.01	27	9390	
	Opportunistic Records Off Site	-6.99	0.43	4.71	0	76	8568	
	Predator Scat	-9	0.52	0	1	10	5779	
	Site Spotlighting	-6.49	0.44	5.76	0	55	6618	
	Transect Spotlighting	-6.44	0.42	6.11	0	134	6542	
Southern Ningaui	Pitfall Trapping	1.18	2.61	0.45	0.65	89	1182	Single
Spotted-tailed Quoll	Cage Trapping	-3.03	0.79	-3.82	0	33	2215	
	Elliott Trapping	-2.73	0.45	-6.1	0	6	7947	
	Hair Sampling Tubes	0.07	0.21	0.31	0.76	90	5989	
	Nocturnal Playbacks	-3.94	0.73	-5.38	0	2	6417	
	Opportunistic Records at Standard Sites	-2.2	0.36	-6.14	0	11	8868	
	Opportunistic Records Off Site	-0.56	0.22	-2.5	0.01	64	7394	
	Predator Scat	0.23	0.21	1.07	0.29	90	4430	
	Site Spotlighting	-3.73	0.73	-5.08	0	2	6186	
Squirrel Glider	Diurnal Herpetofauna	-21.08	2.21	-9.53	0	2	5527	
	Elliott Trapping	-21.61	1	-0.53	0.6	2	9496	
	Incidental Fauna Sighting	-19.4	0.8	2.1	0.04	8	2058	
	Nocturnal Playbacks	-18.09	0.73	4.12	0	37	7367	
	Opportunistic Records at Standard Sites	-19.5	0.77	2.05	0.04	11	9550	
	Opportunistic Records Off Site	-17.94	0.72	4.33	0	45	8696	
	Predator Scat	-19.07	0.78	2.59	0.01	10	5984	
	Site Spotlighting	-17.41	0.72	5.12	0	79	6489	
	Transect Spotlighting	-17.49	0.73	4.96	0	48	6861	
Stripe-faced Dunnart	Elliott Trapping	-145.35	20.71	-7.02	0	2	9838	
	Pitfall Trapping	-144.3	1.05	1	0.32	10	1224	
Sugar Glider	Call Playback	4.88	0.67	7.32	0	18	28	
	Diurnal Herpetofauna	-2.1	0.48	-14.45	0	19	4538	
	Elliott Trapping	-3.42	0.54	-15.34	0	9	7779	

	Incidental Fauna Sighting	0.22	0.47	-9 98	0	25	1940	
	Nocturnal Playbacks	1.6	0.43	-7.68	0	718	5623	
	Nocturnal Streamside	-1.19	0.52	-11.76	0	12	987	
	Opportunistic Records at Standard Sites	-0.29	0.43	-12.01	0	217	7540	
	Opportunistic Records Off Site	0.1	0.43	-11.14	0	293	7950	
	Predator Scat	-0.79	0.44	-12.78	0	66	5342	
	Site Spotlighting	1.52	0.43	-7.88	0	707	4850	
	Transect Spotlighting	1	0.43	-9.04	0	395	6066	
	Walking Spotlight Transect	2.85	0.53	-3.83	0	24	55	
Swamp Rat	Cage Trapping	-24.37	2.28	-10.69	0	5	3203	
	Elliott Trapping	-21.04	0.45	7.37	0	365	8690	
	Hair Sampling Tubes	-23.14	0.47	2.59	0.01	44	7547	
	Opportunistic Records at Standard Sites	-25.27	0.63	-1.42	0.16	5	9240	
	Opportunistic Records Off Site	-23.95	0.51	0.81	0.42	16	8437	
	Pitfall Trapping	-23.01	0.61	2.23	0.03	6	1116	
	Predator Scat	-22.91	0.48	3.05	0	36	5836	
Swamp Wallaby	Diurnal Herpetofauna	-21.74	0.88	3	0	11	4106	
	Hair Sampling Tubes	-20.95	0.31	11.08	0	274	5544	
	Incidental Fauna Sighting	-20.28	0.32	12.88	0	145	1616	
	Nocturnal Playbacks	-23.85	0.38	1.39	0.16	20	5424	
	Nocturnal Streamside	-24.6	0.77	-0.3	0.77	2	942	
	Opportunistic Records at Standard Sites	-20.57	0.3	12.46	0	742	6584	
	Opportunistic Records Off Site	-20.12	0.3	13.95	0	1027	6928	
	Predator Scat	-19.2	0.31	16.94	0	922	3786	
	Site Spotlighting	-21.44	0.31	9.46	0	236	4281	
	Transect Spotlighting	-21.71	0.31	8.43	0	135	5167	
	Walking Spotlight Transect	-20.03	0.5	8.67	0	8	43	
Water Rat	Cage Trapping	-1.61	2.19	-0.74	0.46	2	3259	
	Opportunistic Records at Standard Sites	-0.86	0.76	0.98	0.33	15	9400	
	Opportunistic Records Off Site	-0.79	0.76	1.07	0.28	14	8449	
	Predator Scat	-1.07	0.82	0.66	0.51	6	5988	

	Site Spotlighting	-1.64	0.88	-0.04	0.97	4	6084	
	Transect Spotlighting	-2.18	1	-0.57	0.57	2	6553	
Western Grey Kangaroo	Diurnal Herpetofauna	3.57	2.02	1.76	0.08	2	5571	
	Incidental Fauna Sighting	7.22	0.72	5.03	0	191	1697	
	Opportunistic Records at Standard Sites	6.46	0.75	3.88	0	30	9372	
	Opportunistic Records Off Site	6.29	0.92	2.94	0	4	8459	
	Site Spotlighting	5.02	0.94	1.55	0.12	3	6076	
	Walking Spotlight Transect	11.11	1.36	5.55	0	2	99	
Whip-tail Wallaby	Opportunistic Records at Standard Sites	-37.78	10.18	-3.71	0	13	9390	
	Opportunistic Records Off Site	-36.77	0.32	3.15	0	53	8409	
	Transect Spotlighting	-39.29	0.53	-2.82	0	5	6497	
White-footed Dunnart	Elliott Trapping	-10.83	24.54	-0.44	0.66	3	9813	
	Pitfall Trapping	-7.09	1.32	2.83	0	6	1239	
Yellow-bellied Glider	Call Playback	1.94	1.1	1.76	0.08	3	43	
	Diurnal Herpetofauna	-5.35	1.11	-6.55	0	3	5036	
	Incidental Fauna Sighting	-1.27	1.08	-2.96	0	4	2051	
	Nocturnal Playbacks	-0.7	0.95	-2.77	0.01	338	6497	
	Opportunistic Records at Standard Sites	-2.06	0.95	-4.19	0	152	8450	
	Opportunistic Records Off Site	-0.91	0.95	-2.99	0	368	7862	
	Site Spotlighting	-1.43	0.95	-3.54	0	191	5791	
	Transect Spotlighting	-1.74	0.96	-3.85	0	103	6287	
	Walking Spotlight Transect	0.39	1.03	-1.51	0.13	10	91	
Yellow-footed Antechinus	Diurnal Herpetofauna	-22.86	0.82	-28.04	0	5	5114	
	Elliott Trapping	-17.29	0.46	12.19	0	967	9107	
	Hair Sampling Tubes	-19.47	0.47	7.16	0	66	6971	
	Opportunistic Records at Standard Sites	-20.28	0.49	5.24	0	29	9314	
	Opportunistic Records Off Site	-20.58	0.51	4.51	0	20	8514	
	Pitfall Trapping	-21.87	0.85	1.17	0.24	2	1166	
	Predator Scat	-21.62	0.59	2.09	0.04	7	5693	
	Transect Spotlighting	-22.35	0.68	0.76	0.45	4	6638	

Appendix 3

List of the 18 Bioregions in NSW and their intersection with the core habitat of estimated terrestrial mammal species. Presented are the number of species from each family along with the total number of species and total number of families in each Bioregion.

D	Bioregion	Acrobatidae	Burramyidae	Dasyuridae	Macropodidae	Muridae	Ornithorhynchidae	Peramelidae	Petauridae	Phalangeridae	Phascolarctidae	Potoroidae	Pseudocheiridae	Tachyglossidae	Vombatidae	# Species	# Families
1	Australian Alps	1	1	4	5	4	1	1	2	2	0	1	2	0	1	25	12
2	Brigalow Belt South	1	1	7	6	3	1	0	3	1	1	1	2	1	1	29	13
3	Broken Hill Complex	0	0	4	3	1	0	0	0	0	1	0	0	1	0	10	5
4	Channel Country	0	0	3	2	1	0	0	0	0	1	0	0	1	0	8	5
5	Cobar Peneplain	0	1	4	4	0	0	0	0	1	1	0	0	1	0	12	6
6	Darling Riverine Plains	0	1	7	6	2	1	0	2	1	1	0	0	1	0	22	9
7	Mulga Lands	0	0	5	3	1	0	0	0	0	1	0	0	1	0	11	5
8	Murray Darling Depression	0	0	6	4	1	0	0	0	1	0	0	0	1	0	13	5
9	NSW North Coast	1	1	5	9	7	1	2	3	2	1	2	2	0	1	37	13
10	NSW South Western Slopes	1	1	5	6	6	1	0	3	2	0	1	2	1	1	30	12
11	Nandewar	1	1	4	5	3	1	0	3	1	1	1	2	0	1	24	12

12	New England Tablelands	1	1	3	10	6	1	2	3	2	1	2	2	0	1	35	13
13	Riverina	0	1	5	4	2	1	0	1	1	0	0	1	1	0	17	9
14	Simpson Strzelecki Dunefields	0	0	3	2	1	0	0	0	0	1	0	0	1	0	8	5
15	South East Corner	1	1	4	7	4	1	1	2	1	0	1	2	0	1	26	12
16	South Eastern Highlands	1	1	5	8	6	1	2	3	2	0	1	2	0	1	33	12
17	South Eastern Queensland	1	0	4	8	8	1	2	3	1	1	2	2	0	0	33	11
18	Sydney Basin	1	1	5	8	7	1	2	3	2	1	1	2	0	1	35	13

Appendix 4

Pearson correlation values between coefficient values of each survey techniques with log body mass (g) of species.

Survey Method	R^2	Р	N
Cage Trapping	0.18	0.59	11
Call Playback	0.94	0.23	3
Diurnal Herpetofauna	0.31	0.18	20
Elliott Trapping	0.58	< 0.01	27
Hair Sampling Tubes	0.05	0.81	24
Incidental Fauna Sighting	0.64	0.01	16
Nocturnal Playbacks	0.25	0.29	20
Nocturnal Streamside	0.31	0.35	11
Opportunistic Records at Standard Sites	0.66	< 0.01	39
Opportunistic Records Off Site	0.72	< 0.01	43
Pitfall Trapping	0.71	< 0.01	15
Predator Scat	0.26	0.13	34
Site Spotlighting	0.15	0.47	26
Transect Spotlighting	0.26	0.16	31
Walking Spotlight Transect	0.21	0.53	11

Chapter 3: Improving bioregional frameworks for conservation by

including mammal distributions

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Improving bioregional frameworks for conservation by including mammal distributions Gilad Bino^{1*}, Daniel Ramp^{1, 2} & Richard T. Kingsford¹

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Abstract

Large identifiable landscape units, such as ecoregions, are used to prioritise global and continental conservation efforts, particularly where biodiversity knowledge is inadequate. Setting biodiversity representation targets using coarse large-scale biogeographic boundaries, can be inefficient and under-representative. Even when using fine-scale biodiversity data, representation deficiencies can occur through misalignment of target distributions with such prioritisation frameworks. While this pattern has been recognised, quantitative approaches highlighting misalignments have been lacking, particularly for assemblages of mammal species. We tested the efficacy of Australia's bioregions as a spatial prioritisation framework for representing mammal species, within protected areas, in New South Wales. We produced an approach based on mammal assemblages and assessed its performance in representing mammal distributions. Substantial spatial misalignment between NSW's bioregions and mammal assemblages was revealed, reflecting deficiencies in the representation of more than half of identified mammal assemblages. Using a systematic approach driven by fine-scale mammalian data, we compared the efficacy of these two frameworks in securing mammalian representation within protected areas. Of the 61 species, 38 were better represented by the mammalian framework, with remaining species only marginally better represented when guided by bioregions. Overall, the rate at which mammal species were incorporated into the protected area network was higher (5.1%±0.6sd) when guided by mammal assemblages. Guided by bioregions, systematic conservation planning of protected areas may be constrained in realising its full potential in securing representation for all of Australia's biodiversity. Adapting the boundaries of prioritisation frameworks by incorporating amassed information from a broad range of taxa should be of conservation significance.

Introduction

Establishing protected areas are the cornerstone of conservation strategies (Rodrigues et al. 2004). The development of systematic methods for prioritising conservation areas continues to be a fruitful area of research and improvement (Margules & Sarkar 2007; Pressey & Bottrill 2008; Watson et al. 2011), primarily driven by an increased availability of geographically explicit data along with advances in in the science of conservation planning. Rather than mere theoretical exercises, systematic conservation initiatives are becoming widely adopted, influencing planning and legislation (Pressey & Bottrill 2008). When limited by data, conservation initiatives have relied on classification and demarcation of ecosystems into ecoregions via reoccurring patterns and processes in the landscape (Lindenmayer et al. 2008). These principally reflect the Earth's macroclimate and interactions with elevation, latitude, and continental arrangement (Bailey 2009). Ecoregions can be hierarchically classified, nested into domains, divisions, and provinces (Bailey & Ropes 1998). At regional scales, vegetation and other forms of natural land cover are typically used for classification. Their utility lies in their value in setting conservation priorities, as comparable ecosystems are assumed to incorporate similar biological and environmental processes and therefore respond similarly to management (Bryce et al. 1999). The relative ease in ascribing ecosystems to landscape patterns (Dinerstein et al. 1995) has led to rapid adoption of ecoregions for conservation prioritisation, particularly identification and gazettal of protected areas at various scales (Brooks et al. 2006; Olson & Dinerstein 2002; Olson et al. 2001). At a coarse scale, there are 200 global ecoregions (Olson & Dinerstein 2002), integrating biogeography, habitat, and elevation into landscape units, a particularly attractive and practical approach in data-poor regions (Faith et al. 2001; Jepson & Whittaker 2002). An implicit danger in using these coarse frameworks is the delineation of ecoregion boundaries: primarily derived from perennial patterns in vegetation distribution and geology, they may

not be primary drivers for all facets of biodiversity. This can be especially problematic for fauna (e.g. vertebrates and rare species) as they can occupy multiple vegetation types, resulting in representation bias and inadequacies (Altmoos & Henle 2007; Brooks *et al.* 2004; Lombard *et al.* 2003; Mac Nally *et al.* 2002). Quantitative approaches highlighting these disparities have so far been lacking despite recent advances in distribution modelling.

Australia adopted the Interim Biogeographic Regionalisation for Australia (IBRA) bioregions (Environment Australia 2004) in the 1990s, that were defined from broad, regional-scale natural features and environmental processes. These 85 bioregions were aimed at capturing large-scale geophysical patterns, primarily reflecting vegetation classification (Morgan & Terrey 1992; Thackway & Cresswell 1995). IBRA bioregions are used to assess the comprehensiveness, adequacy, and representation of the national system of protected areas (DEWA 2009; NRMMC 2010). In Australia, State and Territories identify, purchase, and manage protected areas and often obtain matching funding from the Australian government for purchase, after assessment of national priorities against IBRA bioregions. Driven by policy, systematic conservation planning algorithms are employed within the bioregional boundaries to prioritise new areas for protection. These incorporating all available abiotic and biotic data and threats at varying scales, provide sophisticated methods to identify changing priorities for conservation (Pressey, 2009; Pressey, 2002). Moreover, bioregions underpin natural resource management and planning within States and Territories in areas such as fire management, biodiversity monitoring, threatened species management, and control of feral and invasive species (Baker et al. 2005; DEWA 2009; NRMMC 2010). Such reliance on a bioregional framework for conservation management and planning requires critical assessment of effectiveness, including for mobile fauna such as mammals.

There is strong cause for re-examining the efficacy of ecoregions as global threatening processes (e.g. climate change and habitat loss) are increasing extinction rates of

many mammal species (Cardillo *et al.* 2006; Morrison *et al.* 2007). The global conservation status of mammals is poor and worsening; 25% of all mammal species are at risk of extinction and 52% of all known populations are in decline (Schipper *et al.* 2008). Australia's mammal extinction record (over the past 200 years) is the highest in the world (Baillie 1996): 57 species listed on the IUCN Red List (IUCN 2009). To avert this crisis, protected areas and reduction of threatening processes are vital to minimise extinction risk to mammals (Karanth *et al.* 2010). This risk varies with threatening processes across the landscape (McKenzie *et al.* 2007), requiring explicit spatial prioritisation for conservation within Australia (Fritz *et al.* 2009; McKenzie *et al.* 2007; Wilson *et al.* 2005). Such prioritisation should ideally be driven by comprehensive information of mammal distributions.

To this end, we tested the efficacy of the Australian bioregional framework as a spatial framework for conservation prioritisation of fauna. Specifically, we examined whether the bioregional approach maximised representation of mammal species within New South Wales' (NSW) protected areas. To do so we quantified the distributions of terrestrial mammal species and used these to identify reoccurring mammal assemblages that could describe broad variation in species' composition and functional guilds. We then contrasted the efficacy of the bioregional and the mammal driven approach at maximising representation of mammal species within protected areas. This enabled us to compare the different strategies for acquisition of protected areas and the merit of using more faunal information in identifying protected areas.

Methods

Species distribution data

We modelled the distributions of mammal species using presence data recorded across NSW, held within the NSW Atlas database, comprising about 76,000 point locations for 61 native terrestrial mammal species, from 14 families (DECCW 2009). To minimise spatial error, we excluded two categories of records: before 1990 and with a spatial uncertainty of greater than 500m. Records included data from multiple mammal surveys, collected until 2009 by government staff, researchers, naturalists, environmental consultants, land management officers, and the public. Survey method (including opportunistic sightings) was recorded for each point location. A shortcoming of such datasets is the lack of true absence records. To avoid presence-only modelling (Zaniewski et al. 2002), we generated pseudo-absences for each species, using location points for other terrestrial mammal species in the database. To do this, we examined which survey methods were used to detect each species and inferred an absence when those methods were employed but the species was not recorded. Our assumption was that failure to detect a species when a suitable method was employed was a plausible pseudo-absence. To minimise potential false pseudo-absences, we eliminated pseudo-absence points within the home-range of a recorded presence for each species. Homerange areas were obtained from the literature, conservatively using the largest value reported.

Species distribution modelling

We chose six environmental and climate variables covering NSW (800,642km²) for each species, based on their ecology and available data, at a spatial resolution of 250m. With predictor multicollinearity in mind, we attempted to minimise correlation among environmental variables covering NSW (Heikkinen *et al.* 2006). Variables selected included: (1) elevation from a Digital Elevation Model (DEM); (2) average Enhanced Vegetation Index (EVI), calculated for a ten-year period (2000-2009) derived from satellite data obtained from the Terra Moderate Resolution Imaging Spectro-radiometer (MODIS) sensor (Justice *et al.* 1998); (3) annual mean temperature; (4) annual precipitation; (5) annual mean moisture index, all three derived from the correlative modelling tool BIOCLIM 5.1 (Busby 1991); and (6) distance to the nearest water body (floodplains, lakes, reservoirs, lagoons, and main rivers), derived from a classification of spectral classes of Landsat, with ancillary wetland information (Kingsford *et al.* 2004). Lastly, the survey method used to capture the location information (e.g. spotlighting, pitfall trap etc.) for each record was included as a categorical variable. These variables have previously been shown to be associated with mammalian niche envelopes at regional scales (Boitani *et al.* 2008; Guisan & Thuiller 2005).

Advances in a multi-model inference have provided many methods for increasing predictive perfomance and reducing uncertainty in species distribution modelling, including model averaging, cross-validation, and regression regularisation methods (Hastie *et al.* 2009; Reineking & Schröder 2006). We employed Generalised Additive Models (GAMs) to predict distributions of species; these data-driven models deal with highly non-linear and non-monotonic relationships between response and explanatory variables, outperforming other statistical models (Meynard & Quinn 2007). Using GAMs (package _gam⁴,(R Development Core Team 2010)), we used a boot-strapping cross-validation model selection process for each species with all 63 unique combinations (obtained from the six identified predictor variables: 2ⁿ - 1). Each variable was smoothed using the built-in back-fitting algorithm. For each variable combination, we bootstrapped the data 100 times, randomly selecting 63.2% of the data (Hastie *et al.* 2009). The .632 estimator provides good overall model performance, combining low variance with only moderate bias compared to other cross-validation methods (Efron & Tibshirani 1997). We evaluated model performance by examining Akaike's Information Criterion (AIC), trading-off explained variation against model complexity, and

the area under the receiver operating characteristic curve (AUC). We selected the most parsimonious model from a trade-off between the fewest numbers of predictor variables and the lowest average AIC +2 (Burnham & Anderson 2002). Using the final model, probabilities of each species (0-1) were predicted across NSW, at a cell size of 250x250m ($0.0625km^2$). Model performance was good with the majority of AUC values above 0.85 [0.75-0.85 (n=3), 0.85-0.95 (n=30), and 0.95-1 (n=28)].

Identifying mammal assemblages

Using the predicted probabilities of each species within each cell, we employed a clustering procedure to identify statistically reoccurring assemblages of species. To do this, we used the unsupervised Iterative Self-Organizing Data Analysis Technique (ISODATA) (Tou & Gonzales 1974) and ERDAS IMAGINE 9.2 software (Leica Geosystems 2008). The ISODATA method uses a maximum-likelihood decision rule to decide on the number of clusters by calculating class means that are evenly distributed in the data space and then iteratively clustering the remaining pixels, using minimum-distance techniques. Class means are recalculated for every iteration and pixels reclassified with respect to the new means. We continued the process until the number of pixels in each class changes by less than a selected threshold of 5%. To improve the robustness of mammal assemblages in representing spatial variation in mammal distributions, we incorporated a measure of diversity across the range of each assemblage by calculating the sum of occurrence probabilities across all species, in each cell within each assemblage.

While assemblages are a quantitative expression of broad relationships among species, composition analysis can help identify the significant drivers underlying species responses to gradients of change. We determined variation in species composition, across mammal assemblages, using multidimensional scaling (MDS). First, we calculated the dissimilarity among assemblages using the Bray-Curtis index (Bray & Curtis 1957), based on

the average probability of occurrence of each species within each assemblage. Stress configurations were computed from 25 restarts. Two dimensional ordination bi-plots were produced to interpret results, providing an illustration of the species composition in the assemblages. We determined the contribution of each species to the observed differences among assemblages, using a Similarity Percentages analysis (SIMPER). The SIMPER calculates the average Bray-Curtis dissimilarity between all pairs of species found within two compared mammal assemblages. SIMPER was carried out over all paired assemblage comparisons (55) and dissimilarity scores of each species averaged, identifying the main species typifying each mammal assemblage (Supplementary Appendix).

Species diversity may not adequately capture the importance of mammalian presence in the landscape. At an ecoregional scale, conservation priorities, aimed solely at biodiversity may not necessarily conserve optimal levels of the ecosystem services (Naidoo *et al.* 2008). Functional diversity, rather than species diversity, is strongly coupled with ecosystem functioning (Diaz & Cabido 2001). To investigate functional diversity within each assemblage we categorised mammal species into non-mutually exclusive functional feeding guilds: carnivore (prey size > 5g), insectivore (prey size < 5g), folivore, frugivore, graminivore, granivore, nectarivore/palynivore, or fungivore (Jackson 2003; Menkhorst & Knight 2004; Strahan *et al.* 1983). We summed the species probabilities within each feeding guilds across each cell and then within each assemblage. Proportions of feeding guilds within each assemblage were derived by summing species occurrences weighted against their probability of occurrence. We tested for differences among feeding guilds using the independent sample Kruskal-Wallis test.

Critical to effective conservation planning is incorporating threatening processes and relative vulnerability of conservation features (Wilson *et al.* 2005). As the extinction risk of mammals is spatially explicit (McKenzie *et al.* 2007), a key objective of our study was to

determine the vulnerability of mammalian assemblages to extinction. We did this by investigating the composition of species within the critical weight range (CWR) in each assemblage. Many declines and recent extinctions in Australian mammals are associated with a CWR of 35 to 5,500g (Burbidge & McKenzie 1989; Fritz *et al.* 2009). However, this convention has been unclear where evidence suggests extinction risk may not hold a general correlation to body mass (Cardillo & Bromham 2001; Fisher *et al.* 2003). More recent work has shown extinction risk differs between ground-living and arboreal species, as well as for species from low versus high rainfall areas (Johnson & Isaac 2009). In practice, species within the CWR range are more likely assigned to a high-priority conservation group. To complement the presence of CWR species in each of the identified 11 assemblages, we adjusted their proportional contribution by accounting for their relative abundance within each assemblage. We did this by weighting each species by its overall abundance within each assemblage (calculated as the sum of predicted probabilities).

Bioregions and mammal assemblages

We initially quantified the relative accumulated bias in mammal assemblage representation when land prioritisation was solely derived using the bioregional framework while disregarding any knowledge relating to fine-scale distribution of biodiversity. To do this, we quantified the spatial alignment of mammalian assemblages in NSW, relative to the existing bioregional framework. We then selected land parcels of equal sizes (250x250m) using calculated assemblage diversity, representing a new protected area network, equal to federal 10% target of representation of the area of each bioregion. We bootstrapped this process 1,000 times and determined the mean cumulative representation rates of mammal assemblages within them.

Subsequently, we evaluated the species-specific consequences of prioritising land acquisition for protected areas driven by the bioregional framework versus a framework derived from the mammal assemblage. We employed the Marxan software, designed to provide solutions for site selection and reserve design by using a simulated annealing algorithm to select a set of planning units that captures biodiversity targets for a minimum of total cost (Watts et al. 2009). We divided NSW into 5x5km planning units and classified each according to bioregion and mammal assemblage. We tested two scenarios, one targeting 10% representation of each bioregion and another for mammal assemblage. This process was done while building upon the existing protected areas. We set a uniform cost across all planning units and identified an optimal boundary length modifier (0.001) and species penalty factor (10) (Game & Grantham 2008). We iterated each scenario 1,000 times and noted the planning units selected. We then quantified the representation of mammal species found within the selected planning units, based on predicted distributions. To compare the two frameworks, we calculated the rate in which representation of each species accumulated, as a function of number of planning units. We permutated each solution 1,000 times and calculated the rate (the slope of a linear regression) of accumulated representation of each species under each of the two frameworks. For each permutation, we calculated the ratio between of the two and averaged over all permutations:

ratio species_i =
$$\frac{\Delta \text{ representation using mammal regions}}{\Delta \text{ representation using bioregions}}$$

Results

Assemblage composition and structure

The predicted distributions of 61 native mammal species across NSW clustered into 11 reoccurring mammal assemblages (Fig. 1). Three large assemblages (A1-A3) dominated the western and arid parts of the state, while smaller and more intertwined assemblages were scattered across the eastern ranges and coastline of NSW (Table 1). Western assemblages covered much of NSW, with a total area of 517,914km², an order of magnitude larger than

other assemblages (Table 1). Smaller assemblages (A8-A11) were generally in the northeastern regions of NSW, averaging 16,226km² (\pm 3,244sd). NSW's coastline was dominated by one assemblage (A8), while the highlands exhibited a more latitudinal and longitudinal complex structure.

Species richness within assemblages varied along a longitudinal gradient, increasing from west to east (24 to 39 species, respectively) (Table 1). A more subtle variation was observed latitudinally, increasing from south to north (29 to 39 species, respectively). Two distinct groups were apparent (Fig. 2): three western assemblages (A1-A3) and loosely grouped eastern and coastal assemblages, including four more closely related assemblages (A7-A9 and A11). Average dissimilarity between assemblages ranged from 74% (A1, A6) to 14% (A7, A11), with an average dissimilarity of 43.2% (±17.7%sd). Dominant species in the three western assemblages included the western-grey kangaroo (*Macropus fuliginosus*), common dunnart (*Sminthopsis murina*), yellow-footed antechinus (*Antechinus flavipes*), and red kangaroo (*Macropus rufus*). Near the coast, the common wombat (*Vombatus ursinus*), platypus (*Ornithorhynchus anatinus*), yellow-bellied glider (*Petaurus australis*), and bush rat (*Rattus fuscipes*) were more prominent.

There were also variations in how assemblages represented feeding guilds ($\chi^2 = 73.3$. df=7, p<0.001), (Fig. 3). Insectivores dominated all assemblages, with an average proportion of 0.33 \pm 0.02sd, peaking in the mid-west (A3-A5). Folivores (0.13 \pm 0.04sd) and frugivores $(0.16 \pm 0.02 \text{ sd})$ were similarly prevalent, although folivore proportions sharply declined in the east. Carnivore proportions ranged between 0.09 and 0.17 (0.12 \pm 0.03sd), decreasing in the east. Proportions of graminivores (0.08)±0.02), fungivores (0.08) ± 0.02 sd), nectarivores/palynivores (0.05 \pm 0.02sd), and granivores (0.05 \pm 0.02sd) were lower than other feeding guilds and generally higher in eastern than western NSW (Fig. 3). Proportions of species within the CWR captured by the 11 assemblages varied greatly, ranging from 0.29

(A2) to 0.64 (A8, A10) (Table 1). Both total and adjusted proportions of species within the CWR in each assemblage reflected overall species richness, increasing from west to east.

Mammal representation

Large spatial discrepancies were observed between the bioregional framework and representation of mammal assemblages across NSW (Fig. 1, Table 2). The nature of inconsistencies varied between eastern and western NSW. The inadequacy of the bioregional framework resulted from redundancy in western NSW and over-simplification in eastern NSW. Across the western region, three bioregions (Channel Country, Mulga Lands, and Simpson Strzelecki Dunefields) represented only one mammal assemblage (A1) (Fig. 1, Table 2). Overall, the eight western bioregions of NSW represented only three mammal assemblages (Fig. 1). In contrast, the complex structure of mammal assemblages in north-eastern NSW produced several assemblages represented within only single bioregions (e.g., NSW north coast contained seven assemblages) (Fig. 1).

Using the bioregional framework for prioritising may represent some mammal assemblages better than others. By quantifying this, clear partiality emerged in the rate in which mammal assemblage were represented in protected areas (Table 1). For example, the accumulation of conserved area increased fastest for A1, a rate more than ten times greater than for A11. As expected, mammal assemblages represented by several bioregions (i.e., western assemblages: A1-A4) accumulated faster than assemblages in eastern NSW, represented by only a single bioregion. In terms of mammal assemblages, NSW's protected area varied from a low of 1,055km² (A3) to a high of 17,193km² (A7), with an average of 6,168km² (Table 1). The proportional representation of mammal assemblage in the protected area network varied from 0.8% to 36.1% (Table 1). Assemblage A3, stretching across NSW from the north-east to south-west, and associated with central NSW (Fig. 1), had the smallest proportion of protection (0.8%, 1,055km²). There was also low representation of A2 (3.4%,

south-west), A5 (4%, NSW South Western Slopes and South Eastern Highlands), and A1 (4.9%, north-west). Well-represented assemblages (i.e., >25%) included A6 (25.7%, Alpine regions and South Eastern Highlands), A7 (29.2%, South East Corner, Sydney Basin, and New England Tablelands), A9 (32.7%, northern parts of NSW north Coast), and A11 (36.1%, Brigalow Belt South and Nandewar).

When we compared the rate at which individual species were incorporated into the protected area network, the mammal assemblage framework outperformed the bioregional lead spatial prioritisation framework (Fig. 4). Overall, the rates at which mammals were incorporated into a protected area network were slightly higher ($5.1\% \pm 0.6\%$ se), when guided by mammal assemblages. Of the 61 species, 38 were better represented when using mammal assemblages (maximum increased rate of representation was 134%). The remaining 23 species were marginally more efficiently incorporated into the protected area network under the bioregional framework, improving from 0.29% to 7.7%.

Discussion

Using a systematic approach, we found large differences in the efficacy in accumulated representation of mammals in protected areas between the two approaches: the bioregional framework and the mammal assemblage approach (Fig. 4). Disparities were attributed to aggregation of spatially-contiguous regions of mammal assemblages across north-western compared to eastern NSW, creating redundancy in the bioregional framework in the west and inadequate representation in the east (Fig. 1). This misalignment may affect the conservation of mammal species by introducing representation deficiencies and inefficient allocation of funds and effort (Table 1). For instance, northern NSW is recognised for its high diversity of fauna and flora, as well as high levels of endemism (DECCW 2010). It is one of Australia's most diverse regions containing significant areas of rainforest vegetation, with high diversity of frog, reptile, snake, marsupial, and bird species. We identified the same pattern of mammalian biodiversity with relatively small distinct assemblages with high diversity (Table 1). Notably, there was high assemblage turnover (A6-A11), occurring across relatively small spatial scales and indicative of high local endemism (Fig. 2). As a consequence, conservation initiatives dependent on bioregions for the prioritisation and gazettal of land may prove inefficient in adequately protecting mammal species in Australia.

We showed here that a mammal driven framework could overcome this, potentially creating significant improvements in representation of mammal species (Fig. 4). Given Australia's notorious distinction of the worst mammal extinction record of any country (IUCN 2009; Johnson 2006), incorporating such approaches alongside existing frameworks should be a priority. This also raises a more general question relating to the adequacy of the bioregional framework as a spatial prioritisation framework used for assessing the comprehensiveness, adequacy, and representation of protected areas (NRMMC 2010).

Ideally, protected area networks should adequately represent all biodiversity, allowing for long term viability (CBD COP10 2010). We found that only four of the 11 mammal assemblages were adequately represented above recently established targets of 17% (CBD COP10 2010) (Table 1). Results suggest that achieving target representation of bioregions may not adequately represent mammal species. There is clearly a need to review the existing bioregional approach and its efficacy to the gazettal of protected areas, certainly for NSW, and possibly other parts of Australia, for mammals and potentially other biota.

Ideally, prioritisation should strive to move beyond generalisation and simplification and attempt to integrate the complex patterns of biodiversity. Where data are available, attempts are made to utilise all biodiversity data for prioritisation of reserves (Pressey et al. 2009), rather than simple frameworks based on vegetation or other biophysical patterns. Prioritising areas for conservation is now a more quantitative and systematic process, aimed at capturing the biogeographic patterns of biodiversity (Brooks et al. 2006; Pressey et al. 2009; Wilson et al. 2009). Systematic approaches for reserve acquisition have the capacity to minimise representation gaps created through past opportunistic selection and more recent methods driven by vegetation patterns which can be deficient when it comes to accounting for fauna (Margules and Sarkar 2007; Pressey and Bottrill 2008). However, bioregional frameworks continue to operate in policy and management (Morgan & Terrey 1992; NRMMC 2010; Thackway & Cresswell 1995), leading to underrepresentation of certain elements of biodiversity. When systematically prioritising for conservation using fine-scale information relating to mammal distributions, a framework based on mammal assemblages amassed representation of species faster compared to the bioregional framework (Fig. 4). Bioregions defined by dominant vegetation features could be effective for securing representation for the majority of species, but can omit others (Lombard et al. 2003). More so, their efficacy in representing all vegetation species remains to be tested and a similar analysis to ours for mammals may highlight effectiveness at the floristic assemblage level. Efforts should be made to adapt current bioregional approaches with additional taxonomic groups (i.e., mammals, amphibians, reptiles, birds, and flowering plants) to formulate a more comprehensive conservation framework. If alternative prioritisation approaches target different sets of species and areas (Funk & Fa 2010), complementing rather than competing frameworks could minimise wasted conservation efforts (Mace *et al.* 2000). Defined protocols for integrating data sets should be established, facilitating a clear process for boundary modification (WWF 2002). Ultimately, complementary conservation approaches that encompass species-specific and multi-species requirements along with whole ecosystems integrity are desired (Lindenmayer *et al.* 2008). Coordinating assessments and identifying clear criteria are vital for establishing robust units of conservation.

Importantly, continued biotic and climatic change will require managers and stakeholders to adapt existing prioritisation frameworks to maximise effectiveness. Under projected climate change, species distributions are expected to shift according to newly created favourable and hostile conditions (Araújo *et al.* 2006; Root *et al.* 2003). Altough range shifts have occurred for both flora and fauna, mobility and dispersal constraints have translated to considerable differences in the spatial magnitude of shifts (Kelly & Goulden 2008; McCarty 2001). Lack of parity in response to changing conditions and threats can increase misalignemnt between existing employed surrogate approaches and those dependent on species representation. Based on projected predictions and recent evidence of faunal shifts in response to climate change, a static bioregional approach for prioritising future conservation efforts may fail. Potential solutions may rise by integrating changing habitat suitability with landscape and population dynamics, alowing for the combined impacts of climate change on species to be predicted (Franklin 2010).

Effective conservation planning should strive to incorporate threatening processes and relative vulnerability of conservation features (Wilson *et al.* 2005). The Critical Weight Range (CWR) provides one example of an indirect measure of spatio-temporal patterns of both threat and environmental conditions for mammals (Brook *et al.* 2008; Davidson *et al.* 2009; Fisher *et al.* 2003; Johnson 2006; Johnson *et al.* 2002). We showed that the proportion of assemblages within the CWR represented in the protected area network, varied greatly among assemblages (Table 1). Low representation of mammal assemblages associated with higher proportions of species within the CWR (A3, A5, and A10) suggests protected areas may not adequately represent vulnerable species and mitigate extinction risk for these species. More so, prioritising mammal threat mitigation stratified according to bioregions (Dickman *et al.* 2010; McKenzie *et al.* 2007) may result in spatially inefficient action. Tailoring both land prioritisation and management efforts towards distinctive mammal assemblages, prioritised for their vulnerability, may significantly improve mammal conservation outcomes.

Guided by bioregions, a spatial framework of conservation prioritisation, systematic conservation planning of protected areas may be constrained in realising its full potential in securing representation for all of Australia's biodiversity. Prioritisation frameworks should have the capacity to adapt their boundaries by incorporating amassed information from a broad range of taxa. Unfortunately, such frameworks may become well established, making improved approaches difficult to implement. We showed that there are significant implications for mammal conservation in NSW and that future prioritisation of conservation efforts for Australia's mammals can be improved. Continued efforts to adapt the current bioregional approach with approaches using additional taxonomic groups (i.e., mammals, amphibians, reptiles, and birds) in the pursuit of a comprehensive conservation framework should be made a high priority.

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Figures

Figure 1: Eleven mammal assemblages (A1-A11), formed from 61 habitat suitability maps generated for native terrestrial mammal species in NSW and its 18 bioregions, separated by grey lines: AA - Australian Alps, BBS - Brigalow Belt South, BHC - Broken Hill Complex, CHC - Channel Country, CP - Cobar Peneplain, DRP - Darling Riverine Plains, ML - Mulga Lands, MDD - Murray Darling Depression, NAN - Nandewar, NET - New England Tablelands, NNC - NSW North Coast, NSS - NSW South Western Slopes, RIV - Riverina, SSD - Simpson Strzelecki Dunefields, SEC - South East Corner, SEH - South Eastern Highlands, SEQ - South Eastern Queensland, SB - Sydney Basin.

Figure 2: Multidimensional scaling (MDS) showing variation and relationships in species composition among the 11 mammal assemblages, across NSW.

Figure 3: Proportions of feeding guilds within each mammal assemblage. Species occurrence within each assemblage was weighted against its probability of occurrence. Feeding habits were

grouped into eight categories: carnivores (prey size > 5g), insectivores (prey size < 5g), folivores, frugivores, graminivores, granivores, nectarivores palynivores, and fungivores.

Figure 4: Rates of accumulated representation of each species, over selected Planning Units (PUs), were measured when using a systematic process building upon the existing protected areas and guided by fine-scale predictions of mammal distributions. The ratio of rates (precent increase\decrease) was calculated when prioritising mammal assemblages over bioregions, for each of the 61 mammal species.

Figure 1



Figure 2


Chapter 3

Figure 3



Figure 4



Tables

Table 1

Details of identified 11 mammal assemblages: (1) number of species and total area; (2) representation within NSW's protected areas (number of protected areas (*n*), total area (proportion), and proportion of the assemblage's diversity¹); (3) number of mammals in the Critical Weight Range (CWR) and their relative proportions²; and (4) relative rates of accumulated representation (RRAR) when prioritising using the bioregional framework³.

As							
semt	Species	Total Area	п	Area (km ²)	Diversity	CWR	RRAR
olage	<i>(n)</i>	(Km ²)			(%)	#(p/ap)	
A1	25	159,134	14	7,876 (4.9%)	4.9	8 (0.32/0.11)	1
A2	24	223,466	40	7,664 (3.4%)	3.4	7 (0.29/0.15)	0.74
A3	27	135,314	51	1,055 (0.8%)	0.7	10 (0.37/0.16)	0.43
A4	30	75,744	126	7,516 (9.9%)	10	16 (0.53/0.18)	0.50
A5	33	51,437	72	2,072 (4%)	3.8	18 (0.55/0.23)	0.19
A6	29	34,041	95	8,746 (25.7%)	26.5	17 (0.59/0.26)	0.42
A7	32	58,904	156	17,193 (29.2%)	30.1	18 (0.56/0.25)	0.56
A8	39	18,668	194	3,795 (20.3%)	20	25 (0.64/0.28)	0.15
A9	38	18,945	147	6,190 (32.7%)	32.1	24 (0.63/0.36)	0.14
A10	39	15,209	72	1,381 (9.1%)	9.1	25 (0.64/0.35)	0.19
A11	38	12,081	64	4,357 (36.1%)	35.8	23 (0.61/0.29)	0.09
Total				67,845	8.8		

¹Number of species within each assemblage are based on predicted core areas. ²Number of species within the Critical Weight Range (CRW) of 35g to 5,500g are presented along with their corresponding proportions (p) and adjusted proportions (ap) when considering species probabilities of occurrence. ³The relative rates of accumulated representation (RRAR) of each mammal assemblage when land prioritisation is driven by the bioregional framework.

Table 2

Relative area [%] of each of 11 mammal assemblages within each of NSW's 18 Bioregions¹ (left) along with the relative area [%] of each bioregion within each of the mammal assemblages (right).

					Mammal as	ssemblage					
Bioregion	A1	A2	A3	A4	A5	A6	A7	A8	A9	A10	A11
AA	0/0	0/0	0/0	0/0	0/0.2	14.1/96	0.3/3.8	0/0	0/0	0/0	0/0
BBS	0.9/2.4	2/7.8	13.5/32.3	40/53.8	0/0	0.3/0.2	3.3/3.4	0/0	0/0	0/0	0/0
BHC	18/75.4	4.2/24.6	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0
CC	14.7/100	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0
СР	2.1/4.5	25.4/76.9	10.1/18.6	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0
DRP	16.8/28.4	13.5/32.2	27.3/39.3	0.1/0.1	0/0	0/0	0/0	0/0	0/0	0/0	0/0
ML	40.4/97.8	0.6/2.2	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0
MDD	0.5/1.1	34.8/98	0.6/1	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0
NAN	0/0	0/0.1	0.1/0.6	23.5/86	0/0	0.1/0.1	4.7/13.2	0/0	0/0	0/0	0/0
NET	0/0	0/0	0/0	6.7/17.7	0/0	10.1/12.1	26.3/54.2	0/0	6.3/4.2	0/0	28.3/11.9
NNC	0/0	0/0	0/0	2/3.7	0/0	1.5/1.2	7.4/10.9	41.2/19.3	76.2/36.2	27.6/10.5	60.3/18.2
NSS	0/0	0/0.1	28.6/47.3	13.5/12.5	62.1/39	0.3/0.1	1.4/1	0/0	0/0	0/0	0/0
RIV	0/0	19.5/61.9	19.8/38.1	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0
SSD	6.7/100	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0

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SEC	0/0	0/0	0/0	0.1/0.9	0.4/1.8	3.5/10.3	16.3/82.8	2.6/4.1	0/0.1	0/0	0/0
SEH	0/0	0/0	0/0	0.9/1.3	36.6/38.3	67.6/46.8	11.2/13.5	0/0	0/0	0/0	0/0
SEQ	0/0	0/0	0/0	0/0.1	0/0	0/0	0/0.1	11.3/12.6	13.5/15.4	72.4/66.3	7.4/5.4
SB	0/0	0/0	0/0	13.1/26.1	0.8/1.1	2.5/2.3	29.1/45.2	44.9/22.1	3.9/2	0/0	4.1/1.3

¹Bioregion abbreviations are provided in caption of Fig. 1.

Appendix S1

Similarity Percentages (SIMPER) analysis was carried out over all paired assemblage comparisons (55) and dissimilarity scores of each species averaged, identifying the main species typifying each mammal assemblage. Species with an average contribution to dissimilarity score larger than 5% are presented.

Common name	Scientific name	Average dissimilarity		
		\pm SE		
Narrow nosed planigale	Planigale tenuirostris	9.92 ± 0.74		
Dusky antechinus	Antechinus swainsonii	9.52 ±0		
Yellow-footed antechinus	Antechinus flavipes	9.28 ±0.46		
Platypus	Ornithorhynchus anatinus	9.26 ±0.3		
Koala	Phascolarctos cinereus	9.05 ±0.54		
Common wombat	Vombatus ursinus	9 ± 0.46		
Bush rat	Rattus fuscipes	8.09 ± 0.3		
Sugar glider	Petaurus breviceps	7.99 ± 1.14		
Brown antechinus	Antechinus stuartii	7.98 ± 0.5		
Stripe-faced dunnart	Sminthopsis macroura	7.9 ± 1.97		
Greater glider	Petauroides volans	7.63 ±0.48		

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Common dunnart	Sminthopsis murina	7.6 ±1.1
Short-eared possum	Trichosurus caninus	7.36 ± 0.67
Black-striped wallaby	Macropus dorsalis	7.3 ± 0.7
Swamp wallaby	Wallabia bicolor	7.04 ± 0.57
Agile antechinus	Antechinus agilis	7.01 ± 0.47
Common brush tail possum	Trichosurus vulpecula	$6.97\pm\!\!0.28$
Yellow-bellied glider	Petaurus australis	6.93 ± 0.83
Red kangaroo	Macropus rufus	6.8 ± 0.3
Spotted-tailed quoll	Dasyurus maculatus	6.67 ± 0
Common planigale	Planigale maculata	6.46 ±0.21
Red-necked pademelon	Thylogale thetis	6.38 ± 0.41
Fat-tailed dunnart	Sminthopsis crassicaudata	6.3 ±0.45
Common ringtail possum	Pseudocheirus peregrinus	6.25 ±0
Eastern grey kangaroo	Macropus giganteus	5.95 ± 0.35
Squirrel glider	Petaurus norfolcensis	5.81 ±0.25

Chapter 4: Are protected areas adequate for conserving climate

refugia for fauna?

G. Bino, D. Ramp, & R. T. Kingsford

Conservation Biology (under review)

Are protected areas adequate for conserving climate refugia for fauna?

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Key-words: climate change, climate refugia, mammal assemblages, habitat suitability models, protected areas, Marxan.

Word count - 7,227

Are protected areas adequate for conserving climate refugia for fauna?

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Abstract

Predicting effects of climate change on biodiversity is essential for mitigation. Protected areas provide an option but most research has focused on their adequacy in relation to predicted range shifts of single species. There remains considerable uncertainty and limited real-world application in such a focus. Conversely, identifying and protecting areas of climate stability, or refugia, may significantly improve conservation. Such areas are more likely to maintain assemblage structural stability, with persistence of biodiversity and ecosystem function and process. We tested the adequacy of protected areas in conserving existing mammalian terrestrial assemblages under climate change across a large area of Australia. By quantifying assemblage climatic envelopes, we identified areas of potential compositional instability, allowing us to prioritise land acquisition scenarios for climate refugia. Of 11 mammal assemblages, six were currently poorly represented (<10% of total range). Achieving 10% representation required expanding existing protected area network by 122%. Under effects of climate change, considerable reductions in representation of stable assemblages within protected areas by 2050 were predicted. Maintaining adequate mammal representation of 10% under changed conditions required expanding protected areas by 158%. Identifying areas likely to maintain long-term assemblage stability and resilience offers great benefit for conservation planning worldwide and has much to offer over single species assessments. Increased likelihood of long-term representation could be achieved by systematically prioritising land for addition to existing protected areas based on climate refugia for faunal assemblages. This approach has broad application, informing future investments by accounting for both diversity and assemblage resilience simultaneously aimed at maintaining ecosystem function.

Chapter 4

Introduction

Around the world, rapid climate change is changing ranges of many species (Hughes 2000; Kullman 2002; McCarty 2001; Walther et al. 2002), with further range shifts expected (Araújo et al. 2006). Climate change is reorganising species' distributions (Kelly & Goulden 2008; Root et al. 2003), affecting community structure and function (Fox 2007) and driving many to extinction (Malcolm et al. 2006; Parmesan 2006; Thomas et al. 2004). These shifts are primarily driven by species-specific physiological thresholds of temperature and precipitation (Hoffmann & Parsons 1997; Kearney & Porter 2009; Williams et al. 2008), mediated by life history traits, and evolutionary potential. For example, species from cold climates experienced extensive range expansions during glacials and contracted back to cold climate refugia during interglacial periods (Mosblech et al. 2011; Provan & Bennett 2008). Given the severity of current and future climate change on global biodiversity, robust conservation strategies are needed (Dawson *et al.* 2011). Protected areas networks are the cornerstone of climate change conservation efforts for safeguarding biodiversity in situ (Araújo et al. 2011). As distributions of many species change (Bennett & Provan 2008), existing configurations of protected areas will substantially falter in biodiversity representation (Araujo et al. 2004; Hannah et al. 2005), with 6-22% of species failing to meet representation targets in some parts of the world (Hannah et al. 2007). Conservation efforts must ensure maintaining resilience of biodiversity under accelerated human-mediated climate change.

Quantifying biotic impacts to predicted climate change has become a key focus for conservation planning (Bellard *et al.* 2012; McMahon *et al.* 2011). These provide a basis for mitigating the effects of climate change (Pereira *et al.* 2010). A common approach is to model species' distributions under future climate change (Thuiller *et al.* 2005a), allowing for estimating

of predicted range shifts and extinction risks (Thomas *et al.* 2004; Thuiller *et al.* 2005b). These can then be overlayed onto protected network distributions to assess vulnerability and priorities for new protected areas (Araujo *et al.* 2004; Hannah 2008). There are considerable uncertainties and limitations for real-world application (Sinclair *et al.* 2010). For example, species may not be able to immigrate to newly formed suitable habitats (Hoegh-Guldberg *et al.* 2008). Additionally, such single species analysis does not adequately incorporate interactions among species which are a fundamental driver of community structure (Davis *et al.* 1998a; Davis *et al.* 1998b), affected by climate change (Gonzalez-Megias *et al.* 2008; Hughes 2000; Walther *et al.* 2002). A single species focus is particularly problematic for assessing consequences of climate change on communities (Araújo & Luoto 2007; Tylianakis *et al.* 2008). With few resources, conservation planning should prioritise strategies that are most likely to be successful for biodiversity conservation.

One solution is to consider how whole assemblages as a cohesive unit rather than single species behave under predicted future conditions (Ferrier & Guisan 2006; Gilman *et al.* 2010), allowing for the measurement of patterns of species' richness and turnover. Such an approach has considerable value for conservation planning, aimed at representation of multiple species and functions that persist. Adequacy hinges on how well protected areas represent assemblages of species under existing and predicted climatic conditions. Under predicted climate change, some areas across an assemblage's distribution will likely remain stable (climate refugia), while others will change (Keppel *et al.* 2011; Mosblech *et al.* 2011; Shoo *et al.* 2011). Assemblages maybe be replaced or new assemblages develop. In climate refugia, assemblage composition should remain stable and intact because climatic conditions remain within tolerated ranges (Mosblech *et al.* 2011). Importantly, incorporating climate refugia within protected area networks may also

provide sufficient time for species to adapt to newly developed climatic and environmental conditions (Bradshaw and Holzapfel 2006; Mosblech et al. 2011). Identifying climate refugia may have significant implications for ensuring long-term persistence of biodiversity worldwide, and prioritising gazettal of new protected areas.

We investigated the utility of including climate refugia in assessments of protected area adequacy for a large region covering about 10% of Australia, to inform future investments in protected areas. We focused four objectives for terrestrial mammal species across New South Wales (NSW): (a) to quantify mammal co-occurrence patterns and identify regional mammal assemblages from predicted distributions of 61 terrestrial mammal species; (b) to evaluate the adequacy of the existing protected area network to represent the identified mammal assemblages; (c) to identify where mammal assemblage composition changes (unstable) and remains intact (stable) or climate refugia, based on climate change projections, within the current protected area network; and (d) to prioritise protected area acquisition scenarios aimed at ensuring adequate representation (10%) of terrestrial mammals with climate change (CBD COP8 2006).

Materials and Methods

Mammal assemblages as a conservation framework

Large identifiable landscape units, are used to prioritise global and continental conservation efforts, ascribing ecosystems to landscape patterns (Dinerstein *et al.* 1995) and leading to rapid adoption of ecoregions for conservation prioritisation (Brooks *et al.* 2006; Olson & Dinerstein 2002; Olson *et al.* 2001). We have identified 11 mammal assemblages across NSW using species' distribution models, based on Atlas data (Bino *et al.* 2012). Data comprised about 76,000 occurrence records, which were used to produce modelled distributions of 61 native terrestrial mammal species. Using the predicted probabilities of each species within each cell, clustering identified 11 statistically reoccurring assemblages of species (Fig. 1, Appendix 1).

We then used multivariate ordination, Detrended Correspondence Analysis (DCA) (Hill & Gauch 1980), to explore variation among terrestrial mammal assemblages, across the landscape. The response variables were average probabilities of species in each cluster. DCA scores were calculated within the R statistical environment (R Development Core Team 2010) and _vegan' R package (Bradshaw & Holzapfel 2006). Key environmental variables correlated to changes among species' assemblages were identified by correlating the two DCA axes with average monthly precipitation, average monthly maximum temperatures, elevation, and mean EVI.

Climate change

To estimate effects of climate change on assemblage composition, we defined the realised climatic envelope for each mammal assemblage. We used average monthly precipitation (mm) (<u>Rain</u>) and average monthly maximum temperatures (°C) (<u>Tmax</u>); these provide an adequate

summary of bioclimatic relationships at regional scales (Humphries *et al.* 2004). Data for climatic variables were obtained for _current' (1950-2000) and _future' conditions (2050), at a resolution of about one kilometre (30 arc-seconds), from the Worldclim website (Hijmans *et al.* 2005). Future projections were based on the A2A storyline from the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC) (IPCC 2007), using the Commonwealth Scientific and Industrial Research Organisation (CSIRO) global climate models (Gordon & O'Farrell 1997). The A2A scenario, representing a world of independently operating economic oriented nations and continuous population growth, was chosen over the more ecologically friendly B2a storyline as current emission trends are more aligned with the higher emission scenarios developed by the IPCC (Garnaut *et al.* 2008).

We quantified the current climatic envelope for each mammal assemblage by calculating the mean and variance of _Rain' and _Timax' across all cells within each assemblage's range. To identify potential stable areas or climate refugia, we examined projected climatic conditions of _Rain' and _Timax' in each cell. If conditions remained within the assemblage's climatic envelope (5th - 95th percentile), we defined cells as stable (i.e., climate refugia), assuming assemblage composition would persist. Outside an assemblage's climatic envelope, we defined cells as unstable.

Protected area network

We calculated each assemblage's representation within the existing protected area network across NSW (as of 2011), covering 8.45% of the total land area (67,845 km²). Additionally, we incorporated a measure of diversity within each assemblage by quantifying diversity as the sum

of species' predicted occurrence probabilities across all species for each cell and across NSW:

$$SumP_x = \sum_{k=1}^{61} p_{kx}$$
, where k - species, and p_{kx} - predicted probability of species k in cell x.

Prioritisation

We quantified the optimal configuration of land units to achieve 10% representation of mammal assemblages within protected areas. Four scenarios were compared: (a) current climate built on the existing protected area network; (b) current climate starting without existing protected areas; (c) A2A 2050 climate built on the existing protected area network; and (d) A2A 2050 climate without the existing protected areas. We used Marxan (Ball et al. 2009) to run simulations of each scenario. Designed to provide solutions for site selection and reserve design. Marxan uses a simulated annealing algorithm to select a set of planning units that captures a set of biodiversity targets for a minimum of total cost (Ball et al. 2009). To reduce computational requirements, we divided NSW into 5km by 5km planning units (PUs) and summed mammal diversity for each assemblage. We set a uniform cost across all PUs and set representation at 10% for each mammal assemblage. An optimal Boundary Length Modifier (BLM) was selected by running a range of BLMs and identifying the point where boundary length substantially decreased but where total area did not further increase (BLM=0.001) (Ball & Possingham 2000). Similarly, a Species Penalty Factor (SPF) was selected (assemblages replaced species) by considering a range of SPFs and identifying the point where target missing values' substantially decreased but where total cost did not further increase (SPF=10). SPF values must be chosen so that penalties for missing conservation targets are scaled appropriately and relative to each other; too high restricts Marxan's performance, whereas too low can lead to targets not being achieved as often (Ardron et al. 2010). We used NSW's land-use dataset (OEH 2011) to mask out PUs in areas of high urbanisation, intensive farming, and/or cropping. For A2A scenarios (c and d), diversity was calculated after removal of areas where assemblages were unstable. Each of the four scenarios were simulated 100 times to identify areas of repeated selectivity across all solutions, a measure of irreplaceability (Segan *et al.* 2010). Irreplaceability of PUs over the simulations was categorised from selection frequencies as either very low (0-20%), low (21-40%), moderate (41-60%), high (61-80%), or very high (81-100%). Additionally, we examined the average number of PUs required under each scenario to achieve target representation over the 100 possible solutions.

Results

Mammal Clustering

Mammal richness within each assemblage ranged from 24 in the northwest (MA2) to 39 in the northeast and coastal regions (MA8 and MA10), (Fig. 1). Richness was significantly correlated with the average monthly precipitation within each assemblage (r=0.93, F=61.6, df=10, p<0.001) but not with average maximum temperature (F=0.57, df=10, p=0.47). Average monthly precipitation for assemblage regions ranged from 24mm (MA1) to 114 mm (MA9) (72.6mm \pm 31s.d.), while average maximum temperatures ranged from 16.4°C (MA6) to 26.8°C (MA1) (22.4°C \pm 2.9s.d.). Assemblages in arid landscapes (MA1 to MA3, high maximum temperatures and low precipitation) extended across a unique suite of climatic conditions, with little overlap with climatically-adjacent assemblages (Fig. 2). Along the coast, assemblages with increased levels of average monthly precipitation (>60mm) had more overlapping climatic conditions with other assemblages. Unlike arid assemblage regions, assemblage regions with high precipitation (MA9 and MA10) had large climatic envelopes with wide ranges in precipitation and maximum temperatures (Fig. 2). Assemblage regions (Fig. 1), had the largest climatic

envelope, whereas assemblage MA1, in extreme arid areas, had the smallest climatic envelope (Fig. 2).

Eigenvalues of the first two axes of the DCA ordination were 0.43 and 0.09, explaining 68% and 14% of total variance, respectively (Fig. 3). Correlation coefficients for the first two axes revealed that average monthly precipitation and Enhanced Vegetation Index (EVI) were the strongest predictors of Axis 1 (r=-0.97 and -0.98, respectively) (Fig. 3). Average maximum temperatures and elevation were significant predictors of Axis 2 (r=0.84 and -0.89, respectively). The total span of DCA units along Axis 1 (from MA1 to MA9) was 2.9 (Fig. 3), suggesting only partial turnover in species' composition between extremes (Table A1).

Representation

Assemblages varied in area by an order of magnitude: large assemblages (MA1 to MA3) were 135,313-223,465km², while small assemblages (MA8 to MA11) were 12,081-18,668km² (Table 1). The large assemblages dominated the western and more arid parts of the state (covering 65% of NSW), while small intertwined assemblages were more frequent along the eastern ranges and coastline of NSW (Fig. 1). Representation of the 11 mammal assemblages within the protected area network varied from around 1,000km² to 17,000km² (6,168km² ± 4,582s.d.) (Table1). Several assemblages were poorly represented in area and diversity index (i.e., MA3: 0.8 and 0.7%, respectively, and MA2: 3.4 and 3.4%). These were mainly (exception, MA10: 9.1 and 9.1%) in mid-western NSW. Area and diversity index of assemblages were best represented in the northeast NSW (MA9: 32.7 and 32.1% and MA11: 36.1 and 35.8%). The number of protected areas in which each assemblage was represented was not indicative of its area of representation. For example, the three largest assemblages (MA1 to MA3) had the largest area of

representation within protected areas but a few protected areas (14, 40, and 51 respectively; see Table 1).

Climate change

Under the A2A climate scenario, extensive shifts in the climatic across all existing mammal assemblages were predicted (Fig. 2), largely driven by increases in temperature rather than changes in precipitation. Climate across the ranges of assemblages MA1, MA2, and MA10 shifted completely outside their existing climatic envelopes. For most mammal assemblages, climate was predicted to shift into the existing climatic envelopes of other mammal assemblages (MA2, MA6 to MA9, and MA11) (Fig. 2). For example, the current distribution of MA6 has a unique temperature and precipitation envelope but predicted climate change is predicted to overlap with existing climate envelopes of MA5 and MA7 by 2050. Accordingly, significant mixing of mammal species in large parts of NSW is expected to occur by 2050.

Under such 2050 projections, extensive development of unstable conditions for mammal assemblages were predicted across NSW (Fig. 4), predominantly due to rising average maximum temperatures shifting outside current climatic envelopes, especially across northern NSW (Fig. 2). Changes in average precipitation were predicted to lead to relatively small and scattered predictions of instability, while areas responding to changes in maximum temperatures and precipitation were predicted in isolated parts of northern NSW. As a result, total area representation of mammal assemblages within protected areas was predicted to decline by 29%. Reductions in representation varied considerably among assemblages (average reduction of $37.9\% \pm 33.7$ s.d.) (Table 1), including major reductions in area and diversity of assemblages in the northwest (MA1: reductions of 92.7 and 91.9% respectively) and northeast (MA10: reductions of 94 and 94.2% respectively). Representation of MA1 was predicted to decline from

14 to only three protected areas (Table 1) while total area representation of MA10 was predicted to decline by 94% of its current range (1,381km2 to 83km²). In total, 28.8% of currently protected areas and 26.3% of mammal diversity were predicted to be unstable by 2050 under the A2A climate scenario.

Prioritisation

The number and location of PUs for 10% representation of all mammal assemblages, under current conditions, was highly dependent on starting conditions (Fig. 5a-b). Given the existing protected area network, 14.5% of PUs in NSW were selected with _very high' irreplaceability, 36% currently not protected (Table 2). These new PUs mainly occurred along the east coast of NSW, contiguous with existing protected areas. Achieving 10% representation required an average $6,762 \pm 177$ s.d. PUs, more than double the existing protected area network (currently 3,049 PUs). In contrast, where selection was unconstrained by already protected PUs, considerable variation in solutions was reflected by low irreplaceability throughout NSW. However, the average number of PUs required for 10% representation was considerably lower than when constrained by the existing network (2,938 ± 44s.d.).

Under predicted climate change for 2050, 13.7% of PUs in NSW were selected with _very high ' irreplaceability starting from the existing protected area network: 32% of which are not currently protected (Table 2 & Fig. 5c-d). Unstable conditions across the range of assemblage MA1 resulted in areas of high irreplaceability in western NSW, while in eastern NSW, patterns of irreplaceability were similar to those under current climatic conditions. There was a 16% increase in the average number of PUs required to achieve 10% representation compared to those required under current conditions (7,861 \pm 224s.d.). Starting without existing protected areas, the selection of PUs was highly variable. There was the same pattern for western

NSW but several regions in eastern NSW were selected with _very high' irreplaceability, mainly due to the reduction in stable representation of assemblage MA10. Only slightly more PUs were required to achieve representation $(3,206 \pm 111s.d.)$ under this scenario, than under existing conditions.

Discussion

We tested the adequacy of protected areas in conserving a large number of terrestrial mammal species (61 species) across a large area of Australia (~10%). There was a significant underrepresentation (<10% of total range) of more than half the mammal assemblages within NSW (Table 1, 54%). Full representation would require doubling the protected area but could be achieved with an area comparable to the existing network, if begun without the historical base (Table 2). Under-representation was estimated to increase with predicted effects of climate change by 2050, potentially undermining species composition and function (Fig. 4). For some mammal assemblages, representation was predicted to decline by as much as 94% in the protected area network (Table 1). Maintaining adequate representation within the protected area network would require an addition of 122% to the existing protected areas (Fig. 5, Table 1). With projected climate change, an increase of 158% would be required to maintain established adequate representation of 10% (Table 2), (CBD COP8 2006), let alone the 17% targeted by Convention of Biological Diversity (2010).

Given the potential increasing inadequacy of protected area network in the face of climate change, building ecological resilience will be pivotal for ensuring adaptive capacity of biodiversity. This is further complicated by the spatially and temporal variability of impacts. A priority is to identify and protect biodiversity in areas least likely to undergo rapid climate induced changes (Groves *et al.* 2012) and then focus conservation around these climate refugia

(Ashcroft 2010; Keppel *et al.* 2011; Shoo *et al.* 2011; Taylor & Figgis 2007). Such a strategy is better than attempting to predict future shifts of species in response to climate change and capturing new areas in the protected area network (Araujo *et al.* 2004; Hannah 2008). Identifying and protecting refugia for biodiversity offers considerable promise for conservation planning worldwide, potentially reducing the impacts of uncertainties associated with climate change. There is also an added advantage of focussing on climate refugia: it avoids uncertainties and pitfalls relating to complex biotic interactions (Baselga & Araújo 2010; Callaway 2007), rates of dispersal and potential barriers (Hodgson *et al.* 2009). Many areas may become climatically suitable but species' isolation and limited dispersal capacity may hinder potential *ex-situ* colonisation (Honnay *et al.* 2002; Jump & Penuelas 2005; Opdam & Wascher 2004).

We identified climate refugia for mammal assemblages over a large region of Australia under future climate change (Table 2 and Fig. 5). These could form the basis for prioritising future areas for the protected areas network. This needs to be within a systematic planning approach, given limited resources and the need for optimal decisions for a range of conservation goals (Watson *et al.* 2011). We identified refugia which should be the focus of protected area acquisition. These were distributed across NSW's western ranges (Fig 5). Protecting these areas could significantly buffer future climatic impacts and improve prospects for effective biodiversity conservation, including providing sufficient time for adaptation to newly developed climatic and environmental conditions (Bradshaw & Holzapfel 2006; Mosblech *et al.* 2011). Systematic approaches which identify climate refugia will become increasingly important as future expenditure on protected areas diminishes, requiring more scrutiny and justification (Emerton *et al.* 2006; Pressey *et al.* 2007).

The concept of climate refugia is not limited to gazettal of protected areas but could also be the focus for management, particularly mitigation of threatening processes. Prioritising climate-change mitigation strategies should focus on the susceptibility of species to climate change, largely governed by the species' climatic niche (Altmoos & Henle 2007). Across our study area, mammal assemblages were predicted to be unevenly vulnerable to climate change, with some more vulnerable than others (Table 1, Fig 4). Assemblages with a narrow climatic tolerance, especially for temperature variation, were most at risk of compositional change, predicted to undergo large reductions in representation under climate change (Fig. 2). This was most notable for assemblages extending across the western and arid parts of NSW. This is well demonstrated for some organisms at the species level (Thomas et al. 2004), but few studies have extended this across a suite of species (Baselga & Araújo 2010; Gilman et al. 2010). We identified four vulnerable mammal assemblages: MA1, MA2, MA4, and MA10 (Fig. 1). For example, MA10 harboured the largest number of mammal species of the 11 assemblages (Appendix 1) and was already under-represented in the protected area network. It was projected to experience the largest reduction in representation of stable areas (>90%, Table 1). It covers an area strongly associated with dry sclerophyll forests and woodlands and has undergone extensive clearing, fragmentation, and invasion by exotic species (Sattler & Williams 1999). With increasing warming and drying under climate change, fire regimes are likely to intensify, increasing the susceptibility of these dry sclerophyll forests to ecological change (Bradstock 2010). Therefore resilience of MA10 could not only be improved by increasing the area protected but also by focusing resources on invasive species and fire management, similar to efforts in other parts of the world (Heller & Zavaleta 2009; Hellmann et al. 2008; Millar et al.

2007). Safeguarding refugia against changing condition along with monitoring should form a pivotal role for conservation management ensuring they continue to function for resilience.

Conclusions

A considerable opportunity exists to adapt our approach for any large region of the world, using available data. It requires modelling the distributions of multiple species, identifying reoccurring assemblages across the landscape, and applying a systematic prioritisation of land for conservation. Identifying the biogeographic patterns of mammal assemblages provides an intuitive and efficient approach for representing complex spatially-explicit information to stakeholders. Increasing availability of biodiversity and environmental data worldwide (Robertson et al. 2010) means similar approaches could be applied elsewhere, targeting a range of taxonomic groups. By adding other biotic groups, our approach could be more comprehensive for any given region. Such multispecies datasets would help test efficacy of representation of biodiversity in protected area networks. Assessment of climate refugia coupled with flexible and robust investment strategies for protected area acquisition can create a more efficient and robust protected area network (Fuller et al. 2010; Game et al. 2008). Continued data accumulation and the downscaling of climate data will increase identification certainty of micro-refugia and subsequently the robustness of prioritisation efforts (Ashcroft 2010; Maschinski et al. 2006). Protection of climate refugia may be vital for future effective conservation, maintaining ecosystem function and increasing the likelihood for the long-term persistence of biodiversity.

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Chapter 4

Figures

Figure 1: Eleven mammal assemblages (MA1-MA11) formed using the ISODATA algorithm from predicted distributions of 61 native terrestrial mammal species across NSW.

Figure 2: Ellipses representing the climatic conditions (temperature, precipitation) for the 11 mammal assemblages found across NSW, defined by the 5th - 95th percentile of average monthly precipitation and average maximum monthly temperatures for each assemblage. Solid ellipses represent current climatic conditions across the assemblage's extent, while dashed ellipses represent expected climatic conditions in 2050 based on the IPCC's A2A scenario (IPCC, 2007).

Figure 3: Detrended correspondence analysis (DCA) ordination diagrams of terrestrial mammal assemblages (MA1-MA11) across NSW along axis 1 & 2. Included are the Pearson correlations and probabilities between first two DCA axes with environmental attributes (average monthly precipitation - _Rain', average monthly maximum temperatures - _Tmax', Elevation, and Enhanced Vegetation Index - _EVI') within each mammal assemblage.

Figure 4: Effects of potential changes in climatic conditions in 2050 (A2A IPCC scenario) on the stability of 11 mammal assemblages across NSW. Areas with diagonal green lines represent existing protected areas. Coloured shades represent areas where climatic conditions are expected to destabilise composition of current mammal assemblages because of changes in average monthly precipitation (_Rain' - blue), average monthly maximum temperatures (_Tmax' - red), or both (_Rain + Tmax' - black).

Figure 5: Site selection across NSW targeting 10% representation of 11 mammal assemblages within a protected area network. Colour shading represents levels of irreplaceability identified by

the Marxan software for each of four scenarios: (a) current conditions building upon existing protected area network; (b) current conditions without existing network; (c) projected conditions for 2050 building upon existing network; and (d) projected conditions for 2050 without the existing network. Black polygons represent the existing protected area network.

Figure 1










Figure 4



Figure 5a-d



Tables

Table 1

Current and predicted (2050) representation measured as total area (km²), number of protected areas (PAs), and proportion of total

diversity (SumP) of the 11 mammal assemblages in NSW¹.

		(Current conditions		2050							
Assemblage	Total area (km ²)	Number PAs	Area (km ²)	SumP (%)	Number PAs	Area (km ²)	Δ Area (%)	Δ SumP (%)				
MA1	159,134	14	7,876 (4.9%)	4.9	3	577	-92.7	-91.9				
MA2	223,465	40	7,664 (3.4%)	3.4	25	5,701	-25.6	-24				
MA3	135,313	51	1,055 (0.8%)	0.7	23	313	-70.4	-66.2				
MA4	75,744	126	7,516 (9.9%)	10	63	3,984	-47	-44.9				
MA5	51,436	72	2,072 (4%)	3.8	59	1,420	-31.5	-32.4				
MA6	34,042	95	8,746 (25.7%)	26.5	72	8,432	-3.6	-3.2				
MA7	58,905	156	17,193 (29.2%)	30.1	112	15,252	-11.3	-11.5				
MA8	18,668	194	3,795 (20.3%)	20	130	2,810	-26	-25.3				
MA9	18,944	147	6,190 (32.7%)	32.1	110	5,725	-7.5	-7.8				
MA10	15,209	72	1,381 (9.1%)	9.1	20	83	-94	-94.2				
MA11	12,081	64	4,357 (36.1%)	35.8	49	4,021	-7.7	-8.1				
Total	802,941	794	67,845 (8.4%)	8.8		48,316	-28.8	-26.3				

¹ As several protected area represented multiple assemblages; the total number of protected areas was smaller than sum of protected areas representing each assemblage. Percentage representation relative to total assemblage area is given in parentheses.

Table 2

Planning units (PUs, 25 km²) classified according to their irreplaceability across 100 simulated solutions, selected by Marxan to achieve 10% representation of mammal assemblages across NSW. The number of PUs selected, proportion relative to total number of PUs (%PUs), and the proportion represented in protected areas (%PA) are presented for each of the four scenarios: current and projected for 2050, while building upon existing protected area network (Building upon) and starting without the existing protected area network (New).

Irreplaceability	Current						2050						
	Building upon			New			Bui	lding up	on	New			
	PUs	%PUs	%PA	PUs	%PUs	%PA	PUs	%PUs	%PA	PUs	%PUs	%PA	
Very low (0-20)	25149	76.9	0	32564	99.6	9.3	23250	71.1	0	27492	84.1	9.2	
Low (21-40)	1487	4.5	0	121	0.4	13.2	2569	7.9	0	4108	12.6	11.5	
Moderate (41-60)	681	2.1	0	0	0	0	1575	4.8	0	941	2.9	3.6	
High (61-80)	628	1.9	0	0	0	0	810	2.5	0	66	0.2	4.5	
Very high (81-100)	4740	14.5	64.3	0	0	0	4481	13.7	68.0	78	0.2	23.1	

Appendix

Appendix 1

Average probability of occurrence of 61 mammal species across each of 11 mammal assemblages.

Scientific name	Common name	A1	A2	A3	A4	A5	A6	A7	A8	A9	A10	A11
Antechinus agilis	Agile antechinus	0.1	0.3	0.5	0.1	0.7	0.4	0.1	-	-	-	-
Macropus dorsalis	Black-striped wallaby	-	-	-	-	-	-	-	0.1	0.2	0.4	0.2
Pseudomys bolami	Bolam's mouse	0.1	-	-	-	-	-	-	-	-	-	-
Mastacomys fuscus	Broad-toothed rat	-	-	-	-	0.2	0.2	-	-	-	-	-
Antechinus stuartii	Brown antechinus	-	-	0.1	0.1	0.9	0.9	0.8	0.7	0.8	0.7	0.7
Phascogale tapoatafa	Brush-tailed phascogale	-	-	-	-	-	-	-	0.3	0.3	0.8	0.1
Petrogale penicillata	Brush-tailed rock wallaby	-	-	-	0.1	0.1	0.1	0.2	-	-	-	0.4
Rattus fuscipes	Bush rat	-	-	-	0.1	0.7	0.8	0.8	0.9	1	0.9	0.8
Trichosurus vulpecula	Common brush-tail possum	0.3	0.7	0.7	0.7	0.8	0.5	0.4	0.2	-	0.2	0.3
Sminthopsis murina	Common dunnart	0.2	0.9	0.9	0.9	0.7	0.7	0.7	0.5	0.5	0.7	0.8
Planigale maculata	Common planigale	-	-	-	-	-	-	-	0.1	0.5	0.7	0.1
Pseudocheirus peregrinus	Common ring-tail possum	0.6	0.5	0.7	0.3	0.6	0.3	0.2	0.3	0.1	-	-
Macropus robustus	Common wallaroo	0.2	0.2	0.2	0.7	0.3	0.2	0.5	0.1	0.1	0.2	0.6
Vombatus ursinus	Common wombat	-	-	0.2	0.5	0.8	1	0.8	0.3	0.2	0.1	0.5
Antechinus swainsonii	Dusky antechinus	-	-	-	0.1	0.1	0.6	0.2	0.2	0.1	0.2	0.1

Notomys fuscus	Dusky hopping mouse	0.1	-	-	-	-	-	-	-	-	-	-
Pseudomys gracilicaudatus	Eastern chestnut mouse	-	-	-	-	-	-	-	0.1	0.1	0.1	-
Macropus giganteus	Eastern grey kangaroo	0.2	0.3	0.7	0.7	0.7	0.4	0.3	0.2	0.1	0.3	0.2
Cercartetus nanus	Eastern pygmy possum	-	-	0.2	0.8	0.7	0.5	0.6	0.4	0.4	0.1	0.5
Sminthopsis crassicaudata	Fat-tailed dunnart	0.7	0.3	0.1	-	-	-	-	-	-	-	-
Melomys cervinipes	Fawn-footed melomys	-	-	-	-	-	-	-	0.2	0.7	0.7	0.5
Acrobates pygmaeus	Feather-tail glider	0.4	0.3	0.3	0.7	0.6	0.3	0.6	0.7	0.5	0.9	0.6
Leggandina forresti	Forrest's mouse	-	0.1	-	-	-	-	-	-	-	-	-
Melomys burtoni	Grassland melomys	-	-	-	-	-	-	-	-	-	0.1	-
Petauroides volans	Greater glider	-	-	-	0.1	0.3	0.8	0.7	0.4	0.8	0.4	0.8
Pseudomys oralis	Hastings river mouse	-	-	-	-	-	-	-	-	0.2	-	0.2
Phascolarctos cinereus	Koala	0.7	0.8	0.7	0.4	0.2	-	0.1	0.5	0.6	0.7	0.4
Antechinomys laniger	Kultarr	0.1	0.3	-	-	-	-	-	-	-	-	-
Perameles nasuta	Long-nosed bandicoot	-	-	-	-	-	0.1	0.2	0.9	0.9	1	0.6
Potorous tridactylus	Long -nosed potoroo	-	-	-	0.1	0.5	0.1	0.6	0.6	0.7	0.2	0.4
Planigale tenuirostris	Narrow-nosed planigale	0.3	0.1	0.7	0.1	0.5	-	-	-	-	-	-
Pseudomys novaehollandiae	New holland mouse	0.1	0.1	0.1	0.4	0.3	0.1	0.4	0.6	0.1	0.2	0.4
Isoodon macrourus	Northern brown bandicoot	-	-	-	-	-	-	0.1	0.5	0.8	1	0.6
Rattus tunneyi	Pale field rat	-	-	-	-	-	-	-	-	-	0.6	-
Macropus parma	Parma wallaby	-	-	-	-	-	-	-	0.1	0.7	-	0.3
Planigale gilesi	Paucident planigale	0.1	0.3	0.3	-	0.1	-	-	-	-	-	-

Pseudomys pilligaensis	Pilliga mouse	-	0.1	0.2	-	-	-	-	-	-	-	-
Ornithorhynchus anatinus	Platypus	-	-	0.1	0.5	0.8	0.9	0.9	0.9	0.9	0.9	0.9
Macropus rufus	Red kangaroo	0.8	0.4	0.1	-	-	-	-	-	-	-	-
Thylogale stigmatica	Red-legged pademelon	-	-	-	-	-	-	-	0.1	0.7	0.1	0.1
Thylogale thetis	Red-necked pademelon	-	-	-	-	-	-	-	0.2	0.9	0.4	0.4
Macropus rufogriseus	Red-necked wallaby	-	0.1	0.4	0.2	0.7	0.6	0.3	0.1	0.2	0.2	0.3
Aepyprymnus rufescens	Rufous bettong	-	-	-	-	-	-	-	0.2	0.5	0.8	0.9
Pseudomys hermannsburgensis	Sandy inland mouse	0.1	-	-	-	-	-	-	-	-	-	-
Tachyglossus aculeatus	Short-beaked echidna	0.4	0.7	0.6	0.5	0.5	0.3	0.3	0.2	0.1	0.3	0.2
Trichosurus caninus	Short-eared possum	-	-	-	0.1	0.2	0.4	0.4	0.9	1	0.9	0.6
Pseudomys fumeus	Smoky mouse	-	-	-	-	-	-	-	-	-	-	-
Isoodon obesulus	Southern brown bandicoot	-	-	-	-	0.1	0.4	0.1	-	-	-	-
Ningaui yvonneae	Southern ningaui	-	-	-	-	-	-	-	-	-	-	-
Dasyurus maculatus	Spotted-tailed quoll	-	-	-	0.1	0.2	0.6	0.5	0.2	0.8	0.3	0.6
Petaurus norfolcensis	Squirrel glider	-	-	0.1	0.3	0.1	-	-	0.1	-	0.2	-
Sminthopsis macroura	Stripe-faced dunnart	0.5	-	-	-	-	-	-	-	-	-	-
Petaurus breviceps	Sugar glider	0.2	0.3	0.4	0.7	0.4	0.4	0.7	0.9	0.6	0.8	0.8
Rattus lutreolus	Swamp rat	0.5	0.5	0.5	0.4	0.4	0.3	0.4	0.9	0.5	0.7	0.4
Hydromys chrysogaster	Swamp wallaby	0.3	0.2	0.3	0.3	0.2	0.1	0.2	0.3	0.2	0.3	0.2
Macropus fuliginosus	Water rat	0.9	0.9	0.3	-	-	-	-	-	-	-	-
Macropus parryi	Western grey kangaroo	-	-	-	-	-	-	-	-	0.1	0.7	0.7

Sminthopsis leucopus	Whiptail wallaby	-	-	-	-	-	-	0.1	0.1	-	-	-
Petaurus australis	White-footed dunnart	-	-	-	0.3	0.2	0.3	0.8	0.9	0.9	0.9	0.9
Antechinus flavipes	Yellow-bellied glider	0.4	0.8	0.9	0.9	0.5	-	0.1	0.1	0.1	0.5	0.2
Wallabia bicolor	Yellow-footed antechinus	0.1	0.2	0.5	0.8	0.8	0.6	0.7	0.7	0.4	0.2	0.3
Total number of species		25	24	27	30	33	29	32	39	38	39	38

complimentarity

Chapter 5: Niche evolution in terrestrial mammals: clarifying

scale-dependencies in phylogenetic and functional drivers of

assemblages

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Evolutionary Ecology (under review)

Niche evolution in terrestrial mammals: clarifying scale-dependencies in phylogenetic and functional drivers of communities

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Abstract

Ecological and evolutionary mechanisms shaping assemblages of species remain elusive. Interactive forces between competition and habitat filtering are thought to drive many biogeographic patterns over evolutionary time scales. However, the responsiveness of assemblages to these two forces is influenced by spatial scale, forming complex patterns of niche separation. We explored these effects by testing the relative importance phylogeny and functional traits in shaping present day mammal assemblages at multiple scales. Importantly, we aim to identify the spatial scales at which niche evolution operates in shaping present-day assemblages. We modelled the distribution of 53 terrestrial mammal species across New South Wales (800,642 km²), Australia. Using predicted distributions, we estimated the range overlap between each pair of species at increasing cells sizes (~0.8, 5.1, 20, 81,506, 2,025, and 8,100 km²). We employed a decision tree to identify how interactions among functional traits and phylogenetic relatedness translated to levels of sympatry across increasing spatial scales. We find that Australian terrestrial mammals displayed scale-dependent phylogenetic over-dispersion across all spatial scales (~0.8-8,100 km²), decreasing with increasing spatial scale, suggesting ecological processes were more influential than biogeographic sympatry patterns. While the contribution of phylogenetic relatedness to patterns of co-occurrence decreased with increasing spatial scales, habitat preferences increased. Concurrently, dietary preferences operated at the local spatial scales (<10km²), while body mass led to niche overlap at larger spatial scales. Different ecological and evolutionary processes operate at different scales and in different directions. Australian mammals exhibited slower divergence of traits related to the micro-scale niche compared to faster diversification for traits associated with their macro-scale niche. We suggest that body mass played a significant role in reducing competitive pressure for Australian mammals, consequently reducing

phylogenetic clustering. In conclusion, multi-scale analysis is able to provide a clearer relationship between traits and a species ecological niche.

Introduction

Co-occurrences of species are assumed to represent complex non-random evolutionary and ecological processes (Diamond, 1975; Rosenzweig, 1995; Webb et al., 2002), driven partly by species' interactions across evolutionary time scales (Cavender-Bares et al., 2009). Phenotypic or functional similarities found within any given assemblage is both a product of biotic-interactions as well as habitat filtering (Cornwell et al., 2006; Tofts & Silvertown, 2000). Environmental filtering (or habitat filtering), describes the set of abiotic and biotic conditions required by species for survival (Emerson & Gillespie, 2008). Adaptation of cooccurring species to similar abiotic environments can drive species to develop similar ecological preferences and functional traits (phenotypic attraction) (Weiher & Keddy, 1995). In contrast, increased cost of competition for similar resources among co-occurring species can drive phenotypic repulsion (competitive exclusion), constraining coexistence of species (Elton, 1946; Macarthur & Levins, 1967), although strong competitors are able to coexist when certain assumptions are met (Abrams & Rueffler, 2009; Münkemüller et al., 2009). The interactive forces of ecological and evolutionary mechanisms shaping the variety of biogeographic patterns remain elusive. Testing the relative importance phylogeny and traitenvironment matching in shaping present day assemblages can deliver important insights to community structure and composition.

Phylogenetic relatedness can influence assemblage composition in a number of different ways; for example, phylogenetic niche conservatism occurs when closely related species are more ecologically similar than might be expected through a random process of evolutionary diversification (Losos, 2008). However, where competitive exclusion occurs, closely related species may be driven to spatial segregation (i.e., over-dispersion). These ecological and biogeographic processes are highly dependent on spatial scale. Density-dependent interactions among species (e.g. competition), should reduce co-occurrence of

closely related species at small spatial scales, while phylogenetic clustering should increase as spatial scales increase, encompassing both a greater variety of habitats and abiotic conditions exist (Cavender-Bares et al., 2006; Swenson et al., 2006) and eventually encompassing the biogeographic history of the region (Ricklefs, 2004). Understanding mechanisms of species' coexistence could be improved by examining how phylogenetic processes and spatial scale interact with ecological processes that shape assemblages (Ricklefs, 2004). Typically, the mechanisms shaping assemblage structure are considered to operate at three spatial scales (Ackerly et al., 2006; Silvertown et al., 2006): at micro-scales (α -niche), where divergence of resource use allows for co-occurrence of species; at macroscales (β -niche), where divergent habitat use or tolerance of varying environmental conditions produces allopatric distributions of species; and at larger regional-scales (γ -niche), driven by historic biogeographical processes. For a given suite of species, divergence of the α -niche while concurrently preserving or slow evolution of the β -niche should manifest in spatial co-occurrence of closely related species (Emerson & Gillespie, 2008). In contrast, where closely related species are conserved within their α -niche but diverge in their β -niche, they are more likely to display spatial dispersion. Understanding the mechanism and scale is instrumental for understanding species co-occurrence at different spatial scales.

While some traits are strongly tied with a species' tolerance to climate, ultimately affecting their distribution (interpreted as habitat filtering) (Diamond, 1986; Ingram, 2011), others are driven by local competitive regimes and resources exploitation and have little effect on habitat filtering (Ackerly *et al.*, 2006; Losos, 2009). Put simply, while some functional traits operate strongly at the scale of the α -niche, others define the β -niche. Hence, trait contribution to a species' niche (α or β) should vary with spatial scale. It is the interactive contribution of functional traits at different spatial scales that ultimately shapes a species' ecological niche. Despite the considerable benefits in improved evaluation,

determining which traits contribute to the α -niche or β -niche currently remains subjective and ambiguous (Vamosi *et al.*, 2009). The process of separating the α - and β -niche may be overcome by quantifying the scale-dependent contributions of phylogenetic relatedness and individual functional traits to assemblage composition.

Here we examine scale-dependent contributions by quantifying the influence of functional traits (diet, body mass, and habitat preferences) and phylogenetic relatedness in shaping assemblage composition among Australia's native terrestrial mammals at multiple spatial scales. We employed a three-step process: (1) testing for niche conservatism among closely related species; (2) assessing levels of phylogenetic clustering and the effects of mobility; and (3) examining the relative importance of individual functional traits and phylogenetic relatedness in shaping co-occurrence patterns at different spatial scales. We did this by quantifying the spatial distribution of 53 terrestrial mammals and measuring the levels of sympatry between pairs of species within the state of New South Wales (NSW), Australia. By following an analysis at multiple spatial scales and examining individual trait contribution to niche determination, we clarify the evolutionary processes along with their rates and scales in shaping the spatial patterns of present day mammal assemblages.

Materials and Methods

Species distribution data and modelling

We used records for 53 native terrestrial mammal species from the NSW Atlas dataset (DECCW, 2009) between 1990 and 2009 (minimising temporal changes in distributions) and with a spatial accuracy finer than 500m, comprising about 40,000 point locations across NSW (800,642km²). We selected six environmental and climate variables previously shown to provide reasonable representation of mammalian niche envelopes at regional scales (Boitani et al., 2008; Guisan & Thuiller, 2005). Variables selected included: (1) elevation; (2) average ten-year (2000-2009) Enhanced Vegetation Index (EVI) (Justice et al., 1998); (3) annual mean temperature; (4) annual precipitation; (5) annual mean moisture index, all three derived from ANUCLIM 5.1 (Nix, 1986); and (6) distance to the nearest water body (Kingsford *et al.*, 2004). To correctly account for spatial variability of surveys, survey method for record was included as a factor (Bino et al., 2012). We employed Generalised Additive Models (GAMs) to predict distributions of species (package gam, R Development Core Team, 2010). We used a boot-strapping model selection process for each species with all 63 unique combinations (obtained from the six identified predictor variables: 2^{n} - 1) (Steverberg et al., 2001). For each variable combination, we bootstrapped the data 1,000 times, randomly selecting 63.2% of the data (Hastie *et al.*, 2009). The .632+ estimator provides good overall model performance, combining low variance with only moderate bias compared to other cross-validation methods and tests performance when predictions are made to independent data (Efron & Tibshirani, 1997; Leathwick et al., 2006). We evaluated model performance by examining both the Akaike's Information Criterion (AIC), trading-off explained variation against model complexity, and the area under the receiver operating characteristic curve (AUC). We selected the most parsimonious model from a trade-off between the fewest numbers of predictor variables and the lowest average AIC +2 (Burnham

& Anderson, 2002). Using the final model, sighting probabilities (0-1) were predicted across NSW (800,642km²) for each species at a resolution of 250 meters. Model performance were good, with the majority of AUC values above 0.85 [0.75-0.85 (n=1), 0.85-0.95 (n=25), and 0.95-1 (n=27)].

Cross-species similarities

Using predicted distributions, we estimated the range overlap between each pair of species, using ENMTools software (Warren *et al.*, 2010) to measure levels of overlap derived from the Hellinger distance (Van der Vaart, 1998). This was defined as

$$l(p_x, p_y) = 1 - \frac{1}{2} \sqrt{\sum_{i} (\sqrt{p_{x,i}} - \sqrt{p_{y,i}})^2}$$

where *p* was the probability of occurrence for species *x* and *y*, and *I* was the measure range overlap between the two species, ranging from 0 (no overlap) to 1 (complete overlap). To investigate the effects of scale, we measured the overlap index *I* between each pair of species by averaging predicted values for increasing cells sizes of 30, 75, 150, 300, 750, 1500, and 3000 arc seconds (approximately 0.8, 5.1, 20, 81,506, 2,025, and 8,100 km², respectively). These scales enabled us to examine the assemblage's phylogenetic structure at three spatial scales: _community', _regional', and _continental' (Webb *et al.*, 2002).

Species characteristics

We identified relatedness among species for 51 modelled species using a species-level mammalian supertree (Fritz *et al.*, 2009), initially constructed by Bininda-Emonds et al. (2007). To validate the appropriateness of the supertree's phylogenetic relatedness, we independently compared it to genetic similarities among species using the mitochondrial Cytochrome b (cytb) protein sequence. Cytb was selected because it successfully identifies vertebrate species and has the widest taxonomic representation in nucleotide databases

(Bradley & Baker, 2001; Parson *et al.*, 2000). We collated cytb sequences from The Universal Protein Resource (UniProt) (The UniProt Consortium 2009). Only 35 species had complete or partial cytb sequences, and of these, we removed four with less than 90% of their complete sequence available. For the remaining 31 species, we compiled the available protein sequence information (Appendix S1), and used the available online function _ClustalW2^c to align multiple sequences (Larkin *et al.*, 2007). Using these alignments, we identified and retrieved the paired protein sequence similarities (scaled between 0 and 100). Strong correlation was found between phylogenetic relatedness reported in the supertree and that derived from the mitochondrial cytb protein sequence (r=0.85, p<0.001, N=465).

Functional traits for each species were categorized into three commonly used lifehistory traits, reflecting resources used (diet), specific habitat type (habitat), and body mass (Blackburn *et al.*, 2005; Flynn *et al.*, 2009; Sibly & Brown, 2007). Using available literature for each species, we recorded mean body mass, 13 possible dietary preference categories (insect, grass, leaves, roots, fungi, nectar/pollen, bulbs, fruits, arthropods, seeds, ferns, flowers, and vertebrates), and eight key habitat preference categories (closed forest, open forest, woodland, heath, scrub, shrub, grassland, and river) (Australian Faunal Directory, 2009; Jackson, 2003; Menkhorst & Knight, 2004; Strahan, 1984). Species could be assigned to more than one diet or habitat category (Appendix S2).

Testing phylogenetic and niche conservatism

We constructed a distance matrix based on the functional traits associated with each species (habitat, dietary preferences, and body mass), using the Bray-Curtis dissimilarity measure (Bray & Curtis, 1957). We then clustered all species according to their functional distances, using the group average cluster method within the PRIMER-E version 6 software (Clarke & Warwick, 2001). As our data were expressed as pairwise distances among taxa derived from unordered multistate traits, we could not measure the phylogenetic signal using the K statistic

(Blomberg *et al.*, 2003) as it is designed to measure phylogenetic relatedness among continuously varying traits (Harmon & Glor, 2010). We therefore used the Mantel test to test for niche conservatism among closely related species (Bohning-Gaese & Oberrath, 1999; González *et al.*, 2011). We used regression analysis between phylogenetic distance matrix and the three functional distance matrices (diet, habitat, and body mass) and tested for significance using the Mantel test. We tested derived mantel significant levels against a null distribution constructed using 10,000 Monte Carlo randomizations (González *et al.*, 2011). We examined the relationships between functional traits and phylogenetic distances using Generalized Additive Model (GAM) within the R statistical environment (package mgcv', R Development Core Team, 2010). As body mass, the only trait that could be expressed as a continuous variable, was independently tested for phylogenetic signal using the K statistic (Blomberg *et al.*, 2003) in the R package _picante' (Kembel *et al.*, 2010).

We tested for spatial aggregation of closely related species (phylogenetic clustering) by measuring the correlation between phylogenetic relatedness and the degree of spatial overlap (measured as *I*) between all unique pairs of 53 species (1378 combinations). Conceptually, scale and phylogenetic patterning should be strongly tied to the species' ability to disperse, driven by biogeographic history and mobility. As mobility increases, the strength of phylogenetic niche conservatism should decrease (Cavender-Bares *et al.*, 2009). We anticipated that the high mobility of mammal species would result in weak phylogenetic clustering at smaller scales and increasing as examined scale was extended. We repeated regression analyses of phylogenetic clustering at multiple spatial scales.

To quantify how functional traits influence species distribution across spatial scales, we examined the spatial, functional, and phylogenic similarities among unique pairs of the 53 species. We employed a decision tree to identify how interactions among functional traits and phylogenetic relatedness translated to levels of sympatry across increasing spatial scales. The

process split the dependent variable (levels of sympatry) into increasing homogenous subsets using the best split among all variables. Decision trees are a powerful alternative to linear models, identifying nonlinear relationships among multiple correlated predictor variables. They require fewer assumptions than correlational methods, without assumptions of distributions of predictor variables (De'ath & Fabricius, 2000; Olden et al., 2008). Further, decision trees are ideal for phylogeographic analyses as they do not assume data independence, avoiding pseudo-replication and the need for controlling of phylogenetic relatedness of species (Davidson et al., 2009; Jones et al., 2006). To increase the robustness of analyses and interpretation of results, we employed the _random forest' bootstrap approach (Cutler et al., 2007). Using the randomForest package in R (Breiman, 2001; Liaw & Wiener, 2002), we fitted 1,000 decision trees, each time building trees with 63% of the data and fitting to the remaining observations. We extracted the relative importance of each variable, using the average percentage increase in Mean Square Error (MSE) of the bootstrapped predictions when the variable was included. Examining the varying importance of each functional trait across increasing spatial scales can help identify a trait's appropriate spatial scale. As the random forest model scales overall variable contribution but does not provide a single decision tree, interpretation of results are limited. We constructed a single decision tree using the full data set at each spatial scale to provide more detailed information.

Results

Number of mammal species varied mostly along a longitudinal gradient, increasing from east to west. Maximum number of species was dependent on the scale examined (r=0.94, p<0.0001, n=7), ranging from 29 at scales of 30 arc seconds to 42 species at 3000 arc seconds (~0.8km² and 8,100km²), respectively. Mammal body weight considerable varied and ranged from several grams (Dasyuridae sp.) to 20-30 kg (Macropodidae sp.), averaging 5.7 kg ± 10.9 sd. Body mass increased from eastern coastline to the north-western and arid parts of NSW.

Contrary, diversity of dietary and habitat preferences increased towards the eastern coastline of NSW.

Clustering analysis among functional traits of closely related species revealed that the 53 mammal species clearly clustered according to their familial classifications (Appendix S3). Strong clustering (similarity > 90%) was observed among several closely related species (e.g., three glider species in the family *Petauridae*; two Pademelon species with identical functional traits, and the red kangaroo and common wallaroo). Significant niche conservatism among the three functional traits was observed; diet (p<0.001), body mass (Mantel p=0.006, K= 1.63, p=0.01), and habitat (p=0.020). Combined functional traits dissimilarity expressed an increase with phylogenetic distance (deviance explained – 16.6%, F=131.8, p<0.0001). When examiner separately, dissimilarity in diet and habitat increased with phylogenetic distance (Figure 1). The GAM model explained a moderate amount of the deviance (20.8%) and all three functional traits had a significant contribution (diet – F=86.2, p<0.0001; body mass F=9.1, p<0.0001; habitat F=19, p<0.0001).

Phylogenetic clustering and mobility effects were assessed by comparing sympatry and phylogenetic relatedness between species. Across NSW, phylogenetic over-dispersion was observed, as a significant negative correlation existed between phylogenetic relatedness and sympatry (Figure 2). However, strong spatial dependency was observed: as the spatial scale increased (cell size), levels of phylogenetic over-dispersion decreased. As anticipated, the high mobility of the study species resulted in a log-linear pattern where phylogenetic clustering decreased with increasing spatial scale (R^2 =0.95, F=47.9, p<0.0001).

The contribution of functional traits and phylogenetic relatedness to sympatry between pairs of mammal species was dependent upon scale (Figure 3). Phylogenetic

relatedness contributed most to co-occurrence (27.5% MSE) at small (_community'-level) and intermediate (_regional'-level) spatial scales (30–750 arc seconds, ~0.8–506km²), but decreased at larger, biogeographic, scales (24.8% MSE at 3000 arc seconds, ~8,100km²). Contrastingly, the MSE contribution of habitat similarity increased with scale from 25.6% at the smallest scales, surpassing phylogenetic relatedness above 1500 arc seconds (27.2% MSE). Diet and body mass similarity had small but opposing contributions to sympatry, varying differently with spatial scale: dietary similarity decreased with spatial scale (18.4% - 22.1%), while body mass's contribution increased (17.5%-22.5%).

The global decision tree of sympatry grown at the smallest spatial scale (30 arc seconds, ~0.8km²) was first split using habitat distances (Appendix S4). Species more similar in habitat preferences (<2.12 dissimilarity) comprised 86.2% of pairs with a higher, yet still low, level of sympatry (I=0.42), compared to 13.8% of species pairs with low levels of sympatry (I=0.26). The next two splits were made based on the degree of phylogenetic relatedness, dividing the tree into four nodes. Closely related species, belonging to similar genera or families (<61.8 branch length), had low levels of sympatry (I=0.34), while more distant pairs, belonging to similar orders (61.8-212.9 branch length), had somewhat higher levels of sympatry (I=0.48). For even more distant pairs of species from different subclasses (>313.3 branch length), high levels of sympatry occurred (I=0.54), while less distant pairs (212.9-313.3 branch length) had lower levels of sympatry (I=0.34). The final split was made based on similarities in body mass. Species more similar in body mass (<2.26 dissimilarity) had higher levels of sympatry (I=0.37), while those with large differences in body mass (>2.26 dissimilarity) had low levels of sympatry (I=0.25). The decision tree grown at the largest spatial scale (3000 arc seconds, $\sim 0.8 \text{km}^2$) was similar to that at the small spatial scale. Habitat similarities provided the first two splits in levels of sympatry (Appendix S4), while successive splits were shared by both body mass similarities and phylogenetic relatedness.

Again, phylogenetic relatedness was negatively associated with sympatry. Contrastingly, splits based phylogenetic relatedness at large scales were centred on relatively closely related species (branch lengths of 61.8 and 74.3).

Discussion

Species interactions and their biogeographic history play a major role in the evolution of species traits, ultimately shaping sympatry patterns (Ricklefs, 2004). Determining the contribution of multiple traits across multiple scales can shed light on the mechanisms influencing niche determination. Closely related mammal species that were over-dispersed in our study were commensurate with slow rates of divergence along their α -niche and fast rates of β -niche diversification. The conservatism of several functional traits and observed phylogenetic over-dispersion suggest that closely related mammal species across NSW may be competitively excluded. Since Diamond (1986) argued for a habitat first (β -niche) model of speciation, much debate has occurred over the comparative rates of niche evolution. Fast rates of α -niche evolution have been shown to occur in plants (Ackerly *et al.*, 2006; Silvertown *et al.*, 2006), while fast rates of β -niche evolution are evident in vertebrates (Lovette & Hochachka, 2006; Streelman & Danley, 2003). Our findings suggest similar processes in Australia's terrestrial mammals, indicating diversification of the β -niche as a means for alleviating competitive pressures among closely related species.

By comparing the relative importance of three functional traits (diet, body mass, and habitat preferences) at varying spatial scales, we defined the scale and configuration of each niche. Dietary preferences contributed most to shaping a species α -niche (<100 arc seconds, <~10km²), an effect that decreased with increasing spatial scale (Figure 2). In contrast, body mass and habitat preferences contributed most to the β -niche (>100 arc seconds, >~10km²), increasing in importance at large spatial scales. Unsurprisingly, our definition of habitat type

was based on landscape-scale classes, thus potentially confounding the nature of our finding. Finer-scale information on habitat associations may indeed contribute more to the α -niche. Body mass, highly conserved among closely related mammal species (Freckleton & Jetz, 2009), is strongly associated with life-history traits, such as reproduction, longevity, and energy requirements (Blanckenhorn, 2000; Millar & Hickling, 1991; Peters, 1983). Why body mass contributed more to the β -niche rather than the α -niche was intriguing. Logically, the link between energy requirements and body mass should lead to a strong association between body mass and surrogates of habitat productivity (Johnson & Isaac, 2009; Rodríguez et al., 2006). Any changes to a species' body mass would lead to alterations in its distribution. Consequently, habitat productivity acts as a filter for body mass, influencing assemblage composition at large spatial scales. Thus, variation in body mass could be interpreted as evolution along the β -niche axis, manifesting as habitat filtering. In NSW, a sharp gradient in climate and productivity occurs between the western arid and semi-arid regions and the eastern mesic regions (Stern et al., 2000). Our findings suggest this gradient strongly influenced body mass, strongly influencing the large-scale patterns of mammal distributions.

Both phylogenetic clustering and over-dispersion have previously emerged in analysis of phylogenetic patterning (Cooper *et al.*, 2008; Swenson *et al.*, 2006; Webb, 2000). Scaledependencies between local species^c interactions and biogeography have been shown to influence the observed phylogenetic patterns (Cavender-Bares *et al.*, 2006; Swenson *et al.*, 2006; Webb *et al.*, 2002). Across NSW, spanning an area of 800,642km², we found that closely related Australian terrestrial mammal species tended to be spatially segregated, while more distantly related species tended to be highly sympatric. Importantly, the observed pattern was spatially dependent; with phylogenetic over-dispersion of terrestrial mammals decreasing with increasing spatial scale, plateauing at larger scales (Figure 2). Nonetheless, spatial over-dispersion remained prevalent at the largest examined scale (~8,100km²), suggesting that ecological processes, rather than biogeographic were still dominant.

Related species often share similar ecological niches (i.e., phylogenetic signal) across various taxa (Hutchinson, 1957; Losos, 2008; Peterson et al., 1999; Wiens & Graham, 2005). Here, we found evidence that niche conservatism is an important determinant of spatial patterning in Australian mammals, driven by functional traits like body mass, diet, and habitat preferences (Appendix S3 & Figure 1). Closely related mammal species were more likely to share similar functional traits, again plateauing as the phylogenetic distance between two species increased (Figure 3). Phylogenetic niche conservatism is not always prevalent (Freckleton et al., 2002; Graham et al., 2004; Losos et al., 2003; Rice et al., 2003), especially for species with high dispersal capabilities (Cavender-Bares et al., 2009). As mammal species often possess active and high dispersal capabilities (Jenkins et al., 2007), they often exhibit patterns of phylogenetic over-dispersion where co-occurring species tend to be more distantly related than expected by chance (Cooper et al., 2008). Despite this, some variability does exist in the mobility and dispersal capabilities of species within the class Mammalia (Sutherland et al., 2000). If indeed phylogenetic clustering at regional and biogeographic scales is influenced by the mobility of mammalian species, subtle differences among mammalian families should be apparent, presenting a negative relationship between phylogenetic clustering and mobility. Restricted to the speciose families: Dasvuridae (13 species), Macropodidae (12 species), and Muridae (11 species), we examined the phylogenetic clustering at the largest scale possible. Using home range size as a surrogate for dispersal and mobility of a species (Appendix S5), we detected a negative relationship between average home range size and phylogenetic clustering at the family level. *Dasyuridae* and *Macropodidae* with average home-ranges of $589m \pm 59.7s.e.$ and $523m \pm 36s.e.$ respectively exhibited phylogenetic over-dispersion (r=-0.29 & -0.25 respectively).

Conversely, *Muridae* had small average home-ranges ($107m \pm 2.2s.e.$) and no phylogenetic over-dispersion (r=0.06).

Finally, inferences of mechanisms from patterns obtained through analysis carried-out at large biogeographic scales are bound to be weaker compared to those obtained through controlled field manipulations. Additionally, whenever we examined the composition of assemblages at varying scales, only a subset of species are presented to that found within a broader region. Consequently, we restrict our testing to whether examined assemblages show significant structure with respect to their phylogenetic relatedness and composition. Inference from emerging patterns of species⁴ assembly at large scales can nonetheless provide valuable insights into evolutionary processes, rates, and importantly the scales in which they operate in shaping present day assemblages (Cardillo, 2011; Jablonski & Sepkoski, 1996; Webb *et al.*, 2002).

Two summary points are evident for terrestrial mammals in NSW: first, they diverged at a faster rate along their β -niche compared to that of the α -niche and, secondly, divergence of body mass was associated with the β -niche while divergence of dietary preferences with the α -niche. As species under competitive pressure require evolutionary pathways to separate niches, we suggest that body mass for mammals provided such a route, alleviating competitive pressure and reducing phylogenetic clustering. By combining phylogenetic and niche methods through the modelling of species distributions, we addressed a crucial question in community ecology: how do we assess whether specific traits are related to a particular niche? More importantly, by conducting multi-scale spatial analysis, categorical assignment of traits-to-niches are avoided, thus providing a clearer relationship between traits and a species ecological niche and a more precise scaling for the axes of niche evolution.

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Figures

Figure 1: Response shapes in GAM models for branch lengths from the mammalian phylogenetic supertree. The dashed lines are approximate 95% point-wise confidence intervals; tick-marks show the location of observations along the variable range; *y*-axes represent the effect of (a) diet, (b) body mass, (c) habitat, and (d) functional traits combined; s represents smooth term of GAM.

Figure 2: The relationship between phylogenetic clustering and spatial scale (filled circles). Species' phylogenetic clustering was measured as the correlation between genetic relatedness and levels of sympatry. Fitted quadratic regression (dashed) is presented along with a linear reference line (solid) representing expected phylogenetic clustering when species interactions are negligible.

Figure 3: The relative importance of phylogenetic relatedness (supertree branch length) and functional traits (diet, body mass, and habitat), using the average percentage increase in Mean Square Error (MSE) of the bootstrapped predictions when the variable was included. The relative contribution was measured across varying spatial scales (Cell Size [Log ArcSec]), derived from the *randomForest* model. Spatial scales (cells sizes) examined: 30, 75, 150, 300, 750, 1500, and 3000 arc seconds (approximately 0.8, 5.1, 20, 81,506, 2,025, and 8,100 km², respectively).













Appendices / Supporting information

Additional supporting information may be found in the online version of this article:

Appendix S1. Thirty-one species with available Cytochrome B protein sequence information longer than 90% with their sequence length and the accession number. All species had a sequence length of 381, except for the platypus and short-beaked echidna with a sequence length of 379.

Appendix S2: List of 53 mammal species across NSW and their average body mass [g], preferences (1-used, 0-not used) for different habitats (CF=closed forest, OF=open forest, W=woodland, H=heath, SC=scrub, SH=shrub, G=grassland, R=river) and diets (V=vertebrate, I=insect, G=grass, F=fern, L=leaf, FL=flower, N/P=nectar/pollen, FR=fruit, FU=fungi, S=seed, R=root, B=bulbs)

Appendix S3. Cluster analysis for 53 species of terrestrial mammals from NSW, using group average cluster method based on the Bray-Curtis functional trait distances associated with each species (habitat, dietary preferences, and body mass group).

Appendix S4: Decision-trees of levels of sympatry (I) at the smallest scale (30 ArcSec, ~0.8km²) and largest scale (3000arcsec, ~8,100km²), based on functional traits (body mass, diet, and habitat preferences) and phylogenetic relatedness. Details within each node provide: mean, standard deviation, number of cases (n & %). Predictor cut-off values are given above each node.

Appendix S5: Average home-range of the 53 terrestrial mammal species modelled across NSW. Corresponding literary sources are provided in the table followed by the full reference. Minimum home range radius set at 100m. Due to lack of information, home range was estimated for three species (labelled accordingly under source).
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Appendix S1

Thirty-one species with available Cytochrome B protein sequence information longer than 90% with their sequence length and the accession number. All species had a sequence length of 381, except for the platypus and shorth-beaked echidna with a sequence length of 379.

Common Name	UniProt Accession Number
Brown antechinus	P92509
Brush-tailed phascogale	Q35673
Common brush-tail possum	O03503
Common dunnart	Q35886
Common ringtail possum	Q5QS41
Common wallaroo	P92671
Common wombat	Q8W9B2
Dusky antechinus	Q33865
Eastern grey kangaroo	O03473
Fat-tailed dunnart	Q35810
Koala	Q9TEU7
Long-nosed bandicoot	P92717
Long-nosed potoroo	Q5QS02
Narrow-nosed planigale	Q35675
Northern brown bandicoot	Q9B2F7
Parma wallaby	B5KFY8
Paucident planigale	Q35459
Platypus	Q36461
Red kangaroo	O03474
Red-necked pademelon	B5KFZ2
Red-necked wallaby	B5KFY5
Rufous bettong	B8PRU1
Short-beaked echidna	Q8W9G1
Short-eared possum	Q8SEJ1
Spotted-tailed quoll	O03522
Stripe-faced dunnart	O20433
Sugar glider	Q1MWG1
Swamp wallaby	B5KFY9
Water rat	B1P8U7
White-footed dunnart	Q9XP80
Yellow-footed antechinus	Q33706

Appendix S2

List of 53 mammal species across NSW and their average weight [g], preferences (1-used, 0-not used) for different habitats (CF=closed forest, OF=open forest, W=woodland, H=heath, SC=scrub, SH=shrub, G=grassland, R=river) and diets (V=vertebrate, I=insect, G=grass, F=fern, L=leaf, FL=flower, N/P=nectar/pollen, FR=fruit, FU=fungi, S=seed, R=root, B=bulbs)

Common Name	Weight [g]	Habitat Preferences						Dietary Preferences												
		OF	W	Н	G	SC	SH	R	V	Ι	G	F	L	FL	N\P	FR	FU	S	R	В
Agile antechinus	28	1	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
Black striped wallaby	13000	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0
Bolam's mouse	15.5	0	0	0	1	1	1	0	0	1	1	1	0	0	1	0	1	1	1	0
Broad-toothed rat	122	1	0	1	1	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0
Brown antechinus	44	1	1	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
Brush-tailed phascogale	208.5	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
Brush-tailed rock wallaby	6650	1	0	0	1	1	0	0	0	0	1	1	1	0	0	1	0	0	0	0
Bush rat	132.5	1	1	0	0	1	0	0	0	1	1	0	0	0	0	1	1	1	1	0
Common brush-tail possum	2850	1	1	0	0	0	1	0	0	1	0	0	1	1	0	1	1	0	0	1

Common dunnart	19	1	1	1	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0
Common ring-tail possum	875	1	1	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0
Common wallaroo	26375	1	1	0	1	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0
Common wombat	36000	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0
Dusky antechinus	108	1	1	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
Eastern chestnut mouse	82	1	0	1	0	0	0	0	0	1	1	1	0	0	1	0	1	1	1	0
Eastern grey kangaroo	34750	1	1	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0
Eastern pygmy possum	29	1	1	1	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0
Fat-tailed dunnart	15	0	1	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0
Fawn footed melomys	78	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0
Feather-tail glider	12	1	1	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0
Grassland melomys	75	1	1	0	1	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0
Greater glider	1300	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Koala	9500	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Long nosed bandicoot	1200	1	1	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	1
Long nosed potoroo	1050	1	0	1	0	0	0	0	0	1	0	0	0	1	0	1	1	1	0	0

Narrow nosed planigale	7	0	1	0	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0
New holland mouse	23	1	0	1	0	0	0	0	0	1	1	0	0	1	1	0	1	1	1	0
Northern brown bandicoot	1800	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Pale field rat	124	1	0	0	1	0	0	0	0	1	1	0	0	0	0	1	1	1	1	0
Parma wallaby	4550	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0
Paucidentplanigale	11	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
Pilliga mouse	11	1	1	0	0	0	0	0	0	1	1	1	0	0	1	0	1	1	1	0
Platypus	1525	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Red kangaroo	51000	1	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0
Red-legged pademelon	5250	1	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0
Red-necked pademelon	5450	1	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0
Red-necked wallaby	19000	1	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0
Rufous bettong	3500	1	1	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	1	0
Short-beaked echidna	4500	1	1	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Short-eared possum	3500	1	0	0	0	0	0	0	0	1	0	0	1	1	0	1	1	0	0	1
Southern ningaui	7	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0

Spotted-tailed quoll	5500	1	1	0	0	0	0	0	1	1	1	0	0	0	0	1	0	0	0	0
Squirrel glider	245	1	1	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0
Stripe-faced dunnart	20	0	1	0	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0
Sugar glider	123	1	1	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0
Swamp rat	106	0	0	1	0	0	0	0	0	1	1	0	0	0	0	1	1	1	1	0
Swamp wallaby	15400	0	1	1	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	0
Water rat	808	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0
Western grey kangaroo	28250	1	1	0	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0	0
Whip-tail wallaby	16500	1	1	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0
White-footed dunnart	28	1	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0
Yellow-bellied glider	575	1	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0
Yellow-footed antechinus	50	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0

Appendix S3

Cluster analysis for 53 species of terrestrial mammals from NSW, using group average cluster method based on the Bray-Curtis functional trait distances associated with each species (habitat, dietary preferences, and weight group).



Appendix S4

Two decision-trees of levels of sympatry (I) at two smallest scale: (1) 30 ArcSec, $\sim 0.8 \text{km}^2$ and (2) 3000arcsec, $\sim 8,100 \text{km}^2$. Trees were based on functional traits (weight, diet, and habitat preferences) and phylogenetic relatedness. Details within each node provide: mean, standard deviation, number of cases (n & %). Predictor cut-off values are given above each node.





Appendix S5

Average home-range of the 53 terrestrial mammal species modelled across NSW. Corresponding literary sources are provided in the table followed by the full reference. Minimum home range radius set at 100m. Due to lack of information, home range was estimated for three species (labelled accordingly under source).

Order	Family	Scientific name	Common Name	Home range [m]	Source
Dasyuromorphia	Dasyuridae	Antechinus agilis	Agile antechinus	100	(Lazenbycohen & Cockburn 1991)
		Antechinus flavipes	Yellow-footed antechinus	720	(Marchesan & Carthew 2008)
		Antechinus stuartii	Brown antechinus	126	(Lazenbycohen & Cockburn 1991)
		Antechinus swainsonii	Dusky antechinus	100	(Sanecki et al. 2006)
		Dasyurus maculatus	Spotted-tailed quoll	3000	(Belcher & Darrant 2004)
		Ningaui yvonneae	Southern ningaui	150	(Darren & Canhew 2007)
		Phascogale tapoatafa	Brush-tailed phascogale	668	(Soderquist 1994)
		Planigale gilesi	Paucident planigale	205	(Read 1984)
		Planigale tenuirostris	Narrow-nosed planigale	395	(Read 1984)
		Sminthopsis crassicaudata	Fat-tailed dunnart	350	(Read 1984)
		Sminthopsis leucopus	White-footed dunnart	1000	(Lunney & Leary 1989)
		Sminthopsis macroura	Stripe-faced dunnart	300	(Anke & Soderquist 2005)
		Sminthopsis murina	Common dunnart	550	Estimated
Diprotodontia	Acrobatidae	Acrobates pygmaeus	Feather-tail glider	100	(Lindenmayer 1997)
	Burramyidae	Cercartetus nanus	Eastern pygmy possum	100	(Harris et al. 2007)
	Macropodidae	Macropus dorsalis	Black-striped wallaby	540	(Evans 1996)
		Macropus fuliginosus	Western grey kangaroo	1200	(Priddel et al. 1988)
		Macropus giganteus	Eastern grey kangaroo	700	(Moore et al. 2002)
		Macropus parma	Parma wallaby	160	(Lentle et al. 2004)
		Macropus parryi	Whiptail wallaby	460	(Kaufmann 1974)
		Macropus robustus	Common wallaroo	495	(Clancy & Croft 1990)
		Macropus rufogriseus	Red-necked wallaby	480	(Mar et al. 2003)
		Macropus rufus	Red kangaroo	1500	(Priddel et al. 1988)

		Petrogale penicillata	Brush-tailed rock wallaby	220	(Short 1980)
		Thylogale stigmatica	Red-legged pademelon	110	(Vernes et al. 1995b)
		Thylogale thetis	Red-necked pademelon	130	(Vernes et al. 1995a)
		Wallabia bicolor	Swamp wallaby	290	(Troy & Coulson 1993)
	Phalangeridae	Trichosurus caninus	Short-eared possum	125	(McCarthy & Lindenmayer 1998)
		Trichosurus vulpecula	Common brush-tail possum	400	(Mar et al. 2003)
	Phascolarctidae	Phascolarctos cinereus	Koala	970	(Ellis et al. 2002)
	Potoroidae	Aepyprymnus rufescens	Rufous bettong	440	(Tyndale-Biscoe 2005)
		Potorous tridactylus	Long-nosed potoroo	180	(Tyndale-Biscoe 2005)
	Pseudocheiridae	Petauroides volans	Greater glider	115	(Pope et al. 2004)
		Pseudocheirus peregrinus	Common ring-tail possum	100	(Jones et al. 1994)
	Vombatidae	Vombatus ursinus	Common wombat	320	(Murray 2008)
Monotremata	Ornithorhynchidae	Ornithorhynchus anatinus	Platypus	222	(Gust & Handasyde 1995)
	Tachyglossidae	Tachyglossus aculeatus	Short-beaked echidna	565	(Wilkinson et al. 1998)
Peramelemorphia	Peramelidae	Isoodon macrourus	Northern brown bandicoot	130	(Gordon 1974)
		Perameles nasuta	Long-nosed bandicoot	150	(Scott et al. 1999)
		Petaurus australis	Yellow-bellied glider	520	(Goldingay & Kavanagh 1993)
		Petaurus breviceps	Sugar glider	165	(Quin 1995)
		Petaurus norfolcensis	Squirrel glider	165	(Quin 1995)
Rodentia	Muridae	Hydromys chrysogaster	Water rat	180	(DEC. 2009)
		Mastacomys fuscus	Broad-toothed rat	100	(Bubela et al. 1991)
		Melomys burtoni	Grassland melomys	100	(Begg et al. 1983)
		Melomys cervinipes	Fawn-footed melomys	100	(Rader & Krockenberger 2006)
		Pseudomys bolami	Bolam's mouse	100	Estimated
		Pseudomys gracilicaudatus	Eastern chestnut mouse	100	(Strahan et al. 1983)
		Pseudomys novaehollandiae	New holland mouse	100	(Lock & Wilson 1999)
		Pseudomys pilligaensis	Pilliga mouse	100	(Tokushima & Jarman 2008)
		Rattus fuscipes	Bush rat	100	(Maitz & Dickman 2001)
		Rattus lutreolus	Swamp rat	100	(Maitz & Dickman 2001)
		Rattus tunneyi	Pale field rat	100	Estimated

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Chapter 6: Improving conservation outcomes using large data sets

This thesis provided concepts, methods and specific operational guidelines for improving conservation focused on use of multispecies survey data, operating over large scales. Increasingly, it is important to try to maximise value from such data sets that are steadily increasing in size and extent and are primarily at the spatial scale at which major policy and management decisions are made. My research showed improved applications through use of large datasets containing accumulated species' occurrence data. Significant improvements could be made in the monitoring of species, subsequently used for large scale predictions of species' distributions. Furthermore, conservation outcomes could be improved through prioritisation of land specifically for mammal representation under current and projected climate change conditions, using their assemblages rather than the current bioregional framework. Further improvements are possible if different multispecies frameworks are used. Finally, integration phylogenetic and ecological data provided knowledge regarding the processes affecting spatial assemblages of species and the scales in which these operate.

Key findings

Four key analyses were completed on a large data set for this thesis to produce some key findings on the value and methods of analyses for utilising large multispecies data sets. In Chapter 2, I developed a way to prioritise mammalian monitoring techniques when modelling predicted distributions across large scales. Results portrayed considerable variation in the effectiveness of survey techniques for species inventories at regional scales. Unplanned opportunistic sightings were the single largest source of species information, recording 35% of total recorded species. Predator scats, Elliot and pitfall trapping, spotlighting and diurnal herpetofauna surveys were the minimum set of required systematic methods at a regional scale. When employed, these detected all targeted mammal species. While incorporating

opportunistic sightings, systematic surveys could be reduced to only predator scats, Elliot and pitfall trapping. Moreover, spatial variability existed in the utility of survey methods, driven by variation in species inventories within each of 18 bioregions found across NSW. By tailoring survey methods to unique species inventories, monitoring efficacy can considerably be increased. Given survey costs and limited budgets, the analytical approach I used can easily incorporate associated costs with each survey method, providing guidelines for optimal cost\benefit combinations of survey methods at regional and bioregional scales.

In Chapter 3, I tested the efficacy of the existing bioregional framework used in Australia for representing mammal species within protected areas at regional scales. I compared this to an approach based on mammal assemblages and assessed their performances in representing mammal distributions. Results revealed substantial spatial misalignment between the bioregional framework and mammal assemblages. These discrepancies contributed to deficiencies in the representation of as much as half of mammal assemblages, within the existing protected area network. When using a mammal driven framework to prioritise land, significant improvements could be obtained to mammal representation. Of the 61 species, on average, 45 were better represented when using mammal assemblages, while those species better represented when using the bioregions were only marginally better represented over the mammal assemblage framework. Overall, the rates in which mammals were incorporated into a protected area network were higher $(3.8\% \pm 0.7 \text{ sd})$ when guided by mammal assemblages than when using the bioregional framework. Guided by bioregions, systematic conservation planning of protected areas may be constrained in realising its full potential in securing representation for all of Australia's biodiversity. Adapting the boundaries of prioritisation frameworks by incorporating amassed information from a broad range of taxa should be of conservation significance. Rather than a competing approach, I suggested that the mammal assemblage framework could be used to complement existing prioritisation strategies that use

the bioregional framework. More generally, this work advocates for integration of more species-driven data, rather than simply relying on static bioregional frameworks built mainly around vegetation and landscape processes if we are to ensure biodiversity is adequately conserved and represented in our protected areas.

In Chapter 4, I employed the mammalian assemblages based approach to investigate the expected outcomes to mammal representation within the protected area network, as a result of climate change by 2050. I quantified the realised climatic envelope for each mammal assemblage and identified areas expected to shift beyond those climatic envelopes. Those areas were classified as unstable areas for existing mammal assemblages according to climate change projections. Expected alterations in temperature and precipitation are projected to lead to considerable unstable conditions for mammal assemblages across NSW. Using the classification of stable or unstable areas for existing mammal assemblages, I quantified alterations to stable mammal representation (land area and diversity) within protected areas. Total area of mammal assemblages represented in viable refugia declined by as much as 29%, with considerable variation in representation among assemblages (average reduction of $37.9\% \pm 33.7$ s.d.). Importantly, projected impacts of climate change on mammal representation could be minimised by identifying habitat refugia and employing a systematic approach for site selection and representation in the protected area network. Incorporation of habitat refugia in assessments of protected areas increases robustness of conservation outcomes achieved and also safeguards long term persistence of biodiversity within protected areas.

In Chapter 5, I investigated the evolutionary and ecological history shaping presentday mammal occurrence patterns across NSW. Using predicted distributions, I examined the degree of spatial overlap among 53 mammal species and tested the influences of phylogenetic relatedness and functional traits in shaping communities at multiple spatial scales. I found that closely related Australian terrestrial mammal species exhibited phylogenetic overdispersion which was scale dependent, decreasing in effect at increasing spatial scales. Notably, using decision tree analysis, I found scale dependant interactions between phylogenetic relatedness and functional traits. Phylogenetic relatedness, was a predominant contributor to co-occurrence at small and intermediate spatial scales, but decreased at large scales. Nonetheless, spatial over-dispersion remained prevalent at the largest examined scale, suggesting that ecological processes, rather than biogeographic were still dominant. Contrastingly, contribution of habitat similarity increased with scale, surpassing that phylogenetic relatedness at larger scales. Dietary and weight similarity contributed less to explaining co-occurrence, varying differently with spatial scale: dietary similarity decreased with spatial scale, while weight's contribution increased. These results imply that body weight is associated with the β -niche (large scale) while dietary preferences with the α -niche (local scale). This suggests Australian mammals exhibit slower rates of α -niche evolution compared with faster rates of β -niche. The conservatism of several functional traits and observed phylogenetic over-dispersion suggest that closely related mammal species across NSW may be competitively excluded. By exploring a continuous assessment of trait interactions across spatial scales, I avoid a categorical assignation of traits to a specific niche, producing a more precise scaling for evolving determinants of niche overlap.

Promises and pitfalls of SDM's and atlas data

For the conservation of biodiversity to succeed, estimates of its distribution across the landscape are essential. Importantly, understanding how species respond to their environment allows conservation managers to predict how species will respond to threat and environmental change (Guisan and Thuiller 2005). As detailed and complete data of species occupancy are not readily available (Manley, Zielinski et al. 2004; Pressey 2004; Marsh and

Trenham 2008), species distribution modelling (SDMs) are an excellent tool, providing an estimate of occupancy in areas when knowledge is missing or scarce (Elith and Leathwick 2009). They provide a way of scaling up of data to large spatial scales. Considerable application across a broad range of conservation, ecological, and evolutionary themes have resulted in exponential growth of the number of studies employing or referring to SDMs in the past 30 years (Figure 1). SDMs have been deployed in support of reserve design, ecological restoration, invasive species management, species reintroductions and predicting the potential impacts of global environmental change on biogeographical patterns (Pearson 2007; Franklin, 2009).

Figure 1





Establishing protected areas is a key strategy for species protection (CBD COP10 2010), although systematic assessment utilising distribution of species has only recently begun to drive identification and gazettal of protected areas (Pressey 1994). The use SDMs in systematic planning have become common practice (Margules and Pressey 2000; Araújo, Cabeza et al. 2004). SDMs are also used to predict species' invasions (Richardson and

Thuiller 2007), management plans for species recovery and reintroduction (Pearce and Lindenmayer 1998; Hirzel, Posse et al. 2004), and predict the impacts of climate change on species' distributions (Araújo, Thuiller et al. 2006). More recently, improved understanding of complex biogeographic systems has increased the need to incorporate dynamic processes such as dispersal, migration, landscape disturbance, community dynamics and population dynamics (Franklin 2010). For example, the correlative relationship between probability of suitability and population persistence (Araujo, Williams et al. 2002; Cabeza, Araujo et al. 2004) has married SDMs with metapopulation models (Akçakaya 2002; Kramer-Schadt, Revilla et al. 2005). An area likely to experience a continued expansion and development.

Data deficiencies can originate with rarity or restricted range of particular species, detection effectiveness, and a by-product of alternative management targets (Kunin and Gaston 1993; Msoffe, Mturi et al. 2007; Gardner, Barlow et al. 2008). For species with a narrow environmental niche, the penalties associated with few occurrence records are minimal compared to those with broad environmental niches (Kadmon, Farber et al. 2003). Such scarcity of occurrence data can considerably decrease the predictive power of SDMs (Stockwell and Peterson 2002; McPherson, Jetz et al. 2004; Hernandez, Graham et al. 2006; Wisz, Hijmans et al. 2008). While data input are critical to developing SDMs, resulting models can also guide data collection and fieldwork sampling of rare species by identifying areas with high probability of encounter (Le Lay, Engler et al. 2010).

SDM's face considerable challenges dealing with inherit biases present in atlas datasets. These biases are inevitable as atlas datasets are a compilation of occurrence data collected at different spatial and temporal scales for a range of uses and targets. These formed two general deficiency categories: (1) spatial bias in use opportunistic sightings compared to systematic surveys and (2) variation in species detection across habitats. Atlases frequently have the largest source of occurrence data, consisting of systematic and opportunistic records

(Robertson et al. 2010). Systematic surveys, controlled for effort and detection, provide the most reliable estimates of the distribution and density of species (Grantham et al. 2008) but, opportunistic sightings are inexpensive and plentiful although heavily affected by detection and spatial bias (Grand et al. 2007), such as proximity to roads (Austin et al. 1994), and surveours with varying skills (Donald and Fuller 1998). Opportunistic sightings are characteristically spatially auto-correlated (Dormann et al. 2007, Elith and Leathwick 2009) and favour presence' records, inaccurately measuring species' distribution (Hernandez et al. 2006). Effects of spatial bias can be reduced by incorporating background data (i.e., absence data) with similar spatial biases, substantially improving model performance (Phillips et al. 2009). Such geographic sampling bias can be problematic for establishing conservation especially when targeting complimentarity of representation, requiring priority, accountability (Williams, Margules et al. 2002; Reddy and Davalos 2003). Biased occurrence data can severely undermine SDM performance (Edwards, Cutler et al. 2006; Leitão, Moreira et al. 2011). Consequently, biased or incomplete distributional data reduces the predicted efficacy of reserve networks by altering the estimation of species representation (Polasky et al., 2000; Gladstone and Davis, 2003). A priori selection of sampling designs according to prior knowledge and model-based designs can considerably reduce biases (Albert, Yoccoz et al. 2010). However, when using existing data, there are few alternatives beyond discarding biased data, but then the contribution of this approach to management and policy is likely to be limited. Even biased data, such as opportunistic sightings, should be considered, as they often hold the largest source of occurrence data, spanning large spatial extents and have minimal costs compared with systematic surveys. For example in chapter 2, opportunistic sightings of terrestrial mammals formed the largest source of occurrence records (35%) and covered the highest number of species (85%). For 34% of species, opportunistic sightings ranked as the most effective method for regional scale SDM. When employing SDMs,

founded on datasets containing spatial biases, special attention should be made to the statistical analyses and consequent interpretations. One way of doing this is to deal with absences. In this thesis, I modelled mammal distributions using all available data but I generated pseudo-absences containing similar biases and their interaction with the different survey methods (see methods section in research chapters).

Abiotic factors (e.g., climate and soil) determine the species fundamental niche, while constrained by biotic interactions (e.g., competition) to form the realised niche. Biotic interactions are assumed to significantly shape species' distributions (Soberon 2007), with competition, predation, and symbiosis, affecting distributions, and realising the shape of niches (Austin et al., 1990; Davis et al., 1998). Most SDMs do not take this into account, primarily relying on the assumption that abiotic conditions are the primary force shaping the distribution of species (Wiens, Stralberg et al. 2009; Zimmermann, Edwards et al. 2010). Studies investigating multiple spatial scales have suggested that biotic interactions only operate at the smaller scales (Heikkinen, Luoto et al. 2007; Meier, Edwards Jr et al. 2011). However, significant caveats have been raised about neglecting biotic interactions even at macro-ecological scales for extrapolative predictions, most notably predicting the effects of climate change on species distributions (Araújo and Luoto 2007). An example is illustrated by Kissling et al. (2010), presenting significantly stronger bird species loss when their response to climate change is coupled with the response of associated woody plants. As discussed in chapter 4, several methods exist for aggregating multi-species data, potentially integrating biotic interactions as community-level modelling (Ferrier and Guisan 2006; Gilman, Urban et al. 2010). However, incorporating both biotic and abiotic factors in forming ecological communities remains challenging (Callaway 2007; Baselga and Araújo 2010). In chapters 3 and 4, I used a multi-species modelling approach to form distinct mammal assemblages. By taking this approach, I attempted to incorporate biotic interactions through assemblage-level modelling. With respect to conservation, combining complex data large numbers of species into a single manageable entity can ease interpretation and help inform decisions. Additionally, combining species diversity and mammal assemblages enabled a systematic approach for prioritising land acquisition, improving the existing protected areas network. In conclusion, accounting for complex interactions remains a difficult aspect of SDMs, requiring further development of modelling methods and ecological theory. The challenges ahead require moving from single species predictions to a more encompassing understanding of ecosystem-level response to the complex interactions of abiotic and biotic conditions (Montoya and Raffaelli 2010).

Conclusions

Considerable area for improvement still remains in statistical methods (e.g., model and variable selection) and integration of theory (e.g., biotic interaction and functional traits) (Elith and Leathwick 2009; Zimmermann, Edwards et al. 2010). Even so, significant opportunity for enhancements to conservation outcomes presently exist when employing large, readily available, datasets implemented at large scales. This thesis (including accompanying Appendix A) presents only a small fraction of potential applications and avenues of improvement when using SDMs for large scale conservation. By employing a large dataset, I attempted to provide and improving large scale information on the distribution and abundance biodiversity, so that targeted investment in conservation (mitigating threatening processes, gazettal of protected areas) can improve conservation prospects for all biodiversity.

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Appendix: Linking habitat suitability and road mortalities across

geographic ranges

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Appendix

Abstract

Protected areas are established to conserve biodiversity and facilitate resilience to threatening processes. Yet protected areas are not isolated environmental compounds. Many threats breach their borders, including transportation infrastructure. Despite an abundance of roads in many protected areas, the impact of roads on biota within these protected areas is usually unaccounted for in threat mitigation efforts. As landscapes become further developed and the importance of protected areas increases, knowledge of how roads impact on the persistence of species at large scales and whether protected areas provide relief from this process is vital. We took a two-staged approach to analysing landscape-scale habitat use and road-kill impacts of the common wombat (Vombatus ursinus), a large, widely distributed herbivore, within New South Wales (NSW), Australia. Firstly, we modelled their state-wide distribution from atlas records and evaluated the relationship between habitat suitability and wombat road fatalities at that scale. Secondly, we used local-scale fatality data to derive an annual estimate of wombats killed within an optimal habitat area. We then combined these two approaches to derive a measure of total wombats killed on roads within the protected area network. Our results showed that common wombats have a broad distribution (290,981 km²), one quarter (24.9%) of their distribution lies within protected areas, and the percentage of optimal habitat contained within protected areas is 35.6 %, far greater than the COP10 guidelines of 17 %. Problematically, optimal habitat within protected areas was not a barrier to the effects of road-kill, as we estimated that the total annual count of wombat road-kill in optimal habitat within protected areas could be as high as 13.6 % of the total NSW population. These findings suggest that although protected areas are important spatial refuges for biodiversity, greater effort should be made to evaluate how reserves confer resilience from the impacts of roads across geographic ranges.

Introduction

Roads are strongly correlated with both economic growth and natural resource degradation (Wilkie et al. 2000), while their effects on biota can extend outwards from the road edge for hundreds of metres (Bissonette and Adair 2008; Forman and Alexander 1998). Road networks are expanding globally, pressing the need to assess the conservation implications of their impact on biodiversity and existing conservation efforts. To date, most research on road impacts has focussed on localised impacts over small spatial areas (Clevenger and Waltho 2000; Carr and Fahrig 2001; Ramp et al. 2005; Klöcker et al. 2006; Roger and Ramp 2009), but assessment over large geographic regions is critical because road impacts operate along a continuum of scales that includes biogeographic, landscape, and patch-level effects (Trombulak and Frissell 2000; Forman et al. 2003; Grilo et al. 2011). Some notable exceptions do exist where landscape-scale studies on the effects of roads on wildlife have been evaluated (see Kramer-Schadt et al. 2004; Hobday and Minstrell 2008; Eigenbrod et al. 2009 for details). Landscape-scale studies are important in highlighting fragilities at large scales (see van der Ree et al. 2011) that are not apparent because some localised populations appear to be subsisting in road-impacted environments (Roger et al. 2011). Dependencies among adjacent populations across landscapes can destabilise metapopulations when one subpopulation becomes threatened, ultimately leading to a decline in overall species persistence (Gaston and Fuller 2008). In particular, species previously considered (or still considered) common, that have large geographic ranges or are able to disperse (seasonally or permanently), are frequently affected by breakdowns in exchange among populations at landscape scales (Epps et al. 2005).

Appendix

Landscape-scale considerations of the impacts of roads on biodiversity is of direct relevance to global conservation efforts, for which the primary mechanism is the setting aside of protected areas (Regan et al. 2008). Due to the variety and severity of threats facing wildlife, protected areas are instrumental in conferring resilience to threatening processes (McDonnell et al. 2002). Protected areas are at the forefront of many regional and global conservation strategies, such as the tenth annual meeting of the Conference of the Parties (COP 10) on biosafety protocol. Protected areas are not impenetrable and many threatening processes breach their borders (Deguise and Kerr 2006). It is therefore crucial to be able to quantify how effective protected areas are protecting the species within them (Pressey et al. 2000; Crofts 2004; Wilson et al. 2007; Alvaro Soutullo et al. 2008). The impact of roads in protected areas is often overlooked by conservation programmes (Ament et al. 2008), despite many protected areas having surprisingly high densities of roads within them that have been directly linked to population declines (e.g. Ramp and Ben-Ami 2006; Ament et al. 2008). Most protected areas fulfil the dual roles of protecting resource values as well as providing visitor enjoyment, but these roles are often difficult to balance as visitation can impact natural systems (Ament et al. 2008). Globally, road-kill remains a pervasive threat for large numbers of species both outside of and within protected areas (Clevenger et al. 2003; Fahrig and Rytwinski 2009).

The effect of roads on wildlife is often ignored because road fatalities have been considered unlikely to affect persistence of common species; which in most cases constitute the majority of road-kill (Forman and Alexander 1998). Lack of information on threats to common species is not new. Conservation investment routinely targets already threatened species and the areas where they are still found (McKinney and Lockwood 1999; Warren et al. 2001; Devictor et al. 2007), yet threatening processes also impact on common species (Gaston and Fuller 2008; Roger et al. 2011). Common species are defined as those species

Appendix

that are both abundant and widespread (Gaston and Fuller 2007). There is growing evidence that large numbers of species that currently meet these criteria are undergoing substantial decline (Caughley 1994; Gaston and Fuller 2007, 2008); however, responses of common species to land-use change remains largely unexplored (for exceptions see Epps et al. 2005). Given the functional role many common species have in facilitating ecosystem processes (Gaston 2008; Gaston and Fuller 2008), maintaining viable and functional populations of common species is a vital component of biodiversity conservation efforts (Lennon et al. 2004; Lyons et al. 2005; Pearman and Weber 2007).

Our objective was to assess road fatalities rates within protected areas for a common marsupial species, the common wombat (*Vombatus ursinus*); a typical example of a species that is impacted by roads at small scales (Roger et al.. 2011) but for which the implication of road fatalities over large scales has not previously been examined. We focussed on assessing the impact of road fatalities in optimal habitat of protected areas due to the importance of these areas for species persistence. We addressed this landscape-scale question by applying a two-step approach. First we modelled their state-wide distribution from atlas records. We then used this information to evaluate the relationship between habitat suitability and annual wombat road fatalities across their geographic range. Secondly, we used local fatality data to derive an annual estimate of wombats killed within an optimal habitat area. We then combined these two approaches to derive an estimate of the annual total of wombats killed on roads within the protected area network.

Methods

Study species

The common wombat is a large burrowing marsupial and is thought to be both widespread and abundant throughout temperate south-eastern Australia (McIlroy 1995) (Fig. 1), however, informative data describing population distributions across its range is currently lacking (Roger et al. 2007). Despite this, their distribution appears to have contracted southwards since European settlement expansion circa 1860's (McIlroy 1995; Buchan and Goldney 1998). Unlike many native species, common wombats benefit from the clearing of native bushland as it increases foraging habitat (Evans 2008). Their broad niche suggests they are a relatively robust and adaptable species, reflected by their use of agricultural and other modified landscapes (Roger et al. 2007; Roger and Ramp 2009). Adaptation to modified landscapes brings considerable cost, however, as they are frequently killed on roads because they exhibit little road avoidance or aversive behaviour (Roger and Ramp 2009).

Figure 1 approximately here

Study area

Our analysis incorporated both broad-scale and fine-scale analyses. To define the geographic range of the common wombat we set the landscape extent of available habitat to be within New South Wales (NSW) and the Australian Capital Territory (ACT), an area that encompasses approximately half of the species' total distribution (Fig. 1). Given the broad distribution of the species it was not possible to obtain similar quality information on habitat use across the species entire range. NSW is Australia's most populous state and is located on the east coast of the continent with an area of 810,000 km². The ACT is an enclave within NSW with a total land area of 2,400 km². There are 752 protected areas that are greater than 10 km² within the NSW and ACT, with a total area of 86,164 km² for all protected areas. For the purpose of analysis we treated both the ACT and NSW as one modelling domain. To obtain an estimate of the annual total of wombats killed within optimal habitat inside protected areas we used previously published information from a 26-km segment of the Snowy Mountains Highway in Kosciuszko National Park (35°19'S, 148°14'E) (Roger and Ramp 2009).
Modelling common wombat distribution

We used common wombat presence data from records held within the NSW Atlas dataset obtained from the NSW Department of Environment Climate Change and Water (DECCW 2009). Records included data from multiple mammal surveys, collected between 1990 and 2009 by government staff, researchers, naturalists, environmental consultants, land management officers, and the public. To minimise spatial errors, we excluded all records before 1990 and where spatial uncertainty was greater than 500 m. Species occurrence data has been routinely used in species habitat modelling (Guisan and Thuiller, 2005, Robertson et al. 2010) as it provides an estimate of species' distributions across large scales where data are often scarce. We avoided the use of randomly selected pseudo-absence points (see Zarnetske et al. 2007) by locating wombat pseudo-absences from non-wombat sightings within the atlas database. We did this by examining the survey methods used to detect wombats and generated pseudo-absences where terrestrial mammals other than wombats were recorded using survey methods expected to identify the presence of wombats. Although these locations remain pseudo-absences, their selection has advantages over randomly selected points as they are derived from the same dataset as the presence data. To minimise type II errors, we excluded pseudo-absences within 320 m (equivalent to average wombat home range) of a known presence (Roger et al. 2007).

Predictive variables

We collated landscape-scale environmental and climatic variables for the study area using previously published studies of habitat selection by common wombats to guide variable selection (Skerratt et al. 2004; Roger et al. 2007; Evans 2008). Variables included descriptors of geography, vegetation, and climate (Appendix A). A Digital Elevation Model (DEM) was obtained from the Shuttle Radar Topography Mission (SRTM) with a spatial resolution of 3 arc seconds or approximately 90 m (Farr et al 2007). Slope and aspect were derived from the

DEM using ArcGIS 9.2 (ESRI 2007). Indices for topographic wetness (an estimate of the accumulation of overland water flow across catchments), slope steepness (Moore et al. 1991), and roughness (Allmaras et al. 1966) were generated to describe the surface properties of the DEM. We used the Enhanced Vegetation Index (EVI) satellite data obtained from the Terra Moderate Resolution Imaging Spectroradiometer (MODIS) sensor (Justice et al. 1998). Both EVI mean and variance were calculated for a 10-year period (2000-2009) at a resolution of 250m. Digital information for water bodies (floodplains, lakes, reservoirs, and lagoons) was obtained from DECCW, derived from a combination of classification of spectral classes of Landsat MSS and TM imagery, along with ancillary wetland information (Kingsford et al. 2004). A digital image of major rivers was also obtained from DECCW, allowing for distance to water bodies and main rivers to be calculated as predictive variables. Climatic variables across the study area were obtained using the correlative modelling tool BIOCLIM 5.1 (Nix 1986). Twenty seven climatic parameters were interpolated from recorded climatic data and elevation (Nix 1986; Houlder et al. 2000) (Appendix A).

Model development

We avoided collinear variables in any given model by reducing the number of variables prior to the selection of a final model. As we did not wish to subjectively reduce variables, we followed a data-driven pathway to reduce variables prior to model selection (Pinheiro and Bates 2000; Hastie et al. 2001; Thomson et al. 2010). We initially grouped the predictive variables into six collinear categories (geographic, vegetation, temperature, precipitation, moisture, and water). Using a logistic Generalized Additive Model (GAM) within the R statistical environment (package 'gam', R Development Core Team, 2005), we examined the goodness-of-fit values for each variable using the pseudo R^2 . Following this, we selected a single representative variable from each of the six collinear groups to be used in the model selection process (total of six predictors).

We carried out a further model selection process using all 64 unique combinations obtained from the six identified predictor variables (Table 1). To validate the models we ran a bootstrapping procedure using the .632 estimator rule (Hastie et al. 2001), which is suitable when distributions are unknown, and can outperform cross-validation (Efron 1983; Efron and Tibshirani 1997). This approach provides a predictive performance estimate of a model without the expense of collecting a completely new model testing set (Wintle et al. 2005).

#Table 1 approximately here#

We evaluated model performance by calculating the average area under the receiver operating curve (AUC) across all bootstrapped replicates and used this to evaluate the extent to which each model successfully estimated positive and negative observations (Fielding and Bell 1997; Hirzel et al. 2006). A best model set was selected by identifying all models with an AUC value within one standard error from the model with the highest AUC value. The one standard error rule is often used to find a more parsimonious model than the top model selected in the model selection process (Hastie et al. 2001). Selection of a final model from the best model set was made using a trade-off between models in the best model selection was repeated using Akaike's Information Criterion (AIC) to cross-check the model selection process. Hierarchical Partitioning was used to calculate the independent contribution of each variable across all model combinations (Mac Nally 2000). Fitted values of wombat habitat suitability were then predicted across the entire study area at a resolution of 90 m.

The distribution of wombat habitat suitability values was then used to obtain an estimate of the common wombat distribution across the study area. A threshold for occupancy was identified by applying the Jenks' national breaks method, which determines the best arrangement of values into classes by iteratively comparing sums of the squared

difference between observed values within each class and class means (Brewer and Pickle 2002). The geographic range of the wombat within the study area was subsequently defined by suitability values above 0.16.

Linking suitability to road fatalities

To assess fatality rates of common wombats on roads throughout their geographic range we estimated the distribution of wombat fatalities on roads in NSW and the ACT. We obtained information on the distribution of roads within NSW and the ACT from DECCW (Appendix A). The road layer contained 2,632 segments of road throughout NSW (total length 50, 157 km), where segment were defined as sections of road between intersections. There were five categories of roads included in the road layer we used for our analysis: dual carriageway, principal road, secondary road, minor road and track, however, we excluded tracks from the analysis. We grouped dual carriageways and principal roads into highways', secondary roads we labelled major roads' and minor roads were minor roads'. All roads used in the analysis were sealed. To identify collision locations we used the TADS (Traffic Accident Database System of NSW), a database that includes statistics on road traffic accidents in NSW (Appendix A). Collision data between wildlife and vehicles are only included in TADS when reported to NSW Police because of human injury or extensive vehicle damage (Ramp and Roger 2008). There are very few data detailing the frequency of wombat vehicle collisions and the number of associated fatalities across their range, and although TADS considerably underestimates wombat fatalities (most collisions only result in injury to the animal and therefore go unreported), no other state-wide data exist. There were 150 wombat-related accidents recorded in the TADS database for the ten year period between 1996 and 2005. To provide context for this underestimate, Roger and Ramp (2009) reported 209 wombat road fatalities between the period of 1998 and 2005 from a single 40 km stretch of road.

Our approach therefore was to utilise information from TADS to infer the spatial distribution of collision likelihood, rather than using it to infer actual numbers killed annually within the study region. To estimate wombat road fatalities per kilometre of road within NSW we sampled all wombat fatality records contained in the TADS database using ArcGIS. Road segments with no reported collisions were assigned zero. To account for variability in road use (we did not have access to traffic volume data for all roads), the ratio between wombat-related vehicle collisions and all other wildlife-related vehicle collisions recorded in TADS was calculated and standardised by length of road segment.

To assess the relationship between habitat suitability and the mean probability of a wombat fatality, suitability values were averaged for each road segment and weighted by the length of the segment using Hawth's Analysis Tools add-on for ArcGIS (Beyer 2004). We used the Jenks' natural breaks classification to stratify wombat suitability probabilities into four categories: unsuitable (≤ 0.16), medium (≤ 0.45), high (≤ 0.78), and optimal (≤ 1). This enabled us to compare probabilities of wombat fatalities from the TADS database within habitat suitability categories across different road categories. We examined the relationship between habitat suitability groups and the mean probability of a wombat fatality using SPSS (SPSS Inc., 2006). Differences between habitat suitability groups in relation to road class were examined using two-way analysis of variance (ANOVA). Significant differences between means were compared using Tukey's Least Significant Difference (LSD) methods.

Fatality rates within protected areas

To derive a measure of annual wombat road fatalities per kilometre of road within optimal habitat in protected areas we used an additional source of road fatality data (see Roger and Ramp 2009). Fine-scale fatality information across the entire study area and for different levels of habitat suitability, within and outside protected areas, would be optimal but these data do not currently exist. For the purpose of this study, however, identifying the

susceptibility of wombats to fatalities within optimal habitat in protected areas is sufficient. Fatalities of common wombats were recorded on a 26-km segment of the Snowy Mountains Highway within Kosciuszko National Park over a five year period (Fig. 2). Wombat fatalities were recorded using a hand-held global positioning system (GPS) device on average three days per week between 2002 and 2006. Carcases were removed from the roadside after recording to avoid double counting. The road segment was travelled 560 times, recording 117 wombat fatalities. Assuming wombat fatality frequencies were temporally correlated, we calculated monthly frequencies by dividing the recorded number of wombat fatalities with the number of trips each month. The actual number of fatalities per month was estimated by multiplying the monthly ratios with the number of days each month and averaged over the five year period. This resulted in an average fatality rate per month, which we summed to obtain the total rate per year. We then standardised this rate for each kilometre of road by dividing the total rate per year by the total number of kilometres driven each trip.

#Figure 2 approximately here#

We then calculated the total kilometres of road length within protected areas that fell within the optimal suitability category using ArcGIS. Since our fine-scale wombat fatality data came from a road within an optimal habitat area (≥ 0.78), we could only reliably estimate wombat fatalities for optimal suitability areas within NSW in protected areas. As a final measure of range-wide road fatality impacts we multiplied the rate of wombats killed per year from the Snowy Mountains Highway by the total length of roads in protected areas that fall within optimal wombat habitat. We recognise that we had to make several assumptions in order to derive this calculation, and as a result the calculation only serves to provide a rough estimate of the numbers of wombat killed in optimal habitat protected areas. Firstly, we assumed non-stationarity in the relationship between road presence and road-kill, while also assuming equal distribution of wombats across optimal habitat areas.

Results

Wombat habitat suitability model

There was good agreement on the final model among the two methods of model selection: the top AIC model was within 1 SE of the top AUC model. To maximise parsimony we chose the top AUC model which selected mean EVI, mean annual temperature, and mean moisture index of the warmest quarter. The final model explained 70.6% of the deviance (AUC 0.802) (Table 2).

Table 2 approximately here

Mean annual temperature was negatively correlated with wombat habitat suitability, with suitability linearly declining in the warmer regions of north-eastern NSW (Fig. 3). Suitability declined steeply after a mean moisture of 0.4 was reached (mean moisture is scaled from 0-1). Suitability was significantly, but weakly, associated with mean EVI (Fig.3). The inclusion of EVI, a measure of greenness (similar to the normalised vegetation index used in Roger et al. (2007)), indicated that although wombats make use of agricultural land for grazing, their distribution is constrained to wooded areas and/or cleared areas in proximity to remnant vegetation.

Figure 3 approximately here

The habitat suitability model identified areas of optimal habitat mostly within the mountainous regions of the Great Dividing Range and in some coastal temperate regions (Fig. 4). The common wombat distribution appears to be bounded by a large climatic envelope that limits them to the mesic and semi-arid environments of south-eastern Australia, concurring well with expert opinion on common wombat distribution (Triggs 1988).

Figure 4 approximately here

Linking suitability to road fatality

Habitat suitability was positively correlated with fatality likelihood (Fig. 5, $F_{0.030, 2.448} =$ 10.453, *P*<0.001). Results of Tukey's Least Significant Test revealed large differences between the lowest suitability grouping (≤ 0.16) and the highest (≤ 1) as expected. The probability of a wombat fatality also varied among road categories and suitability groupings (Fig. 6). Significant differences between habitat suitability groups in relation to road class were observed ($F_{0.052, 2.426} = 18.515$, *P*<0.001). Significant variation once again occurred between the lowest suitability grouping and the highest.

Figures 5 and 6 approximately here

Distribution and fatality rates in protected areas

Common wombats were predicted to have a geographic range of 290,981km² (areas with habitat suitability above 0.16), distributed throughout eastern NSW and the ACT (Fig. 4) and for which 24.9 % is currently protected as national park or conservation reserve. The component of the total range considered optimal habitat (above 0.78) was calculated as 44,035 km², 35.6 % of which is contained within protected areas.

Using the fine-scale information from the Snowy Mountains Highway we estimated that an average of 8.9 wombats were killed each month (with an annual average of 92.3), equating to 3.53 wombats per km of road per year. Given that there are 804 km of similar roads in optimal habitat within protected areas in the study area, we estimated that a total of 2,841 wombats may be being killed annually in these areas. Previous research in the same optimal habitat area has estimated a density of 1.3 wombats per km² (Roger et al. 2007). Extrapolating this value by the total area of optimal habitat in protected areas (15,676 km²) equates to a population of 20,901 wombats within optimal habitat protected areas. Based on

these figures, it is plausible that the total number of wombats killed annually within optimal habitat in protected areas is around 13.6% of the total population.

Discussion

Empirical examples are needed to support theories developed primarily via simulation (e.g. Roger et al. 2011). Research has focussed on developing models of wildlife fatality hotspots (Ramp et al. 2005; Roger and Ramp 2009), the efficacy of mitigation (Clevenger and Waltho 2005), barrier effects on genetic drift and population viability (Gerlach and Musolf 2000), landscape planning (Jaarsma and Willems 2002), and the effects of road type on population persistence (Jaeger et al. 2005). However, this research is limited in scope and availability of data, and cannot legitimately comment on how road development impacts on biota over larger spatial scales. Continued collation of road kill data along with target monitoring will enable a robust exploration of data-driven parameter bounds, limiting carried uncertainties. Our research is one of the first to begin to quantify landscape extent impacts of roads over this large scale, but some notable exceptions do exist (see Hobday and Minstrell 2008; Fahrig and Rytwinski 2009 for details). Thus, although considerable uncertainty exists (due primarily to data limitations), we believe our two-step approach provides an important basis to begin to quantify how road fatalities impact on biodiversity. Roads will likely increase in significance as a form of disturbance over the coming decades making it all the more crucial.

The wide geographic range (211,107 km²) of common wombats across a range of elevations throughout eastern NSW confirms previous studies describing common wombat extent (Borchard et al. 2008; Buchan and Goldney 1998; Catling et al. 2000; Matthews et al. 2010; Roger et al. 2007). However, contrary to the ecological/biological mechanisms that have been proposed as good predictors of wombat distribution at local scales of analysis (Catling et al. 2000, 2002; Roger et al. 2007), regulation of wombat distributions across their

geographic range is most strongly correlated with climatic controls (Guisan and Thuiller 2005). Further investigation into the influence of ecological/biological mechanisms in shaping large-scale distributions of species is warranted, providing more robust estimates of distribution and abundances (Kearney & Porter 2009). The selection of mean annual temperature suggests that across the species' geographic range it is not extreme temperatures but mean temperatures that drive its distribution. Common wombats are also influenced by vegetation and the inclusion of mean EVI reflects wombat preference for good foraging habitat near cover (Evans 2008). McIlroy (1973) and Buchan and Goldney (1998) considered forest cover important for providing protection from predators and weather conditions. Unfortunately for common wombats, many roadside environments present these attributes by offering cleared land for grazing in close proximity to wooded habitat (Roger et al. 2007), excacerbating the problem of fatalities by attracting wombats to these locations. Given that the geographic range of common wombats has contracted southwards since European settlement (McIlroy 1973), it would be interesting to explore if this southern contraction is a result of changing climatic conditions, human changes in land-use, introduced threats, or a combination of all three.

In this study we assessed the relative abundance of common wombats within protected areas across the study area as well as the percentage of optimal habitat contained within the protected areas network, estimated using a habitat suitability model. We found that one quarter (24.9 %) of common wombat estimated geographic range lies within protected areas, while the percentage of optimal habitat represented within the protected areas network was 35.6 %. Our results suggest that protected areas constitute an important spatial refuge for common wombats and at first glance this seems to bode well for the continued persistence of the species.

Unsurprisingly, we also showed that the probability of a wombat road fatality increases with increasing habitat suitability (Fig. 5). This finding makes sense given that suitable habitat is correlated with higher densities of species, and this in turn can result in increased road fatality rates if animal density is linearly correlated with fatality likelihood (Forman and Alexander 1998). Nevertheless, it was important to demonstrate the link between habitat suitability and the probability of wombat road fatalities which to our knowledge has not been previously demonstrated. In related work, Grilo et al (2011) observed a higher frequency of road fatalities on roads traversing continuously forested habitat. The authors highlighted that road networks in well-connected landscapes appear to be a serious threat to long-term population stability and viability. Although not specific to protected areas, their finding provides further evidence that road fatalities in areas considered important for species conservation are of concern for a wide range of species.

The relationship between road category and suitability grouping allowed us to demonstrate that the probability of a wombat fatality within highly suitable habitat remains high despite road category (Fig. 6). This is important for management which may not have considered major and minor roads as significant locales of wombat fatalities. The relationship between road category and road fatality is not linear, with various hypotheses presented to predict the effects of traffic on road-kill probability (see Seiler 2004; Jaeger et al 2005 for details). How important road category is in terms of contributing to the frequency of road fatality seems highly dependent on species, with road avoidance behaviour likely playing a large role in determining susceptibility (Jaeger et al. 2005). By broadening the scope of study, research can begin to quantify landscape extent impacts of roads on populations and how patterns of habitat use and selection change with road-based fatality rates. It is vital that we develop an understanding of the motivations behind animal presence and movement to fully comprehend how roads interact with susceptible species. If species are highly susceptible to

the impacts of roads then both rare and abundant species are potentially at great threat especially if their reproductive rates or recruitment rates are low.

A common assumption of protected area networks is that they act as sources for species across their geographic ranges, particularly if they constitute substantial components of the remaining or better quality habitat (Gaston 2008). We found strong support for this assumption with wombats favouring protected areas, but the number of fatalities occurring within these areas is problematic. Indeed, we previously reported that annual road fatalities within a 30 km^2 protected area appeared to match the total population estimate for this area (Roger et al 2007), a finding that implies that dispersal to this location was the only explanation for their continued existence there. This raises the question of whether protected areas that are infiltrated by roads may themselves contain localised population sinks, and effort should be expended in evaluating how protected areas confer resilience from the impacts of roads. Unfortunately, to test this theory for common wombats we currently lack information on how many are killed outside protected areas. We cannot assume that the relationship between density and fatality rates is linear, and hence a comparison of fatality rates for different habitat suitability and population densities across their geographic range would be a valuable contribution to the research. Likewise information on traffic volume (which we are lacking) has been shown to be important in assessing road impacts (Seiler 2004; Jaeger et al. 2005).

In a review of the ecological effects of roads, Forman and Alexander (1998) considered road fatalities unlikely to affect persistence of common species because birth rates were presumed to exceed road fatality rates for many species. As a result, species level conservation in road-impacted environments has remained focused on species already threatened with regional extinction in the near future (Forman et al. 2003). However, like the common wombat, a number of studies have recently documented population level depletions

of common species as a result of road impacts at local scales (Jones 2000; Ramp and Ben-Ami 2006; Fahrig and Rytwinski 2009; Roger et al. 2011). There is a pressing need to quantify how different forms of land-use impact on biodiversity and how ultimately common species will persist as processes that underpin their decline intensify. How the threat of roads within protected areas impacts on species persistence should be of vital interest to conservation practitioners around the world.

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Tables

Table 1.

Model results for wombat sighting probability. Table presents the number of models within one standard error (1SE) of the best model and the number of times each variable was selected within 1SE of the best model for AUC (AIC results are also presented for comparison).

DIS_RIV	ELEV	EVIM	AMT	VAR_P	MIWQ	AUC	AIC
1	1	1	1	0	1	0.802	16756.95
1	1	0	1	0	1	0.802	16898.99
0	0	1	1	0	1	0.802	17206.19
1	0	1	1	0	1	0.802	17037.78
	-		-		-		

1	1	1	1	0	1	0.803	16582.55
0	1	1	1	0	1	0.803	16889.4
0	1	0	1	0	1	0.805	17667.73
1	1	0	1	0	1	0.805	17477.6
0	1	1	1	0	1	0.805	17575.49
1	1	1	1	0	1	0.806	1744.28
1	0	0	1	0	1	0.806	18119.16
1	0	1	1	0	1	0.806	18002.43
0	0	0	1	0	1	0.810	18244.57
0	0	1	1	0	1	0.810	18126.3

Symbols for predictor variables occurring in model set are distance to rivers (DIS_RIV), elevation (ELEV), mean EVI (EVIM), annual mean temperature, (AMT), Precipitation Seasonality (VAR_P), and mean moisture index of warmest quarter (MIWQ). The variable VAR-P was not selected in any of the models within one standard error (1SE) of the best model

Table 2.

Variable coefficients and chi-square scores for the top wombat sighting probability model.

The AUC value for the final model was 0.80243.

Variable	Coefficie	Chi-square	pvalue	Independent
	nts			contribution
Intercept	4.72			
Annual mean temperature (ºC)	-0.38	457.18	<0.001	71.68
Mean moisture index of warmest quarter	-0.46	803.54	<0.001	25.17
(MI)				
Mean EVI	0	304.08	<0.001	3.15

The deviance explained by the final model was 70.6 %. Null deviance was 61,640 (df=44,462) and residual deviance was 18,140 (df=44,438).

MI = (1-exp(soilb×store/maxstore))/(1-exp(soilb)), where

maxstore is the maximum soil water availability in mm and soilb depends on soil type.

Figures

Fig. 1 Sighting locations of common wombats across their range throughout continental south-eastern Australia from 1990 to 2009. The boxed area represents the location of the local scale fatality data. The abbreviations are those used for the eastern states and territory of Australia: ACT (Australian Capital Territory); NSW (New South Wales); VIC (Victoria); SA (South Australia); and QLD (Queensland).

Fig. 2 Fatality data was collected from the Snowy Mountains Highway in southern NSW. The sampled road segment as well as protected area boundaries are displayed.

Fig. 3 The partial residual plot shows the relationship between a given independent variable and the response variable given that other independent variables are also in the model. The x-axis represents the range of values for each environmental variable, (3a) mean annual temperature (°C), (3b) mean moisture index of warmest quarter (($1-e^{soilb*store/maxstore}$) / ($1-e^{soilb}$), and (3c) mean EVI. The y-axis displays the smoothed environmental variable.

Fig. 4 Habitat suitability values (probabilities) across NSW and ACT. Major protected areas networks within NSW and the ACT are also shown.

Fig. 5 Mean probability and standard error of a wombat fatality within protected areas plotted against stratified suitability groupings.

Fig. 6 Mean probability and standard error of a wombat fatality within protected areas plotted against road category and suitability groupings. Highways were omitted from the optimal suitability grouping due to their absence in protected areas.

Fig. 1



Fig. 2







Fig. 4





Fig. 5







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Variable	Resolution	Source	Category
Elevation	90 m	SRTM	Geographic
Slope	90 m	SRTM	Geographic
Aspect	90 m	SRTM	Geographic
Surface Roughness	90 m	SRTM	Geographic
Wetness Index	90 m	SRTM	Geographic
Mean yearly EVI	250m	DECCW	Vegetation
Mean yearly variance of EVI	250m	DECCW	Vegetation
Annual Mean Temperature	90 m	AnuClim	Temperature
Mean Diurnal Range (Mean(period max-min))	90 m	AnuClim	Temperature
Isothermality 2/7	90 m	AnuClim	Temperature
Temperature Seasonality (C of V)	90 m	AnuClim	Temperature
Max Temperature of Warmest Period	90 m	AnuClim	Temperature
Min Temperature of Coldest Period	90 m	AnuClim	Temperature
Temperature Annual Range (5-6)	90 m	AnuClim	Temperature
Mean Temperature of Wettest Quarter	90 m	AnuClim	Temperature
Mean Temperature of Driest Quarter	90 m	AnuClim	Temperature
Mean Temperature of Warmest Quarter	90 m	AnuClim	Temperature

Mean Temperature of Coldest Quarter	90 m	AnuClim	Temperature
and a composition of Control Quarter	<i>y</i> u		10
Annual Precipitation	90 m	AnuClim	Precipitation
Precipitation of Wettest Period	90 m	AnuClim	Precipitation
Precipitation of Driest Period	90 m	AnuClim	Precipitation
Precipitation Seasonality(C of V)	90 m	AnuClim	Precipitation
Precipitation of Wettest Quarter	90 m	AnuClim	Precipitation
Precipitation of Driest Quarter	90 m	AnuClim	Precipitation
Precipitation of Warmest Quarter	90 m	AnuClim	Precipitation
Precipitation of Coldest Quarter	90 m	AnuClim	Precipitation
Annual Mean Moisture Index (M.I.)	90 m	AnuClim	Moisture
Highest Period Moisture Index	90 m	AnuClim	Moisture
Lowest Period Moisture Index	90 m	AnuClim	Moisture
Moisture Index Seasonality (C of V)	90 m	AnuClim	Moisture
Mean Moisture Index of High Quarter	90 m	AnuClim	Moisture
Mean Moisture Index of Low Quarter	90 m	AnuClim	Moisture
Mean Moisture Index of Warm Quarter	90 m	AnuClim	Moisture
Mean Moisture Index of Cold Quarter	90 m	AnuClim	Moisture
Distance to major rivers in New South Wales		DECCW	Water
Distance to water bodies in New South Wales		DECCW	Water
Distance to Road Layer of New South Wales		DECCW	
Reserve Layer of New South Wales		DECCW	

Traffic and Accident Database System

Roads and Traffic Authority of NSW

of New South Wales

Variables and their source used in the habitat suitability model

All variables used were for the extent of NSW. The three layers provided by DECCW were

for Australia and clipped to the NSW extent.