RESOURCES, DATA RESOLUTION AND SMALL MAMMAL RANGE DYNAMICS

Nerissa Haby

B. Env. Sci. (Hons)

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for the degree of Doctor of Philosophy

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Ecology and Evolutionary Biology

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Table of contents

Detailed revisions made to 'Resources, data resolution and small mammal range dynamics ' in response to general (a) and minor comments (b), included in Examiner 1 and 2 reports.

E	Comment	Response	Pg
a. General comments			
1	P 10. last paragraph: What does it mean that SDM should be readily generalised? Should an even more important attribute be that species models produce distribution maps that are accurate?	Reworded: ' ..should produce more accurate geographic maps of species distributions across its range. and over time. that can be reliably interpreted..'	11
1	P 11. last paragraph: How might the fragmentation of habitat effect occupancy predicted in a SDM?	The effects of habitat fragmentation on predicted occupancy were already highlighted in the Discussion section 'Capacity to improve model interpretation through realised niche characteristics': 'In addition. the history of vegetation clearance in the landscape may cause the reasonably dispersal limited *I. o. obesulus. R. f. greyi* and *R. l. lutreolus* to be absent from suitable patches due to local extinctions. or occupy suboptimal habitat. All of these dynamics lead to more complex species responses to environmental gradients (Holt et al. 2005). increased uncertainty or bias in SDM predictions.'	21
1	P 12. 26. 42. 58: More detail on techniques used to define 'absence' data.	Additional justification was added to p12. p42 and p58 in the revised thesis. but not p26 where a different dataset was used.	
1	P20. third paragraph: Most empirical investigations describe how species live and use resources with all the constraints that are imposed on them by the presence of competitors. predators. resource shifts and the like (realised niche). Although this difference is clarified in later chapters. most readers are likely to have in mind the classical Hutchinsonian niche concept rather than newer (and still debated) concepts that are assumed here.	Reworded: 'First. empirical investigations into species' resource use and life history attributes would indicate variables required for basic survival and reproduction '	20
1	P40 and 41. Table 1: Which local investigations provided the information on demographic parameters (p43)? Some of the data look a bit unusual. For example. the 8 young used per female for *Antechinus flavipes* seems low: the species usually has litters of 10-12. I was a bit surprised also that Rmax values from voles and muskrats had been substituted for values for native Rattus. Has Rmax not been estimated from local studies for *R. fuscipes. R. lutreolus* or other native species?	The core references used in compiling this table have been added to a new Appendix XII in the revised thesis. These references should aid in conveying the balance of information incorporated into the population viability models. such as reproductive rates being set to take into account mortality in developmental stages. In the case of *A. f. flavipes* that can give birth to 8-10 young. they have on average 7.6 young (Smith 1984). All population viability analysis models were set to support stable populations (long-term density equilibrium. with stochastic variability). with information on species ecology incorporated where available. Unfortunately. Rmax values have not been estimated for most native species. which lack long-term time-series data due to field surveys being predominantly short-term and localised. For this investigation. the values adopted from species with similar ecology were similar to estimates calculated for these species based on aspects of their biology (Table 1. p61). but since they were obtained from ongoing monitoring programs. thought to be more realistic.	
1	P 56. top: Most small mammals in arid. alpine, temperate and other environments use burrows and shelter and are nocturnal, so these traits may not be adaptations to desert life *per se* but may just be adaptive in any environment.	Reworded: 'Additional behavioural adaptations that aid species' persistence in these harsh environments. include..'	56

E	Comment	Response	Pg
1	P59, Table 1: Flooding and small and spatially explicit refugia may be extremely important to small mammal dynamics in the Channel Country IBRA region. Depending on when field sampling was carried out, animals could appear to be associated with quite different sets of climatic and-especially-environmental variables. Is it possible to define the conditions that prevailed when species' sampling was carried out and obtain better model fits by running analyses for data obtained during dry and wet periods?	Unfortunately available data were obtained from different times that don't align well. However, areas most likely to be flooded and refugia were represented in the existing SDM by including: i) elevation and distance to watercourse, and ii) vegetation community mapping and soil water holding capacity *A. laniger*, *D. byrnei* and *N. cervinus* all demonstrated a positive correlation with distance to watercourse that likely represents the dynamics of gibber plains rather than flood dynamics, while species occurrence was positively correlated with soil water holding capacity of the solum. Areas with higher soil water holding capacity are likely to indicate preferred habitat, either for shelter or ready source of food (refugia). The occurrence of both *L. forresti* and *S. macroura* was poorly predicted, however, the species' association with understorey was reflected in the positive correlation with shrubland and hummock grassland (Table 2: Appendix XXIV), respectively. However, it is likely the SDMs were lacking key variables, or that the areas surveyed within the Channel Country IBRA region contained sub-quality habitat for these species that is only occupied during periods of greater resource availability	
1	Finally the poor model fit for *L. forresti* and *S. macroura* is almost certainly not because these species have distributional gaps in or near the Channel Country (p68, bottom): the Channel Country IBRA region is a stronghold for both species. The gap that appears in distribution maps for these species is in the Simpson-Strzelecki IBRA region, which was not modelled here.	This is an important point to clarify. This sentence has been removed.	
2	The introduction does not clearly state the aims of the thesis or provide direction for the thesis. While each chapter states the hypothesis being explored, it would have been useful to include this in the Introduction to a) tie the chapters together and b) show the thought process that the candidate went through to develop a set of cogent, related research chapters.	In the revised version, the clarity of the overall direction of the thesis has been improved by collating and representing the aims in the Introduction.	6-7
2	I found it confusing following the progression of SDMs through Chapters 1-3. Providing a general outline of the development of the SDMs in the Introduction would have made this clearer.	The data used in each chapter differs. Because of this, the detailed descriptions of how the datasets were derived are left to the respective methods sections, including figures to illustrate points where possible. Given the thesis structure, I have not included a summary in the Introduction. However, the overall clarity of the role and differences between each chapter has been improved in the revised thesis by summarising aims in the Introduction and the merger of tables into Appendix IV	
2	There are multiple versions of the table describing landscape variables applicable to Chapters 1-3.	No merged into a single appendix (Appendix IV)	
b. Minor comments			
1	Pii and 57, bottom: *N. cervinus* does eat a lot of seed, but it has been (tentatively) classified as an omnivore. See Murray et al. 1999 Wildlife Research 26: 421-437.	*N. cervinus* has been classified a granivore on the basis of its diet consisting of up to 95% seed, some plant material and <5% invertebrates (Watts 1970). The evidence used to support omnivores diet in Murray et al. 1999 is based on *N. alexis*, a species that consumes a broader range of items (Murray and Dickman 1994a; 1994b). Giver this, I have left *N. cervinus* being summarised as a 'granivore', as it is this aspect of its ecology that I was interested in exploring in SDMs and relative to the other species.	

E	Comment	Response	Pg
1	P3 (117), 4 (18), 43, 72 (L12), 85: replace effect, effected, or effecting with affect, affected, affecting.	Fixed	
1	P4. L5: A range shift reflects species maintaining its niche by tracking suitable climatic or environmental conditions.	Fixed: '... tracking suitable climatic or environmental conditions may become increasingly difficult ...'	4
1	P5. point v: Australia does not have a majority of the World's marsupials (Aust 157. Sth America and New Guinea 172)	Reworded: 'Approximately 85 % of Australian mammals are endemic to the continent. including many of the world's marsupials and monotremes (Steffen *et al* 2009).'	5
1	P12. last line: replace measured with measures.	Fixed	
1	P14. first line: Check spelling of imperial.	Fixed	
1	P24. line 13:insert on. between effect and the.	Fixed	
1	P39. L19: delete in.	Fixed	
1	P39. bottom line: insert fine between relatively and environmental.	Fixed	
1	P52. L8: replace influences with influence.	Fixed	
1	P68. two lines from bottom: replace there with these	Fixed	
1	P68: bottom paragraph: a couple of references are made to Kotler and Brown 1988 and to Shenbrot et al 1999 suggesting that these authors have worked on Australian native mammals. However, they have not, so attributing specific observations on N. cervinus and other native species to these authors is not correct.	Reworded to clarify these citations support the advantages associated with bipedal gait. '*N. cervinus* builds deep burrows. and has a bipedal gait that enables species to better exploit patchy and sparse resources and better escape predation (Kotler and Brown 1988: Shenbrot et al. 1999).'	67
1	P72. Abstract: Opening sentences difficult to follow	Rewritten: 'In many correlative species distribution models biotic factors are excluded as interactions that have a secondary influence on species' occurrence via the *realised niche*. irrespective of a species' ecology. Over time biotic interactions can drive natural selection and changes within the *fundamental niche*. resulting in a contemporary dependency on resource availability for survival or reproduction. Resource availability may not be closely correlated with coarse climate variables. but represent the dynamics of nutrients and water availability cascading through trophic webs...'	71
1	P74. 10 lines from the bottom: the sentence beginning 'Over evolutionary time..." makes no sense.	Rewritten: ' Where resource selection improves survival or reproductive success of a species. natural selection can lead to phylogenetic and ontogenetic adaptations. polymorphism, adaptive radiation. or divergence. changes that are directly reflected in the *fundamental niche* '	73. 80
1	P78. L7: insert of between range and adaptations.	Fixed	
1	P82: Please explain the shading in Table 1.	Added: 'Shaded values indicate no support for the methods indicated.'	81
2	The recommendations mentioned in the introduction abstract and text haven't been identified. but trends have been.	Reworded: 'To determine whether recommendations derived from world-wide or international investigations can be applied in an Australian context...'	3
		' How suitable are world-wide recommendations for Australia's mammals?'	5
2	Justify the selection of the three climate variables have been used. and why not climatic variability.	Available spatial layers representing climatic variability in the Channel Country were highly correlated with mean values (mean Pearson's *r* for MT 0.85. RS 0.98). and when used in place of mean variables, produced similar results (i.e. within 1.6% DE for all species models. excluding the *N. cervinus* climate-only model that increased by 3.8% DE using climate variables. but was insufficient to outperform the climate-and-landscape model). Overall. while local rainfall events drive resource pulses vital for the long-term	

E	Comment	Response	Pg
		persistence of species in the region. the climate in this region is highly variable (Morton et al. 2011), and broad-scale climate patterns are yet to be accurately predicted. This information has been added to Appendix IV.	
2	Chap 2. Table 1. p29: Shouldn't the root zone water holding capacity read that a value of 0 was applied to polygons where > 50% of the area had moderate to very low capacity? It is currently written as <50%.	Fixed	
2	Chap 3. p39: word missing between relatively and environmental.	Fixed	
2	P51. The first sentence of the discussion needs rewording.	Reworded: 'This investigation detected a number of scale-dependent inconsistencies that related small changes in a landscape populated by fewer. more isolated populations with greater estimated rates of decline in the number of individuals and range shift (when detected) using coarse-scale environmental information.'	50

References not cited in the thesis

Murray BR. Dickman CR (1994*a*) Granivory and microhabitat use in Australian desert rodents. are seeds important? Oecologia 99:216-225

Murray BR. Dickman CR (1994*b*) Food preferences and seed selection in two species of Australian desert rodents. Wildlife Research 21:647-655.

Abstract

Extensive range shift and mass extinctions resulting from climate change are predicted to impact all biodiversity on the basis of species distribution models of wide-spread and data-rich taxa (i.e. vascular plants, terrestrial invertebrates, birds). Cases that both support and contradict these predictions have been observed in empirical and modelling investigations that continue to under-represent small mammal species (Introduction). Given small mammals are primary or higher order consumers and often dispersal limited, incorporating resource gradients that define the *fundamental niche* may be vital for generating accurate estimates of range shift. This idea was investigated through the influence of coarse to fine resolution, landscape- and quadrat-scale data on the range dynamics of four temperate- and five arid-zone small mammals.

This investigation determined:

i. Landscape-scale edaphic and biotic factors improved model fit, robustness and transferability for five species, especially arid species, via improved discrimination of unsuitable habitat (specificity) or suitable habitat for a wet-heath specialist (*Rattus lutreolus lutreolus*; Chapters 1 & 4)
ii. Quadrat-scale biotic factors improved model fit for three species; a dense understorey preferring species (*Isoodon obesulus obesulus*), granivore (*Notomys cervinus*) and insectivore (*Sminthopsis macroura*; Chapters 2 & 4),
iii. Coarse or fine resolution environmental data were more strongly correlated with the occurrence of different species across variables, reflecting the known ecology of these species (Chapters 2 & 4), and
iv. Fine resolution environmental data directly affected the spatial representation of available habitat in a coupled niche-population model, resulting in smaller shifts being detected for a greater number of species (Chapter 3).

Biotic interactions can drive adaptations that can lead to species becoming dependent on resource availability for survival or reproduction (Chapter 5). Complex ecosystem dynamics can make it difficult to distinguish resource partitioning caused by specialist adaptations (*fundamental niche*) from contemporary interactions (*realised niche*). In this investigation, evidence of biotic environmental variables defining the *fundamental niche* was provided by improved model transferability: representing direct (e.g. suitable habitat - *R. l. lutreolus*) or indirect influences on species' occurrence (e.g. rainfall via food availability on *I. o. obesulus*, *N. cervinus* and *Dasyuroides byrnei*). In addition to better representing resources, fine-scale environmental data affected the spatial configuration of available habitat, leading to smaller estimates of range shift. Hence, it is vital to consider species-environment relationships and conceptualise direct or proximal variables in order to construct robust SDMs. Improving this practice will also identify key relationships that influence community dynamics and require further empirical research (Chapter 5).

Acknowledgements

This PhD has been a wonderful experience for broadening my understanding of ecosystem dynamics, ecological theory and analyses, coding and trouble-shooting in new software packages. For this opportunity I sincerely thank my supervisors Barry Brook and Jeff Foulkes, and those who supported my application (Anita Smyth and the University of Adelaide, Divisional Scholarship).

I would also like to express my thanks to a wide range of additional collaborators:

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Co-authors- Tom Prowse, Stephen Gregory, Michael Watts, Steve Delean and Damien Fordham.

Manuscript reviewers- Mark Hutchinson, Charley Krebs, Stephen Gregory, Donna Harris, Bill Breed, Barry Fox, Sonia Croft, Robert Brandle, Bert Harris, Salvador Herrando-Pérez, Sharn Lucas, journal editors and reviewers (e.g. Joseph Merritt, Journal of Mammalogy).

Data used under licence agreement were sourced from the Biological Databases of SA (Dept. of Environment and Natural Resources, SA), Atlas of Victorian Wildlife (Dept. of Sustainability and Environment, Vic), Atlas of NSW Data (Dept. of Environment and Climate Change), Wildnet database (Dept. of Environment and Resource Management, Qld), NT Atlas and Spatial Databases (Dept. of Natural Resources, Environment, The Arts and Sport, NT).

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Declaration

This work contains no material which has been accepted for the award of any other degree or diploma in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text.

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* Haby, N.A., Delean, S. & Brook, B.W. 2011. Specialist resources are key to improving small mammal distribution models. Austral Ecology 37, 216-226.

[redacted] 30 Apr 2012

Nerissa Ann Haby Date

Introduction

HOW WELL DO EXISTING EVALUATIONS OF CLIMATE CHANGE IMPACTS ON RANGE DYNAMICS REPRESENT AUSTRALIAN SMALL MAMMALS?

N.A. Haby[1], J. Foulkes[2], B.W. Brook[1]

The Environment Institute[1] and Terrestrial Ecosystem Research Network[2],
School of Earth & Environmental Sciences, University of Adelaide,
Adelaide SA 5005, Australia

In review: Australian Mammalogy

STATEMENT OF AUTHORSHIP

HOW WELL DO EXISTING EVALUATIONS OF CLIMATE CHANGE IMPACTS ON RANGE DYNAMICS REPRESENT AUSTRALIAN SMALL MAMMALS?

In review: Australian Mammalogy

N.A.H. conceptualised and wrote the manuscript and is corresponding author. J.F. and B.W.B. provided editorial comments.

All contributors certify that the statement of contribution is accurate and give permission for the inclusion of this material in the thesis.

Signed [redacted] *Date* 27 Apr 2012
Haby, N.A. (Candidate)

Signed [redacted] *Date* 26/4/12
Foulkes, J.

Signed [redacted] *Date* 27/4/12
Brook, B.W.

Abstract

Australian mammals are unique in many respects and may not be well represented by current world-wide forecasts of the impact of climate change on range shifts, or empirical investigations that have detected changes in mammal morphology, phenology, density and distribution. World-wide predictions are typically biased towards plant, bird and invertebrate taxa with wide ranges, while empirical investigations target species that are charismatic, threatened, data deficient, have unique characteristics or are associated with the spread of disease. To determine whether recommendations derived from world-wide or international investigations can be applied in an Australian context, we need to consider how well Australian mammals with unique ecology and natural history are represented, and if not, ensure these species are sufficiently represented in prioritising national efforts to conserve native wildlife.

Introduction

The decline in Australian mammals over the last 200 years has been dire: 27 species or subspecies have become extinct, contributing a high proportion of all recorded global vertebrate extinctions (Short and Smith 1994, Johnson 2006). Another 94 species are recognised as threatened under the EPBC Act (www.environment.gov.au/epbc/, accessed on 31 January 2012), which is likely to be an underestimate as many species are being increasingly effected by the additional threat of climate change (Steffen *et al*. 2009, Burbidge *et al*. 2008).

Empirical support for and against the effects of climate change on range-shifts

A number of empirical investigations have already detected affects of recent climate change on mammal morphology, phenology, density and distribution (see reviews by Root *et al.* 2003, Parmesan and Yohe 2003, Isaac 2008). These changes may be driven via changes in habitat availability supporting activity periods and reproduction (e.g. ground squirrels and lemmings; Steenhof *et al*. 2006, Kausrud *et al*. 2008), the distribution of food resources (e.g. mat forming lichens for reindeer, Heggberget *et al*. 2002), or quality (e.g. nutrient availability for herbivores; Hughes 2003, Prowse *et al*. 2009). Ultimately, these changes are expected to cause further extensive restructuring of mammal communities and distributions (Levinsky *et al*. 2007, Lawler *et al*. 2009, Blois *et al*. 2010, McCain and Colwell 2011, Svenning *et al*. 2011).

Range shifts have been confirmed for a number of species, including rodents in a tropical valley in Senegal, Africa (over a 30 year period; Thiam *et al*. 2008), and various small mammals along an elevation gradient in Yosemite National Park, California, USA (over a 90 year period; Moritz *et al*. 2008). Shifts in species' ranges have led to hybridisation between species (e.g. flying squirrels; Garroway *et al*. 2010) and restrictions in the distribution of generalist species to narrow climatic zones with limited habitat diversity, leading to species being misidentified as habitat specialists (e.g. a sub species of *Peromyscus* mouse; Yang *et al*. 2011). From the range shifts observed to date, a rate of 0.4 - 2.1 km yr^{-1} has been estimated (based on 20 small to medium-sized mammals in northern Indiana, USA, from 1930s to 1970s; Francl *et al*. 2009). In future, the rate of range shift is expected to increase considerably to up to 4 km yr^{-1} (Francl *et al*. 2009); tracking suitable climatic or environmental conditions may become increasingly difficult due to dispersal limitations and other factors such as Allee effects at the expanding range margin (e.g. range pinning, Keitt *et al*. 2001).

Other landscape dynamics can induce range shifts and affect whether range shifts in response to climate change are realised. In a mountainous area experiencing increasingly warmer and drier climates, xeric species (arid-adapted) were expected to expand their ranges upslope, but instead mesic species (adapted to wetter environments) increased in abundance (Rowe *et al*. 2010). In another investigation, small mammals occupying a fragmented landscape in mesic environments demonstrated a greater resilience to climate change than species occupying relatively undisturbed arid environments (McKenzie *et al*. 2007). These results were attributed to mesic species responding to a landscape recovering from intensive grazing (Rowe *et al*. 2010) and regional differences in productivity (McKenzie *et al*. 2007), respectively.

Environmental and taxonomic variability in predicted range shifts

Regional differences in the direction and rate of shift in mammal species distributions are predicted worldwide (Burrows *et al*. 2011). For example, the proportion of mammals predicted to go extinct by 2050, include between 2 - 20 % in Mexico, but 24 - 59 % in South Africa, 10 - 80 % in Queensland, Australia (the latter estimated from dispersal scenarios only; Thomas *et al.* 2004) and 10 -15 % all of Africa (Thuiller *et al*. 2006). The susceptibility of mammal populations to climate change may further differ at a bio- or ecoregion scale (e.g. between 10 and over 90 % species turnover between regions; Lawler *et al*. 2009). At the bio- or ecoregion scale (Olsen and Dinerstein 1998), a unique composition of mammal richness (and subsequently range size), habitats and climate can be found (Smith *et al*. 1994, Williams *et al*. 2003) and more accurate climate change projections developed (e.g. rainfall projections obtained in Mediterranean ecosystems; Yates *et al*. 2010), which enable vulnerable ecosystems to be identified (e.g. alpine zone, coastal fringe, freshwater systems, wet tropics and south-west Western Australia; Hughes 2011).

In additional to regional variability, ecological traits are likely to drive variability across species (Davidson *et al*. 2009). Many species-specific investigations into range shift have targeted charismatic species (e.g. moose and koala; Darimont *et al*. 2005, Adams-Hosking *et al*. 2011), threatened species (endangered lagomorphs and Iberian desman; LaFever *et al*. 2007, Anderson *et al*. 2009, Morueta-Holme *et al*. 2010), data deficient species (African forest squirrels; Peterson and Martinez-Meyer 2007), carnivores (marten and lynx; Carroll 2007), volant species (European bats; Rebelo *et al*. 2010) and species associated with the potential spread of diseases (e.g. rodents; Lijun *et al.* 2010). Additional investigations into demographic factors that influence abundance and therefore distribution (i.e. survival and reproduction) have also targeted charismatic and threatened species (polar bear, wild ass and lemur; Molnar *et al*. 2010, Saltz *et al*. 2006, Dunham *et al*. 2011). However, this small (and as a consequence taxonomically and evolutionarily biased) sample of investigations represents only a fraction of the world's total mammalian diversity.

How suitable are world-wide recommendations for Australia's mammals?

Existing reports of the global-scale effects of climate change on biodiversity typically target specific regions and taxa (see Root *et al*. 2003, Isaac 2008, Parmesan and Yohe 2003). These investigations are unlikely to represent trends in Australian mammals for a number of reasons:

i. Mammals are rarely included in meta-analysis (e.g. 1 out of 143 species: Root *et al*. 2003) or are represented by rodents (e.g. McCain and Colwell 2011). Forecasts based on rodents may overestimate rates of adaptation by other taxa or, if biased towards dietary specialists, underestimate use of new habitats (Cameron and Scheel 2001).

ii. Coarse-scale investigations can exclude narrow-ranged species. For example, only mammals occupying more than 125 000 km^2 had sufficient data to be included in the evaluation by Lawler *et al*. (2006). An analysis at this scale, if applied to Australian non-volant terrestrial mammals, would exclude over 43 % of species (Murray and Dickman 2000).

iii. Forecasts derived at coarse resolutions (50 km, 100 km and 200 km; Lawler *et al*. 2006), may not incorporate suitable habitat (e.g. rock outcrops; Smith *et al.* 1994), limiting the benefits of integrating population demographics, dispersal, and other ecological and life-history details required for robust estimates of range shift (Huntley *et al*. 2010).

iv. Australian species range dynamics are influenced by climate variability, correlated with distance from the coast, unlike in other areas where species range dynamics follow generalised patterns, such as decreasing range size with latitude (Rapoport's rule; Smith *et al.* 1994, Brown *et al.* 1996).

v. Approximately 85 % of Australian mammals are endemic to the continent, including many of the world's marsupials and monotremes (Steffen *et al*. 2009).

vi. Finally, extinctions of Australian mammals are uniquely biased towards the loss of small- to medium-sized mammals (e.g. 35 g to 5.5 kg; Short and Smith 1994, Chisholm and Taylor 2010).

Conclusion

Better understanding the unique ecology and natural history of many small to medium-sized Australian mammals is key to enabling the adoption of forecasts derived from areas outside of Australia, understanding regions with contrasting historic and future (predicted) sensitivity of species loss (e.g. arid regions; Thomas *et al*. 2004, McKenzie *et al*. 2007), and informing ecologically realistic species distribution models (e.g. see Austin and van Neil 2011) that aid in conserving our native wildlife into the future.

Overview of the goals of this investigation

The influence of small mammal ecology on estimated range dynamics were investigated through the hypotheses:

1. That the addition of landscape variables to a climate-only model will improve both model accuracy and transferability tested in a rigorous out-of-region validation (Chapter 1),

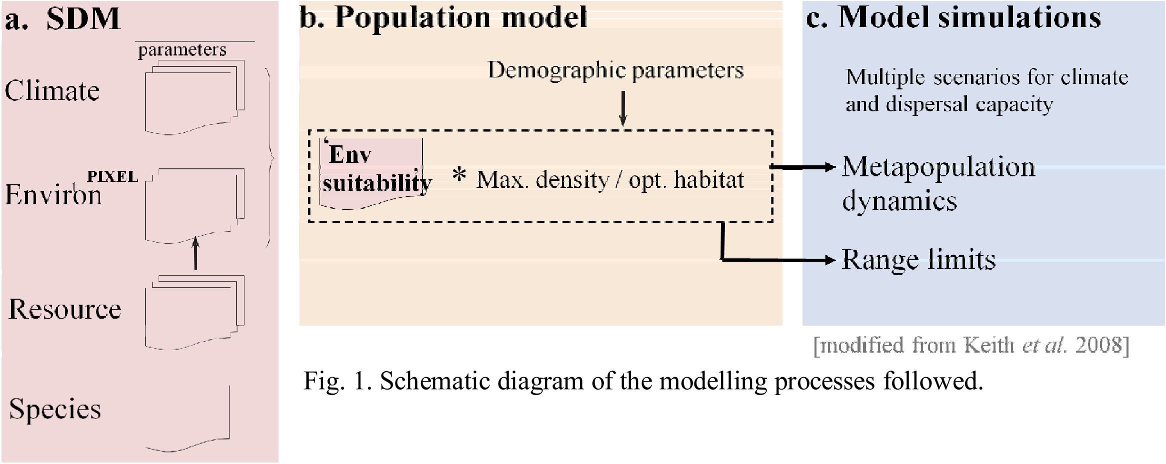
2. That abiotic and biotic landscape and quadrat-scale environmental data, sampled at high-resolution, more effectively represents the ecology of small mammals and improve SDM accuracy (Chapter 2), and

3. That finer-resolution data used in species distribution models produces a more complex spatial configuration of predicted available habitat (via increased patch number and patch variability), leading to improved connectivity between patches to facilitate dispersal across the landscape in response to a changing climate (Chapter 3).

The relationship between these hypotheses is illustrated in Fig. 1. These investigations targeted four temperate-zone mammals, which may not represent dynamics influencing arid-zone mammals. As a result the following hypothesis was raised:

4. That given adaptations of small mammals in the arid-zone, additional (landscape) features are more important than climate variables in predicting species distribution, and that these correlations are best represented at finer scales despite animals being relatively mobile (Chapter 4).

Finally, the importance of considering species' ecology and biotic resources when modelling small mammal range dynamics as a result of the temporal relationship between biotic interactions, evolution and SDMs was reviewed (Chapter 5).



[modified from Keith *et al.* 2008]

Fig. 1. Schematic diagram of the modelling processes followed.

Chapter 1

IMPROVING PERFORMANCE AND TRANSFERABILITY OF SMALL-MAMMAL SPECIES DISTRIBUTION MODELS

N. A. Haby, S. Delean, B. W. Brook

The Environment Institute and School of Earth & Environmental Sciences,
University of Adelaide, Adelaide SA 5005, Australia

In review: Acta Oecologia

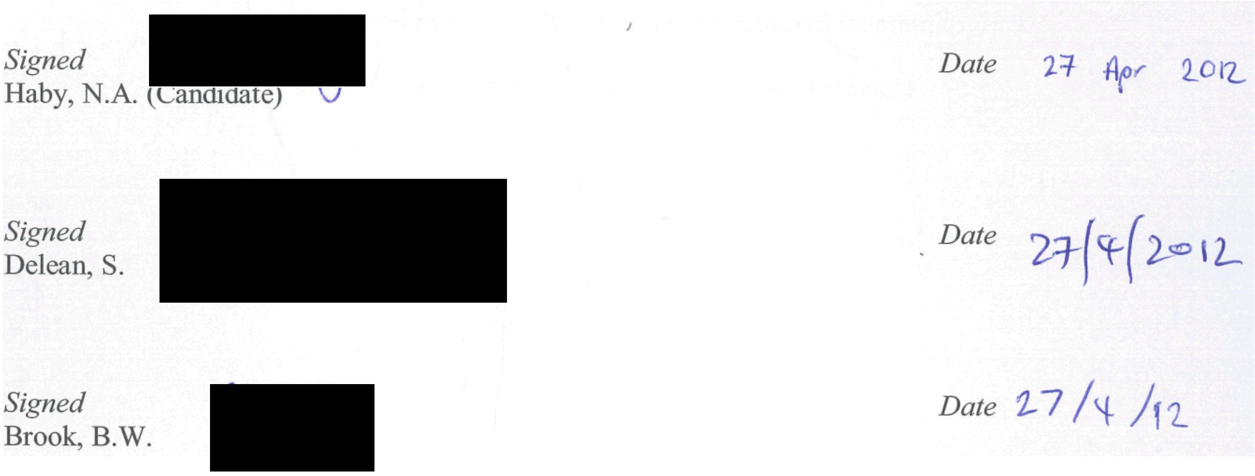
STATEMENT OF AUTHORSHIP

IMPROVING PERFORMANCE AND TRANSFERABILITY OF SMALL-MAMMAL SPECIES DISTRIBUTION MODELS

In review: Acta Oecologia

N. A.H. collated and prepared data, performed analyses, interpreted data, wrote manuscript and is corresponding author. S.D. contributed to conceptualising the manuscript, planning the analyses and provided editorial comments. B. W. B. contributed to conceptualising the manuscript and provided editorial comments.

All contributors certify that the statement of contribution is accurate and give permission for the inclusion of this material in the thesis.



Signed [redacted]
Haby, N.A. (Candidate)
Date 27 Apr 2012

Signed [redacted]
Delean, S.
Date 27/4/2012

Signed [redacted]
Brook, B.W.
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Abstract

In theory, interpretation and transferability of species distribution models (SDMs) should be improved by including abiotic and biotic factors that directly influence a species' *fundamental niche*. We tested this expectation by investigating whether the addition of topographic, soil and vegetation variables to a climate-only model improved model performance and predictive capacity in a rigorous out-of-region validation for four coastal small mammal species. We used two commonly applied methods for species distribution models: generalised linear models (GLM) and boosted regression trees (BRT). The inclusion of landscape variables improved the structural goodness of fit for all four species (e.g. 2.6 – 47.6 % increase in deviance explained), and the information-theoretic rankings (based on AIC_c, BIC and DIC) for the wet-heath specialist (Muridae, *Rattus lutreolus lutreolus*) and peramelid (Peramelidae, *Isoodon obesulus obesulus*). For both species, improved model performance transferred to improved predictive capacity in the out-of-region validation (increase in the area under the curve, AUC). However, this result was poorly supported by trends in the successful classification of presences and absences (kappa), which often reflected trends in specificity (classification of absences), indicating a modelling bias caused by low prevalence of species occurrence. Across all SDMs additional abiotic and biotic landscape variables contributed more than 5 % explanatory strength. Our results supported the expectation that additional landscape variables can have a more direct influence on the *fundamental niche* as demonstrated by increased model fit and transferability. Additional abiotic and biotic landscape variables may enhance correlative SDM robustness in assessments of the impact of climate change on species' distributions.

Introduction

Species distribution models (SDM) are a tool used to describe the factors underpinning a species' spatial distribution and extent, and for investigating the potential effect of management scenarios and climate shifts (Guisan and Thuiller 2005; Peterson 2006). Typically, SDMs incorporate climate variables which are: (i) considered to have a direct influence on flora (e.g. through plant productivity) (Austin 1985) at coarse scales (Franklin 1995), (ii) were easily obtained (Austin 2002) and (iii) have a wide coverage, to facilitate out-of-region predictions (Austin and Meyers 1996). These principles governing climate data use in SDMs have continued to be used to generate estimates of the potential impact of climate change on species distributions at the global scale (Pearson and Dawson 2003). However, these models may not be sufficiently accurate at a fine scale to inform on-ground conservation actions (e.g. Ellis 2011).

More robust SDMs can, in principle, be developed using factors that define the *fundamental niche* that underpins the *realised niche* and distribution of a species (Pearson and Dawson 2003; Araújo and Guisan 2006; Austin 2007). The *fundamental niche* in which a species can theoretically survive and reproduce is defined by a suite of environmental factors (Hutchinson 1957; Pulliam 2000). Ideally, these factors will have a physiological influence on a species either directly (are not consumed) or via resource availability (consumed), therefore enabling causal (proximal) rather than correlated (distal) relationships to be incorporated in SDMs (Franklin 1995; Guisan and Zimmermann 2000; Austin 2002). The development of SDMs of plants using climatic variables alone follows this biologically informed logic, given these primary producers are directly influenced by these abiotic variables (Austin 2002). However, climate-only analyses have been applied extensively in vertebrate SDMs without strong justification, and have constrained the perception of environmental factors that influence the *fundamental niche* to abiotic variables (e.g. Sillero 2011).

There are several limitations to using climate-only data to represent the *fundamental niche* of small mammals in SDMs. First, climate variables are often distally correlated with the distribution of terrestrial vertebrates, via their effect on shelter or food availability (Hirzel and Le Lay 2008). Second, variables such as temperature or precipitation can be influenced by local topography (e.g. elevation, slope and aspect) (Franklin 1995; Hirzel and Le Lay 2008). Consequently, any SDMs created using only climate variables may not be representative across regions or time periods (Austin 2002; Guisan and Thuiller 2005). In addition, to better define a species' *fundamental niche* by incorporating more appropriate environmental factors, it may be necessary to reconsider the scale used to sample the data (Wiens et al. 1987; Pearson and Dawson 2003; Guisan and Thuiller 2005). Microclimate variables have already been used to better represent mechanistic influences on the physiology of an ectotherm (Kearny 2006).

Environmental factors used to define the *fundamental niche* do not need to be abiotic (Hutchinson 1957; Pulliam 2000). An example of a resource provided by a biotic factor that influences the *fundamental niche*, is the presence of a host plant on the survival of a parasitic vine or shrub, such as mistletoes, order Santalales; or native cherry, *Exocarpos cupressiformis*. Biotic factors that characterise required habitat (Dennis et al. 2003), or limited resources (Orians and Wittenberger 1991), have been found to improve model fit in a variety of mammals and bird investigations (e.g. vegetation communities; Ford et al. 2006; Luoto et al. 2007). Direct and resource gradients should also improve model transferability (Guisan and Zimmermann 2000). However, the application of less rigorous evaluation techniques (cross-validating or bootstrapping the original dataset), compared with using a wholly independent dataset (Guisan and Thuiller 2005), has made it difficult to assess the value of additional landscape variables on model transferability (out-of-region predictions), leading, in turn, to a lack of agreement on whether biotic variables are useful (e.g. Thuiller et al. 2004).

Well-designed models that reflect our current understanding of species ecology and are underpinned by adequate data for parameter estimation should produce more accurate geographic maps of species distributions across its range, and over time, that can be reliably interpreted (Caughley et al. 1988; Araújo and Guisan 2006). As landscape variables may have a direct or proximal influence on small mammal occurrence, representing gradients of the *fundamental niche*, we propose the addition of these variables to a climate-only model will improve both model accuracy and transferability tested in a rigorous out-of-region validation. To investigate these hypotheses, we evaluated model performance (fit to observations, and predictability in an out-of-region validation) for a climate-only and a climate-and-landscape variable model, for four small ground dwelling mammals.

Materials and methods

Study area

This investigation targeted several coastal subregions of the Interim Biogeographic Regionalisation of Australia (Fig. 1, Appendix I). These encompassed naturally occurring subsets in the distribution of four mammal species, fragmented by the Coorong, Gulf St Vincent and Spencers Gulf of the state of South Australia.

Fig. 1 Map of Interim Biogeographic Regionalisation of Australia (IBRA) sub-regions used to parameterise the species distribution models (dashed lines) and those used for out-of-region validation of the model predictions (stippling). The IBRA sub-region codes shown represent Eyre Hills (EYB3), Talia (EYB4), Mount Lofty Ranges (FLB1), Kangaroo Island (KAN1), Fleurieu (KAN2), Bridgewater (NCP1), Glenelg Plain (NCP2), Lucindale (NCP3) and Mount Gambier (VVP2).

General small mammal ecology

The southern brown bandicoot, *Isoodon obesulus obesulus* (Peramelidae; Shaw 1797), yellow-footed antechinus, *Antechinus flavipes flavipes* (Dasyuridae; Waterhouse 1838), bush rat, *Rattus fuscipes greyi* (Muridae; Gray 1839), and swamp rat, *Rattus lutreolus lutreolus* (Muridae; Gray 1841), are four of South Australia's more widespread coastal mammals (Robinson et al. 2000). These species currently occupy remnants within FLB1, KAN1-2, NCP1-3 and VVP2; FLB1, KAN2 and NCP2-3; EYB3-4, FLB1, KAN1-2, NCP1-3 and VVP2; and KAN2, NCP1-3 and VVP2, respectively (refer to Fig. 1, with further detail on these species provided in Appendix II).

Available data

Presence locations of each species were determined from a baseline inventory of the distribution of South Australia's flora and fauna (Biological Databases of South Australia, December 2008). This inventory contains data from a variety of sources, including systematic regional biological surveys of representative, intact vegetation communities (Heard and Channon 1997; Owens 2000), and opportunistic records from the South Australian Museum and a variety of other sources. Only records collected using reliable methods, < 100 m location accuracy and post-1970 were used (Appendix III). Where areas were subject to more intensive survey or monitoring effort (e.g. Belair National Park), records were restricted to a random sub-set to retain a more consistent density of records across the study area.

To assist in identifying less suitable habitat (Barry and Elith 2006), sufficient information was available to determine a selection of 'true absences' (rather than 'pseudoabsences' that are often defined without any on-ground verification). These absence sites were defined as biological survey sites trapped for a minimum of four nights, using Elliott or cage traps, that failed to capture the target species. These criteria reflect a reasonable opportunity to capture the target species if it was present in the area at the time of the survey. This systematic approach reduces the risk of including false absences as *Rattus* spp. are often quick to detect, facilitated by Elliott traps being placed in run-ways. Resident *Antechinus f. flavipes* are often detected within four nights (Marchesan and Carthew 2008), while the less abundant *I. o. obesulus* can also be detected by other methods used (e.g. hair tubes and signs of diggings). Finally, to reduce influence of false absences and maximise the benefit of a limited number of presences on model outputs, we used the Maximum Sum of Sensitivity and Specificity threshold (MSS; calculated in R using `PresenceAbsence`) to identify presences because it has been shown to down weight the influence of false-absences (Freeman 2007).

Presence and absence data were used to sample information from a selection of available vector and raster environmental spatial layers using ArcInfo 9.2 (ESRI 2009; Appendix IV). Altogether, these variables represented climate, topography, soil and vegetation that may influence or represent required resources, such as preferred habitat (e.g. woodland or wetland), food (e.g. invertebrates, fungi, plant material) or shelter (e.g. understory cover and tree hollow availability).

Species distribution model comparison

Data from the northern extent of the survey area (EYB3-4, KAN1-2, FLB1; see Fig. 1), represented the range of values across the study area and were used to create two candidate models specifying species distribution as a function of available climate variables (MT, RW, RS) (Model 1) or combination of abiotic (MT, RW, RS, E, S, lnWC, M and H) and biotic (GEN) landscape variables (Model 2) (Appendix IV).

Species occurrences were modelled with generalised linear models (GLM) using a binomial error distribution and logit link function, fitted in R v2.8.0 (R Core Development Team 2009; www.r-project.org). Overall model structural goodness of fit was assessed based on the per cent deviance explained relative to the null model (% DE). The model with the best predictive capacity was identified using several measures of fit (R v2.8.0, R Core Development Team 2009; WinBUGS v1.4, Imperial College and MRC 1996): Akaike's Information Criterion (corrected for small sample sizes), Bayesian Information Criterion and Deviance Information Criterion presented as the difference from the highest-ranking model (ΔAIC_c, ΔBIC, ΔDIC), and weight scaled to a sum of 1 ($wAIC_c$, *w*BIC, *w*DIC). The AIC_c involves information-theoretic bias correction, which implicitly accounts for model parsimony. The BIC gives it a more conservative response to the inclusion of additional parameters (Burnham and Anderson 2002). The DIC (following McCarthy 2007) was also calculated initially to provide a third value for comparison, derived from a different statistical framework.

To avoid generating biased results due to assuming linear species response curves, a complementary approach was also used; the more flexible boosted regression trees (BRT) (Guisan and Zimmermann 2000). BRTs were fitted using the R package 'GBM' (Elith et al. 2008; Ridgeway 2009). Optimal tree complexity and learning rate were selected by within-sample cross-validation for each species (Appendix V), bag fractions were set at 0.5 and the relative proportion of deviance explained by each model was calculated from the summary statistics (J. Elith, University of Melbourne, pers. comm., 2009).

Out-of-region validation

Out-of-region validation was used to test the predictive ability of the SDMs fitted via GLM and BRT in the IBRA units NCP1-3, VVP2 (see Fig. 1); implemented using R packages 'PresenceAbsence' (Freeman 2007) and 'GBM' (Elith et al. 2008; Ridgeway 2009). The range of data values in this geographic region were considered sufficient for a relative comparison of model performance. Several species had low prevalence in this area (0.08-0.24), increasing the risk of variable validation statistics and difficulty in assessing performance (Liu et al. 2005; Meynard and Quinn 2007). Therefore, three methods were used to evaluate relative predictive performance: a) the mean difference between the predicted probability of occurrence and the actual value (0 or 1), b) the area under the receiver-operating characteristic curve (AUC) (independent of prevalence, Manel et al. 2001), and c) Kappa, sensitivity and specificity statistics (Fielding and Bell 1997). To calculate the last three statistics, the Maximum Sum of Sensitivity and Specificity (MSS) threshold was calculated using the R package 'PresenceAbsence' (Freeman 2007) given its suitability for small datasets (Jiménez -Valverde and Lobo 2007).

Identifying model bias

To determine whether model bias affected estimates of Kappa, sensitivity and specificity statistics, and their subsequent trends when comparing between models, the predicted values were compared to the mean of each statistic's empirical distribution, generated by re-applying the two models to 1 000 bootstrapped samples from the original dataset.

Contribution of variables

The explanatory strength (relative importance) of each variable in describing the four species' distributions was calculated as the combined change in per cent deviance explained (% DE) when each variable was removed from the saturated GLM and added to the null (intercept only) GLM (Garnett and Brook 2007). For comparison, the 'relative influence values' from BRT summary outputs are also presented (Elith et al. 2008). Variable odds ratios and 95 % confidence intervals were also derived for the saturated model (Model 2) using GLM.

Results

Influence of landscape variables on model performance

Overall, the climate-only GLM (Model 1) explained between 16.5 and 43.8 % of the deviance in species' occurrence (Table 1). A further 2.6 – 47.6 % of deviance, across species, was explained after incorporating additional landscape variables into the model (Model 2; Table 1). The $w\text{AIC}_c$ values showed Model 2 to be the highest-supported model (for most species). The stronger penalty of additional parameters in Model 2 applied using *w*BIC and *w*DIC, resulted in only a slight disagreement between the $w\text{AIC}_c$, *w*BIC and *w*DIC values for *I. o. obesulus* and *R. f. greyi* (of < 7 % and 34 %, respectively), however, a substantial disagreement for *A. f. flavipes* suggesting a less parsimonious representation of variation in the occurrence of this species (97 %; Table 1).

The BRT models, which allow implicitly non-linear responses and interactions, outperformed GLM (based on % DE) when using the climate-only model to describe the distribution of the dense understorey preferring *I. o. obesulus* and *R. f. greyi* (Table 1). Adding landscape variables to the climate-only BRT improved model-fit (1.3 – 13.0 %), with the most substantial improvement being for the wet-heath specialist *R. l. lutreolus*.

Table 1 Explanatory strength of null and *a priori* predictive generalised linear models (GLM) and boosted regression trees (BRT) containing climate-only (Model 1: Species ~ MT + RS + RW) or climate and landscape parameters (Model 2: Species ~ MT + RS + RW + E + S + lnWC + GEN + M + H). Shown are the number of parameters (*k*), minimised negative log-likelihood (-LL), Akaike's information criterion corrected for small sample sizes, Bayesian Inference Criterion and Deviance Information Criterion presented as the difference from the highest-ranking model (ΔAIC$_c$, ΔBIC, ΔDIC) and weight scaled to a sum of 1 (*w*AIC$_c$, *w*BIC, *w*DIC), and the per cent deviance explained by the model relative to the null (% DE) for each method.

model	*k*	-LL	ΔAIC$_c$	*w*AIC$_c$	ΔBIC	*w*BIC	ΔDIC	*w*DIC	% DE GLM	% DE BRT
I. o. obesulus (323 presence : 393 absence sites, 716) (prevalence 0.45)										
Model 1	4	-364.4	36.8	0.00	5.1	0.07	36.7	0.00	26.1	41.4
Model 2	11	-338.9	0.0	1.00	0.0	0.93	0.0	1.00	31.2	42.7
A. f. flavipes (72 presence : 354 absence sites, 426) (prevalence 0.17)										
Model 1	4	-108.8	6.7	0.03	0.0	1.00	7.2	0.03	43.8	41.9
Model 2	11	-98.2	0.0	0.97	21.1	0.00	0.0	0.97	49.3	45.8
R. f. greyi (145 presence : 299 absence sites, 444) (prevalence 0.33)										
Model 1	4	-234.3	0.0	0.72	0.0	1.00	0.0	0.66	16.5	26.1
Model 2	12	-227.0	1.9	0.28	34.7	0.00	1.4	0.34	19.1	27.4
R. l. lutreolus (21 presence : 411 absence sites, 429) (prevalence 0.05)										
Model 1	4	-68.7	68.4	0.00	31.5	0.00	66.4	0.00	18.3	25.4
Model 2	12	-28.7	0.0	1.00	0.0	1.00	0.0	1.00†	65.9	38.4

MT, average monthly minimum temperature; RS / RW, average monthly rainfall during summer (Nov-Jan) and winter (Jun-Aug); E, elevation; S, slope; lnWC, distance from nearest water course or body transformed using the natural log; GEN, broad vegetation community; M, root zone water holding capacity; H, soil acidity.

†Obtained from 45 235 out of the intended 100 000 runs (following a 10 000 run 'burn-in') due to the limited presence data in some parameters.

Influence of additional landscape variables on out-of-region predictive performance

Additional abiotic and biotic landscape variables improved the out-of-region classification of species occurrence (based on AUC) for the understorey-preferring *I. o. obesulus* and wet-heath specialist *R. l. lutreolus*, had little effect on the classification of the woodland generalist *A. f. flavipes* occurrence and reduced the classification of the understorey-preferring *R. f. greyi* occurrence (Fig. 2). Positive or negative trends in AUC were reflected in the Kappa statistics in some cases (*I. o. obesulus*, GLM; *R. l. lutreolus*, BRT; *R. f. greyi*, BRT), but appeared driven by specificity, indicating the low prevalence of species records affected the classification of species' occurrence, despite using the MSS threshold (Fig. 3). Additional support for improved classification of species' presence was provided by increased sensitivity statistics in the case of *I. o. obesulus* (BRT) and *R. l. lutreolus* (GLM) (Fig. 3). While these results focus on an increase in validation metrics with the addition of landscape variables to the climate-only model, the decline in AUC and sensitivity for *R. f. greyi* may better align with the low explanation of deviance in species occurrence and also support improved model performance.

Fig. 2 Out-of-region predictive performance of fitted species distribution models, measured as the difference between area under the curve (AUC) values obtained from the prediction of occupancy for Model 1(M1) and Model 2 (M2) using generalised linear modelling (GLM) and boosted regression trees (BRT). AUC values range from 0.5 to 1.0, representing random discrimination by the model to perfect discrimination, respectively (Fielding and Bell 1997). Error bars are calculated as standard deviation. For model definitions, see Table 2.

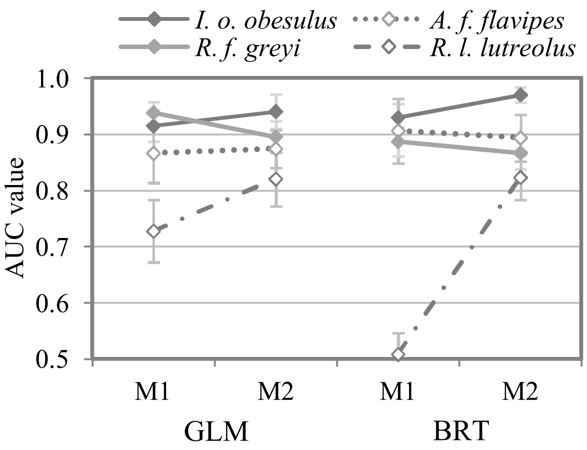
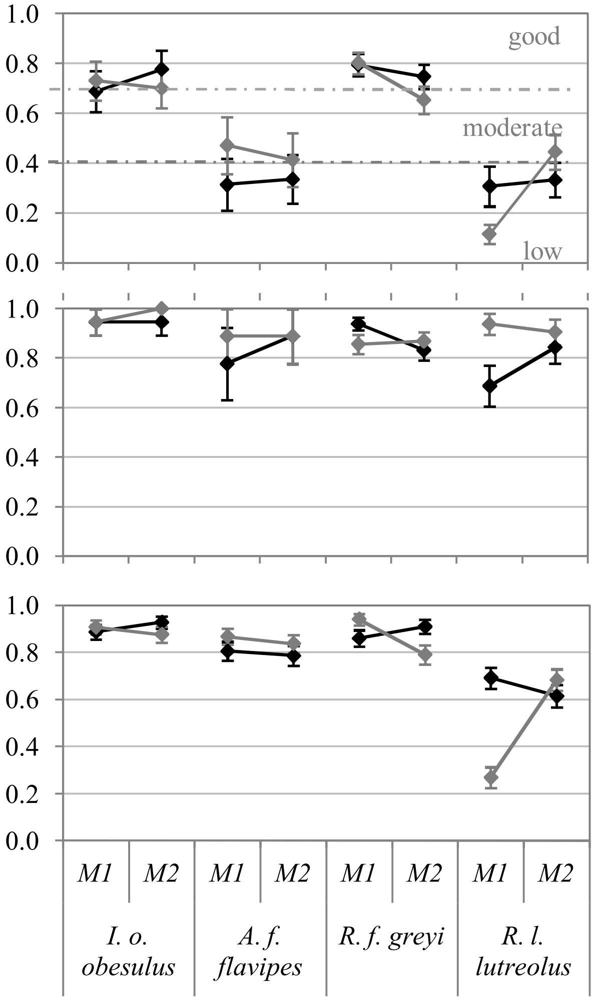


Fig. 3 Out-of-region predictive performance, illustrated using three measures of agreement: Kappa (top), sensitivity (middle) and specificity statistics (bottom; Fielding and Bell 1997). These metrics were derived from probability estimates using the Maximum Sensitivity and Specificity threshold (MSS) for each model (generalised linear modelling, black line and boosted regression tree modelling, grey line) and species where *I. o. obesulus*, *A. f. flavipes*, *R. f. greyi* and *R. l. lutreolus* have 0.08, 0.16, 0.46 and 0.24 prevalence in the predict region, respectively. Error bars are calculated as standard deviation.



Resolving model bias

The Kappa, sensitivity and specificity statistics generated were mostly unbiased. A comparison of the predicted validation statistics to the mean of their empirical distributions identified bias in the climate-only model for *R. l. lutreolus* (GLM) (Fig. 4), leading to slightly lower Kappa and specificity statistics and higher sensitivity statistics. This slight bias would reduce the increase in sensitivity and decrease in specificity and Kappa when comparing the climate-only and climate-and-landscape models, but not sufficiently to alter the trend observed.

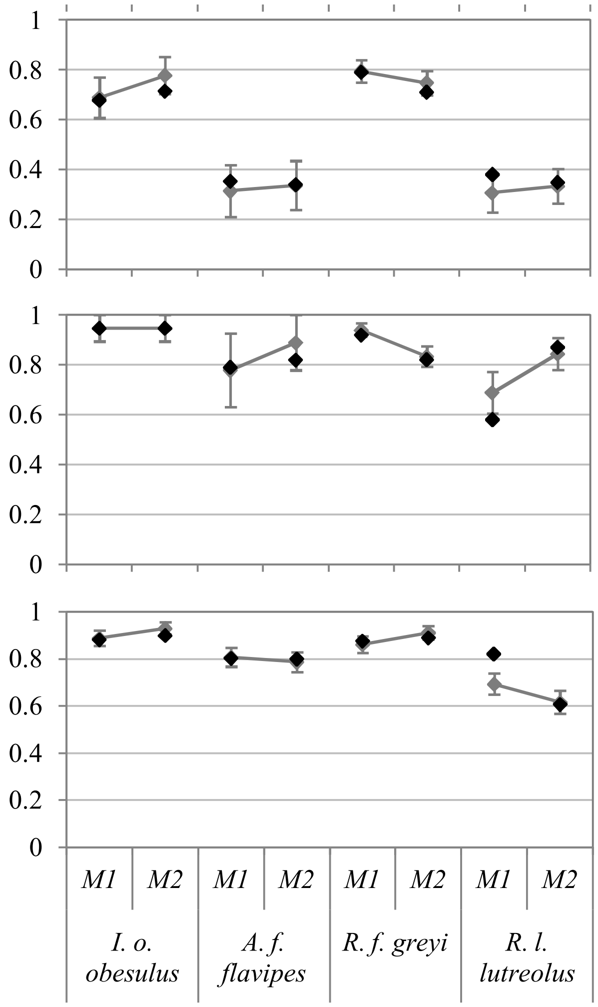


Fig. 4 Illustration of model bias using average generalised linear modelling-generated statistics, based on 1 000 bootstrap samples (black diamonds), and the initial predict values (grey diamonds) calculated using the Maximum Sensitivity and Specificity threshold (MSS) for each model. Shown are the Kappa (top), sensitivity (middle) and specificity statistics (bottom). Error bars are calculated as standard deviation

Core influential variables

On average, seasonal rainfall (RS, RW), elevation (E) and log-distance to water course (lnWC) were consistently ranked in the top four variables explaining species occurrences across all species and regardless of the type of statistical model used (Table 2). Soil acidity (H) or broad vegetation description (GEN) were the next-highest ranked explanatory variables, using GLM or BRT, respectively. Variable effect size (expressed as odds ratios) varied between SDMs and indicated useful contributions particularly from climate variables, forest and mallee forest and soil acidity in describing *I. o. obesulus* occurrence; climate variables, distance to water course, forest and mallee forest and root zone water holding capacity for *A. f. flavipes*; climate variables for *R. f. greyi*, and climate variables, distance to water course, sedgeland, fernland and grassland and shrubland, root zone water holding capacity and soil acidity for *R. l. lutreolus* (Appendix VI).

Discussion

The inclusion of available abiotic and biotic landscape variables to a climate-only model improved the predictive ability of SDMs for four small mammal species from Australia's southern sclerophyll habitats. Our results supported the expectation that additional abiotic and biotic landscape variables increased model fit (% DE and $w\mathrm{AIC}_c$) and predictive performance assessed in an out-of-region validation, indicating better representation of causal influences or resources that define the *fundamental niche*. Improved model fit was demonstrated for three of the four species; the wet-heath specialist, *R. l. lutreolus*, dense understorey-preferring *I. o. obesulus* and woodland generalist *A. f. flavipes*. Predictive performance measured by AUC values on out-of-region validation were comparable to those estimated by Wintle et al. (2005) (0.75 – 0.77) and Gibson et al. (2004) (0.66 – 0.86), and occasionally exceeded 0.9, suggesting these models were successfully transferred (Manel et

Table 2 Explanatory strength of each variable calculated using generalised linear modelling (GLM) and boosted regression tree (BRT) modelling. The explanatory strength for each variable was derived in GLM by combining the per cent deviance explained (% DE) when a variable is deleted from the saturated model with the % deviance explained when adding that variable to the null model and dividing that value by the degrees of freedom (as per Garnett and Brook 2007). The explanatory strength of each variable using BRT was derived from the relative influence values (RI) calculated using the package 'GBM' in R (Elith et al. 2008; Ridgeway 2009).

		I. o. obesulus		*A. f. flavipes*		*R. f. greyi*		*R. l. lutreolus*		Ave. across species		Rank across species	
Variable	*df*	GLM % DE	BRT % RI	GLM % DE	BRT % RI	GLM % DE	BRT % RI	GLM % DE	BRT % RI	GLM	BRT	GLM	BRT
RS	1	31.6	40.2	47.3	53.4	19.3	44.5	30.7	32.1	30.8	42.6	1	1
RW	1	21.3	16.0	31.7	9.9	12.9	17.0	1.1	4.6	17.4	11.9	2	3
E	1	18.3	10.7	23.3	13.5	8.7	20.7	12.3	19.7	14.9	16.2	3	2
lnWC	1	8.3	10.7	12.4	7.1	3.0	5.0	13.9	12.1	10.3	8.7	4	4
H	1	10.4	1.5	10.5	0.0	4.4	0.6	12.0	1.2	10.1	0.9	5	9
M	1	0.7	0.9	9.9	1.2	2.1	0.1	10.9	5.0	6.8	1.8	6	8
MT	1	10.5	8.9	11.0	1.8	4.2	5.0	0.1	5.2	6.5	5.2	7	7
GEN*	2, 2, 3, 3	2.6	3.6	5.0	7.5	0.8	2.1	8.3	15.4	3.8	7.2	8	5
S	1	7.1	7.5	5.3	5.6	2.2	5.0	0.2	4.6	3.7	5.7	9	6

MT, average monthly minimum temperature; RS / RW, average monthly rainfall during summer (Nov-Jan) and winter (Jun-Aug); E, elevation; S, slope; lnWC, distance from nearest water course or body transformed using the natural log; GEN, broad vegetation community; M, root zone water holding capacity; H, soil acidity.
*Only communities represented by both presence and absence records are included for each species.

al. 2001; Vanreusel et al. 2007). However, additional indicators of predictive performance that were more sensitive to the number and prevalence of species occurrences (Kappa, sensitivity, specificity) demonstrated only limited support. As such, while these additional landscape variables arguably improved SDM performance and transferability, they only partially resolve the current difficulty in modelling small mammal distributions using available environmental data.

As SDMs are correlative, it is not at first clear whether strong support for a variable reflects direct or resource gradients on a species, or whether it acts as a surrogate for indirect variables influencing the *realised niche*. In this study, there was strong support for climate variables used in all four species SDMs we developed. Austin (2002) argued that variables often do not fit exclusively into a specified category (direct, resource or indirect), using water as an example: it acts as a resource gradient when in low availability, or indirect gradient when abundant, causing water logging and anaerobic conditions for plants. Without an ecologically thoughtful consideration of the relationships between species and their environments, climate variables may represent a direct influence on the physiological tolerances of a species or substantial indirect (bionomic) variables (e.g. physiological tolerances of a key competitor).

There are several ways through which the known ecology of a species should provide insight into the relationships represented by available data. First, empirical investigations into species' resource use and life history attributes would indicate variables required for basic survival and reproduction. For example, soil water holding capacity may represent increased availability of invertebrate prey for *I. o. obesulus* and *A. f. flavipes* and plant material consumed by *R. l. lutreolus*. Second, it may be possible to use similarities between species. In the case of soil water-holding-capacity, the lack of support across burrowing species (*R. l. lutreolus* and *R. f. greyi*) suggests this variable does not singly represent ease of burrow construction. Finally, improved representation of biotic interactions and therefore, representation of the *realised niche* in the geological landscape should be less likely for small mammals that co-occur in their native range (i.e. already established different niche position and breadth), and especially for strong competitors (e. g. *R. l. lutreolus* that can outcompete *R. f. greyi*).

In addition to species' ecology, statistical tools should help evaluate whether variables included in a SDM have enhanced the representation of the *fundamental niche* or *realised niche*. In both cases model performance should increase. However, only models with improved representation of the *fundamental niche* should demonstrate an increase in validation statistics used to measure model transferability.

The failure of additional variables expected to directly influence a species *fundamental niche* to improve SDM may assist in identifying gaps in data availability and resolution. For example, the biotic variable, broad vegetation community, captured more than 5 % of the deviance for the wet-heath specialist *R. l. lutreolus* and woodland generalist *A. f. flavipes.* This variable appeared to more adequately represent nesting sites and specialised habitat required by these species, than the low diverse understorey preferred by *I. o. obesulus* or *R. f. greyi*. Given this, it is reasonable to assume additional variables describing more detailed components of the environment (e.g. understorey) are required to further improve model performance and transferability.

Limited data availability for ground-dwelling small mammals

Detailed statistical models can be developed if there are sufficient location data to support a range of abiotic and biotic predictive variables. Data are often difficult to obtain for rare or sparsely-distributed species (e.g. Barry and Elith 2006); however, threatened species, such as the endangered *I. o. obesulus*, often receive additional targeted survey and monitoring effort, and are the focus of the development and implementation of species-specific sampling methods (e.g. Haby 2006). In this study, records for this species exceeded the number and spatial coverage of *A. f. flavipes* (vulnerable), *R. l. lutreolus* (rare) and *R. f. greyi* (not currently threatened) records. These last three species can be locally common and do co-occur with *I. o. obesulus*, suggesting these species are not recorded as comprehensively or data collated adequately during field surveys. This potentially jeopardises further investigations relating to their conservation. To date, few surveys have targeted less threatened or common native mammals in southern Australia, thus limiting our understanding of relationships between the distribution of small mammal species and the common drivers of these distributions.

Capacity to improve model interpretation through realised niche characteristics

SDM performance is limited by available data for fitting (see below), and the failure to (parsimoniously) include important factors that modify the *fundamental niche* when modelled across the landscape (i.e. the *realised niche*); including biotic interactions, dispersal, or catastrophic events (Araújo and Luoto 2007; Barry and Elith 2006; Brooker et al. 2007; Elith and Lethwick 2009; Fox and Monamy 2007; Pulliam 2000). For example, competition between *R. l. lutreolus* and *R. f. greyi,* may restrict *R. f. greyi* from suitable habitat (Maitz and Dickman 2001; Manley et al. 2002). Another common but difficult-to-quantify problem is the representation of transient individuals detected in unsuitable habitat during field surveys. *Antechinus f. flavipes* may fall into this category where surveys were performed during the breeding season when males are dispersing. In addition, the history of vegetation clearance in the landscape may cause the reasonably dispersal limited *I. o. obesulus*, *R. f. greyi* and *R. l. lutreolus* to be absent from suitable patches due to local extinctions, or occupy suboptimal habitat. All of these dynamics lead to more complex species responses to environmental gradients (Holt et al. 2005), increased uncertainty or bias in SDM predictions.

Chapter 2

SPECIALIST RESOURCES ARE KEY TO IMPROVING SMALL MAMMAL DISTRIBUTION MODELS

N. A. Haby, S. Delean, B. W. Brook

The Environment Institute and School of Earth & Environmental Sciences,
University of Adelaide, Adelaide SA 5005, Australia.

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STATEMENT OF AUTHORSHIP

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All contributors certify that the statement of contribution is accurate and give permission for the inclusion of this material in the thesis.

Signed [redacted] *Date* 27 Apr 2012
Haby, N.A. (Candidate)

Signed [redacted] *Date* 27/4/2012
Delean, S.

Signed [redacted] *Date* 27/4/12
Brook, B.W.

Abstract

Small ground-dwelling mammals can have complex ecological relationships with environmental factors that limit the usefulness of coarse data in predictive species distribution models (SDM). We investigated the relative importance of available abiotic and biotic, landscape and quadrat-scale data for predicting the distributions of four small mammals using data at three resolutions: 150 m, 500 m and 1 000 m. At 150 m, the inclusion of landscape-scale data to a climate-only model improved the predicted occurrence of the wet heath specialist and woodland generalist, but not the two dense understorey species. Limited improvement was obtained with the inclusion of available quadrat-scale data (possibly due to missing or insufficiently detailed descriptive variables). As the models of best fit were re-applied to lower resolution environmental data (500 m and 1 000 m), the variance explained decreased for the wet heath specialist and two dense understorey species. These trends corresponded with reduced variance explained predominantly by biotic variables or abiotic landscape variables, respectively. In contrast, the resolution of environmental data had no effect on the woodland generalist SDM, indicating the habitat for this more mobile species was sufficiently represented at the lowest resolution (1 000 m). These results highlight the potential value of landscape and finer-scale variables in modelling the distributions of small mammals. Where such variables are unavailable, higher-resolution climate data could better represent resource availability (indirectly) or suitable microclimates (directly), especially for more vulnerable, above-ground nesting species. We encourage the collection of additional detailed and high-resolution environmental information to facilitate the development of more accurate models of the extent and distribution of small mammals.

Introduction

The performance and accuracy of species distribution models (SDM) depend on the ecological relevance of the data used to build them (e.g. Austin 2002). Abiotic factors typically used in SDM tend to have an indirect influence on terrestrial mammal habitat (Fox 1998, Andrews & O'Brien 2000), so including biotic environmental data with a proximal (causal) influence should enhance their accuracy (Austin 2002, Beever *et al.* 2003, Farraz *et al.* 2009). Adding complexity is that the resources represented by abiotic and biotic environmental data will be patchily distributed throughout the landscape, at a range of scales (Kotliar & Wiens 1990). The appropriate scale at which to represent environmental data for any one species may be challenging to identify (Morris 1987, Wiens *et al.* 1987, Orians & Wittenberger 1999).

Landscape-scale, abiotic climate and topographic data have been used successfully to model the distribution of several small mammal species (Carbajo & Pardiñas 2007, Kirk & Zielinski 2009). Higher-resolution climate data are also increasingly being used (Orrock *et al.* 2000) to indirectly represent food resources or levels of predation pressure (Haythornthwaite & Dickman 2006, Southgate *et al.* 2007), and low resolution biotic environmental data (e.g. vegetation communities represented at

> 1 km^2; Anderson *et al.* 2002, Acevedo *et al.* 2007), to represent more proximal influences on species occurrence (Caughley *et al.* 1987). Landscape-scale abiotic and biotic environmental data could improve SDM for small, predominantly ground-dwelling mammals with a clear dependency on specific features in the landscape. For example, in Australia the swamp rat, *Rattus lutreolus lutreolus,* depends on resources provided in wet heath communities (Taylor & Calaby 1988). A SDM for *R. l. lutreolus* should, therefore, be improved by including additional biotic environmental data representing this vegetation community.

Fine-scale data, representing more detailed features within the landscape, are difficult to acquire and implement statistically, and so are often ignored (Santos & Beier 2008). Such data, however, could strengthen the ecological foundation of SDMs (Austin 2002), improve our ability to model generalist species (Manning & Edge 2004), facilitate our interpretation of habitat suitability maps (Dennis *et al.* 2003, Hirzel & Le Lay 2008) and may even be necessary to distinguish between distribution models for different species using similar input data (Traba *et al.* 2010). A variety of fine-scale environmental data can be used to represent proximal relationships with small mammals (Catling *et al.* 2000, Larrucea & Brussard 2008). For example, understorey cover may represent suitable habitat in Australia for the southern brown bandicoot, *Isoodon obesulus obesulus*. Hence, models for small ground-dwelling mammals that respond to subtle changes in the environment may be improved by including fine-scale environmental data.

We expected abiotic and biotic landscape and quadrat-scale environmental data, sampled at high-resolution, to more effectively represent the ecology of small mammals and improve SDM accuracy. To investigate this we aimed to quantify the predictive performance of a set of *a priori* models, created using available landscape and quadrat-scale variables at three resolutions (i.e. 150 m, 500 m or 1 000 m) for four small mammals.

Methods

Study area and species

This investigation targeted several coastal sub-regions of the Interim Biogeographic Regionalisation of Australia (Fig. 1, Appendix I). This area encompassed naturally occurring subsets in the distribution of four mammal species, fragmented by the Coorong, Gulf St Vincent and Spencers Gulf. The four species were *Rattus fuscipes greyi, Rattus lutreolus lutreolus*, *Antechinus flavipes flavipes* and *Isoodon obesulus obesulus* (details on species ecology are provided in Appendix II).

Fig.1 Interim Biogeographic Regionalisation of Australia (IBRA) sub-regions used to define the study area (see Appendix I).

Species presence and absence

Both landscape and quadrat-scale environmental data were only available at Biological Survey of South Australia (BSSA) survey sites (see Heard & Channon 1997, Owens 2000). Species 'presences' were then defined as BSSA survey sites within a radius of 150 m, 500 m, and 1 000 m of a known species record locality, obtained from the Biological Databases of South Australia (December 2008) (Fig.2). The three resolutions aimed to maximise the number of available records (150 m), more liberal dispersal (500 m), and what is often referred to in the literature as 'fine-scale' (1 000 m). The remaining BSSA survey sites that were more than the specified distance from a known record locality (i.e. 150 m, 500 m or 1 000 m) were used to represent species 'absence'. While species absence is difficult to determine, there had been no captures of any of the target species during a four night survey using cage or Elliott traps at these sites (see Owens 2000).

Available environmental data

A range of available landscape and quadrat-scale data were used to generate individual spatial layers from which the values at BSSA survey sites were extracted in ESRI ArcGIS 9.2 (Appendix IV). Landscape-scale climate layers were derived by fitting thin-plate spline models to meteorological station data (Australian Bureau of Meteorology) and elevation (250 m Digital Elevation Model; Geoscience Australia 2008) (see Fordham *et al.* In press). Topographic features, included higher resolution elevation, slope and distance to water course. Soil and vegetation mapping were modified to create a series of simple spatial layers representing root zone water holding capacity, soil acidity and general vegetation community.

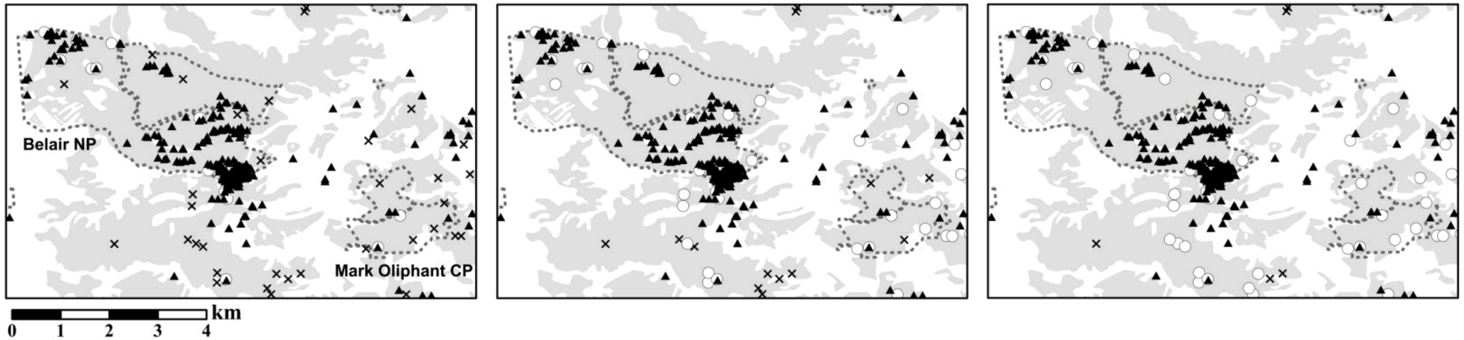


Fig. 2 In order to determine the influence of spatial resolution on multiple-scale environmental data used in SDMs, and that was only available from Biological Survey of South Australia survey sites, species record localities (▲) were used to reclassify survey sites as 'presences' and 'absences'. Survey sites that fell within a radius of 150 m (left panel), 500 m (centre panel) and 1000 m (right panel) of a known record locality of a species were reclassified as 'presences' (○), while survey sites outside of these distances were retained as 'absences' (✕). To illustrate this point, *I. o. obesulus* record localities, and corresponding 'presences' and 'absences', are shown in the vicinity of Belair National Park and Mark Oliphant Conservation Park, approximately 13 km south-east of Adelaide (hatched lines).

A range of quadrat-scale data (30 x 30 m) were available from regional BSSA surveys conducted across the state (Heard & Channon 1997). From these a selection was made following a series of preliminary investigations (using the 150 m dataset). Initial data exploration identified variables with incomplete data that could be removed. Scatter-plots identified variables with no or few species presences, or that did not appear to be correlated with species presence / absence. Compositional analysis (Resource Selection for Windows; Leban 1999) and principal component analysis (PCA, R Core Development Team 2009), did not further refine the number of variables because all variables were used disproportionately to their availability, or variability within the dataset, respectively. Finally, the variables were discussed with a botanist (P. Lang, Department of Environment and Natural Resources, pers. comm., 2009), to identify those representing unique floristic or structural components that would complement available landscape data (Appendix IV).

Categorical landscape and quadrat-scale variables were simplified to reduce the number parameters that would be included in the SDMs. For example, to account for observer error when sampling open sclerophyll native flora in South Australia (P. Lang, Department of Environment and Natural Resources, pers. comm., 2009), understorey cover in the 30-70 % and 70 – 100 % Muir code categories (Muir 1977 in Heard & Channon 1997) were combined. Binomial thresholds were applied to other variables. For example, soil acidity was initially comprised of multiple categories reflecting surface and sub-soil acidity, neutrality or alkalinity. These categories were grouped to whether the sub or surface-soil was acidic (1), or neutral or alkaline (0) (Appendix IV).

Model selection

A series of simple candidate models was derived *a priori* to represent a gradient of increasing emphasis on finer-scale and biotic information, including a climate-only landscape model (average monthly minimum temperature, MT; average rainfall during summer, RS), an abiotic landscape variable model (RS; distance to watercourse, lWC; slope, S; root zone water holding capacity, M; soil acidity, H), a mixed abiotic and biotic landscape variable model (including broad vegetation description, GEN), and a mixed abiotic and biotic landscape and quadrat-scale variable model (including diversity of flora taller than 2 m, C3; shrub cover between 0.5 - 1.0, SC; or sedge cover under 0.5 m, VL) (Table 1). The number of sites occupied by each of the four species was generally small (between 35 and 197), so to reduce the risk of over-fitting we restricted the number of parameters in any given model to better accommodate the recommended 10 records per parameter (see Wintle et al. 2005). Correlated variables ($r > 0.6$) were not used in the same candidate model. Throughout, modelling was performed in R v2.8.0 (R Core Development Team 2009).

We predicted species occurrence using both linear and nonlinear modelling approaches. Generalised linear models (GLM) were used to predict species occurrence for the highest resolution date (i.e. 150 m scale) using a binomial error distribution and logit-link function. Overall model fit was assessed as per cent deviance explained relative to the null model (% DE) (Garnett & Brook 2007). The model with the highest predictive capacity was identified using the difference in Akaike's Information Criterion (corrected for small sample sizes, ΔAIC_c) and relative model weight ($wAIC_c$). Bayesian Information Criterion and Deviance Information Criterion are also reported in Appendix VII.

To avoid generating biased results caused by assuming linear species response curves, boosted regression trees (BRT) (Guisan & Zimmermann 2000) that implicitly account for nonlinearity and interactions were used. BRTs were fitted using the R package GBM (Ridgeway 2009) (following Elith *et al.* 2008). Optimal tree complexity and learning rate were selected by cross-validation for each species (Appendix VIII), bag fractions were set at 0.5 and the relative proportion of deviance explained by each model was calculated from the summary statistics (J. Elith, University of Melbourne, pers. comm., 2009).

Model and variable performance at multiple scales

To determine whether the resolution of environmental data affected our ability to accurately model species distributions, we also fitted GLMs to the 500 m and 1 000 m resolution datasets (Fig. 2). The model fitted to each of these datasets contained the same terms from the most parsimonious GLM identified using the 'within 150 m' data (and its corresponding set of single variable models). We calculated the difference in overall model fit by subtracting the value derived when using the 150 m and 500 m datasets from the 1 000 m dataset.

Results

Effect of additional abiotic and biotic variables on model performance

Abiotic and biotic landscape and quadrat-scale variables explained substantial variation in the presence of some of the species (Table 1, Appendix VII, VIII). The biotic landscape variable (GEN) contributed to the model of best fit (identified as the top ranking model in % DE and $wAIC_c$) for the wet heath specialist *R. l. lutreolus* (M4) and mobile woodland generalist *A. f. flavipes* (M3). The inclusion of (biotic) quadrat-scale variables slightly improved model performance for the less specialist species, occupying dense understorey (*I. o. obesulus*, M4: *R. f. greyi*, M5 GLM), but was most noticeable in contributing to relative model performance for the wet heath specialist (M5-7).

Table 1 Explanatory strength of null and *a priori* generalised linear models, where 'occupied sites' are represented by survey sites within 150 m of a known record locality. Shown are the number of parameters (*k*), minimised negative log-likelihood (-LL), the difference between the Akaike's infor-mation criterion corrected for small sample sizes and the highest-ranking model (ΔAIC_c), weight scaled to a sum of 1 ($wAIC_c$), and the per cent deviance explained by the model relative to the null (% DE) for each method (GLM and BRT) and species.

Model	Variables	*k*	-LL	ΔAIC_c	$wAIC_c$	% DE GLM	% DE BRT
I. o. obesulus (35 presences : 473 absence sites) (prevalence 0.07)							
Null	~ 1	1	-127.4	65.6	0.00		
M1	~ MT + RS	3	-93.8	2.5	0.14	26.4	27.5
M2	~ RS + lWC + H	4	-93.3	3.5	0.09	26.8	26.8
M3	~ RS + GEN	4	-92.3	1.5	0.24	27.5	26.8
M4	~ RS + lWC + C3	4	-92.1	0.0	0.51	27.7	25.9
M5	~ RS + SC	5	-93.9	6.8	0.02	26.3	25.6
A. f. flavipes (66 presences : 440 absence sites) (prevalence 0.13)							
Null	~ 1	1	-195.9	166.4	0.00		
M1	~ MT + RS	3	-114.8	8.2	0.02	41.4	45.6
M2	~ RS + lWC + H	4	-117.6	15.9	0.00	40.0	39.7
M3	~ RS + lWC + H + GEN	6	-107.6	0.0	0.98	45.1	47.6
M4	~ RS + lWC + H + C3	5	-117.2	17.1	0.00	40.2	38.9
M5	~ RS + lWC + H + SC	7	-114.5	15.9	0.00	41.5	38.5
R. f. greyi (197 presences : 388 absence sites) (prevalence 0.34)							
Null	~ 1	1	-373.7	146.4	0.00		
M1	~ MT + RS	3	-298.5	0.0	1.00	20.1	32.4
M2	~ RS + S + M + H	5	-307.9	22.8	0.00	17.6	23.6
M3	~ RS + S + M + H + GEN	8	-306.9	27.0	0.00	17.9	23.5
M4	~ RS + S + M + H + C3	6	-307.4	23.9	0.00	17.8	24.7
M5	~ RS + S + M + H + SC	8	-302.5	18.3	0.00	19.0	24.9
R. l. lutreolus (63 presences : 504 absence sites) (prevalence 0.11)							
Null	~ 1	1	-197.8	146.7	0.00		
M1	~ MT + RS	3	-173.2	101.5	0.00	12.5	27.2
M2	~ RS + S + lWC	4	-152.5	62.3	0.00	22.9	28.9
M3	~ RS + S + M + H	5	-143.1	45.4	0.00	27.7	29.5
M4	~ RS + S + M + GEN	7	-118.3	0.0	1.00	40.2	39.3
M5	~ RS + S + M + C3	5	-133.9	27.0	0.00	32.3	30.3
M6	~ RS + S + M + SC	7	-128.3	19.9	0.00	35.1	32.8
M7	~ RS + S + M + VL	6	-144.9	51.2	0.00	26.7	29.1

MT, average monthly minimum temperature; RS, average monthly rainfall during summer (Nov-Jan); S, slope; lWC, distance from nearest water course or body transformed using the natural log; GEN, broad vegetation community; M, root zone water holding capacity; H, soil acidity; C3, diversity of flora taller than 2 m; SC, shrub cover between 0.5 – 1.0 m in height; VL, sedge cover under 0.5 m.

Effect of decreasing resolution of environmental data on model and variable performance

Declining resolution of environmental data affected model performance for each species to varying degrees (Fig. 3, Appendix IX, X). Model performance deteriorated for the wet heath specialist (*R. l. lutreolus* ~ RS + S + M + GEN) and a dense understorey species (*I. o. obesulus* ~ RS + lWC + C3, *R. f. greyi* ~ MT + RS). These trends corresponded with reduced variance explained by biotic landscape and quadrat-scale variables and abiotic landscape variables, respectively (Fig. 4, Appendix XI). In contrast, model performance improved slightly for the mobile woodland generalist (*A. f. flavipes* ~ RS + lWC + H + GEN), suggesting the variables used to represent interactions with their environment were adequately represented at a low-resolution (1 000 m).

Discussion

Abiotic and biotic landscape and quadrat-scale environmental data, sampled at high-resolution, can be used to represent specialised resource requirements and improve the accuracy of small mammal SDM. Support for this increases with the degree of specialised habitat, diet and shelter required across the four small mammals targeted in this investigation, from the wet heath specialist and herbivore (*R. l. lutreolus*), woodland generalist and insectivore (*A. f. flavipes*), dense understorey omnivore (*I. o. obesulus*), and more widespread, dense understorey omnivore (*R. f. greyi*).

The benefits of including abiotic and biotic landscape and quadrat-scale environmental data were species specific. Abiotic and biotic landscape-scale information improved the SDM for the wet heath specialist and woodland generalist, but not for either dense understorey species. Additional biotic quadrat-scale data again contributed somewhat to the wet heath specialist SDM and negligibly for the dense understorey species SDM. These results encourage us to more carefully consider the ecology of species being modelled, rather than targeting utmost specialists as easier subjects to model (e.g. Swihart *et al.* 2006).

Lower-resolution environmental data caused the model performance to deteriorate for the wet heath specialist and both dense understorey species. These trends corresponded with fine-scale interactions that suggest habitat for the wet heath specialist was defined by features within the landscape other than climate, while indirect or proximal influences of climate on the dense understorey species were better represented at a higher-resolution (especially for the more vulnerable above-ground nesting species). In contrast, low-resolution environmental data had minimal effect on the woodland generalist *A. f. flavipes*, indicating that coarse environmental data sufficiently described its distribution, or that there were additional limitations, not represented in the SDM, that prevented improved model performance (see below).

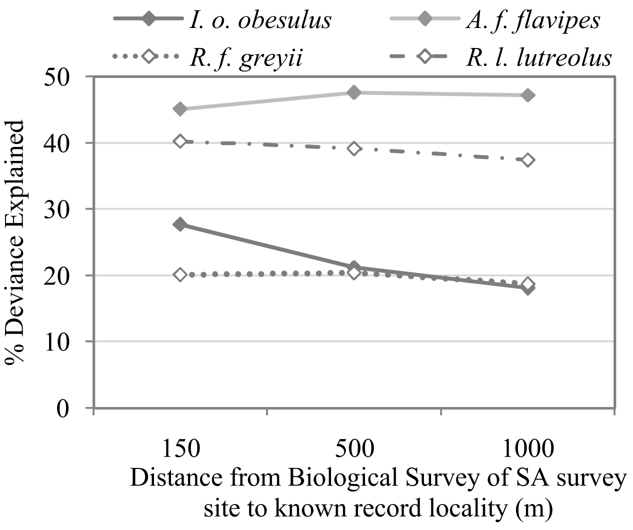


Fig. 3 Change in deviance explained (% DE) by the single best (identified as the top ranking model in % DE and AIC_c) model for each species applied to datasets where species occupancy is represented at three different levels of association (i.e. species 'presence' was adjusted to survey sites with complete environmental data at 150 m, 500 m and 1000 m from original species record localities).

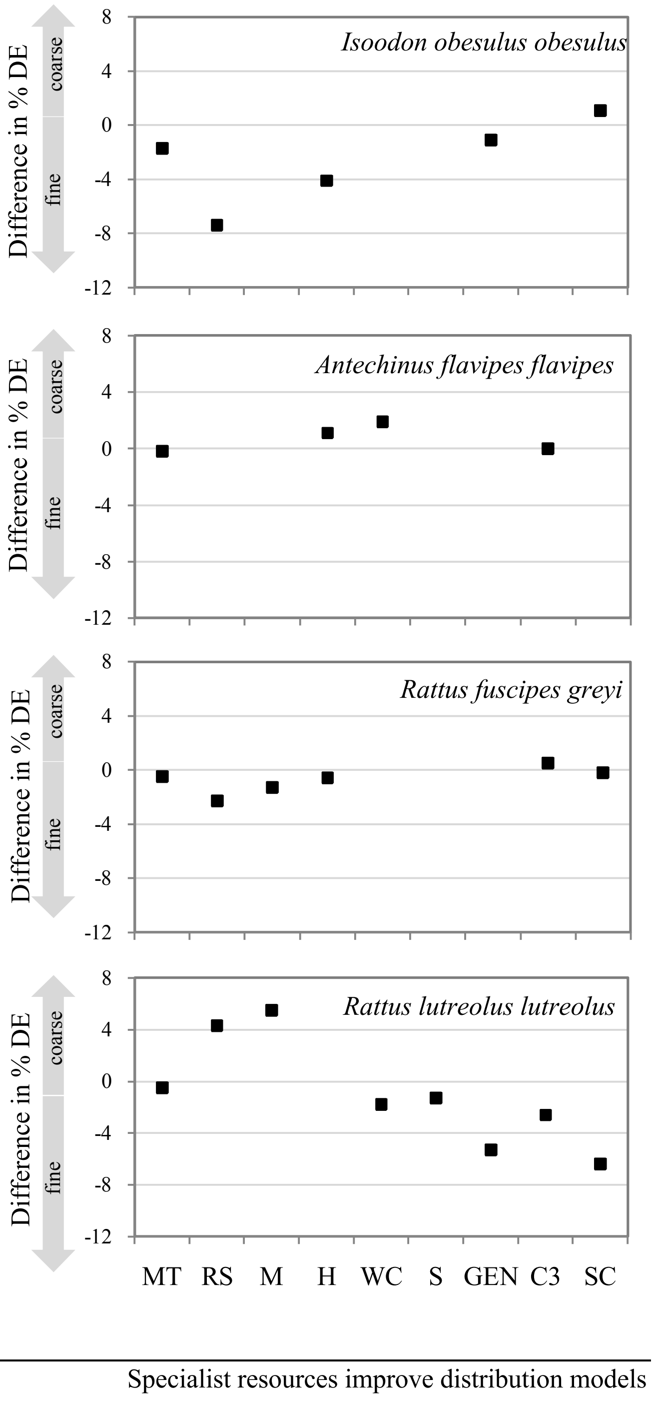


Fig. 4 Change in deviance explained by single-variable models based on decreasing resolution of environmental information (% DE at 1000 m - % DE at 150 m). Only variables demonstrating a consistent increase (coarse-scale correlation) or decrease (fine-scale correlation) in % DE are shown. The remaining variables either had a variable response across these scales, or were not used in any of the candidate models (Appendix IX). The variables shown on the x-axis are: MT, average monthly minimum temperature; RS, average monthly rainfall during summer (Nov-Jan); S, slope; lWC, distance from nearest water course or body transformed using the natural log; GEN, broad vegetation community; M, root zone water holding capacity; H, soil acidity; C3, diversity of flora taller than 2 m; SC, shrub cover between 0.5 – 1.0 m; VL, sedge cover under 0.5 m.

Despite potential limitations, the SDMs used in this investigation appeared to predict some niche separation between the four species. This was illustrated in the direction of change in model performance when lower-resolution landscape and quadrat-scale variables were used to predict species occupancy. The presence of *I. o. obesulus* appeared to be strongly correlated at a fine-to-coarse-scale across these variables; a pattern that was weaker for *R. f. greyi,* not apparent for *A. f. flavipes* and reversed for *R. l. lutreolus*. This result indicates that ecological relationships are at least partially represented in simple *a priori* SDMs, especially when comparing SDMs for different species.

Model limitations and further research

The most obvious limitation to model performance is that key environmental data were missing from the candidate models for each species. A variety of fine-scale variables are known to influence species occurrence, including floristics and cover, understorey stem density, fallen wood and litter moisture (Orrock *et al.* 2000, Mac Nally *et al.* 2001, Manning & Edge 2004, Brannon 2005, Haythornwaite & Dickman 2006, Larrucea & Brussard 2008, Mapelli & Kittlein 2009). The importance of fine-scale variables like these, have even been demonstrated for the generalist species, mulgara, *Dasycercus cristicauda*, and hairy-footed dunnart, *Sminthopsis hirtipes* (Masters 2008, Pearson & McKenzie 2008). However, data representing these features were unavailable for these SDMs, or had insufficient detail.

Quadrat-scale data are often recorded in the field using coarse categories, making them less suitable for modelling (Bowman *et al.* 2001, Pearce *et al.* 2001). In this investigation, the variable shrub cover between 0.5 and 1.0 m (SC) represented the 60 - 70 % understorey cover preferred by *I. o. obesulus* (Paull 1992) within a single broad 30 - 70 % Muir cover category (Heard & Channon 1997). A lack of sufficient detail to represent ecological relationships may explain why, contrary to expectations, the inclusion of quadrat-scale variables provided limited or no improvement to SDMs. Examples include, the importance of vegetation cover in defining *A. f. flavipes* and *R. f. fuscipes* habitat (Catling *et al.* 2000), and floristic composition and structure and *R. l. lutreolus* habitat (Cockburn 1981, Braithwaite & Gullan 1978). For fine-scale variables to contribute to SDMs, more appropriately scaled (Jorgensen 2004), detailed or continuous data are required, especially since interactions between species and environmental factors are often unknown prior to field surveys. Furthermore, spatially explicit maps of fine-scale variables are required to generate maps of the extent and distribution of a species. This remains a challenging task.

Model performance may also be limited by demographic stochasticity and dispersal. Tyre *et al.* (2001) found these factors restricted the variance explained to < 50 %, when modelling greater glider, *Petauroides volans*, habitat. This may be further exaggerated in a fragmented landscape, since small mammals can be sensitive to connectivity (e.g. Fitzgibbon *et al.* 2007). However, the degree of effect of these factors on SDM performance requires further research.

Another factor potentially limiting model performance is biotic interactions, such as competition and predation, masking the influence of environmental variables on species occurrence (Pulliam 2000). For example, *R. l. lutreolus* can outcompete *R. f. greyi* (Maitz & Dickman 2001), which may initially enhance our confidence in building a SDM for *R. l. lutreolus,* but not *R. f. greyi*. However, model performance may be further confounded by local interactions with predators (Fox & Monamy 2007). It is difficult to determine the distribution, density and behaviour of widespread predators from available presence and absence data. Typically, detailed information on biotic interactions are generally only obtained from long-term demographic investigations (e.g. Brook *et al.* 2000). However, for some species, environmental variables may represent both habitat preference (directly) and biotic interactions (indirectly) (Orrock *et al.* 2000).

Conclusion

Abiotic and biotic landscape (coarse-scale) and quadrat-scale (fine-scale) environmental information can be valuable contributors when predicting the occurrence of small mammals. However, the value of incorporating fine-scale information will depend on the level of detail it represents. For fine-scale variables to be successfully used in SDMs, more detailed descriptive or continuous data collected at appropriate scales are required, particularly when interactions between species and environmental factors are often unknown prior to field surveys. Where data representing core aspects of a species ecology are unavailable, or model complexity is limited by the number of species occurrences, model accuracy can still be improved by using high-resolution environmental data. For example, general climatic variables, such as rainfall during summer, were found to influence *I. o. obesulus* and *R. f. greyi* at a fine-scale in this investigation. Ultimately, environmental data used to create SDMs should be justified by the ecology of the target species.

Chapter 3

SCALE DEPENDENCY OF METAPOPULATION MODELS USED TO PREDICT CLIMATE CHANGE IMPACTS ON SMALL MAMMALS

N. A. Haby[1], T. A. A. Prowse[1], S. D. Gregory[1], M. J. Watts[1],
S. Delean[1], D. A. Fordham[1], J. Foulkes[2] and B. W. Brook[1]

The Environment Institute[1] and Terrestrial Ecosystem Research Network[2],
School of Earth & Environmental Sciences, University of Adelaide,
Adelaide SA 5005, Australia

In review: Ecography

STATEMENT OF AUTHORSHIP

SCALE DEPENDENCY OF METAPOPULATION MODELS USED TO PREDICT CLIMATE CHANGE IMPACTS ON SMALL MAMMALS

In review: Ecography

N. A. H. conceptualised manuscript, performed analysis on all samples, interpreted data, wrote manuscript and is corresponding author. T. A. A. P. was available to discuss life history tables, refining analyses in Vortex and provided editorial comments. S. D. G. was available to discuss troubleshooting in R code and provided editorial comments. M. J. Watts contributed tools to aid in extracting select results from RAMAS-GIS output files and provided editorial comments. S. D. provided earlier analytical support and editorial comments. D. A. F. generated climate data (spatial) and provided editorial comments. J. F. Provided editorial comments and B. W. B. contributed to conceptualising the manuscript and provided editorial comments.

All contributors certify that the statement of contribution is accurate and give permission for the inclusion of this material in the thesis.

Signed [redacted] *Date* 30 Apr 2012
Haby, N.A. (Candidate)

Signed [redacted] *Date* 30/4/2012
Prowse, T.A.A.

Signed [redacted] *Date* 26/4/12
Gregory, S.D.

Signed [redacted] *Date* 30/4/12
Watts, M.J.

Signed [redacted] *Date* 27/4/2012
Delean, S.

Signed [redacted] *Date* 27/4/2012
Fordham, D.A.

Signed [redacted] *Date* 26/4/12
Foulkes, J.

Signed [redacted] *Date* 27/4/12
Brook, B.W.

Abstract

For investigating potential range shifts in a changing climate it is becoming increasingly common to develop models that account for demographic processes. Metapopulation models incorporate spatial configuration of occupied habitat (i.e. arrangement, size and quality), population demography, and inter-patch dispersal making them suitable for investigating potential threats to small mammal range and abundance. However, the spatial scale (resolution) used to represent species-environment dynamics may affect estimates of range shift and population resilience by failing to represent stepping stones of suitable habitat and refugia, respectively. We aimed to determine whether relatively fine-scale environmental information and associated model resolution influenced predictions of metapopulation persistence and range shift. The case study includes four small terrestrial mammals from southern Australia. Species distribution models were constructed using environmental predictors measured at 0.01 or 1 km^2 resolution and combined with demographic information to parameterise coupled niche-population models (using RAMAS-GIS). These models simulated population dynamics projected over 40-years under both a stable and changing climate. The total area of predicted available habitat was similar at both spatial scales. However, at the fine-scale, more patches were modelled (ca. 10 times) and were more variable in shape (range in perimeter : area 0.032 at the fine-scale; 0.002 coarse-scale), leading to increased connectivity between patches (ave. no. patches within dispersal distance, < 57 fine-scale; 0 coarse-scale). At the fine-scale, small patches were not more prone to extinction (i.e. per cent loss of populations ~ habitat), although species vulnerability was greater (higher rate of population decline and lower expected minimum abundance). Despite this, greater range shifts were measured at the coarse-scale (for species illustrating a shift at both scales). These results illustrate that potential range shifts and species vulnerability information may be misrepresented if more advanced modelling techniques that incorporate species demographics and dispersal inadequately represent the scale at which these processes occur.

Introduction

Anthropogenic climate change is forecast to cause contractions in the range of many species of mammals (e.g. Levinsky et al. 2007). Whether these changes occur depends on the capacity of a species to track a suitable climate envelop within the landscape: a reflection of not just climatic suitability, but additional factors including the configuration of suitable habitat and demographic and dispersal dynamics within and between patches (Huntley et al. 2010). Depending on these conditions, populations may persist, decline or disappear across a species' range. Metapopulation models provide a framework to explore simultaneously the multiple factors that influence species extinction risk (including synergistic effects; Keith et al. 2008, Fordham et al. 2012) and have been successfully used to explore rates of change in the leading and trailing edges of a species' range (Anderson et al. 2009).

Metapopulation models are often underpinned by species distribution models (SDM; Franklin 2010): the accuracy and relevancy of which is influenced by the scale (resolution) of environmental data used to represent species – environment dynamics (Huntley et al. 2010, Austin and van Niel 2011a, Haby et al. 2012). Coarse-scale climate information is considered to be the predominant factor affecting species distribution and useful for avoiding biotic interactions (Pearson and Dawson 2003). However, climate is most likely to influence species such as small ground-dwelling mammals via resource (food) availability (Claridge et al. 2008), which can fluctuate at a finer scale than a species' home range (Kotlier and Wiens 1990, Claridge et al. 2002).

The use of overly coarse environmental information in SDMs can limit the strength of correlation between environmental variables and species' occurrence (e.g. Haby et al. 2012), under-represent factors influencing species survival (e.g. human resources on winter opossum survival; Kanda et al. 2009), and directly affect the predicted extent and distribution of suitable habitat (Kriticos and Leriche 2010). This includes misrepresenting key microrefugia with stable climates that buffer against stochasticity and potentially enable persistence in a changing climate (Randin et al. 2009, Willis and Bhagwat 2009, Sublette Mosblech et al. 2011). Microrefugia can be especially important for the persistence of poor dispersers (Ashcroft 2010). Using coarse environmental information can also lead to low cohesion between patches of suitable habitat that prevent simulated populations from tracking suitable habitat in a changing climate (Sondgerath and Schroder 2002, Opdam and Wascher 2004), while allowing large scale, extreme weather events to cause large gaps of unoccupied habitat within in a species' range (Opdam and Wascher 2004). Overall, these limitations can lead to underestimates or overestimates of extinction risk (Sublette Mosblech et al. 2011).

Generally, small mammal populations are suitable candidates for metapopulation models because they have limited dispersal capacity and short generation times (Olivier et al. 2009). Indeed, a number of investigations have focused on metapopulation function and dynamics (e.g. Brito and da Fonseca 2007), including the potential effects of development and management programs on small mammal persistence (e.g. Anderson et al. 2009). The scale of environmental data used to define the spatial configuration of available habitat incorporated into metapopulation models may be, however, particularly important for small mammals because they may occupy habitat that is not well represented by currently available data.

While fine-scale environmental information used in modelling species' distributions has previously been represented at 1 km^2 (e.g. for a rare species, Lomba et al. 2010), we expected finer-resolution data to represent a more complex spatial configuration of available habitat (via increased number of patches that are more variable in size and shape), leading to improved connectivity between patches to facilitate dispersal across the landscape in response to a changing climate. To investigate this, coupled niche-population models were constructed in RAMAS-GIS (Akçakaya 2005), and run over 40-years of simulated climate change. These models integrated SDMs built with environmental information sampled at 0.01 or 1 km^2 resolution. The 1 km^2 'coarse' resolution represents a scale often reported in SDM investigations (e.g., Lomba et al. 2010), above which little change has been found on representing landscape parameters (i.e. between 1-3 km; Price et al. 2010). The 0.01 km^2 'fine' resolution was expected to better represent the ecology of the species (e.g. dispersal capacity; Table 1), and factors driving their patchy occupation of remnant habitat (e.g. Gooch and Haby 2003), while being computationally feasible. As a case study, we considered differences and similarities among four small mammal species across two regions of southern Australia. Several outputs at each scale were compared for each species (as recommended by Beissinger and Westphal 1998) to investigate differences in the spatial configuration of available habitat (i.e. patch number, size, shape and connectivity), and population vulnerability via: i) rate of change in abundance, ii) expected minimum abundance (McCarthy and Thompson 2001), and iii) shifts in regional range centroids and boundary.

Methods

Study species

The four small terrestrial mammals (two marsupials and two rodents) we modelled have differing autoecological and life history traits (Table 1, Appendix XII). Habitat loss and fragmentation for agricultural production has resulted in the southern brown bandicoot (Peramelidae, *Isoodon obesulus obesulus*) being listed as endangered (*Environment Protection and Biodiversity Conservation Act 1999*), and the yellow-footed antechinus (Dasyuridae, *Antechinus flavipes flavipes*) and swamp rat (Muridae, *Rattus lutreolus lutreolus*) regionally vulnerable and rare, respectively (*South Australia National Parks and Wildlife Act 1972*). The bush rat (Muridae, *Rattus fuscipes greyi*) is common.

Coupled niche-population model

Species presence and absence data and available environmental information were used to generate a species distribution model (SDM) for each species. SDMs were combined with a stage-structured stochastic and demographically explicit population viability analysis model to create a coupled niche-population model in RAMAS-GIS (Akçakaya 2005).

Species presences and absences

SDM are ideally based on presence-absence data (Kent and Carmel 2011), but absences are usually unavailable, unreliable or limited (Lobo et al. 2010, Kent and Carmel 2011). The Biological Survey of South Australia presents a unique opportunity to extract presence-absence data from an extensive, systematic baseline survey of intact, remnant vegetation communities (Heard and Channon 1997, Owens 2000). Additional records of occurrence were sourced from local survey and monitoring programs, and the South Australian Museum (Biological Databases of South Australia, December

2008). Records were limited to those collected using reliable methods (e.g. captures, sightings and signs unlikely to be confused with other species), < 100 m location accuracy and post-1970. Species absences were represented by biological survey sites that incorporated four nights trapping, using Elliott, cage traps and pitfall traps, and failed to capture the target species. This systematic approach reduces the risk of including false absences as *Rattus* spp. are often quick to detect, facilitated by Elliott traps being placed in run-ways. Resident *Antechinus f. flavipes* are often detected within four nights (Marchesan and Carthew 2008), while the less abundant *I. o. obesulus* can also be detected by other methods used (e.g. hair tubes and signs of diggings). Finally, to reduce influence of false absences and maximise the benefit of a limited number of presences on model outputs, we used the Maximum Sum of Sensitivity and Specificity threshold (MSS; calculated in R using `PresenceAbsence`) to identify presences because it has been shown to down weight the influence of false-absences (Freeman 2007).

Environmental data

Features within the environment representing climate, topography, soil and vegetation types were available in a series of spatial layers (Appendix IV). These spatial layers were resampled to 0.01 and 1 km^2 pixel resolution using ArcInfo 9.3 (ESRI 2009).

Species distribution model and patch structure

SDMs were constructed using all available occurrence data and environmental variables previously found to be correlated with species occurrence (Chapter 1). The generalised linear models (GLM) with a binomial error distribution and logit link function were fitted in R v2.13.1 (R Core Development Team 2011; www.r-project.org; Chapter 1). The model structure goodness-of-fit was reported as the per cent deviance explained relative to the null model (% DE) and performance statistics calculated (area under the receiver curve (AUC), Kappa, sensitivity and specificity) using a Maximum Sum of Sensitivity and Specificity threshold calculated using the R package PresenceAbsence (Freeman 2007). The performance of each of these SDMs is evaluated in Appendix XIII.

Each SDM was then predicted across 0.01 and 1 km^2 pixel environmental data that included climate projections from 2001 to 2041 and the MSS threshold used to convert probability values into binomial habitat suitability maps. Habitat patches were then created by grouping pixels of suitable habitat within frequent dispersal distance likely to represent contiguous populations using the neighbourhood cell distance parameter (Table 1).

Stage-matrix parameters

An age-structured post-breeding matrix population model was constructed for each species using available information on fertility and mortality of subadult and adults (Table 1). Juvenile mortality was then adjusted in a cohort life table until a stable population was reached (Caughley 1977). As these species establish independent home ranges that may overlap with individuals with the opposite sex, the population demographic models were limited to one sex (females).

Table 1 Demographic parameters applied in the coupled niche-population models using RAMAS-GIS. This process requires a habitat suitability map generated using a species distribution model. Once a threshold value is applied, the map represents unsuitable and suitable habitat (0 and 1, respectively) and habitat pixels combined into patches using the neighbourhood distance. These patches then form the basis of the population demographic model. Where two parameters are presented, the left and right values were applied to the 0.01 and 1 km^2 models, respectively.

	A. f. flavipes	*I. o. obesulus*	*R. f. greyi*	*R. l. lutreolus*
Species biology				
Family	Dasyuridae	Peramelidae	Muridae	Muridae
Status	VU (Sth Aust.)	EN (Aust.)	No listing	Rare (Sth Aust.)
Weight (g)	21 - 79	400 - 1850	40 - 225	50 - 200
Habitat preference	structurally complex	dense and low vegetation	dense and low vegetation	tall grass and sedge
Diet	insectivorous and carnivorous	omnivorous	omnivorous	herbivorous
Shelter	tree hollows, *Xanthorrhoea* spp.	mounds of leaf litter, dense shrubs	burrows	burrows
Habitat suitability index				
Number of records[b]	80:390 or 293	209:426 or 317	198:344 or 260	52:446 or 338
Regions of occurrence included in models[c]	FP, SE	FP, KI, SE	EP, FP, KI, SE	FP, SE
Threshold (MSS)	0.15[a], 0.17[a]	0.39 [a], 0.43[a]	0.565 [a], 0.61[a]	0.07, 0.115
Neighbourhood distance	2.5, 1.5	1.5, 1.5	1.5, 1.5	1.5, 1.5
Population demographic parameters				
Life history table / stage matrix				
• No. stages	3 (≤ 2 yr)	4 (≤ 3 yr)	3 (≤ 2 yr)	4 (≤ 3 yr)
• Age at first breeding	1	1	1	1
• Fertility (/yr) (young*litters/♀)	(8*1)/2 = 4	(3.1*3)/2 = 4.62 Don't breed in 4th breeding season	(5*3.5)/2 = 8.75 Don't breed in 2nd breeding season	(5*2)/2 = 5 Don't breed in 3rd breeding season
SD	± 33.75 %	± 36 %	± 30 %	± 30 %

(cont.)

(cont.) **Table 1**

	A. f. flavipes	*I. o. obesulus*	*R. f. greyi*	*R. l. lutreolus*
Survival rates (%)	24.7 (0 – 1) 1.72 (1 yr)	10.5 (0 – 1) 65 (1+ yr)	11.2 (0 – 1) 2.53 (1+ yr)	12.47 (0 – 1) 60.1 (1+ yr)
SD	± 5 %	± 5 %	± 5 %	± 5 %
Rmax	1.574 (biol.)	1.72 (biol.)	2. 075 (oregan vole; biol. 2.25)	1.243 (ave. watervole muskrat; biol. 1.78)
Initial abundance & carrying capacity (K)	2 ha^{-1}, 200 km^{-1}	3 ha^{-}1, 300 km^{-1}	10 ha^{-1}, 1000 km^{-1}	7 ha^{-1}, 700 km^{-1}
Dispersal function, Mij = a.exp(-Dij$^{c/b}$), where D is the distance from patch i to j	0.8.exp(-Dij$^{0.6/0.24}$)	0.5.exp(-Dij$^{0.95/0.1}$)	0.5.exp(-Dij$^{0.6/0.2}$)	0.5.exp(-Dij$^{0.9/0.1}$)
Max. dispersal (Dmax)	1.55 km	0.6 km	0.75 km	0.45 km

[a]Threshold used to convert probabilities into suitable and unsuitable habitat.

[b]The limited number of presences available was retained at both scales by manually inserting missing environmental data no longer represented at 0.01 or 1 km^2 resolution before the species distribution models were created.

[c]Region codes represent Eyre Peninsula (EP), Fleurieu Peninsula (FP) Kangaroo Island (KI) and South East (SE).

Initial abundance, carrying capacity and density dependence

Demographic parameters were sourced from local investigations that generally targeted good quality habitats. As a result, all habitats modelled were assumed to represent good quality habitat capable of supporting a high density of individuals at carrying capacity (i.e. number of cells*density; Table 1). Without considering a range of habitat qualities and the subsequent effect on survival and reproduction parameters, the estimated number and size of populations is likely to be overly optimistic (e.g. Southwell et al. 2008). In addition, all patches of suitable habitat were allowed to be occupied at the start of the simulation (excluding single-pixel populations at the fine resolution; see ‘Stochasticity’ below). To ensure a stable metapopulation structure prior to the integration of a changing climate, the initial abundance of single-pixel populations were set to 0 at the first time step for models built at the fine-scale. The occupancy of these patches would then be driven by immigration during a 20-year burn-in period of stable climate preceding each simulation (see ‘Simulation’ below). Over-estimating patch occupancy and animal abundance is not expected to inhibit a relative comparison of model function at two scales, however, these results should not be considered absolute representations of species distributions.

Density dependence was assumed as scramble competition (i.e. Ricker logistic), whereby resources available to all individuals decrease as abundance of ‘all stages’ increases , affecting all vital rates (only survival rate for *R. l. lutreolus*). The theoretical maximum possible increase of a population completely unconstrained from intraspecific competition (Rmax) was estimated for each species from literature on their biological constraints, or selected from long-term monitoring programs of species with similar biological traits where available (Herrando-Perez et al. Unpubl.).

Stochasticity

Environmental stochasticity was simulated as a correlated lognormal distribution around survival and fertility rates. There was no correlation set between populations, stochasticity in carrying capacity or dispersal.

Dispersal

Field-based programs rarely estimate the proportion of individuals that disperse from natural populations or the distance travelled. However, estimates of maximum dispersal were available and were used in a negative exponential dispersal functions to calculate the proportion of individuals moving between patch edges (i.e. edge to edge dispersal; Table 1). These values may over-estimate actual dispersal capacity represented by a single case within contiguous vegetation (Jacobson and Peres-Neto 2010), or underestimate dispersal ability (e.g. for the banner-tailed kangaroo rat; Winters and Waser 2003).

Simulation

The coupled niche-population models were constructed at each resolution, for each species, across two regions that encompass natural subsets in the distribution of the species (Fleurieu Peninsula and South East), using a stable climate scenario and 40-years of climate change based on a no-climate-policy reference (no stabilization) scenario (MiniCAM Ref.; Clark et al 2007). Maggicc/Scengen v5 (Fordham et al. 2012) was used to generate multi-model climate averged annual forecasts (2001 - 2041) based on seven general circulation models, previously shown to be suitable for Australia (Fordham et al. 2011). Each simulation incorporated a 20-year burn-in period over a stable climate (held constant at 2001 level), followed by 40-years climate change (time step = 1 year) or stable climate, and 1000 replications. The only case where these parameters were not applied was for *R. l. lutreolus* in the South East, which were constrained to 35 years climate change due to limitations in program capacity when modelling populations at a finer resolution.

Sensitivity analyses

Additional sensitivity analyses included indirectly enhancing patch connectivity by increasing maximum dispersal (Dmax) to 5 km, but altering the dispersal-distance function to retain the same proportion of individuals dispersing (i.e. same area under the curve; SA 1), increased variation in survival rates from 5 % to 10 % (SA 2) and a combination of these (SA 3). Maximum dispersal and survival were chosen for the sensitivity analyses to indirectly represent habitat not represented at these scales (e.g. along roadsides) that would facilitate dispersal in a fragmented landscape and adult survival is the governing vital rate in the stability of *r*-selected species.

Evaluating spatial and temporal changes in the metapopulation

Extent and configuration of available habitat

Differences in the spatial configuration of available habitat were evaluated through their effect on range extents and landscape metrics describing the distribution of available habitat at the two scales. Landscape metrics such as number of patches, were obtained from RAMAS-GIS output files, and additional 'patch area' and 'perimeter-to-area ratio' metrics in R using packages raster (Hijmans and van Etten 2011), maptools (Lewin-Koh et al. 2011) and SDMtools (VanDerWal et al. 2011). The 'minimum distance between patches' exported from RAMAS-GIS was calculated using the R package raster. The range medoid of available habitat was generated using a euclidean distance dissimilarity matrix across latitude and longitude values of patch centroids within an entire region (i.e. the number of clusters equalled 1; using R package cluster (Maechler et al. 2011).

Shifts in range centroids and margins

The range centroid of occupied habitat was derived from RAMAS-GIS output files at the first and last time step and the northern, southern, eastern and western range extents were calculated from the centroids of occupied patches (using the 'GetMeans' and 'GetNonzeroPoints' tools available at purl.oclc.org/globalecology/ramas/). The 'GetMeans' tool extracts from RAMAS-GIS output files the centroid of occupied populations at the initial time step and measures the relative shift for each subsequent time step. The 'GetNonzeroPoints' tool extracts the centroids of populations (i.e. occupied habitat), enabling the northern, southern, eastern and western populations to be identified. All spatial coordinates were converted back to latitude and longitude (GDA 94) in Microsoft Excel for comparison with available habitat.

Metapopulation abundance and patch occupancy

Changes in the abundance of individuals and populations were extracted from RAMAS-GIS. The rates of decline (or increase) in the number of populations and individuals over time were explored using a simple linear regression in R. Patch occupancy was explored as a function of patch metric variables using a non-parametric Cox proportional hazards regression (survival package in R; Lumley 2011), which accounts for time dependent data and the 40-year, right-censored data. The overall model structure goodness of fit was reported as the per cent deviance explained relative to the null model (%

DE), along with the predictive capacity represented by the Akaike's Information Criterion (corrected for small sample sizes, ΔAIC_c) and relative model weight ($wAIC_c$). The explanatory strength (relative importance) of each variable in describing the average occupancy duration of a patch was calculated as the combined change in deviance explained when each variable was removed from the saturate model and added to the null (intercept only) model (Garnett and Brook 2007).

In addition, the expected minimum abundance was extracted from RAMAS-GIS, which provides a measure of species vulnerability more resilient to changes in mean population growth rate than extinction risk (McCarthy and Thompson 2001).

Results

Effect of patch metrics on the duration of local occupancy

Habitat area estimated according to fine-scale SDMs was similar to that estimated at the coarse-scale (Table 2). Differences in estimates of areas occurred between species; a larger area was estimated at the fine-scale than coarse-scale in one case (*R. l. lutreolus*, FP), similar area in two cases (*A. f. flavipes*, FP; *R. l. lutreolus*, SE), and smaller area by approximately 10 % for three cases (*I. o. obesulus*, *R. f. greyi*, FP), or 21 % and 35 % for the remaining cases (*R. f. greyi*, SE and *A. f. flavipes*, SE, respectively; Appendix XIII). The general similarity of habitat area between scales was reflected in the initial total number of individuals (slightly scaled for each species; Fig. 1a), but not in the total number of patches and occupied populations which were an order of magnitude higher at the finer scale (Fig. 1b, Table 2).

Available habitat was found to be more irregularly shaped at the fine-scale than at the coarse-scale, based on the greater perimeter-to-area ratios (Table 2) and lower correlation between patch area and perimeter-to-area ratio (mean Pearson's r -0.36 and -0.66, respectively). This enabled greater opportunities for dispersal between neighbouring patches, with no dispersal possible at the coarse-scale (i.e. distance between patches exceeded maximum dispersal capacity; Table 2).

At the fine-scale, environmental stochasticity drove local extinctions in the stable population demographic models within the 40-years of stable climate simulations for each species. This enabled patch occupancy (i.e. 'duration of local occupancy') to be explored as a function of landscape metrics. Larger and less-isolated patches (influenced by irregular shape and the presence of small patches of suitable habitat to act as 'stepping stones') were expected to persist for longer. Patch occupancy was most strongly correlated with patch area, followed by the perimeter-to-area ratio (X-CH; Fig. 2). Average patch occupancy duration was strongly correlated with minimum distance between neighbouring patches for the more mobile woodland generalist *A. f. flavipes* and *R. f. greyi*.

The strength of correlation between patch occupancy during climate change and patch metrics was weaker relative to the stable climate scenario, illustrating an indiscriminate effect of climate change on population persistence at a regional scale (CH; Fig. 2).

Effect of scale on persistence and population dynamics in a changing climate

Over 40-years of simulated climate change, the number of small mammals declined at both scales (Fig 1a). The rate of decline was lower at the fine-scale (especially in the FP; Table 2, Appendix XIII), but was associated with greater population loss (Table 2) and lower median expected minimum abundance (%) after 40-years of simulated climate change (Fig. 3), especially in the South East. These results were obtained despite more frequent movement of animals into available patches generated as a consequence of fragmentation, new habitat becoming suitable within dispersal distance or recolonisation of previously suitable habitat (Fig. 1b, Table 2). Results obtained from the sensitivity analyses supported elevated metapopulation abundance for some species at the fine-scale in response to increased dispersal capacity (SA1, SA3; Appendix XIV).

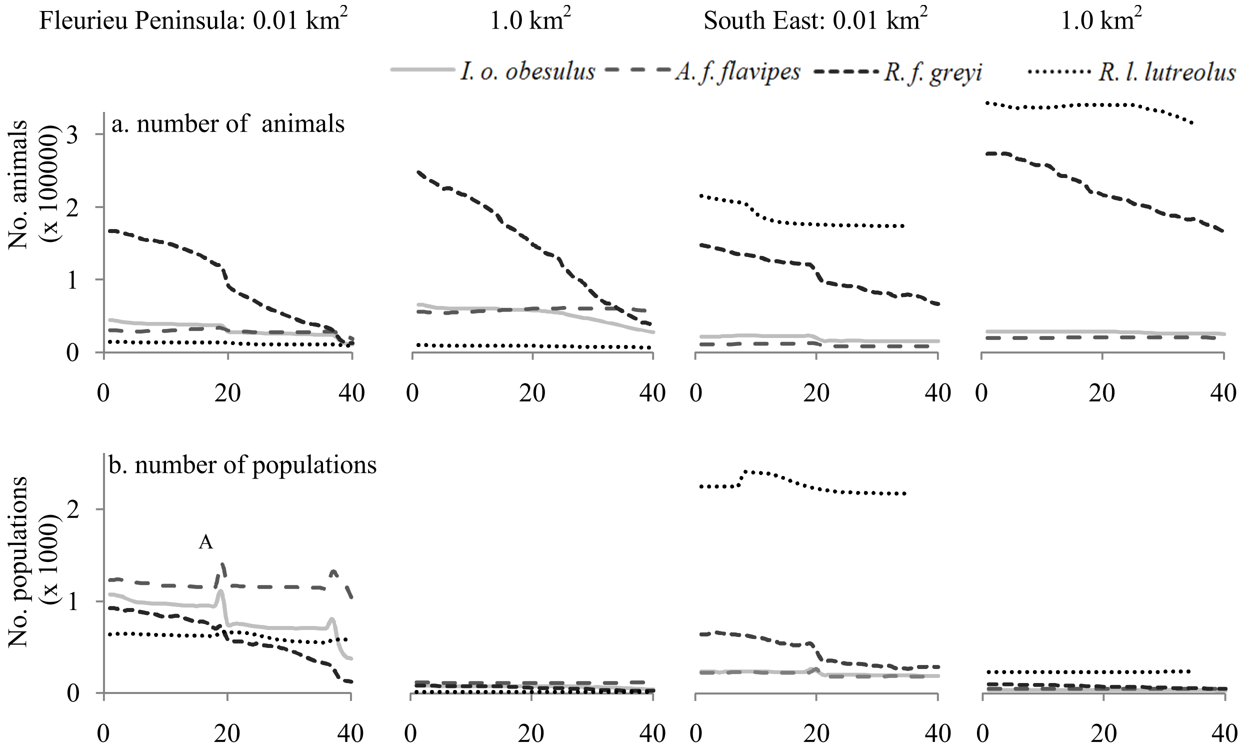


Fig. 1 Number of a) individuals, and b) populations simulated over 40-years of projected climate change using coupled niche-population models incorporating environmental information at two scales of spatial resolution (0.01 and 1 km^2). Temporary peaks (e.g. A) indicate time steps where habitat suitability of many pixels falls below threshold, leading to a substantial alteration in the configuration of available habitat and temporarily increasing the number of transitional populations. Unsustainable populations perish in the subsequent time steps. The absence if these peaks from trends at the coarse resolution are an additional reflection of low metapopulation function.

Table 2 Summary of the a) initial habitat and population, and b) changes over 40-years of projected climate change (1000 simulation iterations, for the species' range on the Fleurieu Peninsula and South East. Values are calculated across species and include the average (SD) or median (min-max) values. More detailed values are provided in Appendix XIII.

	Fleurieu Peninsula		South East	
resolution:	0.01 km^2	1.0 km^2	0.01 km^2	1.0 km^2
a. Initial spatial configuration of available habitat and number of occupied patches:				
Ave. habitat area (km^2)	193 (121)	199 (128)	221 (212)	244 (198)
Ave. no. patches	1123 (148)	72 (41)	919 (1112)	98 (83)
Ave. no. popn[1]	943 (238)	72 (41)	787 (899)	98 (83)
Ave. max no. patches within dispersal dist.	57 (56)	0 (0)	17 (7)	0 (0)
Median patch area (hectares)	2.75 (1-4246)	100 (100-3675)	3.75 (1-2947)	125 (100-3425)
Median p:a ratio	0.032 (0.008-0.04)	0.004 (0.002-0.004)	0.028 (0.002-0.04)	0.004 (0.002-0.004)
Median distance between patches (km)	0.3 (0.2-5.7)	3.6 (1.8-15.2)	0.3 (0.2-7.8)	2.6 (1.8-14.7)
b. Changes following 40 years of climate change:				
Total available habitat that is occupied (%)	78 (27)	92 (4)	73 (14)	92 (4)
Patch no. (%)	-55 (30)	-41 (28)	-23 (22)	11 (88)
Habitat area (%)	-67 (24)	-47 (35)	-35 (18)	-16 (18)
Population no. (%)	-44 (38)	-37 (29)	-25 (22)	-15 (23)
No. new populations created	744 (417)	15 (10)	168 (74)	8 (6)
Ave. abund. animals yr^{-1}	-1329 (2041)	-3733 (2497)	-897 (918)	-804 (1304)
No. occupied popns yr^{-1}	-9 (9)	-1 (1)	-5 (5)	0 (1)
Expected minimum abundance (%)	37 (25)	49 (30)	64 (14)	78 (15)

[1] Averaged from 1000 simulations over the burn-in period

The difference between habitat loss (%) and the decline in the number of populations (%) indicates increased fragmentation of populations at both scales (Fig. 4). There was no indication that a loss of smaller populations was more prevalent at the fine-scale.

Range shift to track habitat availability

The largest shifts in the range centroid (influenced by both the extent and density of occupied populations) were towards the north-east (higher elevation) in the Fleurieu Peninsula and south-east in the South East region (Fig. 5). At the finer scale, predicted changes in the range centroid (unweighted by abundance) were often less than observed at the coarse-scale (more resilient), but detected additional changes for *A. f. flavipes* (more sensitive; Fig. 5). This was also the case for detecting changes in the centroid of available habitat (Appendix XV), which in most cases, shifted NE or SE at a faster rate than occupied patches. Results obtained from the sensitivity analyses generally agreed with these values (Appendix XV).

The NE range shift in the Fleurieu Peninsula and SE shift in the South East coincided with contracting SW and NW range edges, respectively, for some species (Fig. 6, Appendix XVI). At the fine-scale, contractions were lower than illustrated at the coarse-scale in the Fleurieu Peninsula, while the reverse was true for the South East. More instances of range contractions in available habitat were also detected at the fine-scale (i.e. *R. l. lutreolus* in the Fleurieu Peninsula and *A. f. flavipes* in the South East; Appendix XVI).

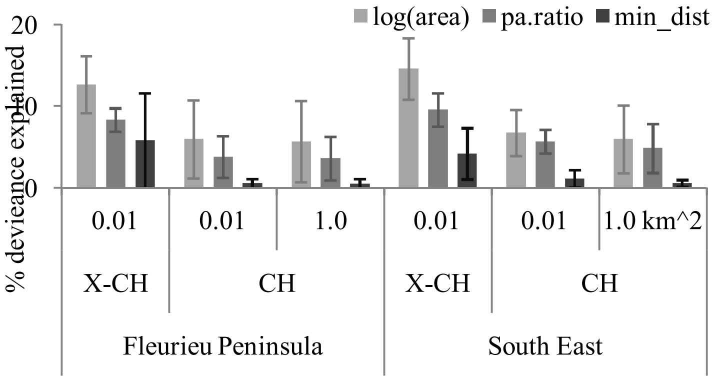


Fig. 2 Average (SD) strength of each landscape variable in explaining the patch occupancy predicted during the stable climate (X-CH) and 40 years of projected climate change (CH) at 0.01 and 1 km^2 resolution (there was insufficient environmental variability to cause local extinctions at 1 km^2 in the X-CH scenario). Variables include the natural log of patch area, perimeter-to-area ratio and minimum distance between patches. These variables were uncorrelated at 0.01 km^2, but correlated at 1 km^2 (mean Perason's r -0.36 and -0.66, respectively). Patch metrics from transitional populations are not included.

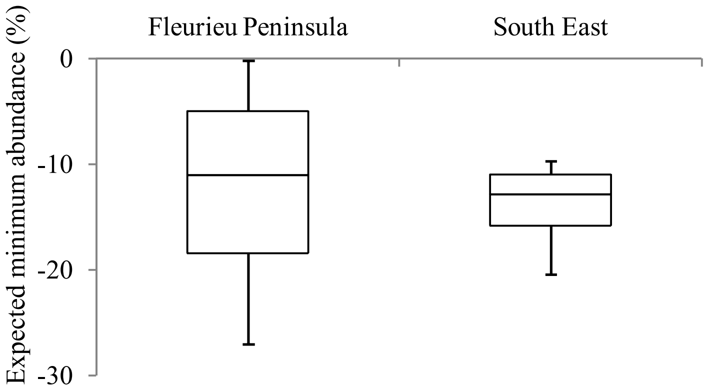


Fig. 3 Difference between per cent expected minimum abundance (EMA) at 0.01 and 1 km^2 following 40-years of climate change.

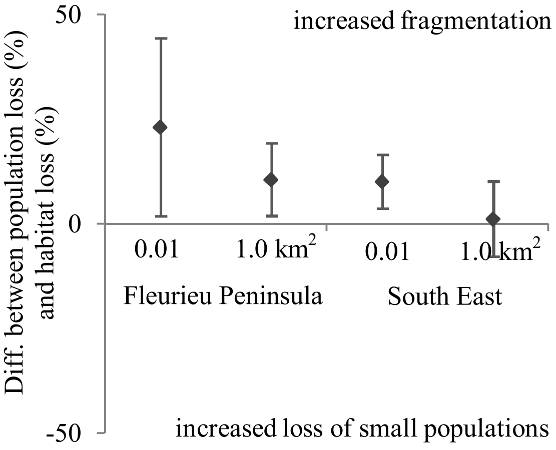


Fig. 4 Test for bias in loss of small populations (decline in number of populations > decline in available habitat). A greater loss of small populations at the fine-scale is not evident. Instead, a greater loss in available habitat (%) than number of populations (%) indicating increased habitat fragmentation is shown across all scales and regions.

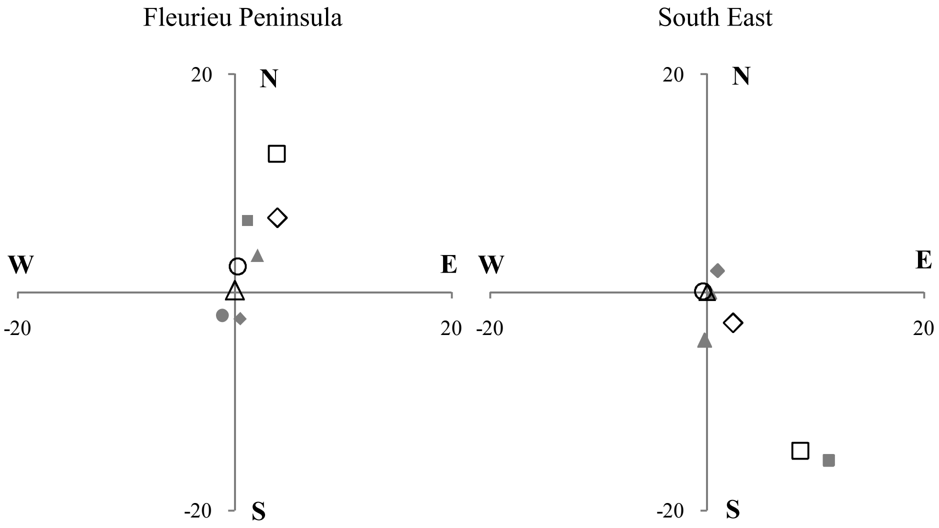
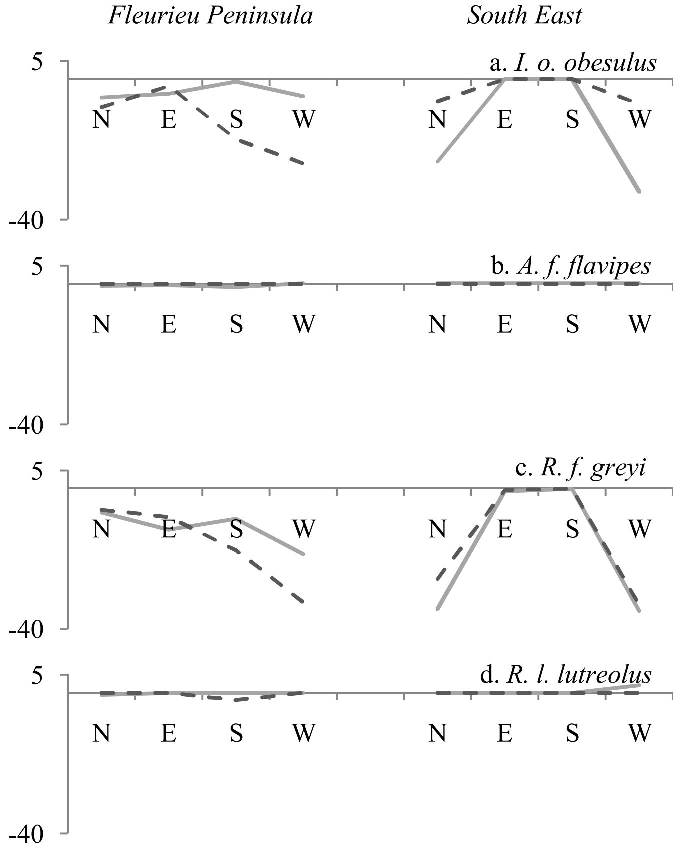


Fig. 5 Shift in the centre-point of occupied habitat at 0.01 and 1 km^2 resolution (solid or hollow symbols, respectively), in the two study areas: Fleurieu Peninsula and South East. Shift is greater at the coarse resolution for species illustrating a shift at both scales, contrary to evidence supporting increased patch connectivity at the fine-scale (i.e. greater number and variability in shape within dispersal distance). Species are represented by diamonds (*I. o. obesulus*), triangles (*A. f. flavipes*), squares (*R. f. greyi*) or circles (*R. l. lutreolus*).

Fig. 6 Contractions in the extent of occupied habitat at 0.01 km^2 (grey solid line) and 1 km^2 resolution (dark grey dashed line), within the Fleurieu Peninsula, and South East. Contrary to expectations greater contractions were detected at the coarse-scale in the Fleurieu Peninsula. Only minor range expansions were predicted (positive values). In the South East, expansion in the south-easterly direction is constrained by the coast (south) and this investigation being constrained by a state boundary (east).



Discussion

This investigation detected a number of scale-dependent inconsistencies that related small changes in a landscape populated by fewer, more isolated populations with greater estimated rates of decline in the number of individuals and range shift (when detected) using coarse-scale environmental information.

At both scales the average total area of available habitat and maximum patch size were similar (Table 2). However, patches of available habitat defined at the fine-scale were i) much greater in number (ca 10 times) and included small patches that may act as stepping stones for shifting populations, ii) more irregularly shaped (greater range of p:a values), iii) had a greater core area (max p:a 0.04 at a fine-scale; 0.004 coarse-scale), and iii) were more often within dispersal distance (>200 m fine-scale; >1800 m coarse-scale).

The greater number of populations modelled at the fine-scale declined at a faster rate (Table 2) and had a lower expected minimum abundance (Fig. 3). The higher vulnerability of populations at this scale may reflect the increased sensitivity of small populations to stochastic extinction events (e.g. containing 10-20 individuals; Brito and da Fonseca 2007), which can increase the extinction risk of metapopulations comprised of small populations (Forys and Humphry 1999). However, a greater rate of loss of small populations relative to habitat fragmentation is not supported in this investigation (Fig. 4). This is reassuring as colonisations of very small populations can aid in species' persistence (Crone et al. 2001). Furthermore, the abundance of individuals declined at a slower rate (Table 2), suggesting higher resilience in this parameter when measured using finer-scale models.

The faster rates of decline in the number of populations estimated at the fine-scale were associated with higher rates of translocations caused by fragmentation of existing patches, dispersal to newly available habitat or recolonisation of previously occupied habitat. There were several indications of increased translocation, including i) a sharp increase in population abundance in response to a sudden loss of habitat and subsequent change in habitat configuration (e.g. Fig 1 "A"), ii) a greater number of transitionary populations (Appendix XIII), iii) increased rates of fragmentation (Fig. 3), and iv) increased occupation of available habitat in response to altered dispersal capacity (i.e. SA 1 and 3; Appendix XIV).

Increased translocation implies increased cohesion within the metapopulation with the potential to facilitate inter-patch movements and range shift (Opdam and Wascher 2004). Based on this, we would expect range shifts to be greater at a fine-scale than coarse-scale. This was the case for one species that was not detected to shift at the coarse-scale (*A. f. flavipes*), however, lower range shifts were predicted for species illustrating a shift at both scales (Fig. 5). The exaggerated range shifts at the coarse-scale supports the assertion that coarse environmental data risks overestimating species' extinction risk (Austin and van Niel 2011b).

Although potentially more realistic, models that integrate climate, habitat, demographic and population dynamics, especially at fine spatial scales, obviously require more data (Huntley et al. 2010), in particular, demographic information such as population growth rates and vital rates (e.g. Coulson et al. 2001), habitat requirements, availability and quality (Southwell et al. 2008), and information on inter-patch dispersal (Jacobson and Peres-Neto 2010). This information is likely to influence estimates of species persistence in different ways. Empirical investigations have illustrated the influence of patch size on occupancy, patch area, habitat quality and distance to ditches on extinction risk, and connectivity and patch occupancy on recolonisation rates (e.g. muskrats; Schooley and Branch 2009).

Overall, the coupled niche-population models showed the highest sensitivity to climate change for *R. f. greyi*, followed by *I. o. obesulus*, *R. l. lutreolus* and *A. f. flavipes* (based on the per cent loss of populations and habitat, Appendix XV; range shift, Fig. 5 and contractions of range edge, Fig. 6). This ranking is the reverse of SDM predictive capacity (% DE; Appendix XIIa), but reflects species SDMs influenced more by climate variables, indicating additional environmental variables can confound predictions (e.g. topographic, soil and vegetation variables for the wet-heath specialist, *R. l. lutreolus* and *A. f. flavipes*). The importance of fine-scale information representing habitat geometry and quality and subsequently population demography and dispersal potential has empirical support across a variety of additional taxa (e.g. Löbel et al. 2006, Hokit et al. 2010, Baguette et al. 2011).

This investigation focused on a relative comparison of multiple points of reference to determine the influence of scale on metapopulation persistence, function and shift in a changing climate. We found greater inter-patch dispersal, lower rates of decline (in individual abundance) and range shift represented at the fine-scale. Consequently, where little is known of the ecology of a species to parameterise a metapopulation model, environmental information is too coarse to enable dispersal and regions where the effects of climate change may over-ride the influence of landscape metrics on patch occupancy (as indicated in this investigation; Fig. 2) we recommend simple SDMs be used to approximate species' distributions.

Chapter 4

LESSONS FROM THE ARID ZONE: USING CLIMATE VARIABLES TO PREDICT SMALL MAMMAL OCCURRENCE IN HOT, DRY ENVIRONMENTS

N.A. Haby[1], J. Foulkes[2], B.W. Brook[1]

The Environment Institute[1] and Terrestrial Ecosystem Research Network[2],
School of Earth & Environmental Sciences, University of Adelaide,
Adelaide SA 5005, Australia

In review: Landscape Ecology

STATEMENT OF AUTHORSHIP

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N. A. H. conceptualised the manuscript, performed analyses, interpreted data, wrote manuscript and is corresponding author. J. F. and B. W. B. provided editorial comments.

All contributors certify that the statement of contribution is accurate and give permission for the inclusion of this material in the thesis.

Signed [redacted] *Date* 27 Apr 2012
Haby, N.A. (Candidate)

Signed [redacted] *Date* 26/4/12
Foulkes, J.

Signed [redacted] *Date* 27/4/12
Brook, B.W.

Abstract

The direct and synergistic effects of anthropogenic climate change are forecast to cause temperatures to rise and rainfall to become less reliable, threatening many species. Hot and highly variable rainfall already defines the climate of arid Australia, leading to the evolution of various physiological and behavioural adaptations by small mammals to survive in this environment (e.g. insectivorous diets, torpor, nocturnal activity and sheltering in burrows). Features within the landscape associated with these traits may be critical for predicting the distribution of arid species. Here we explored the contribution of landscape and quadrat-scale environmental variables, sampled up to 10 000 m from known records, in a range of small mammal species distribution models (SDMs). The inclusion of landscape variables increased the per cent deviance explained (% DE) in species occurrence by up to 55.2 % using generalised linear modelling (GLM) and 24.7 % using boosted regression trees that included complex, non-linear interactions (BRT). These improvements were supported by increased discrimination of species occurrence in an out-of-sample cross-validation (i.e. area-under-the curve, Kappa) for *Antechinomys laniger*, *Dasyuroides byrnei* and *Notomys cervinus*. For these species, model performance (% DE) increased with the resolution of environmental data used (< 5 000 m for the endemic *D. byrnei*), reflecting a coarse-scale relationship with distance to watercourse (e.g. at 1 000 m), but masking a fine-scale relationship with rainfall during winter (at 150 m). Our results show that additional (landscape) features can be more important than climate variables in predicting the distribution of arid mammals within their existing range. Useful variables included environmental gradients that vary over finer scales (i.e. strata richness or cover). However, species–environment correlations varied across scales, indicating while additional data may be useful at coarse scales, accurate fine scale data may be required to represent climate–species relationships.

Introduction

Anthropogenic climate change is forecast to produce a warmer, drier and more variable climate in Australia (Dunlop and Brown 2008); potentially leading to the loss of many native species (Williams et al. 2003; Sander and Wardell-Johnson 2011). However, the mean and variability in temperature and rainfall differ between regions (CSIRO and Bureau of Meteorology 2007). Arid environments are defined by high temperatures, intense solar radiation, lack of water and high evaporation rates (Bartholomew and Dawson 1968), with high spatial and temporal variability (Morton et al. 2011). These factors have a strong influence on biotic resource productivity and availability (Kotler and Brown 1988). In order to exploit these unpredictable environments, small mammals have had to be flexible and adaptive.

Small terrestrial mammal communities within the arid zone of Australia are dominated by dasyurids (Dasyuridae) and rodents (Baverstock 1982; Morton 1982). Species have evolved to consume a broader range of foods (i.e. insectivorous and carnivorous dasyurids; Bartholomew and Dawson 1968;

Baverstock 1982), produce more concentrated urine (esp. rodents; Baverstock 1982), store fat in their tail (Morton 1982), have thicker fur (Dawson and Dawson 1982), produce more than one litter a year (Morton 1982), and/or undergo torpor to conserve up to 97 % of metabolic energy (dasyurids only; Morton et al. 1989; Geiser and Kortner 2010). Additional behavioural adaptations that aid species' persistence in these harsh environments, include nocturnal activity (Bartholomew and Dawson 1968), use of burrows and plant cover for shelter (Bartholomew and Dawson 1968; Baverstock 1982; Morton 1982), nest sharing (including *Sminthopsis crassicaudata* with *Mus musculus*; Wallis 1982), and increased mobility in the landscape (Morton 1982).

As a result of these multiple adaptations, the influence of rainfall on species survival is confounded by complex interactions that vary across species, space and time (Foulkes et al. 1995; Dickman et al. 1999; Thibault et al. 2010; Morton et al. 2011). Rainfall increases primary productivity and availability of food resources: followed by eruptions of desert rodents and to a lesser degree dasyurids, and their predators (Predavec 1994; Letnic et al. 2005; Haythornthwaite and Dickman 2006). Although species responses might follow a lag period (e.g. Dickman et al. 2001), or be further influenced by interspecific interactions influencing population demographics (Abramsky 1988; Letnic et al. 2005; Lima et al. 2008).

Some of these relationships can be adequately or best represented using coarse-scale environmental data. Species can respond to large-scale climatic events with long-term environmental variation (e.g. rodent abundance has been correlated with El Nino Southern Oscillation; Brown and Heske 1990; Letnic et al. 2005; Orland and Kelt 2007; Magnusson et al. 2010). Large-scale topographic features can also influence small mammal abundance and diversity through providing refuge habitat (e.g. active or inactive floodplains, respectively; Finlayson 1939; Denny 1975; Ellison and van Riper III 1998); distribution (e.g. high ground during floods; Dickman et al. 1993); foraging behaviour (e.g. kangaroo rats; Sullivan et al. 2001) and movement (i.e. along low-lying floodplains, claypans and gibber plains; Finlayson 1939).

However, environmental gradients can also vary at much finer scales. Rainfall regimes can differ within 50 km (Letnic and Dickman 2005) or less, with most rainfall coming from thunderstorms less than 8 km in diameter (Noy-Meir 1973). At even finer scales, micro-relief (2cm) can influence flooding and vegetation growth (Williams 1982; Tongway and Hindley 2004), and combined with the influence of soil, provide suitable microclimates for shelter, nesting material and prey (e.g. cracks and burrows; Hoover et al. 1977; Read 1984): influencing foraging (e.g. *Sminthopsis* spp. in cracking clay soil cracks or granivores via soil particle size; Read 1984; Kotler and Brown 1988), caching and pilfering behaviour of small mammals (e.g. desert rodents; Swartz et al. 2010). As a result, characteristics of the microhabitat (“small-scale, fine-grained, and quantifiable variation in floral and edaphic characteristics of communities”) can act on species independently of macrohabitat (e.g. in rodent species composition; Stevens and Tello 2009).

Finally, species persistence in the arid zone is likely to be facilitated by metapopulation dynamics (Brandle and Moseby 1999), including local extinctions (e.g. 1-3 km from suitable habitat; Milstead et al. 2007), and dispersal (facilitated by rainfall) from suitable (refuge) habitat (Dickman et al. 1995; Dickman et al. 2011). These dynamics may only be recognisable at fine scales (Kotler and Brown 1988).

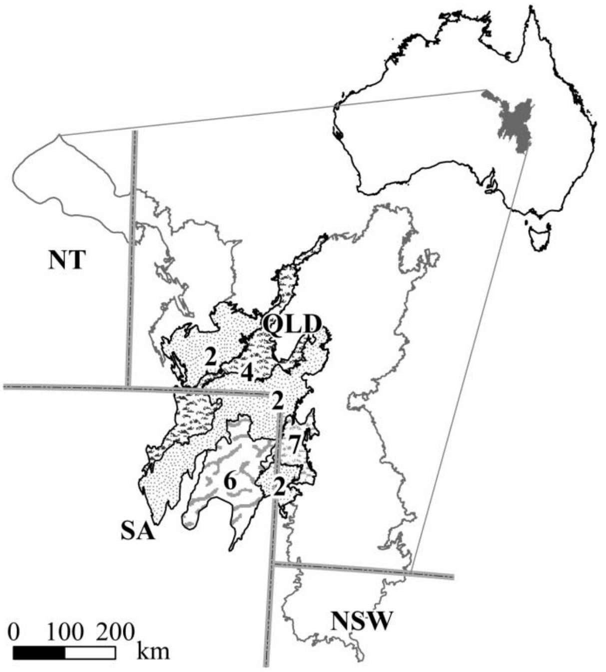
As vegetation and soil influence resources available for small mammals, we propose a) additional (landscape) features are more important than climate variables in predicting the distribution of arid mammals within their existing range, and b) that these correlations are stronger at finer scales despite animals being relatively mobile. To investigate these hypotheses, we evaluated model performance (fit to observations, and predictability in a cross-validation) for a climate-only and a climate-and-landscape variable model, for five small ground dwelling mammals. We then assessed the predictions of a set of *a priori* models, created using available landscape and quadrat-scale variables, sampled at increasingly distant sites from the original species record (i.e. 150 m, 500 m, 1 000 m, 5 000 m and 10 000 m) for five small mammals in the Channel Country of Australia. Identifying environmental factors that have a proximal, direct influence on species occurrence is critical in determining robust SDMs required for predicting the effects of climate change (Austin 2002), especially for species that have evolved strategies to survive in climatically unpredictable environments.

Methods

Study area and species

We targeted five species of small mammal within several arid sub-regions of the Channel Country Interim Biogeographic Regionalisation of Australia region (Fig. 1, Appendix XVII). The climate is defined by hot dry summers and short, dry, moderately cool winters (Brandle 1998). Rainfall is temporally and spatially highly variable (Allan 1982). Geological features include stony (gibber) plains, rocky outcrops and sand ridges and plains intersected by ephemeral creeks and permanent water holes (Morton 1982; Brandle 1998). This area supports a high diversity of patchily distributed habitats with unique floristic or structural composition, dominated by low open chenopod shrubland and grassland (Brandle 1998; Williams 1982). In this region soil texture and landform type have been correlated with plant diversity that together influence the small mammal community (Brandle 1998). The species we modelled included two species endemic to the Channel Country IBRA region (a carnivore, *Dasyuroides byrnei*, Dasyuridae, and a granivore *Notomys cervinus*, Muridae) and three widespread but uncommon species (two insectivores *Antechinumys laniger* and *Sminthopsis macroura*, Dasyuridae, and an omnivore *Leggadina forresti,* Muridae; information on individual species' ecology is provided in Appendix XVII).

Fig. 1 This investigation targeted species occurrence and environmental information from the South Australian extent of the Coongie (6), Diamantina-Eyre (4), Lake Pure (7) and the Sturt Stony Desert (2) Interim Biogeographic Regionalisation of Australia (IBRA) sub-regions of the Channel Country region (defined in Appendix XVII).



Species presence and absence and environmental data

Species occurrence was initially determined from a baseline inventory of the distribution of South Australia's flora and fauna (Dataset 1; Biological Databases of South Australia, December 2010). This inventory contains data from a variety of sources, including the Biological Surveys of South Australia (BSSA; Heard and Channon 1997; Owens 2000). Presences were represented by records collected using reliable methods, < 100 m location accuracy and post-1980 (Appendix XIX). Absences were defined as BSSA survey sites trapped for a minimum of four nights, using Elliott traps and pit fall traps, that failed to capture the target species (see p12).

To permit species-environment relationships to be modelled at multiple scales, a second dataset was used (Dataset 2). 'Presences' were reclassified as BSSA survey sites within a radius of 150 m, 500 m, 1 000 m, 5 000 m and 10 000 m of a known species record locality (more detail provided in Haby et al. 2012). As more sites were generally within the radius of known records at greater distances, the number of presences increased with resolution. BSSA survey sites that were more than the specified distance from a known record locality remained 'absence' sites.

Presence and absence data were used to sample information from a selection of climate, topography, soil and vegetation data available from vector and raster spatial layers using ArcInfo 9.3 (ESRI 2009; Appendix IV).

Comparison of climate-only and abiotic-and-biotic landscape variable models (dataset 1)

Model selection

The initial dataset (excluding the 20 % reserved for out-of-sample validation) was used to construct models that specified species distribution as a function of available climate variables (RS, RW) (Model 1) or combination of abiotic (RS, RW, E, lnWC and PAWHC) and biotic (GEN) landscape variables (Model 2; Appendix IV).

Species occurrences were modelled with generalised linear models (GLM) using a binomial error distribution and logit link function, fitted in R v2.8.0 (R Core Development Team 2009; www.r-project.org). Overall model structural goodness of fit was assessed based on the per cent deviance explained relative to the null model (% DE). The best-supported model was identified using Akaike's Information Criterion (corrected for small sample sizes) and Bayesian Information Criterion, both represented as relative model weight ($w\mathrm{AIC}_c$, wBIC).

To allow non-linear species response curves to be fitted, a complementary regression approach was also used; boosted regression trees (BRT) (Guisan and Zimmermann 2000). BRTs were fitted using the R package 'GBM' (Elith et al. 2008; Ridgeway 2009). Optimal tree complexity and learning rate were selected by within-sample cross-validation for each species (Appendix XXa), bag fractions were set at 0.5 and the relative proportion of deviance explained by each model was calculated from the summary statistics (J. Elith, University of Melbourne, pers. comm., 2009).

Cross-validation

Cross-validation was done on the remaining 20 % of data to test the predictive ability of the SDMs fitted via GLM and BRT; implemented using R packages 'PresenceAbsence' (Freeman 2007) and 'GBM' (Elith et al. 2008; Ridgeway 2009). Several species had low prevalence in the cross-validation dataset (0.01-0.30), increasing the problem of variable validation statistics and difficulty in assessing performance (Meynard and Quinn 2007; Liu et al. 2005). Therefore, three methods were used to evaluate relative predictive performance: a) the mean difference between the predicted probability of occurrence and the actual value (0 or 1), b) the area under the receiver-operating characteristic curve (AUC) (independent of prevalence, Manel et al. 2001), and c) Kappa, sensitivity and specificity statistics (Fielding and Bell 1997). The last three statistics required probability values to be transformed into predicted presence and absence values by specifying a Maximum Sum of Sensitivity and Specificity (MSS) threshold (calculated using the R package 'PresenceAbsence'; Freeman 2007), recommended for small datasets (Jiménez -Valverde and Lobo 2007).

Checking for model bias

To determine whether model bias affected estimates of Kappa, sensitivity and specificity and their subsequent trends when comparing between models, the predicted values were compared to the mean of each statistic's empirical distribution, generated by re-applying the two models to 1 000 bootstrapped samples from the original dataset.

Evaluating variable contribution

The explanatory strength (relative importance) of each variable in describing the five species' distributions was calculated as the combined change in per cent deviance explained (% DE) when each variable was removed from the saturated GLM and added to the null (intercept only) GLM (following Garnett and Brook 2007). For comparison, the 'relative influence values' presented in BRT summary outputs (Elith et al. 2008) are also presented.

Comparison of mixed landscape and quadrat-scale variable models (dataset 2)

Using the second dataset, a series of simple candidate models was derived *a priori* to represent a gradient of increasing emphasis on finer-scale and biotic information, including a climate-only landscape model (RS, RW), an abiotic landscape variable model (RS, lnWC, PAWHC), a mixed abiotic and biotic landscape variable model (including GEN), and a mixed abiotic and biotic landscape and quadrat-scale variable model (C2, SD; Appendix IV). Species occurrence was represented by 167 sites (2 to 50 presences). To reduce the issue of over-fitting, we restricted the dimensions any given model to at least 10 records per fitted parameter (see Wintle et al. 2005) and avoided using correlated variables ($r > 0.6$) in the same candidate model. The candidate SDMs for each species were originally generated using 150 m resolution data and linear and nonlinear modelling approaches and compared using the methods specified above in R v2.8.0 (R Core Development Team 2009; Appendix XXb).

Model and variable performance at multiple scales (dataset 2)

To determine whether the resolution of environmental data affected our ability to model species distributions accurately, we also fitted GLMs using the 500 m, 1 000 m 5 000 m and 10 000 m resolution datasets. The model fitted to each of these datasets contained the same terms from the most parsimonious GLM (based on AIC_c) identified using the 'within 150 m' data (and its corresponding set of single variable models). We calculated the difference in overall model fit by subtracting the value derived when using the 150 m and 500 m datasets from the 1 000 m dataset (Haby et al. 2012).

Results

Influence of additional landscape variables on SDM performance

Model performance

Overall, the climate-only GLM (Model 1) explained less than 4.5 % of the deviance in species' occurrence (Table 1). A further 5.2 – 55.2 % of deviance was explained across species after incorporating additional landscape variables into the model (Model 2; Table 2). The $w\mathrm{AIC}_c$ values showed Model 2 to be the highest-supported model for *A. laniger, D. byrnei* and *N. cervinus*. The stronger penalty of additional parameters in Model 2 applied using *w*BIC resulted in a disagreement between the $w\mathrm{AIC}_c$ and *w*BIC values for *L. forrest*, suggesting a less parsimonious representation of variation in the occurrence of this species (Table 1). However, BIC-selected models based on small to modest sample sizes (~22 to 200 samples), as used in this investigation, can be biased (Burnham and Anderson 2004).

Table 1 Explanatory strength of null and *a priori* generalised linear models (GLM) and boosted regression trees (BRT) containing climate-only (Model 1: Species ~ RS + RW) or climate and landscape parameters (Model 2: Species ~ RS + RW + E + lnWC + GEN + PAWHC; see Appendix IV for variable definitions). Shown are the number of parameters (*d.f.*), minimised negative log-likelihood (-LL), Akaike's information criterion (corrected for small sample sizes) and Bayesian Inference Criterion represented as the difference from the highest-ranking model ($\Delta\mathrm{AIC}_c$, ΔBIC), weight scaled to a sum of 1 ($w\mathrm{AIC}_c$, *w*DIC), and the per cent deviance explained (% DE) by the model relative to the null for each method.

model	*d.f.*	-LL	$\Delta\mathrm{AIC}_c$	$w\mathrm{AIC}_c$	ΔBIC	*w*BIC	% DE GLM	% DE BRT
A. laniger (41 presence : 117 absence sites, 158) (prevalence 0.26)								
Model 1	3	-86.3	70.8	0.00	53.5	0.00	4.5	29.5
Model 2	9	-44.4	0.0	1.00	0.0	1.00	50.9	43.6
D. byrnei (19 presence : 127 absence sites, 146) (prevalence 0.13)								
Model 1	3	-55.7	45.9	0.00	29.1	0.00	1.3	18.5
Model 2	9	-26.3	0.0	1.00	0.0	1.00	53.4	43.2
L. forresti (24 presence : 106 absence sites, 130) (prevalence 0.19)								
Model 1	3	-61.2	3.3	0.12	7.8	0.02	1.6	7.6
Model 2	9	-53.1	0.0	0.56	20.7	0.00	14.7	6.3
N. cervinus (19 presence : 126 absence sites, 145) (prevalence 0.13)								
Model 1	3	-56.3	49.1	0.00	32.4	0.00	0.0	43.0
Model 2	9	-25.2	0.0	1.00	0.0	1.00	55.2	55.2
S. macroura (45 presence : 89 absence sites, 134) (prevalence 0.34)								
Model 1	3	-84.6	2.3	0.23	8.0	0.02	1.1	2.2
Model 2	9	-80.1	6.7	0.03	28.4	0.00	6.3	2.9

The climate-only BRT models, which allow implicitly non-linear responses and interactions, explained greater variation in species occurrence for all climate-only GLMs (Table 1). However, additional landscape variables improved model-fit (0.7 – 24.7 % DE), especially for *A. laniger*, *D. byrnei* and *N. cervinus* (> 12.2 % DE).

Cross-validation predictive performance and model bias

Additional abiotic and biotic landscape variables predominantly improved the classification of *A. laniger, D. byrnei* and *N. cervinus* occupancy as illustrated by both increased AUC (Fig. 2) and Kappa (Appendix XXI), although, Kappa closely reflected specificity, indicating these validation statistics were affected by the low prevalence of species records, despite using the MSS threshold.

To identify bias in the Kappa, sensitivity and specificity, the estimated validation statistics were compared to the mean of their empirical distributions. Estimates were least biased for species with good model and predictive performance (i.e. *D. byrnei, A. laniger* and *N. cervinus*; Appendix XXII). Bias was detected in the estimates for *A. laniger* (inflating M2 sensitivity), the data-poor *N. cervinus* (inflating M2 Kappa), and species with poor model performance: *L. forresti* (inflating sensitivity and lessening specificity of M1) and *S. macroura* (inflating sensitivity and lessening specificity of M2; Appendix XXII). The effect of this bias on the direction of trends discussed was negligible for *N. cervinus*, but masked lower sensitivity of M2 for *A. laniger* and improved sensitivity of M2 for *L. forresti*.

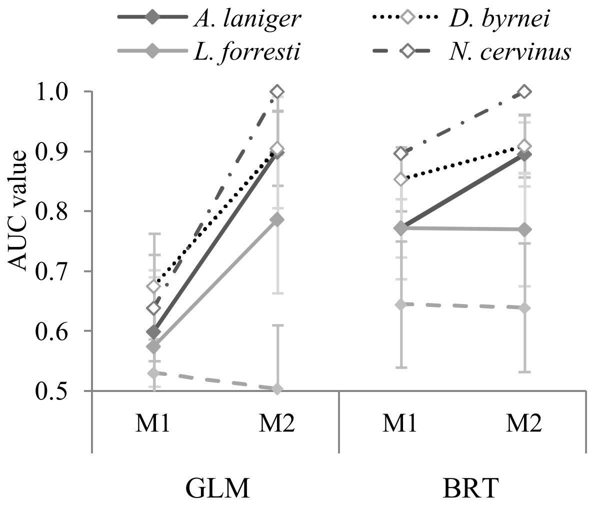


Fig. 2 Out-of-region predictive performance, measured as the difference between area under the curve (AUC) values obtained from the prediction of occupancy for Model 1(M1) and Model 2 (M2) using generalised linear modelling (GLM, black) and boosted regression trees (BRT, grey; Table 1). AUC values range from 0.5 to 1.0, representing random discrimination by the model to perfect discrimination, respectively (Fielding and Bell 1997). Error bars are calculated as standard deviation.

Identifying influential variables

Distance to watercourse or body (lnWC) was the top ranking variable explaining species' occurrence using both GLM and BRT (Table 2). This variable was followed by soil water holding capacity of the solum (PAWHC), broad vegetation community (GEN) and rainfall during summer (RS) using GLM, or rainfall during winter (RW), RS and elevation (E) using BRT. Variable effect size (coefficient and standard error) indicated useful contributions particularly from lnWC for modelling the occurrence of *A. laniger, D. byrnei* and *N. cervinus*; RS for *A. laniger* and PAWHC for *A. laniger* (Appendix XXIII).

Value of additional quadrat-scale biotic variables

Abiotic and biotic landscape and quadrat-scale variables explained substantial variation in the presence of some of the species. The abiotic variables lnWC and PAWHC contributed to the model of best fit (top ranking model based on % DE and $w\text{AIC}_\text{c}$) for *A. laniger*, *D. byrnei* and *N. cervinus* (M2 GLM; Table 3). GEN was present in the top-ranking *L. forresti* model (M4, GLM and BRT); and the biotic quadrat-scale variable C2 contributed to the top ranking model for *N. cervinus* (M3, GLM), and SD for *S. macroura* (M5, GLM) and *A. laniger* (M5, BRT). These variables explained reasonable amount of variance in species occurrence (up to 15.4 % RI (BRT) and 12.7 % DE (GLM) for C2 and SD, respectively; Table 4). However, the improvement in model performance was insufficient to overcome the stronger penalty applied using *w*BIC, or the small sample size limiting the effect of variables being detected in the model, resulting in the null model ranking highest for *N. cervinus, L. forresti* and *S. macroura* (150 m candidate models, Appendix XXIV).

Table 2 Independent explanatory strength of each variable calculated using generalised linear models (GLM) and boosted regression trees (BRT). The explanatory strength for each variable was derived in GLM by combining the per cent deviance explained (% DE) when a variable is removed from the saturated model with the % DE when adding to the null model and dividing that value by the degrees of freedom (as per Garnett and Brook 2007). The explanatory strength of each variable using BRT was derived from the relative influence values (% RI) calculated using the package 'GBM' in R (Ridgeway 2009) (Elith et al. 2008). Variables are defined in Appendix IV.

		A. laniger		*D. byrnei*		*L. forresti*		*N. cervinus*		*S. macroura*		Average		Rank	
Variable	*df*	%DE	% RI	%DE	%RI	%DE	%RI	%DE	%RI	%DE	%RI	GLM	BRT	GLM	BRT
RS	1	10.0	16.0	4.8	3.8	2.2	15.6	1.0	0.8	2.8	10.2	4.2	9.3	4	3
RW	1	1.3	7.4	1.5	6.3	0.1	49.3	0.9	2.3	0.5	37.5	0.9	20.6	6	2
E	1	2.8	8.6	0.2	9.7	1.1	11.2	2.4	0.9	0.6	11.3	1.4	8.3	5	4
lnWC	1	44.0	49.1	50.6	70.1	1.9	12.4	78.8	95.9	0.4	29.8	35.1	51.5	1	1
GEN	3	7.2	2.0	9.3	5.0	6.2	7.5	5.6	0.1	2.7	10.4	6.2	5.0	3	5
PAWHC	1	23.3	16.9	21.3	5.0	5.2	4.0	8.7	0.1	0.5	0.8	11.8	5.4	2	6

Table 3 Explanatory strength of null and *a priori* generalised linear models (GLM) and boosted regression trees (BRT), where 'occupied sites' are classified as BSSA survey sites within 150 m of a known species record locality. Shown are the number of parameters (*d.f.*), minimised negative log-likelihood (-LL), the difference between the Akaike's information criterion corrected for small sample sizes and the highest-ranking model ($\Delta\mathrm{AIC}_c$), weight scaled to a sum of 1 ($w\mathrm{AIC}_c$), and the per cent deviance explained by the model relative to the null (% DE) for each method and species. Variables are defined in Appendix IV.

Model	Variables	*d.f.*	-LL	$\Delta\mathrm{AIC}_c$	$w\mathrm{AIC}_c$	% DE GLM	% DE BRT
A. laniger (17 presences : 150 absence sites) (prevalence 0.11)							
Null	~ 1	1	-54.9	28.8	0.00		
M1	~ RS + RW	3	-48.2	19.4	0.00	12.3	11.5
M2	~ RS + lnWC + PAWHC	4	-37.4	0.0	0.97	31.8	23.1
M3	~ RS + lnWC + C2	4	-41.1	7.2	0.03	25.3	28.3
M4	~ RS + GEN	5	-42.8	12.9	0.00	22.0	42.8
M5	~ RS + SD	5	-45.5	18.2	0.00	17.2	46.7
D. byrnei (11 presences : 156 absence sites) (prevalence 0.07)							
Null	~ 1	1	-40.6	26.4	0.00		
M1	~ RS + RW	3	-36.3	22.0	0.00	10.5	NA
M2	~ RS + lnWC + PAWHC	4	-24.2	0.0	0.89	40.2	NA
M3	~ RS + lnWC + C2	4	-26.3	4.2	0.11	35.0	NA
M4	~ RS + GEN	5	-31.4	16.4	0.00	22.7	43.1
M5	~ RS + SD	5	-36.7	26.9	0.00	9.6	43.4
L. forresti (27 presences : 140 absence sites) (prevalence 0.16)							
Null	~ 1	1	-73.9	3.9	0.07		
M1	~ RS + RW	3	-71.6	3.4	0.09	3.1	11.9
M2	~ RS + lnWC + PAWHC	4	-70.0	2.4	0.16	5.3	4.4
M3	~ RS + lnWC + C2	4	-71.1	4.6	0.05	3.8	18.6
M4	~ RS + GEN	5	-67.7	0.0	0.52	8.3	24.3
M5	~ RS + SD	5	-69.3	3.1	0.11	6.2	23.1
N. cervinus (2 presences : 165 absence sites) (prevalence 0.01)							
Null	~ 1	1	-10.8	2.8	0.11		
M1	~ RS + RW	3	-9.9	5.1	0.03	8.3	NA
M2	~ RS + lnWC + PAWHC	4	-6.4	0.0	0.42	41.3	NA
M3	~ RS + lnWC + C2	4	-6.3	0.0	0.43	41.5	NA
M4	~ RS + GEN	5	-9.0	7.4	0.01	17.0	79.5
M5	~ RS + SD	5	-10.0	9.5	0.00	7.6	36.4
S. macroura (50 presences : 117 absence sites) (prevalence 0.30)							
Null	~ 1	1	-101.9	1.7	0.23		
M1	~ RS + RW	3	-100.5	3.0	0.12	1.4	3.9
M2	~ RS + lnWC + PAWHC	4	-100.4	4.9	0.05	1.5	1.2
M3	~ RS + lnWC + C2	4	-100.6	5.4	0.04	1.3	4.6
M4	~ RS + GEN	5	-99.7	5.6	0.03	2.2	4.0
M5	~ RS + SD	5	-96.9	0.0	0.54	5.0	2.0

Table 4 Independent explanatory strength of each variable calculated using generalised linear models (GLM) and boosted regression trees (BRT). The explanatory strength for each variable was derived in GLM by combining the per cent deviance explained (% DE) when a variable is removed from the saturated model with the % DE when adding to the null model and dividing that value by the degrees of freedom (as per Garnett and Brook 2007). The explanatory strength of each variable using BRT was derived from the relative influence values (RI) calculated using the package 'GBM' in R (Ridgeway 2009) (Elith et al. 2008). Variables are defined in Appendix IV.

		A. laniger		*D. byrnei*		*L. forresti*		*N. cervinnus*		*S. macroura*		Average		Rank	
Variable	*df*	%DE	%RI	%DE	%RI	%DE	%RI	%DE	%RI	%DE	%RI	GLM	BRT	GLM	BRT
RS	1	20.1	43.1	9.8	22.3	3.1	16.4	1.4	NA	1.5	14.5	7.2	24.1	5	2
RW	1	0.1	6.2	9.0	18.1	1.0	38.2	10.6	NA	0.6	30.5	4.3	23.3	6	3
lnWC	1	18.1	33.4	35.8	47.2	0.2	5.7	61.8	NA	0.0	21.4	23.2	26.9	1	1
PAWHC	1	12.6	7.6	18.9	5.3	12.2	7.6	5.6	NA	1.5	3.3	10.2	6.0	3	6
C2	1	1.7	6.1	0.7	3.1	2.2	15.0	0.4	NA	0.2	15.4	1.0	9.9	7	4
GEN	3	16.5	2.9	20.0	3.8	16.0	9.1	17.2	NA	2.3	9.0	14.4	6.2	2	5
SD	1	12.7	0.7	4.5	0.2	7.1	7.9	6.4	NA	8.5	5.9	7.8	3.7	4	7

Effect of decreasing resolution of environmental data on model and variable performance

Increasing the resolution of environmental data resulted in an increase in out-of-sample performance of the models that better explained species occurrence (*A. laniger*, *D. byrnei* and *N. cervinus*; Fig. 3). A threshold was apparently reached for the endemic *D. byrnei* (around 5 000 m), but not the endemic and data poor *N. cervinus* (prevalence also increased from 0.01 to 0.1 at 150 m and 10 000 m, respectively; Appendix XXIV). The trend for increased model performance with resolution had mixed support from the single-variable models: lnWC was more correlated with *A. laniger, D. byrnei* and *N. cervinus* occurrence at a coarse scale and RW with *D. byrnei* and *N. cervinus* at a fine scale (Fig. 4). These trends altered with the definition of 'coarse' and 'fine' scales (e.g. 1 000 m or 5 000 m for coarse-scale; Fig. 4b).

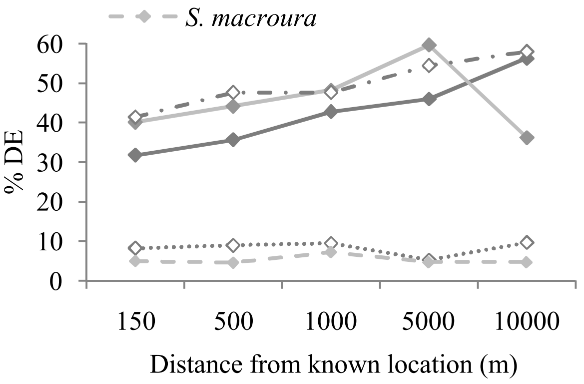
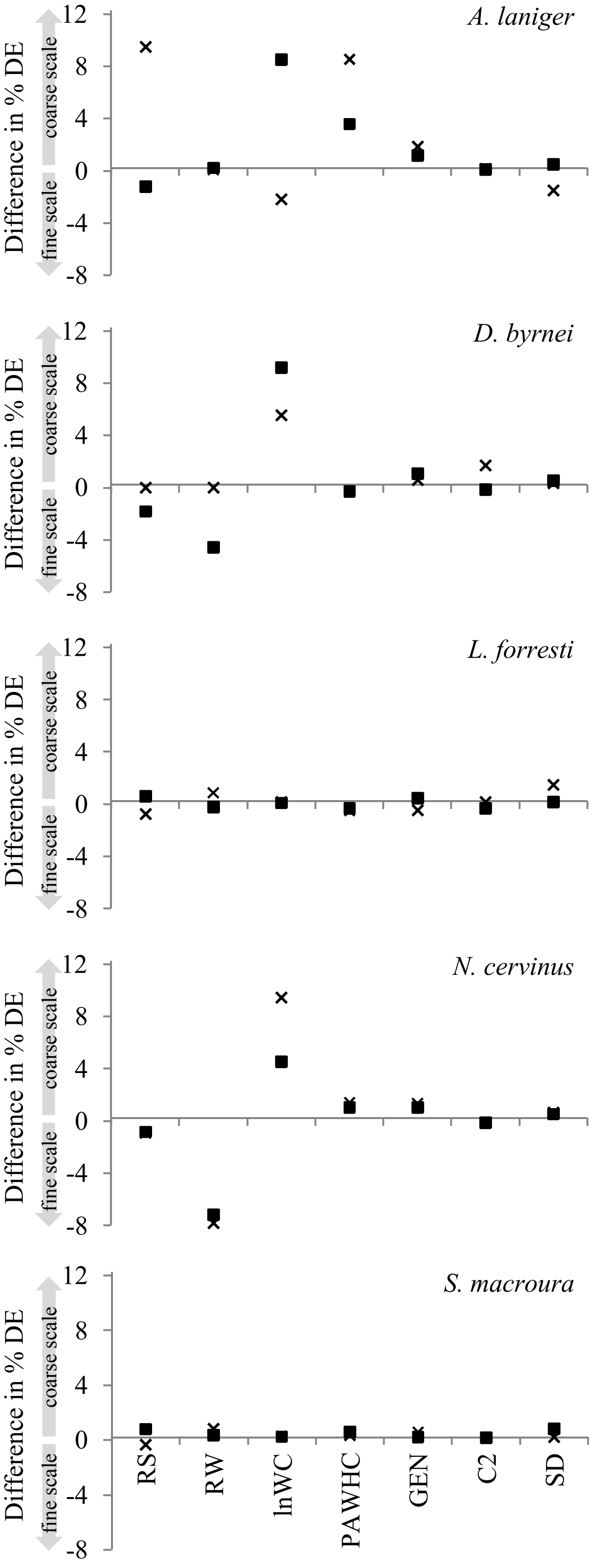


Fig. 3 Change in deviance explained (% DE) by the single best model (based on % DE and AIC$_c$) applied to datasets where species 'presence' was classified as survey sites with complete environmental data at 150 m, 500 m, 1 000 m, 5 000 m and 10 000 m from original record localities.

Fig. 4 Difference in per cent deviance explained by single-variable models based on increasingly coarse environmental data (squares: % DE at 1 000 m - % DE at 150 m, crosses: % DE at 5 000 m - % DE at 150 m). Where RS, ave. monthly rainfall during summer; RW, ave. monthly rainfall during winter; lnWC, dist. from watercourse/body; PAWHC, root zone water holding capacity; GEN, broad vegetation community; C2, diversity of shrubs < 2m; SD shrub cover < 0.5 m.



Discussion

Our results show that additional (landscape) features can be more important than climate variables in predicting the distribution of arid mammals within their existing range. Useful variables included environmental gradients that vary over finer scales (i.e. strata richness or cover). However, species–environment correlations varied across scales, indicating additional coarse-scale data can assist in modelling species occupancy, but that accurate fine scale data may be required to represent climate–species relationships.

In the naturally highly variable climate of the Channel Country IBRA region, climatic factors alone were insufficient to describe the occurrence of a range of small dasyurids and rodents (i.e. < 4.5 % DE, GLM). Species occurrence was considerably better represented using BRT that allow for more complex species response curves (< 43.0 % DE), but for all five small mammal species, a variety of landscape environmental variables representing climate, topography, soil and vegetation better modelled occurrence (< 55.2 % DE, GLM, BRT; Table 1). Further support for improved representation of species occurrence was provided in the out-of-sample cross-validation and increased AUC and Kappa for *A. laniger*, *D. byrnei* and *N. cervinus*.

The distribution of the best modelled species (*A. laniger*, *D. byrnei* and *N. cervinus*) was mostly explained by the variables distance to watercourse (lnWC), soil water holding capacity of the solum (PAWHC), rainfall during summer (RS, excluding *N. cervinus*) and broad vegetation community (GEN; GLM, Table 2). The relative rank of variables as determined using BRT differed, especially in regards to broad vegetation community (decreased). Using a second dataset that allowed additional quadrat-scale variables to be considered within the candidate set, top ranking models (based on % DE, $w\text{AIC}_c$) included diversity of shrubs under 2 m (C2; *N. cervinus*) and shrub cover under 0.5 m (SD; *A. laniger*, BRT and *S. macroura,* GLM; Table 3). These variables also ranked within the top four (based on their independent contribution to a saturated model) for *L. forresti*, and *S. macroura* (GLM; Table 4).

The relationships detected reflect species distribution and ecology (see Appendix XVIII). The best modelled species were endemic or occurred throughout the Channel Country IBRA region (*D. byrnei* and *N. cervinus* or *A. laniger*, respectively). *D. byrnei* is carnivorous and capable of exploiting smaller mammals and reptiles as additional food source. This larger species is also capable of sprinting faster than the other small mammals targeted in this investigation (Garland et al. 1988). *N. cervinus* builds deep burrows, and has a bipedal gait that generally enables species to better exploit patchy and sparse resources and better escape predation (Kotler and Brown 1988; Shenbrot et al. 1999). *A. laniger* also has bipedal gait and generalist diet of more readily available invertebrates. The two remaining species were poorly modelled: *L. forresti* and *S. macroura*. Both *L. forresti* and *S. macroura* are quadrupeds, the slowest sprinters of the five species and construct only shallow burrows (Garland et al. 1988). As a result these species require cover to provide food resources, avoid predation and shelter from environmental fluctuations (Kotler and Brown 1988). It is likely the SDMs were lacking key variables representing refuge habitat, or that the areas surveyed within the Channel Country IBRA region contained sub-quality habitat for these species that is only occupied during periods of greater resource availability.

Substrate and vegetation have an important influence on arid rodents (e.g. Munger et al. 1982, Shenbrot 1992; Orland and Kelt 2007), reflecting a long period of evolution and speciation in a challenging and sometimes extreme environment (e.g. dasyurids, Cramb et al. 2009). This could explain why additional environmental variables improved the SDMs; by enhancing the representation of a species' *fundamental niche* (see Hutchinson 1957 and related papers). Unfortunately, the potential additional influence of environmental variables on predation risk, and competition, and therefore *realised niche*, may make it difficult to identify the value of environmental factors in terms of the fundamental or *realised niche* (Munger et al. 1982).

Fine scale variability in substrate and vegetation can affect resource availability (e.g. Price 1978; Kotler and Brown 1988; Tongway and Hindley 2004). This effect was not supported by model performance increasing with data resolution (Fig. 3). However, this relationship could reflect i) the low prevalence of data, which also increased with resolution, or ii) improved correlations for some dominant environmental variables that were better represented at a coarser resolution (e.g. distance to watercourse at 1 000 m). Stronger correlations were detected between species and rainfall during winter at a fine scale (150 m), providing further support that the influence of environmental gradients at different scales is species-specific (see also Haythornthwaite and Dickman 2006).

Adaptations to arid environments may enhance the resilience and preservation of small mammals in a changing climate. Heterothermic capabilities (e.g. torpor) have been attributed to a species ability to resist extinction processes (e.g. Geiser and Kortner 2010**).** Fewer species are expected to go extinct in hot deserts compared with other biomes across the world (Thomas et al. 2004). However, most surveys in the arid zone have occurred during relatively wet conditions (e.g. decadal average rainfall; Kerle et al. 2007, Bureau of Meteorology 2012), where current climate variability facilitates population persistence though allowing for one good season in seven generations (e.g. Morton 1982). Given this context, as the climate becomes more variable (e.g. Chesson et al. 2004), arid species may become increasingly sensitive to a changing climate.

Chapter 5

ECOSYSTEM DYNAMICS, EVOLUTION AND DEPENDENCY OF HIGHER TROPHIC ORGANISMS ON RESOURCE GRADIENTS

N.A. Haby[1], J. Foulkes[2], B.W. Brook[1]

The Environment Institute[1] and Terrestrial Ecosystem Research Network[2],
School of Earth & Environmental Sciences, University of Adelaide,
Adelaide SA 5005, Australia

In review: Global Ecology and Biogeography

STATEMENT OF AUTHORSHIP

ECOSYSTEM DYNAMICS, EVOLUTION AND DEPENDENCY OF HIGHER TROPHIC ORGANISMS ON RESOURCE GRADIENTS

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All contributors certify that the statement of contribution is accurate and give permission for the inclusion of this material in the thesis.

Signed [redacted] *Date* 27 Apr 2012
Haby, N.A. (Candidate)

Signed [redacted] *Date* 26/4/12
Foulkes, J.

Signed [redacted] *Date* 27/4/12
Brook, B.W.

Abstract

In many correlative species distribution models biotic factors are excluded as interactions that have a secondary influence on species' occurrence via the *realised niche*, irrespective of a species' ecology. Over time biotic interactions can drive natural selection and changes within the *fundamental niche*, resulting in a contemporary dependency on resource availability for survival or reproduction. Resource availability may not be closely correlated with coarse climate variables, but represent the dynamics of nutrients and water availability cascading through trophic webs. Identifying biotic resources might therefore be key to understanding the distributions of many competitively dominant specialists and generalists in environments where limiting resources are rare (e.g. pollinators in degraded systems). Further empirical investigations into species interactions are required to distinguish between limiting resources (e.g., food, space, nutrients, nest sites) verses constraining biotic interactions considered to affect species abundance. In the mean-time, species for which we can have a reasonably good understanding of the possible mechanisms driving the evolution of traits may provide biologically realistic case-studies in the development of community models.

Introduction

Species distribution models (SDMs) may have reached their limit as a guide for policy makers and managers involved in species conservation (Sinclair et al. 2010). Most SDMs are based on climate data, which is believed to underpin species' morphological and physiological adaptations and range boudaries, and be an important driver of future change (Parmesan 2006; Sexton et al. 2009). The use of SDMs at relatively coarse scales has allowed simple spatial models of complex systems to be created, while avoiding finer-scale stochastic influences of biotic interactions (Pearson and Dawson 2003). In modelling the impact of climate change, observed correlations between climate and a species' current distribution are projected forward, transferring the rate of change in climatic variables to the rate of change in a species' distribution. However, the influence of climate on species can be buffered by adaptations (e.g. controlled hypothermia, torpor; Chaplin 1976; Kelm and von Helversen 2007), resulting in climate variables being correlated with or out performed by other environmental factors in SDMs (e.g. Beale et al. 2008; Heikkinen et al. 2010). Climate change can affect species physiology, phenology or range through a number of mechanisms that cannot yet be explained (Sexton et al. 2009).

SDMs were originally developed to investigate drivers of ecological patterns (Elith and Leathwick 2009). However, the adequacy of geographical range shifts predicted using SDMs is questioned in the literature because they ignore or oversimplify biotic interactions, habitat heterogeneity and connectivity, dispersal, disturbances, history of occupancy, extinction debt, evolutionary change, glacial refuges and diseases (e.g. Sinclair et al. 2010). Recommendations have been made repeatedly to strengthen the overall ecological foundations of SDMs (e.g. Austin 2007; Austin and van Niel

2011a). One way to develop more robust and accurate models is to identify ecological variables that have a direct, proximal influence on species distributions (Austin 2002). Variables can include biotic factors, which have been shown to improve SDM performance at a continental scale (e.g. dominant vegetation providing denning and nutritional requirements of arboreal mammal; Kearney et al. 2010). Additional biological realism can be achieved using new techniques and incorporating more information on species ecology (Elith and Leathwick 2009; Ellis 2011).

Here we review recent efforts to better capture the temporal relationship between biotic interactions, evolution and SDMs. This pioneering work is expected to be critical for improving models of specialist species or narrow-range species where limiting resources (including those of biotic origin) may impose strong constraints.

Application of niche in SDMs

The use of biotic factors as direct, causal factors that can be usefully incorporated within SDMs has been limited by the confusion of the niche concept (Whittaker et al. 1973; Araújo and Guisan 2006) and its representation in SDMs (Morrison 2001; Austin 2002; Elith and Leathwick 2009). The 'fundamental (Grinnellian) niche' is the ecospace within which a species can theoretically survive and reproduce and have positive population growth (Hutchinson 1957; Whittaker et al. 1973; Pulliam 2000; Holt 2009). The most appropriate factors that define this space cause a physiological species' response, either directly or through resource availability (e.g. nutrients and water; Guisan and Zimmermann 2000; Austin 2002). Yet abiotic physical variables are often considered the primary drivers of species survival, reproduction, physiology and behaviour (e.g. Soberón and Peterson 2005): generally represented by climate variables (i.e. temperature and precipitation) or indirectly via topography and soil variables. Resources are rarely included and are often assumed to influence species abundance or, in the case of resources provided by living (biotic) components of the system, misrepresented as biotic interactions influencing the *realised niche* (e.g. Whittaker et al. 1973; Soberón and Peterson 2005; Colwell and Rangel 2009). The 'realised (Eltonian) niche' represents the *fundamental niche* in geographic space after it has been modified by additional biotic interactions, dispersal dynamics, source-sink dynamics and other real-world constraints (Whittaker et al. 1973; Pulliam 2000; Pearman et al. 2008).

There are two main problems with the interpretation of fundamental and *realised niche*s in SDM. First, the tendency to treat all biotic factors as interactions that influence the *realised niche* ignores the evolution of intrinsic characteristics dependent on biotic components of the environment (e.g. environmental tolerance, resource requirements, life history, demographic and dispersal; Munger et al. 1983; Brown et al. 1996). Second, the predominant role of climatic gradients on evolution and the *fundamental niche* is typically justified on the basis of plant physiology (e.g. Austin 2002). The effect of climate on non-primary producers can be complex and indirect via food and shelter (Noy Meir

1974; Morton et al. 2011). As a result, climate-primary producer interactions may not represent consumer species dependent on biotic resources for nutrients (e.g. parasitic plants or animals) or factors associated with germination, anchoring or reproduction (Colwell and Fuentes 1975; Catling et al. 2002).

Trophic interactions leading to the evolution of adaptive traits

Species can interact when their *fundamental niche*s overlap along a gradient, either partially or completely for one or both species (i.e. ‘niche inclusion’, ‘reciprocal niche overlap’, or ‘coextensive niches’, respectively), and can result in the *realised niche* of a species being constrained (i.e. as a result of competition, predation or parasitism; Colwell and Fuentes 1975). Alternatively, interactions can have an important, facilitative influence on species niche dynamics (e.g. mutualism, pollinators, soil mycorrhizal fungi, ecosystem engineers; Hooper et al. 2005; Lavergne et al. 2010), or contribute stochastic elements to community composition (e.g. mimicry, prey switching, pollinators forming search images, and demographic specific interactions; Colwell and Fuentes 1975). Overall, the outcome of species interactions may be difficult to understand with some interactions having a direct or combined influence on multiple species and change under different conditions (Hooper et al. 2005; Thorpe et al. 2011; McCluney et al. 2011).

In many cases, interactions may cause temporary responses in foraging behaviour and predator avoidance through segregating resources or habitat (e.g. Huh and Kitting 1985; Korpimäki 1987; Majolo and Ventura 2004; Sundell et al. 2008). Alternatively, natural selection may limit co-evolution. For example, herbivory may drive natural selection for increasing tolerance, cuing of compensatory growth and seed production or anti-herbivore defences (de Mazancourt et al. 2005; Farji-Brener 2007). The development of an antagonistic response is illustrated by *Carduus nutans* plants that germinate in leaf-cutting ants waste areas developing more abundant and longer spines, and tougher leaves (Farji-Brener 2007).

Where resource selection improves survival or reproductive success of a species, natural selection can lead to phylogenetic and ontogenetic adaptations, and promote polymorphism, adaptive radiation, or divergence: changes that are directly reflected in the *fundamental niche* (functional habitat) (Holt and Gaines 1992; Brown et al. 1996). For example, intraspecific competition broadens niches, leading to adaptive radiation or changes in life-history strategies (Alley 1982), and interspecific competition to divergence and narrower niches along an environmental gradient and interspecific and intrasexual variation in foraging behaviour (Colwell and Fuentes 1975; Feinsinger et al. 1979; Rusterholz 1981). Predatory risk can also result in morphological adaptations (e.g. bipedal locomotion and enlarged auditory bullae; Kotler and Brown 1988) or behavioural adaptations (e.g. predator mobbing; Eberle and Kappeler 2008). Overall, competition and predation can result in segregation of resources and habitat (e.g. Pianka and Pianka 1976; Hallett 1982; Schmitt and Coyer 1982; Holmes and Robinson

1988). The temporal relationship between species interactions and the evolution of functional traits relating to the *fundamental niche* is illustrated in Table 1.

Species-specific interactions can evolve relatively quickly (e.g. < 10 years), and once evolved, the associated traits are likely to continue being improved rather than replaced, supporting conservation of the *fundamental niche* (Holt and Gaines 1992; Wiens et al. 2010; Thorpe et al. 2011). There are several additional factors that contribute to niche conservatism, including a strong phylogenetic signal, history of stabilising selection (e.g. regeneration niches), a large difference in survival and reproduction, or extreme rare or frequent inter-population dispersal (Pearman et al. 2008; Holt 2009). Overall, the dynamics of the *fundamental niche* are generally assumed to be conservative, as illustrated by species tracking suitable environments during past phases of climate change, such as during the Pleistocene glacial-interglacial cycles (Pearman et al. 2008).

Table 1 Examples of competitor and predator influence on the *realised niche* (occupancy of suitable environment) and *fundamental niche* (via evolution).

	Realised niche	Fundamental niche
Competition	Time-varying alteration in foraging periods, patterns or diet, reduced abundance, local extinction	Specialisation (e.g. metabolic adaptations, increased aggression), diversification (e.g. shift in resource use or phenology) or generalisation (e.g. increased diversification, mobility and capacity to exploit environmental variability)
Predation	Retreat to shelter, reduced abundance, local extinction	Change in morphology (e.g. camouflage, locomotion), phenology, recognise environmental cues
Empirical test	Competitor or predator release	No release
SDM test	Non-transferable	Transferable

→ evolution

Evolved dependency on biotic factors for survival or reproduction

Morphological, physiological or behavioural adaptations may correspond to physiological tolerance, growth form, diet breadth, habitat selection, host use, resource selection and susceptibility to pathogens (e.g. Futuyma and Moreno 1988). Resources associated with these traits may be non-limiting when specialisation in one species coincides with interactions with generalist species (asymmetric interactions, Bascompte and Jordano 2007). For example, the least weasel is a specialist predator that is capable of prey switching (type III functional response) between rodents (Sundell and Ylönen 2008). However, the specialisation of coexisting species can, in rare cases, lead to potential critical dependency on another species for survival (Howe 1984; Kotler and Brown 1988; Bascompte and Jordano 2007). For example mutually dependent species, including plants and mycorrhizal fungi (e.g. recruitment, Diez 2007), leaf-cutting ant and fungus (food and microclimate, Farji-brener 2007), and long-tongued fly and its primary food plant (food and pollination, Anderson and Johnson 2008).

In some cases these relationships have become obligatory for pollination or reproduction (e.g. fig and wasp, McLeish et al. 2010), nutrients (e.g. nectar bat and long-tubed flowers, Muchhala and Thomson 2009), or dispersal (e.g. mistletoe birds, Barea and Watson 2007).

In other cases, obligate, one-sided mutualism may occur where one species becomes dependent on another with high tolerance (e.g. host, de Mazancourt et al. 2005), or many others (e.g. vertebrate dispersers, Gautier-Hion and Maisels 1994). Avian brood parasites are dependent on their hosts to incubate and rear their young (Rothstein 1990). As the cost to the host is high via brood loss, reduced population and possible extinction (Siepielski and Benkman 2007), the host is under pressure to develop anti-parasitism adaptations (e.g. recognition of parasite eggs, increased inter-clutch variation), resulting in further adaptations via natural selection in the brood parasite (e.g. increased mimicry, Takasu 2005).

Resources and associated traits are especially important for species with distinct niches (McGill et al. 2006). These effects may be observed across taxonomic groups, such as the dependency of arboreal mammals on nesting hollows (Dueser and Shuggart 1979), Australian typhlopid snakes on ant pupae and larvae (Shine and Webb 1990), amphibians and salamanders on cool moist microhabitats and ponds (Bartelt et al. 2010, Dillard et al. 2008), and butterflies on a variety of resources (Dennis et al. 2003). In other cases, resources may be sought by rare, competitively dominant specialists within a group of coexisting species or guild (e.g. Hallett 1982). The occurrence of species with specialised resource requirements depends on resource availability, with upper limits in abundance set by social components (Dueser and Shuggart 1979). Some of the resources that have been recognised to date include a variety of nutrients (flowers, fruits, seeds, insects, animal carcasses, dung, urine, small mammals, coral spawning; Yang et al. 2008; Table 2). Individual traits that form an important component in ecological networks (e.g. Hooper et al. 2005), may assist in identifying limiting resources required to represent the *fundamental niche* in SDMs better (Fig. 1).

Case study: Arid systems

The relationship between climate and consumers is well illustrated in ecosystem dynamics in arid environments. Here, community structure is driven by water availability (rainfall and flooding, soil, nutrients and topography), supporting primary productivity (plants, seeds), primary consumers (insects, rodents) and their predators (insectivores, carnivores) (Noy Meir 1973; Letnic and Dickman 2010; Morton et al. 2011). Consequently, the effect of rainfall on vertebrates is via food availability or quality (Previtali et al. 2009; Dickman et al. 2011).This bottom up effect of resources on higher trophic levels is accentuated by resource pulses caused by rare, intense (extreme), brief events that are not predicted by associated resource consumers and so exceed the amount that can be used, initiating substantial bottom up effects and delayed top down effects (Yang et al. 2008). Yet while these

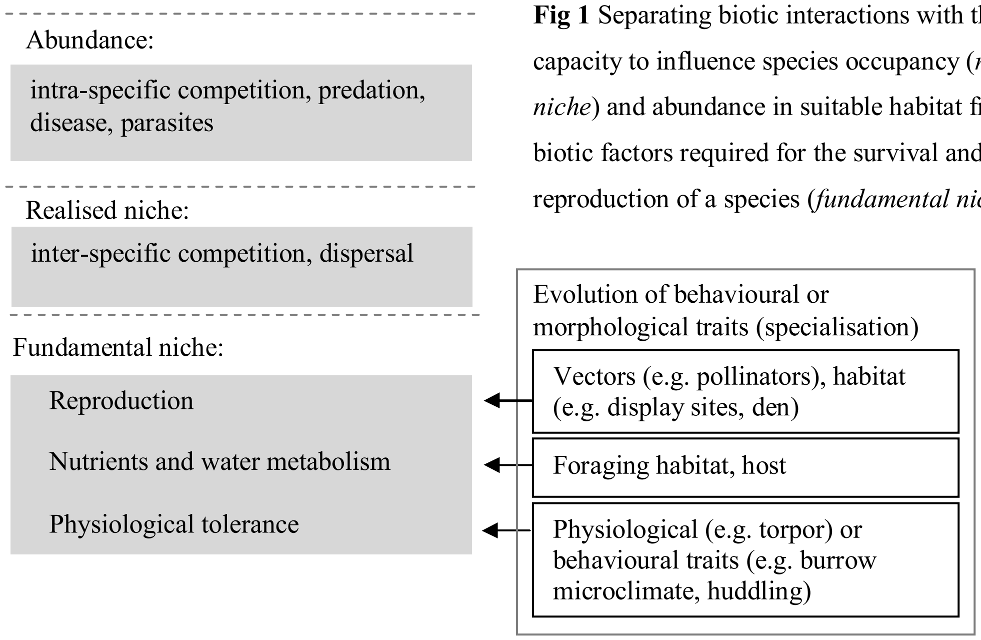


Fig 1 Separating biotic interactions with the capacity to influence species occupancy (*realised niche*) and abundance in suitable habitat from biotic factors required for the survival and reproduction of a species (*fundamental niche*).

Table 2 Examples of additional non-climatic resources required for survival and reproduction and therefore have a stronger influence on a species' distribution through the *fundamental niche*. Associations may primarily reflect required microhabitat (m), nutrients (n) or water (w) or features that facilitate predator aversion or reproduction.

Link	Abiotic or biotic resource	Species	Source
m	rocky areas	snow vole, black mongoose	Luque-Larena et al. 2002; Rathbun and Cowley 2008
m	trapdoor spider burrows	pygmy bluetongue lizard	M. Hutchinson pers. comm. 2012
m	sandy, small particle soils	desert pocket mouse	Hoover et al. 1977
m, n	soft soils, vegetation	Mendoza tuco-tuco	Albanese et al. 2010
m, p	habitat complexity	rock wallaby	Murray et al. 2008
n	genus/species-specific hosts	buloke mistletoe, creeping mistletoe	T. Croft pers. comm. 2012
n	mistletoe	painted honeyeater	Barea and Watson 2007
n	plant	pollen-specialising bee	Strickler 1979
n	bamboo	giant panda	Loucks et al. 2003
n	rabbit	Spanish imperial eagle, Iberian lynx	Ferrer and Negro 2004
n	few hard coral species	Chevon butterflyfish	Lawton et al. 2011
w	cactus	Santiago Galapagos mouse	Gregory and Macdonald 2009
p	*Triodia* spp.	Ningaui	Bos et al. 2002
r	avian hosts	brood parasites	Rothstein 1990
r	pebble mounds	*Pseudomys* spp.	Ford and Johnson 2007
r	Tasmanian blue gum	swift parrot	Hingston et al. 2004
r	hunting perches, gecko prey, sites for drumming displays	Mauritius kestrel, ruffed grouse	Burgess et al. 2011; Zimmerman and Gutierrez 2008
r, n	black-tailed prairie dogs	burrowing owls	Lantz et al. 2007

relationships sound direct, they are confounded by synergistic effects (e.g. between intensity of rainfall, soil structure, nutrients and seeds in the seed back on primary productivity, Noy Meir 1973; Munger et al. 1983; Letnic and Dickman 2010), lags in response times (Southgate and Masters 1996) and negative interactions (e.g. abundant rain degrading food resources, Kelt 2011), which may be conditional or accentuated by interspecific interactions (e.g. animals that create pits while foraging, caching behaviour effects plant species, James et al. 2009; Kelt 2011).

To survive in this environment small mammals have developed a range of adaptations to efficiently use and conserve moisture and energy (e.g. torpor, highly concentrated urine, nocturnal activity, subterranean habits), and reliance on ephemeral (response to environmental cues, increased mobility, opportunistic breeding strategies, generalist diets, food caching) or perennial resources (sap or nectar specialists, insectivores, Noy Meir 1973; Dickman et al. 1995; Körtner and Geiser 2009; Kelt 2011; Morton et al. 2011). In addition to environmental gradients, adaptations form in response to interspecific interactions over evolutionary time, such as anti-predator behaviours (e.g. foraging under shelter) and morphology (e.g. faster bipedal locomotion and increased auditory sensitivity, Kotler et al. 1994; Shenbrot et al. 1999; Kelt 2011). Species' response can be further confounded by relative changes in abundance of food resources, parasites, pathogens, predators and population density during dry periods (Southgate and Masters 1996). However, climate driven resource variability can override effects of interactions and nutrient limitations (Noy Meir 1974; Kelt 2011).

The concurrent influences of environmental gradients and interactions on species' survival and reproduction can result in mechanisms being hard to identify and species specific responses that are difficult to predict (Munger et al. 1983; Price and Brown 1983; Holt et al. 1995). Yet, the distribution of reliable nutrients and moisture available in specific habitats can form refugia, allow coexistence, support a greater number of omnivores or opportunistic species sensitive to predation, and provide a temporal niche required for ongoing existence (e.g. recruitment) (Yang et al. 2008; Letnic and Dickman 2010; Kelt 2011): a species' dependency on these resources can be exploited for the creation of robust SDMs reflecting species' *fundamental niche*. For example, food resources for rodents are more directly represented by ephemeral plants which encompass the interactions and lag between rainfall, soil and vegetation properties; perennial plants may be closely correlated with invertebrate food sources or shelter for dasyurids, and additional prey dynamics may be required for improved SDM of higher order predators.

Discussion

The selection of traits based on past biotic interactions, may result in contemporary resource availability strongly affecting a species' survival or reproduction, and therefore improve SDM performance via the *fundamental niche*. Identifying biotic resources might therefore be key to understanding the distributions of specialists (Boulangeat et al. 2012). The effects of resource limiting generalists may be apparent only during the initial colonisation period, after which a range of biotic interactions may provide a stable supply of resources (e.g. pollinators, Lavergne et al. 2010). However, even in this case, continual changes to community composition and dynamics might lead to relatively generalised interactions becoming limiting (Lavergne et al. 2010). The loss of effective seed dispersers has already been recorded in some systems (Meehan et al. 2002), and along with the potential loss of pollinators can induce cascading effects (Bascompte and Jordano 2007). As a result, drivers associated with conservative niche dynamics (i.e. endemic specialists) or becoming limited through deteriorating community dynamics with may be vital for confidently extrapolating SDMs across the landscape (Angilletta and Sears 2011).

Naturally dynamic systems drive the path and rate of evolution, extinction and phylogenetic divergence (Alley 1982); this moderates the impact of biotic interactions, stabilises food webs and shapes species' ecology (Lavergne et al. 2010; Wiens et al. 2010). Relationships between abiotic and biotic interactions that lead to the development (or maintenance) of traits are poorly understood (Hooper et al. 2005; Angilletta and Sears 2011). This increases the risk of misinterpreting interactions, which in turn effects assumptions made about a species' fundamental or *realised niche*. For specialists, sufficient information may be already available to improve conceptual models by distinguishing resources driving the *fundamental niche* from facilitative biotic interactions influencing the *realised niche* (e.g. woodpeckers creating nesting sites for boreal owls, Heikkinen et al. 2007). To remedy this problem for other species, further investigations are required into the demographic response to environmental gradients that may define the niche, how flexible those responses are across sites and given current and ongoing species evolution (Schmitt and Coyer 1982; Morrison 2001; Holt 2009).

Identifying general mechanisms underlying the evolution of traits can aid in understanding and modelling community dynamics (McGill et al. 2006; Eronen et al. 2010; Wiens et al. 2010) and determining whether niches are likely to be conservative in novel environments (Lavergne et al. 2010; Sinclair et al. 2010). Yet the mechanisms may be difficult to identify, especially given each species has a unique niche within which it survives and reproduces (Holt et al. 1995; Brown et al. 1996). To overcome this sizeable challenge, recommendations have been made to focus on key evolutionary traits and ecological consequences (Price 1986; Kotler and Brown 1988). This should aid in rationalising gradients (recommended by Brown et al. 1996; Austin and van Niel 2011a), and identifying biologically useful and correctly scaled gradients (e.g. nectar availability, Zimmerman and Pleasants 1982; Dennis et al. 2003).

Overall, this review builds on Holt (2009) by i) expanding on the role biotic interactions have on the development of adaptive traits over evolutionary time, leading to dependency on resources by higher trophic species, and ii) explaining why we should not be surprised when the inclusion of these factors improves SDMs (e.g. Pauses et al. 1997, Heikkinen et al. 2007, Dillard et al. 2008, Kearney et al. 2010).

Conclusion

RESOURCES, DATA RESOLUTION AND SMALL MAMMAL RANGE DYNAMICS

Conclusion

Ongoing confusion regarding the niche concept and its representation in species distribution modelling (SDM) has led to biotic factors being considered only in terms of interactions relating to the *realised niche*. However, over time, biotic interactions can drive natural selection of traits that enhance resource exploitation, competitive dominance or predator avoidance. In these cases a species' dependence on resource availability for positive population growth may outweigh the secondary effects of constraining interactions (e.g. competition and predation); especially for species that are mutually dependent, competitively dominant specialists, or generalists occupying degraded communities with limited species performing ecosystem functions (e.g. pollinators). This work evaluates the influence of landscape- and quadrat-scale data at varying resolutions on modelled range dynamics of nine species of temperate- and arid-zone small mammals.

Do biotic factors influence the fundamental niche?

Investigations into the relative contribution of additional edaphic and biotic factors (vegetation community structure) to climate-only species distribution models (SDM) determined improved performance for all temperate- and arid-zone small mammals (Chapters 1 & 4; Table 1). Most support was obtained for two endemic species (*Dasyuroides byrnei* and *Notomys cervinus*), a wet-heath specialist (*Rattus lutreolus lutreolus*), opportunistic insectivore (*Antechinomys laniger*) and understorey preferring *Isoodon obesulus obesulus* (i.e. increase in metrics reflecting strength of statistical evidence and structural goodness-of-fit: $w\mathrm{AIC}_c$ wBIC and Δ % DE). For these five species improved model fit transferred to improved predictability of species occurrence in an independent dataset (measured using AUC and Kappa scores): most noticeably for the three arid species (out-of-sample validation). However, improved Kappa scores reflected improved discrimination of absences (specificity), except *R. l. lutreolus*, where it was instead associated with improved discrimination of presences (sensitivity). These trends were only weakly influenced by model bias, which predominately affected sensitivity estimates for species represented by few presences records and species with poor model performance (*Leggadina forresti* and *Sminthopsis macroura*). Overall, support for increased discrimination of the occurrence of three arid and two coastal species, tested in a rigorous out-of-region (coast) or out-of-sample validation (arid), demonstrates improved model robustness as expected in the case of enhanced representation of the *fundamental niche*.

For those SDMs that were enhanced by the addition of topographic, soil and vegetation variables (based on model fit and transferability), the contributions of individual variables are shown in Table 2. In general, climate variables were most useful in SDMs within the coastal Mediterranean environment and of little value in the arid Channel Country IBRA region where rainfall and flooding events are unpredictable. In both regions additional topographic, soil and vegetation data contributed more than 5 % explanatory strength to many SDMs, while variables indirectly representing refuges were particularly valuable in the arid region (distance to watercourse and soil water holding capacity). This pattern supports the dynamic interaction of moisture, soil and species on resource availability in arid ecosystems and importance of refuges harbouring populations during periods of drought (e.g. Morton et al. 2011, Dickman et al. 2011).

A second dataset that represented species presence determined by proximity to known records (i.e. within 150 m) was used to explore the value of additional quadrat variables to landscape-scale SDMs (i.e. diversity of flora > 2 m or < 2 m, shrub cover < 0.5 m or 0.5-1.0 m; Chapters 2 & 4). Quadrat-scale variables were present in the top ranking models for some species (*I. o. obesulus, N. cervinus* and *S. macroura*; Table 3). However, support was not unanimous across all information theoretic measures ($w\mathrm{AIC}_c$, *w*BIC), indicating improved model performance was insufficient to overcome the additional penalty applied when using a greater number of parameters by the BIC, or the small sample size limiting the effect of variables being detected in the model. In these cases, there was no validation performed.

Table 1 Improved discrimination of species occurrence following the addition of topographic, soil (edaphic), and vegetation variables illustrated for species with improved model performance (a), and supported by an independent validation (b). Shown are the Akaike's information criterion (corrected for small sample sizes) and Bayesian Inference Criterion represented as the weight scaled to a sum of 1 ($w\mathrm{AIC}_c$, *w*BIC), the per cent deviance explained (% DE) by the fitted model relative to the null (mean field) model, the difference in % DE of the climate-and-landscape model relative to the climate-only model (Δ % DE), the area under the curve (AUC) and Kappa metrics, and Sensitivity (Sens) and Specificity (Spec) statistics (generated using a Maximum Sensitivity and Specificity threshold). Shaded values indicate no support for the methods indicated.

	a. Model performance (e.g. GLM)				b. Trend[1] and bias[2] in validation statistics			
	$w\mathrm{AIC}_c$	*w*BIC	% DE	Δ % DE	AUC	Kappa	Sens	Spec
Coastal mammals (out-of-region validation)								
I. o. obesulus	1.00	0.93	31.2	5.1	1	1	0	2
A. f. flavipes	0.97	0.00	49.3	5.5	0	0	1	-1
R. f. greyi	0.28	0.00	19.1	2.6	-1	-1	2	1
R. l.lutreolus	1.00	1.00	65.9	47.6	1	0	2^{B+}	-2^{B-}
Arid mammals (out-of-sample validation)								
N. cervinus	1.00	1.00	55.2	55.2	2	2^{B+}	0^{B+}	2^{B+}
D. byrnei	1.00	1.00	53.4	52.1	2	2	-1	2
A. laniger	1.00	1.00	50.9	46.4	2	2	0^{B-}	2^{B+}
L.. forresti	0.56	0.00	14.7	13.1	1	2	0^{B+}	2^{B-}
S. macroura	0.03	0.00	6.3	5.2	-1	-1	2^{B+}	-2^{B-}

[1] Direction and strength of trend: 2-increase (beyond S.D.), 1-slight decrease, 0-no change, -1-slight decrease, -2-decrease (beyond S.D.).

[2] Model bias indicating the trend should be in a negative direction (B-) or positive direction (B+).

Table 2 Independent contribution of climate, topographic, soil and vegetative variables in the saturated SDMs of coastal (a) and arid (b) mammals, where it performed better than the climate-only model (See Table 1). Shown are the per cent deviance explained values (%DE).

	Coastal mammals				Arid mammals			
	I. o. obesulus	*A. f. flavipes*	*R. l. lutreolus*	Ave.	*A. laniger*	*D. byrnei*	*N. cervinnus*	Ave.
MT	10.5	11.0	0.1	7.2				
RS	31.6	47.3	30.7	36.5	10.0	4.8	1.0	5.3
RW	21.3	31.7	1.1	18.0	1.3	1.5	0.9	1.2
E	18.3	23.3	12.3	18.0	2.8	0.2	2.4	1.8
S	7.1	5.3	0.2	4.2	na	na	na	na
lnWC	8.3	12.4	13.9	11.5	44.0	50.6	78.8	57.8
PAWHC	na	na	na	na	23.3	21.3	8.7	17.8
H	10.4	10.5	12.0	11.0	na	na	na	na
M	0.7	9.9	10.9	7.2	na	na	na	na
GEN	2.6	5.0	8.3	5.3	7.2	9.3	5.6	7.4

Climate variables: ave. minimum temperature (MT), ave. monthly rainfall during summer (RS) and winter (RW). Topographic variables: elevation (E), slope (S), distance to watercourse or line (lnWC). Soil (edaphic) variables: root zone water holding capacity (M or PAWHC), soil acidity (H). Vegetation (biotic) variables: broad vegetation community (GEN).

Table 3 Performance of top-ranking models relative to a climate-only model. Shown are the Akaike's information criterion (corrected for small sample sizes) and Bayesian Inference Criterion represented as the weight scaled to a sum of 1 (wAIC$_c$, wBIC), the per cent deviance explained (% DE) by the model relative to the null and the difference in % DE of the top-ranking model relative to the climate-only model.

	Top ranking model	wAIC$_c$	wBIC	% DE	Δ %DE
Coastal mammals					
I. o. obesulus	~ RS + lnWC + C3	0.51	0.04	27.7	1.3
A. f. flavipes	~ RS + lnWC + H + GEN	0.98	0.10	45.1	3.7
R. f. greyi	~ MT + RS	1.00	1.00	20.1	0.0
R. l. lutreolus	~ RS + S + M + GEN	1.00	1.00	40.2	27.7
Arid mammals					
N. cervinus	~ RS + lnWC + C2	0.43	0.04	41.5	33.2
D. byrnei	~ RS + lnWC + PAWHC	0.89	0.89	40.2	29.7
A. laniger	~ RS + lnWC + PAWHC	0.97	0.97	31.8	19.5
L. forresti	~ RS + GEN	0.52	0.02	8.3	5.2
S. macroura	~ RS + SD	0.54	0.01	5.0	3.6

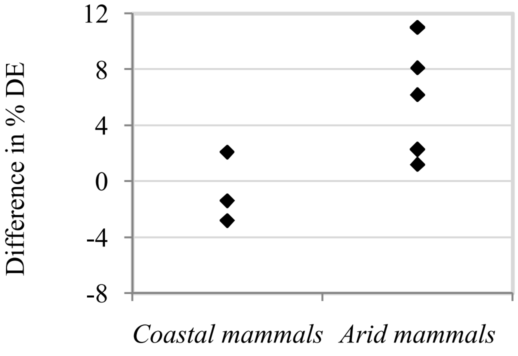
Additional climate variables not already defined in Table 2: Root zone water holding capacity of the solum (PAWHC), diversity of flora > 2 m (C3) or < 2 m (C2), shrub cover < 0.5 m (SD) or 0.5-1.0 m (SC).

In both the landscape-only and landscape-and-quadrat-scale models, not all patterns expected based on the ecology of these small mammals were apparent. For example, 'broad vegetation community' aided in describing the occurrence of the wet-heath specialist (*R. l. lutreolus*), but not an understorey preferring species (*I. o. obesulus*), which also failed to be aided by the addition of 'shrub cover between 0.5 and 1.0 m' (SC). The failure of these models to represent known species-environmental relationships reflects either i) limitations in the resolution of the available data (i.e. vegetation community mapping and classification biased towards the upper structural layer (canopy) and use of broad categories to estimate cover in the field, e.g. 30 – 70 % cover), or ii) that these relationships are minor in comparison to others being detected, including indirect representation of resource availability by climate variables (e.g. by complex species response curves in BRT).

Influence of scale on the representation of species-environmental interactions

To explore the effects of scale on SDM performance, the landscape-and-quadrat-scale models of best fit previously identified were re-applied using datasets where species occurrence was represented at a lower resolution (i.e. by environmental features within 500 m and 1 000 m of known species records; Chapters 2 & 4). With decreasing resolution, model performance decreased for the wet-heath specialist (*R. l. lutreolus*) and two dense-understorey species (*I. o. obesulus* and *R. f. greyi*; negative values), but increased for the remainder (positive values; Fig. 1). The latter trend can be explained by the ecology in some cases (e.g. the more mobile woodland generalist, *A. f. flavipes*, may obtain sufficient prey and nest sites from neighbouring woodland remnants), or potential data limitations in other cases (e.g. inconsistencies in the increase in model performance for two arid endemic species, *D. byrnei* and *N. cervinus*).

Fig. 1 Change in deviance explained (% DE) by the single best model (identified as the top ranking model in % DE and AIC$_c$) based on the dataset representing species presence within 150 m of known records relative to the dataset containing species presence within 1000 m.



To verify increased model performance with decreasing resolution, the explanatory strength of individual single-variable models were compared (Chapters 2 & 4). Patterns varied between species and variables, but indicated the trend of improved model performance with decreasing resolution for the arid species was being driven by the species response to distance to water-course variable (lnWC; Fig. 2). Overall, climate variables were closely associated with some species at a coarse resolution (e.g. RS-*R. l. lutreolus*), and others at a fine resolution (e.g. RS-*I. o. obesulus*). These patterns are supported by the ecology of these species: *R. l. lutreolus* prefers wet-heath and sedgeland (represented by GEN, C3 or SC), which is dependent on water channelled into these habitats from across the catchment (explaining the weaker association with RS). The fine-scale association between rainfall and *I. o. obesulus* and *D. byrnei* may represent the influence of soil moisture for sustaining food availability over dry periods (fungi and invertebrates) or increased abundance of vertebrate prey (e.g. rodents, Letnic et al. 2005), respectively.

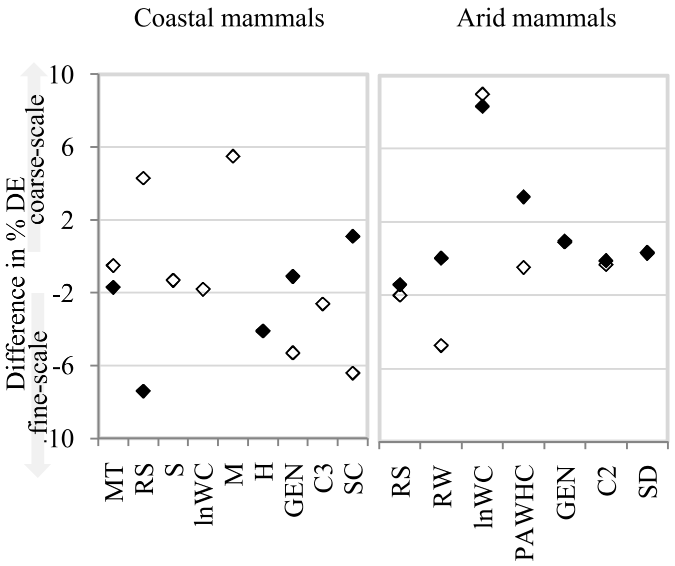


Fig. 2 Change in deviance explained by single-variable models with decreasing resolution of environmental information at known sites (% DE at 1000 m - % DE at 150 m). Illustrated are trends for (left) two coastal species, *I. o. obesulus* (solid diamonds) and *R. l. lutreolus* (hollow diamonds), and (right) two arid species, *A. laniger* (solid diamonds) and *D. byrnei* (hollow diamonds). Variable codes are described in Table 3.

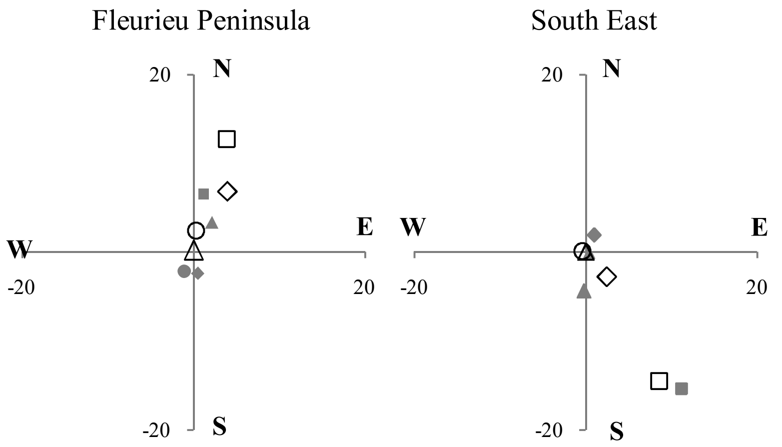
Influence of scale on detecting range shift during a period of simulated climate change

The scale used in SDMs also directly influenced the extent and distribution of available habitat, which therefore affected estimates of population persistence and range shift predicted to occur in a changing climate (Chapter 3). This was demonstrated in coupled niche-population models simulating population dynamics projected over 40-years of a stable and of a changing climate. The underlying SDMs based on 100 m^2 or 1000 m^2 resolution environmental data predicted a similar area of available habitat (Table 4). However, at the fine scale, more patches were modelled (ca. 10 times) that were more variable in shape (range in perimeter : area 0.032 at the fine-scale; 0.002 coarse-scale), leading to increased connectivity between patches (average number of patches within dispersal distance, < 57 fine-scale; 0 coarse-scale). As a result lower rates of decline in animal abundance and range shifts were forecast (although range shifts were detected for more species than at the coarse scale; Table 4, Fig. 3). These results illustrate that potential range shifts and species vulnerability information may be misrepresented if more advanced modelling techniques incorporating species demographics and dispersal inadequately represent the scale at which these processes occur.

Table 4 Summary of the a) initial habitat and population, and b) changes over 40-years of projected climate change (1000 simulation iterations, for the species' range on the Fleurieu Peninsula and South East. Values are calculated across species and include the average (SD) or median (min) values. More detailed values are provided in Table 1 of Chapter 3 and Appendix XIII.

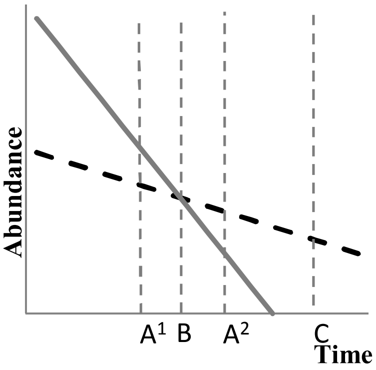
	Fleurieu Peninsula		South East	
resolution:	100 m^2	1000 m^2	100 m^2	1000 m^2
a. Initial spatial configuration of available habitat and number of occupied patches:				
Ave. habitat area (km^2)	193 (121)	199 (128)	221 (212)	244 (198)
Ave. no. patches	1123 (148)	72 (41)	919 (1112)	98 (83)
Median p:a ratio	0.032 (0.008)	0.004 (0.002)	0.028 (0.002)	0.004 (0.002)
Median distance between patches (km)	0.3 (0.2)	3.6 (1.8)	0.3 (0.2)	2.6 (1.8)
Ave. max no. patches within dispersal dist.	57 (56)	0 (0)	17 (7)	0 (0)
b. Changes following 40 years of climate change:				
Habitat area (%)	-67 (24)	-47 (35)	-35 (18)	-16 (18)
Patch no. (%)	-55 (30)	-41 (28)	-23 (22)	11 (88)
Population no. (%)	-44 (38)	-37 (29)	-25 (22)	-15 (23)
Ave. abundance animals yr^{-1}	-1329 (2041)	-3733 (2497)	-897 (918)	-804 (1304)
No. occupied populations yr^{-1}	-9 (9)	-1 (1)	-5 (5)	0 (1)

Fig. 3 Shift in the centre-point of occupied habitat at 100 m^2 and 1000 m^2 resolution (hollow or solid symbols, respectively), in the Fleurieu Peninsula and South East. Species are represented by diamonds (*I. o. obesulus*), triangles (*A. f. flavipes*), squares (*R. f. greyi*) or circles (*R. l. lutreolus*).



The consequence of inaccurate initial abundance and rates of change on model outcomes will depend on the duration of forward predictions. For example, at points in time along simulations at two scales (Fig. 4), estimates may be greater at one scale than another (e.g. A), produce similar results (B), or predict species extinction in one case (C). The risk of generating inaccurate results and misinforming policy further highlights the importance of: i) creating robust SDMs based on ecologically relevant predictors (e.g. Austin 2007, Ford and Johnson 2007, Angilletta and Sears 2011), and ii) continuing to acquire more accurate estimates of the initial parameters and confidence intervals (e.g. effect of environmental predictors on population fitness; Järemo et al. 1999, Ylönen et al. 2003, Gaillard et al. 2010).

Fig. 4 Illustration of the confounding effect of time on estimates of abundance and extinction using two different models with different initial abundances and slope.



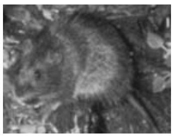
Overall, the coupled niche-population models showed the highest sensitivity to climate change for *R. f. greyi*, followed by *I. o. obesulus*, *R. l. lutreolus* and *A. f. flavipes* (Table 5; Chapter 3). This ranking was the reverse of SDM predictive capacity, but reflects the result that SDMs for these species were most influenced by climate variables. For the remaining species, the addition of static non-climate variables can stablise predictions (e.g. topographic, soil and vegetation variables for the wet-heath specialist, *R. l. lutreolus*, and woodland generalist, *A. f. flavipes*). The importance of fine-scale information to represent habitat geometry and quality, and the subsequent effects on population demography and dispersal potential has empirical support across a variety of additional taxa (e.g. Löbel et al. 2006, Hokit et al. 2010, Baguette et al. 2011).

Future directions: improving SDMs and priorities for empirical research

The use of SDMs for forecasting range shifts under global change is an important and established method, yet they often do not adequately reflect the ecology of a species' niche. Morrison (2001) and others have recommended that in each investigation: i) the niche being referred to is clearly defined (also Elith and Leathwick 2009), ii) a conceptual model relating the target species to the ecosystem is provided (also Austin 2007), iii) the relationships under investigation are described (including the direction of influence; Chapter 5), and iv) limiting resources required for positive population growth (e.g., food, nutrients, nest sites) are clearly identified and distinguished from secondary constraining biotic interactions (e.g. competition and predation), or other spatial or temporal influences (e.g. dispersal potential, history of disturbance).

For some small mammals, analysis of currently available data may adequately characterise species' distributions where environmental factors directly influence species occurrence (e.g. suitable microclimates on nest site availability for non-fossorial species *I. o. obesulus*), or are associated with resources: proximally (e.g. woodland communities representing nest sites for the mobile, woodland generalist, *A. f. flavipes*), or distally (e.g. the influence of suitable microclimate on subterranean fungi and invertebrate availability for *I. o. obesulus*). However, where environmental factors have an indirect or distal indirect influence on species occurrence, forecast changes in range dynamics

Table 5 Relative species ranks obtained from outputs derived at the fine-scale species reflecting model performance (a) and impacts predicted following 40-years of simulated climate change (b). Top ranking species are indicated by the arrow head or 1.

	Confidence ranking			
				
Species	*A. f. flavipes*	*R. l. lutreolus*	*I. o. obesulus*	*R. f. greyi*
Family	Dasyuridae	Muridae	Peramelidae	Muridae
Status	VU	Rare	EN	
Habitat preference	complex	tall grass sedge	dense, low veg	dense, low veg
Diet[1]	I, C	H	O	O
Shelter	hollows, *Xanthorrhoea* spp.	burrows	leaf litter, shrubs	burrows
a. Initial extent:				
SDM performance	◄	—	—	
Contribution of: MT[2]	1		2	3
RS[2]	1	2	3	4
RW[2]	1		3	2
Propn of climate: total	2	3	1	4
Area predicted	1	4	3	2
b. Simulated climate change				
Habitat loss	—	—	►	
Population loss	3	4	2	1
Centroid shift			2	1
Fragmentation	1	1	1	2

[1] H-herbivore, O-omnivore, I-insectivore, C-carnivore

[2] Climate variables are defined in Table 2.

with climate change should be treated with caution (i.e. where climate is the only dynamic variable, imposing direct, immediate rates of change on species' occupancy).

Collecting empirical data continues to be an essential component of improving SDMs; by increasing the number of localities available to represent occurrence of data poor species, through to obtaining empirical information on demographic response to appropriately scaled environmental factors that represent direct, proximal influences on species population growth rates, or secondary biotic interactions (e.g. competition, predation and diseases) (Chapters 1 to 4). This information will improve our confidence in SDM forecasts, assist in redressing current bias in models towards data-rich taxa (plants, birds and invertebrates), and may become more important as ecosystems become degraded reducing the number of species performing ecosystem functions. However, the logistical difficulties in achieving have been long recognised (e.g. Brown et al. 1996). To address this problem Austin and van Niel (2011a) suggested standardising environmental data used to represent gradients in SDMs. Another suggestion would be to target empirical investigations into functional guilds and mammalian species with key traits that are currently poorly represented in SDMs.

Overall, the work in this thesis determined landscape- and quadrat-scale edaphic and biotic factors (including vegetation community structure, floristics and cover) can improve model fit and transferability. Cases of improved model robustness (transferability) imply improved integration of gradients that define the *fundamental niche*. The strength of species-environment relationships varied with resolution of environmental variables relative to known record localities: examples of improved correlation at fine and coarse scales were evident for many variables, including mean rainfall. In addition, the resolution of environmental data influenced habitat geometry, metapopulation function and estimates of range shift. As a result, appropriately scaled, ecologically relevant environmental data are required to redress the under-representation of small mammals in SDMs used to evaluate species sensitive to climate change.

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Appendix I Landscape and vegetation characteristics of the Interim Biogeographic Regionalisation for Australia (IBRA) v6.1 sub-regions (Australian Government Department of the Environment, Water, Heritage and the Arts) spanning the study area.

Appendix II Ecology of the four mammal species targeted in this investigation.

Southern brown bandicoot, *Isoodon obesulus obesulus* (endangered, *Environment Protection and Biodiversity Conservation Act 1999*)

In general terms, *I. o. obesulus* occupies scrub, heath and ecotones, low ground cover, open paddocks and urban environments (Heinsohn, 1966). Suitable habitat usually incorporates a mosaic of communities (Broughton and Dickman 1991) and some component of mature vegetation (Stoddart and Braithwaite 1979; Lobert 1985; Claridge and Barry 2000). The understorey is required to support at least 50 % cover, preferably 60 – 70 % cover (Moro 1991; Paull 1992), or a certain floristic composition for species occurrence in poor quality habitats (Braithwaite and Gullan 1978). This territorial medium-sized ground-dwelling mammal is omnivorous, forages on a selection of invertebrates, fungi, plant material and small vertebrates and constructs nests using available leaf litter (Wood-Jones, 1924; Heinsohn 1966). The species currently occupies remnants within FLB1, KAN1-2, NCP1-3 and VVP2 (Fig. 1).

Yellow-footed antechinus, *Antechinus flavipes flavipes* (vulnerable, *South Australia National Parks and Wildlife Act 1972*)

Antechinus f. flavipes is a generalist (Wood-Jones 1923) and occurs in a variety of vegetation communities (Hockings 1981). The species prefers structurally complex vegetation (Stokes et al. 2004) with dense understorey (Hockings 1981), high ground leaf litter cover (Kelly and Bennett 2008) and *Xanthorrhoea* spp. or tree hollows for nest sites (Marchesan and Carthew 2004). Males of the species are capable of seasonal dispersal between patches of remnant vegetation (average 352 m) (Marchesan and Carthew 2008). The species is primarily insectivorous and carnivorous (Wood-Jones 1923) and currently occupies remnants within FLB1, KAN2 and NCP2-3 (Fig. 1).

Swamp rat, *Rattus lutreolus lutreolus* (rare, *South Australia National Parks and Wildlife Act 1972*)

Rattus l. lutreolus occurs in similar habitats to *R. f. greyi,* but where *R. f. greyi* will occur in woodlands (Maitz and Dickman 2001), the former prefers wetter environments with tall grasses, sedges (Braithwaite and Gullan 1978) and dense (low) understorey (Hockings 1981; Norton 1987a; Monamy 1995; Holland and Bennett 2007). Individuals of the species actively deter those of *R. f. greyi* or younger *R. l. lutreolus* from preferred habitat (Maitz and Dickman 2001), but can occupy a broader range of habitats where *R. f. greyi* are absent (Lunney 2008b). The species is herbivorous and consumes plant material, some insects and fungi (Norton 1987b; Taylor and Calaby 1988b) and currently occupies remnants within KAN2, NCP1-3 and VVP2 (no suitable records were available to represent the species' distribution in KAN1 and the extensive Murray Lakes and Coorong sub region was excluded for containing only a few *R. lutreolus lutreolus* records) (Fig. 1).

Bush rat, *Rattus fuscipes greyi* (not currently threatened)

Rattus f. greyi is widely distributed (Wood-Jones 1925; Lunney 2008a) and occupies a range of vegetation communities (Watts and Aslin 1981; Taylor and Calapy 1988a) in increasing abundance from rainforest, shrubland, forest, heathland to sedgeland (Lindenmayer et al. 2008). This reflects a preference for dense and diverse low vegetation (Stewart 1979; Hockings 1981; White et al. 1996; Spencer et al. 2005; Holland and

Bennett 2007). The species is associated with *Xanthorrhoea* spp. and the presence of fallen logs (Spencer et al. 2005; Frazer and Petit 2007). A generalist fungivore, *R. f. greyi* has a seasonally variable diet of fungi, grasses, sedges, seed and arthropods, with increasing consumption of grasses over autumn and winter (Cheal 1987; Carron et al. 1990) when food is generally limited (Braithwaite and Lee 1979). Individuals construct burrows and are able to climb (Warneke 1971), but have limited dispersal between remnants (Bentley 2008). The species currently occupies remnants within EYB3-4, FLB1, KAN1-2, NCP1-3 and VVP2 (Fig. 1).

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Appendix III Species occurrence data from the South Australian biological survey and additional site opportunistic data incorporated within the Biological Databases of South Australia (BDBSA, extracted 18th December 2008).

	I. o. obesulus	*A. f. flavipes*	*R. f. greyi*	*R. l. lutreolus*
Year range	1975 – 2008	1972 – 2004	1971 – 2008	1972 -2004
Filters	≤ 100 m location accuracy, single observation per location			
Sampling method				
• Cage trap	104	-	17	1
• Elliott trap	8	61	183	55
• Pit trap	-	2	14	1
• Roadkill	30	-	-	-
• Observed (incl. spotlighting)	93	-	4	3
• Sign-diggings	113	-	-	2
• Sign-dropping	2	-	-	-
• Sign-hair tube	10	-	-	-
• Sign-nest (in-active)	2	-	2	-
• Sign-track tube	7	-	-	-
• Sign-within scat	2	-	-	-
• Unknown / unspecified	26	20	19	4
Total	397	83	239	66

Appendix IV Spatial landscape variables used, including categorical variables that were simplified to avoid over-parameterising models.

Variable	Description	Method of creation and data source	Range (min-max)			
			a.[A]	b.	c.[B]	d.[C]
Landscape-scale data						
Climate						
MT	Ave. monthly min. temp.	Baseline climate layers were created from meteorological station data (Australian Bureau of Meterology), combined with elevation from a 250 m DEM (Geoscience Australia 2008) and interpolated across the region using thin plate smoothing splines in ANUSPLIN to a 1 km resolution (Hutchinson 2006; Fordham et al. In press).	11.7-15.9 °C	11.7-15.9 °C	6.5-7.9 °C	4.07-8.65 °C
RS	Ave. monthly summer rainfall (Nov - Jan)		40.3-97.0 mm	40.3-96.3 mm	15.3-30.5 mm	16.2-31.7 mm
RW	Ave. monthly winter rainfall (Jun - Aug)	These were used to generate the initial SDMs. An ensemble of the top ranking global climate models (GCM) in Australia was then used to predict future climate using parameters from several climate change scenarios. A period of 40 years from the no-policy-change 'reference' scenario (Fordham et al. 2011) was extracted for this investigation.	126.4-490.6 mm		9.4-16.4 mm	42.0-132.4 mm
Topography						
E	Elevation	Elevation and slope were derived from a 25 m DEM and the distance from the nearest watercourse from available watercourse and body vector information (Department for Environment and Natural Resources, DENR), using ArcGIS 9.2 (ESRI 2006). Values were transformed using the natural log. These finer scale topographic variables are more likely to represent the patchy distribution of available shelter and food for some species (eg *R. l. lutreolus*).	0-694 m		17.2-197.2 m	-4.0-703.0 m
S	Slope		0.0-30.6°	0.0-30.6°		
lnWC	Distance from nearest water course / body		1.3-4.5	3.0-10.3	3.0-6.0	2.9-8.3

(cont.)

(cont.) **Appendix IV**

Soil						
M	Root zone water holding capacity	Soil vector data were available from PIRSA (2001). Categorical root zone water holding capacity values were reclassified to1 where > 50 % area within a mapped polygon had high root zone water holding capacity, and 0 for polygons where > 50 % area had moderate to very low water holding capacity. Categorical soil acidity data were reclassified to 1 where polygons contained > 20 % acidic surface and sub-surface soil cover, and 0 where > 20 % of the area, neutral of alkaline soils. These finer scale soil variables were mapped with reference to the distribution of vegetation communities, but were selected to represent possible relationships with soil type preferred for burrowing, subterranean food availability and shelter.	0, 1	0, 1		0, 1
H	Soil acidity		0, 1	0, 1		0, 1
PAWHC	Root zone water holding capacity of the solum	In the Channel Country IBRA region soil vector data were available from the Atlas of Australian Soils (www.asris.csiro.au), representing root zone water holding capacity of the solum (A and B horizons) and cracking clay, red duplex and sandy soils types. The latter was strongly correlated and not used.			0-157.0	
Vegetation						
GEN	Broad vegetation community	Vegetation communities > 15 ha were mapped from 1: 40 000 aerial photographs (1987), with assistance from the classification of structural and floristic data (Foulkes and Heard 2003). Categorical data were reclassified as 1, sedgeland, fernland or grassland; 2, woodland or mallee woodland; 3 forest or mallee forest; 4 shrubland. As *I. o. obesulus* and *A. f. flavipes* were absent from GEN1, this variable category was removed from the respective SDM. This finer scale variable was selected to directly represent preferred habitat, including available shelter (such as hollow), and food resources. In the Channel Country IBRA region, categorical data were reclassified as 1, woodland; 2, shrubland > 1 m; 3 shrubland < 1 m; 4 hummock grassland.	0,1, 2, 3, 4	0,1, 2, 3, 4	0,1, 2, 3, 4	0,1, 2, 3, 4

(cont.) **Appendix IV**

Quadrat-scale data				
C3	Diversity of flora > 2 m	Point data were available from DENR Biological Survey of South Australia (BSSA) sites. Prior to extraction this dataset was validated by a botanist (N. Neagle, DENR, pers. comm., 2011, P. Lang, DENR, pers. comm., 2009). C3 represented counts of tree, mallee and large shrub species taller than 2 m, and C2 shrub species richness < 2 m. Point data were available from DENR BSSA survey sites containing modified Muir categories (1-10 %, 10-30 %, 30-70 % and 70-100 %) (Heard & Channon, 1997) condensed to (0, 1-10 %, 10-30 %, > 30-70 %).	0-10 species	
C2	Diversity of shrubs < 2 m			1-67 species
SC	Shrub cover 0.5 – 1.0 m		0, 1, 2, 3	
SD	Shrub cover < 0.5 m			0, 1, 2, 3
VL	Sedge cover < 0.5 m		0, 1, 2	

[A] Some variables shared some correlation (r > 0.6), including between MT and RS (-0.60), RS and RW (0.77), RS and E (0.78), RW and E (0.82), RW and H (0.64).

[B] Correlated variables (i.e. MT and RS r 0.85, PAWHC and soil type r 0.96) were not included in the same model.

[C] Variables representing climate variability was also trialed, but found to be highly correlated with mean values (mean Pearson's r for MT 0.85, RS 0.98), and when used in place of mean variables, produced simular results (≤ 1.6% DE for all models, excluding the *N. cervinus* climate-only model that increased by 3.8% DE and was insufficient to outcompete the climate-and-landscape model).

Appendix V Explanatory strength of *a priori* predictive boosted regression tree models using climate (Model 1; ~ MT + RS + RW) and landscape parameters (Model 2 ~ MT + RS + RW + E + S + WC + GEN + M + H). Shown are the optimal tree complexity (number of nodes) and learning rate (number of trees added to the model) used to apply the BRT model, the resultant number of trees required and the percentage deviance explained (% DE).

	I. o. obesulus		*A. f. flavipes*		*R. f. greyi*		*R. l. lutreolus*	
	Model 1	Model 2	Model 1	Model 2	Model 1	Model 2	Model 1	Model 2
Tree complexity	5	3	2	2	4	3	2	2
Learning rate	0.01	0.01	0.005	0.005	0.01	0.005	0.01	0.005
No. trees	750	1250	1450	1400	1200	1100	500	1350
% DE	41.4	42.7	41.9	45.8	26.1	27.4	25.4	38.4

MT, average monthly minimum temperature; RS / RW, average monthly rainfall during summer (Nov-Jan) and winter (Jun-Aug); E, elevation; S, slope; lnWC, distance from nearest water course or body transformed using the natural log; GEN, broad vegetation community; M, root zone water holding capacity; H, soil acidity.

Appendix VI Coefficients estimated for each parameter of the more complex generalised linear model for each species (Model 2 ~ MT + RS + RW + E + S + WC + GEN + M + H), standard error (SE), z score and the associated p-value. Also shown are the effect size as an odds ratio, and 95 % confidence intervals around the odds ratio.

	Coefficient	SE	z score	Pr(>|z|)	Odds ratio	95 % CI
a. *I. o. obesulus*						
(Intercept)	-27.411	3.564	-7.7	<0.000	<0.0	0.000-0.000
MT	1.201	0.193	6.2	<0.000	3.3	2.274-4.860
RS	0.103	0.014	7.5	<0.000	1.1	1.079-1.139
RW	0.012	0.003	4.4	<0.000	1.0	1.007-1.017
E	-0.003	0.001	-2.5	0.011	1.0	0.995-0.999
S	0.007	0.020	0.3	0.727	1.0	0.968-1.048
lnWC	0.009	0.076	0.1	0.910	1.0	0.869-1.171
GEN3	-1.388	0.282	-4.9	<0.000	0.2	0.144-0.434
GEN4	0.066	0.368	0.2	0.857	1.1	0.518-2.202
M1	0.283	0.278	1.0	0.308	1.3	0.770-2.290
H1	0.851	0.250	3.4	0.001	2.3	1.434-3.824
b. *A. f. flavipes*						
(Intercept)	-22.326	6.476	-3.4	0.001	<0.0	0.000-0.000
MT	0.788	0.384	2.0	0.040	2.2	1.033-4.677
RS	0.154	0.029	5.3	<0.000	1.2	1.101-1.235
RW	0.001	0.006	0.2	0.839	1.0	0.989-1.014
E	-0.001	0.002	-0.3	0.727	1.0	0.995-1.003
S	0.029	0.034	0.9	0.385	1.0	0.964-1.100
lnWC	-0.337	0.158	-2.1	0.033	0.7	0.523-0.974
GEN3	1.235	0.446	2.8	0.006	3.4	1.433-8.259
GEN4	0.316	0.741	0.4	0.670	1.4	0.320-5.883
M1	0.865	0.434	2.0	0.046	2.4	1.013-5.574
H1	0.481	0.454	1.1	0.290	1.6	0.663-3.951

(cont.) **Appendix VI**

	Coefficient	SE	z score	Pr(>|z|)	Odds ratio	95 % CI
c. *R. f. greyi*						
(Intercept)	-25.559	3.340	-7.7	<0.000	<0.0	0.000-0.000
MT	1.081	0.187	5.8	<0.000	3.0	2.041-4.256
RS	0.104	0.012	8.4	<0.000	1.1	1.083-1.137
RW	0.013	0.003	4.8	<0.000	1.0	1.008-1.019
E	-0.005	0.001	-3.8	<0.000	1.0	0.993-0.998
S	-0.003	0.025	-0.1	0.898	1.0	0.950-1.046
lnWC	0.030	0.079	0.4	0.702	1.0	0.883-1.203
GEN3	-0.027	0.330	-0.1	0.934	1.0	0.509-1.856
GEN1	0.075	0.554	0.1	0.892	1.1	0.363-3.194
GEN4	0.199	0.312	0.6	0.524	1.2	0.661-2.250
M1	0.322	0.305	1.1	0.290	1.4	0.759-2.508
H1	0.062	0.272	0.2	0.820	1.1	0.624-1.813
d. *R. l. lutreolus*						
(Intercept)	-44.914	8.701	-5.2	<0.000	<0.0	0.000-0.000
MT	2.099	0.476	4.4	<0.000	8.2	3.203-20.776
RS	0.191	0.032	6.0	<0.000	1.2	1.137-1.288
RW	0.011	0.006	2.0	0.050	1.0	1.000-1.022
E	-0.018	0.004	-5.0	<0.000	1.0	0.976-0.989
S	-0.073	0.073	-1.0	0.317	1.0	0.805-1.073
lnWC	-0.525	0.181	-2.9	0.004	0.6	0.415-0.844
GEN3	0.194	0.727	0.3	0.789	1.2	0.291-5.064
GEN1	3.934	0.829	4.7	<0.000	51.1	10.037-260.470
GEN4	3.796	0.694	5.5	<0.000	44.5	11.386-173.923
M1	1.848	0.533	3.5	0.001	6.4	2.227-18.103
H1	2.638	0.700	3.8	<0.000	14.0	3.533-55.327

MT, average monthly minimum temperature; RS / RW, average monthly rainfall during summer (Nov-Jan) and winter (Jun-Aug); E, elevation; S, slope; lnWC, distance from nearest water course or body transformed using the natural log; GEN, broad vegetation community; M, root zone water holding capacity; H, soil acidity.

Appendix VII Explanatory strength of null and *a priori* generalised linear models, where 'occupied sites' are represented by survey sites within 150 m of a known record locality. Shown are the number of parameters (*k*), minimised negative log-likelihood (-LL), Akaike's information criterion corrected for small sample sizes (AIC_c), Bayesian Inference Criterion (BIC), Deviance Information Criterion (DIC), difference from the highest-ranking model (ΔAIC_c, ΔBIC, ΔDIC), weight scaled to a sum of 1($w\text{AIC}_c$, *w*DIC, *w*BIC), and the percentage deviance explained (% DE) by the model relative to the null.

Model	Variables	*k*	-LL	AIC_c	ΔAIC_c	$w\text{AIC}_c$	BIC	ΔBIC	*w*BIC	DIC	ΔDIC	*w*DIC	%DE
I. o. obesulus (35 presence : 473 absence sites) (prevalence 0.07)													
Null	~ 1	1	-127.4	256.8	65.6	0.00	261.0	54.7	0.00	256.8	64.4	0.00	
M1	~ MT + RS	3	-93.8	193.7	2.5	0.14	206.3	0.0	0.75	193.8	1.4	0.18	26.4
M2	~ RS + lWC + H	4	-93.3	194.7	3.5	0.09	211.5	5.2	0.06	194.6	2.2	0.12	26.8
M3	~ RS + GEN	4	-92.3	192.7	1.5	0.24	209.5	3.2	0.15	192.7	0.3	0.31	27.5
M4	~ RS + lWC + C3	4	-92.1	191.2	0.0	0.51	212.2	5.9	0.04	192.4	0.0	0.36	27.7
M5	~ RS + SC	5	-93.9	198.0	6.8	0.02	219.0	12.7	0.00	198.0	5.5	0.02	26.3
A. f. flavipes (66 presence : 440 absence sites) (prevalence 0.13)													
Null	~ 1	1	-195.9	393.9	166.4	0.00	398.1	149.8	0.00	393.9	166.5	0.00	
M1	~ MT + RS	3	-114.8	235.7	8.2	0.02	248.3	0.0	0.90	235.4	8.1	0.02	41.4
M2	~ RS + lWC + H	4	-117.6	243.3	15.9	0.00	260.1	11.8	0.00	243.3	16.0	0.00	40.0
M3	~ RS + lWC + H + GEN	6	-107.6	227.4	0.0	0.98	252.6	4.3	0.10	227.3	0.0	0.98	45.1
M4	~ RS + lWC + H + C3	5	-117.2	244.6	17.1	0.00	265.6	17.3	0.00	244.8	17.5	0.00	40.2
M5	~ RS + lWC + H + SC	7	-114.5	243.3	15.9	0.00	272.7	24.4	0.00	243.2	15.9	0.00	41.5

(cont.) **Appendix VII**

Model	Variables	k	-LL	AIC$_c$	ΔAIC$_c$	wAIC$_c$	BIC	ΔBIC	wBIC	DIC	ΔDIC	wDIC	%DE
R. f. greyi (197 presence : 388 absence sites) (prevalence 0.34)													
Null	~ 1	1	-373.7	749.5	146.4	0.00	753.8	137.7	0.00	749.5	146.8	0.00	
M1	~ MT + RS	3	-298.5	603.0	0.0	1.00	616.1	0.0	1.00	602.6	0.0	1.00	20.1
M2	~ RS + S + M + H	5	-307.9	625.8	22.8	0.00	647.6	31.5	0.00	625.8	23.2	0.00	17.6
M3	~ RS + S + M + H + GEN	8	-306.9	630.0	27.0	0.00	664.8	48.7	0.00	629.9	27.3	0.00	17.9
M4	~ RS + S + M + H + C3	6	-307.4	626.9	23.9	0.00	653.0	36.9	0.00	626.9	24.2	0.00	17.8
M5	~ RS + S + M + H + SC	8	-302.5	621.3	18.3	0.00	656.1	40.0	0.00	621.2	18.5	0.00	19.0
R. l. lutreolus (63 presence : 504 absence sites) (prevalence 0.11)													
Null	~ 1	1	-197.8	397.6	146.7	0.00	401.9	120.9	0.00	397.6	146.9	0.00	
M1	~ MT + RS	3	-173.2	352.4	101.5	0.00	365.3	84.3	0.00	352.5	101.8	0.00	12.5
M2	~ RS + S + lWC	4	-152.5	313.1	62.3	0.00	330.4	49.4	0.00	313.0	62.3	0.00	22.9
M3	~ RS + S + M + H	5	-143.1	296.2	45.4	0.00	317.8	36.8	0.00	296.1	45.4	0.00	27.7
M4	~ RS + S + M + GEN	7	-118.3	250.8	0.0	1.00	281.0	0.0	1.00	250.7	0.0	1.00	40.2
M5	~ RS + S + M + C3	5	-133.9	277.9	27.0	0.00	299.5	18.4	0.00	306.3	55.6	0.00	32.3
M6	~ RS + S + M + SC	7	-128.3	270.8	19.9	0.00	301.0	19.9	0.00	270.7	20.0	0.00	35.1
M7	~ RS + S + M + VL	6	-144.9	302.0	51.2	0.00	327.9	46.9	0.00	301.9	51.2	0.00	26.7

MT, ave. monthly minimum temperature; RS, ave. monthly rainfall during summer (Nov-Jan); S, slope; lWC, distance from nearest water course or body transformed using the natural log; GEN, broad vegetation community; M, root zone water holding capacity; H, soil acidity; C3, diversity of flora taller than 2 m; SC, cover of shrubs between 0.5 – 1.0 m in height; VL, sedge cover under 0.5 m.

Appendix VIII Explanatory strength of null and *a priori* boosted regression tree models, where 'occupied sites' are represented by survey sites within 150 m of a known record locality. Shown are the optimal tree complexity (number of nodes) and learning rate (number of trees added to the model) used to apply the BRT model, the resultant number of trees required and the per cent deviance explained (% DE). Model composition follows that listed in Table 1.

	M1	M2	M3	M4	M5	M6	M7
I. o. obesulus							
Tree complexity	1	2	1	1	1	-	-
Learning rate	0.005	0.005	0.005	0.005	0.005	-	-
No. trees	2200	550	1900	1000	800	-	-
% DE	27.5	26.8	26.8	25.9	25.6	-	-
A. f. flavipes							
Tree complexity	2	2	2	4	2	-	-
Learning rate	0.010	0.005	0.005	0.005	0.005	-	-
No. trees	1600	1350	2950	700	850	-	-
% DE	45.6	39.7	47.6	38.9	38.5	-	-
R. f. greyi							
Tree complexity	2	4	5	3	4	-	-
Learning rate	0.010	0.005	0.005	0.005	0.005	-	-
No. trees	2100	950	1050	1050	850	-	-
% DE	32.4	23.6	23.5	24.7	24.9	-	-
R. l. lutreolus							
Tree complexity	2	3	2	3	3	2	4
Learning rate	0.010	0.010	0.005	0.005	0.005	0.005	0.005
No. trees	1950	1450	1050	800	1000	800	900
% DE	27.2	28.9	29.5	39.3	30.3	32.8	29.1

Appendix IX Explanatory strength of the null and *a priori* generalised linear models, where 'occupied sites' are represented by survey sites within 150 m, 500 m and 1000 m of a known record locality. Shown are the minimised negative log-likelihood (-LL), Akaike's information criterion corrected for small sample sizes (AIC$_c$), Bayesian Inference Criterion (BIC), Deviance Information Criterion (DIC), difference from the highest-ranking model (ΔAIC$_c$, ΔBIC, ΔDIC), weight scaled to a sum of 1(*w*AIC$_c$, *w*DIC, *w*BIC), and the percentage of the deviance explained (% DE) by the model relative to the null.

a. I. o. obesulus	Model	*k*	-LL	AIC$_c$	ΔAIC$_c$	*w*AIC$_c$	BIC	ΔBIC	*w*BIC	DIC	ΔDIC	*w*DIC	%DE
	~ 1	1	-127.4	256.8	65.6	0.00	261.0	54.7	0.00	256.8	64.4	0.00	
	~ MT + RS	3	-93.8	193.7	2.5	0.14	206.3	0.0	0.75	193.8	1.4	0.18	26.4
150 m	~ RS + lWC + H	4	-93.3	194.7	3.5	0.09	211.5	5.2	0.06	194.6	2.2	0.12	26.8
	~ RS + GEN	4	-92.3	192.7	1.5	0.24	209.5	3.2	0.15	192.7	0.3	0.31	27.5
35 pres : 473 abs	~ RS + lWC + C3	4	-92.1	191.2	0.0	0.51	212.2	5.9	0.04	192.4	0.0	0.36	27.7
prevalence 0.07	~ RS + SC	5	-93.9	198.0	6.8	0.02	219.0	12.7	0.00	198.0	5.5	0.02	26.3
	~ 1	1	-212.0	426.0	88.2	0.00	430.3	79.7	0.00	426.0	88.3	0.00	
	~ MT + RS	3	-165.9	337.8	0.0	0.76	350.5	0.0	0.98	337.7	0.0	0.77	21.8
500 m	~ RS + lWC + H	4	-168.0	344.1	6.3	0.03	361.1	10.6	0.00	344.1	6.4	0.03	20.7
	~ RS + GEN	4	-166.8	341.8	4.0	0.10	358.8	8.3	0.02	341.7	4.0	0.10	21.3
73 pres : 454 abs	~ RS + lWC + C3	4	-167.0	342.0	4.2	0.09	363.2	12.7	0.00	342.1	4.5	0.08	21.2
prevalence 0.14	~ RS + SC	5	-168.3	346.7	8.9	0.01	367.9	17.4	0.00	346.6	9.0	0.01	20.6
	~ 1	1	-300.7	603.3	118.0	0.00	607.6	109.4	0.00	489.1	4.1	0.11	
	~ MT + RS	3	-239.6	485.3	0.0	1.00	498.2	0.0	1.00	485.1	0.0	0.88	20.3
1 000 m	~ RS + lWC + H	4	-245.9	499.8	14.5	0.00	517.0	18.7	0.00	499.8	14.8	0.00	18.2
	~ RS + GEN	4	-246.0	500.0	14.7	0.00	517.2	19.0	0.00	500.0	15.0	0.00	18.2
129 pres : 425 abs	~ RS + lWC + C3	4	-246.1	501.4	16.1	0.00	522.9	24.6	0.00	500.2	15.2	0.00	18.1
prevalence 0.23	~ RS + SC	5	-244.1	498.2	12.9	0.00	519.7	21.5	0.00	498.2	13.2	0.00	18.8

(cont.)

(cont.) **Appendix IX**

b. A. f. flavipes	Model	k	-LL	AIC$_c$	ΔAIC$_c$	*w*AIC$_c$	BIC	ΔBIC	*w*BIC	DIC	ΔDIC	*w*DIC	%DE
	~ 1	1	-195.9	393.9	166.4	0.00	398.1	149.8	0.00	393.9	166.5	0.00	
	~ MT + RS	3	-114.8	235.7	8.2	0.02	248.3	0.0	0.90	235.4	8.1	0.02	41.4
150 m	~ RS + lWC + H	4	-117.6	243.3	15.9	0.00	260.1	11.8	0.00	243.3	16.0	0.00	40.0
	~ RS + lWC + H + GEN	6	-107.6	227.4	0.0	0.98	252.6	4.3	0.10	227.3	0.0	0.98	45.1
66 pres : 440 abs	~ RS + lWC + H + C3	5	-117.2	244.6	17.1	0.00	265.6	17.3	0.00	244.8	17.5	0.00	40.2
prevalence 0.13	~ RS + lWC + H + SC	7	-114.5	243.3	15.9	0.00	272.7	24.4	0.00	243.2	15.9	0.00	41.5
	~ 1	1	-216.9	435.9	196.2	0.00	440.1	180.8	0.00	435.9	196.2	0.00	
	~ MT + RS	3	-120.3	246.6	7.0	0.03	259.3	0.0	0.94	246.3	6.6	0.04	44.6
500 m	~ RS + lWC + H	4	-123.8	255.6	16.0	0.00	272.5	13.2	0.00	255.6	16.0	0.00	42.9
	~ RS + lWC + H + GEN	6	-113.7	239.7	0.0	0.97	264.9	5.6	0.06	239.7	0.0	0.96	47.6
77 pres : 436 abs	~ RS + lWC + H + C3	5	-123.2	256.6	16.9	0.00	277.6	18.4	0.00	256.7	17.0	0.00	43.2
prevalence 0.15	~ RS + lWC + H + SC	7	-119.3	252.7	13.1	0.00	282.2	22.9	0.00	252.8	13.1	0.00	45.0
	~ 1	1	-234.6	471.3	211.5	0.00	475.5	195.0	0.00	471.3	211.6	0.00	
	~ MT + RS	3	-130.9	267.8	8.0	0.02	280.5	0.0	0.91	267.4	7.7	0.02	44.2
1 000 m	~ RS + lWC + H	4	-133.2	274.5	14.7	0.00	291.4	10.9	0.00	274.6	14.9	0.00	43.2
	~ RS + lWC + H + GEN	6	-123.8	259.8	0.0	0.98	285.1	4.6	0.09	259.6	0.0	0.98	47.2
87 pres : 549 abs	~ RS + lWC + H + C3	5	-132.8	275.7	15.9	0.00	296.8	16.3	0.00	275.7	16.1	0.00	43.4
prevalence 0.14	~ RS + lWC + H + SC	7	-130.3	274.8	14.9	0.00	304.3	23.8	0.00	274.8	15.1	0.00	44.5

(cont.)

(cont.) **Appendix IX**

c. R. f. greyi	Model	*k*	-LL	AIC$_c$	ΔAIC$_c$	*w*AIC$_c$	BIC	ΔBIC	*w*BIC	DIC	ΔDIC	*w*DIC	%DE
	~ 1	1	-373.7	749.5	146.4	0.00	753.8	137.7	0.00	749.5	146.8	0.00	
	~ MT + RS	3	-298.5	603.0	0.0	1.00	616.1	0.0	1.00	602.6	0.0	1.00	20.1
150 m	~ RS + S + M + H	5	-307.9	625.8	22.8	0.00	647.6	31.5	0.00	625.8	23.2	0.00	17.6
	~ RS + S + M + H + GEN	8	-306.9	630.0	27.0	0.00	664.8	48.7	0.00	629.9	27.3	0.00	17.9
197 pres : 388	~ RS + S + M + H + C3	6	-307.4	626.9	23.9	0.00	653.0	36.9	0.00	626.9	24.2	0.00	17.8
absprevalence 0.34	~ RS + S + M + H + SC	8	-302.5	621.3	18.3	0.00	656.1	40.0	0.00	621.2	18.5	0.00	19.0
	~ 1	1	-413.3	828.6	164.3	0.00	833.0	155.5	0.00	828.5	135.2	0.00	
	~ MT + RS	3	-329.1	664.3	0.0	1.00	677.5	0.0	1.00	663.8	-29.6	1.00	20.4
500 m	~ RS + S + M + H	5	-341.6	693.3	29.1	0.00	715.4	37.9	0.00	693.3	0.0	0.00	17.3
	~ RS + S + M + H + GEN	8	-340.0	696.3	32.0	0.00	731.4	54.0	0.00	696.2	2.8	0.00	17.7
241 pre : 377 abs	~ RS + S + M + H + C3	6	-340.1	692.4	28.2	0.00	718.8	41.3	0.00	692.2	-1.1	0.00	17.7
prevalence 0.39	~ RS + S + M + H + SC	8	-338.3	692.7	28.5	0.00	727.9	50.4	0.00	692.6	-0.7	0.00	18.2
	~ 1	1	-450.9	903.8	164.9	0.00	908.2	155.9	0.00	903.7	165.4	0.00	
	~ MT + RS	3	-366.4	738.9	0.0	1.00	752.3	0.0	1.00	738.4	0.0	1.00	18.7
1 000 m	~ RS + S + M + H	5	-381.4	773.0	34.1	0.00	795.3	43.0	0.00	772.9	34.5	0.00	15.4
	~ RS + S + M + H + GEN	8	-379.9	775.9	37.0	0.00	811.6	59.3	0.00	775.8	37.4	0.00	15.8
290 pres : 367 abs	~ RS + S + M + H + C3	6	-377.5	767.1	28.2	0.00	793.9	41.6	0.00	767.0	28.7	0.00	16.3
prevalence 0.44	~ RS + S + M + H + SC	8	-378.1	772.5	33.6	0.00	808.2	55.9	0.00	772.4	34.0	0.00	16.1

(cont.)

(cont.) **Appendix IX**

d. R. l. lutreolus	Model	k	-LL	AIC$_c$	ΔAIC$_c$	*w*AIC$_c$	BIC	ΔBIC	*w*BIC	DIC	ΔDIC	*w*DIC	%DE
	~ 1	1	-197.8	397.6	146.7	0.00	401.9	120.9	0.00	397.6	146.9	0.00	
	~ MT + RS	3	-173.2	352.4	101.5	0.00	365.3	84.3	0.00	352.5	101.8	0.00	12.5
	~ RS + S + lWC	4	-152.5	313.1	62.3	0.00	330.4	49.4	0.00	313.0	62.3	0.00	22.9
150 m	~ RS + S + M + H	5	-143.1	296.2	45.4	0.00	317.8	36.8	0.00	296.1	45.4	0.00	27.7
	~ RS + S + M + GEN	7	-118.3	250.8	0.0	1.00	281.0	0.0	1.00	250.7	0.0	1.00	40.2
	~ RS + S + M + C3	5	-133.9	277.9	27.0	0.00	299.5	18.4	0.00	306.3	55.6	0.00	32.3
63 pres : 504 abs	~ RS + S + M + SC	7	-128.3	270.8	19.9	0.00	301.0	19.9	0.00	270.7	20.0	0.00	35.1
prevalence 0.11	~ RS + S + M + VL	6	-144.9	302.0	51.2	0.00	327.9	46.9	0.00	301.9	51.2	0.00	26.7
	~ 1	1	-250.3	502.5	183.7	0.00	506.9	157.6	0.00	502.5	183.9	0.00	
	~ MT + RS	3	-212.1	430.2	111.3	0.00	443.3	94.0	0.00	430.0	111.4	0.00	15.3
	~ RS + S + lWC	4	-193.5	395.1	76.3	0.00	412.6	63.3	0.00	395.1	76.4	0.00	22.7
500 m	~ RS + S + M + H	5	-176.7	363.6	44.7	0.00	385.4	36.0	0.00	363.5	44.8	0.00	29.4
	~ RS + S + M + GEN	7	-152.3	318.9	0.0	1.00	349.3	0.0	0.97	318.7	0.0	1.00	39.1
	~ RS + S + M + C3	5	-162.1	334.3	15.5	0.00	356.1	6.8	0.03	363.4	44.8	0.00	35.2
89 pres : 510 abs	~ RS + S + M + SC	7	-167.8	349.9	31.0	0.00	380.3	31.0	0.00	349.8	31.2	0.00	32.9
prevalence 0.15	~ RS + S + M + VL	6	-177.6	367.3	48.4	0.00	393.4	44.1	0.00	367.2	48.6	0.00	29.0
	~ 1	1	-308.2	618.4	218.1	0.00	622.8	191.7	0.00	618.4	218.2	0.00	
	~ MT + RS	3	-256.0	518.1	117.8	0.00	531.3	100.2	0.00	518.1	117.9	0.00	16.9
	~ RS + S + lWC	4	-236.5	481.1	80.8	0.00	498.7	67.6	0.00	481.0	80.8	0.00	23.3
1 000 m	~ RS + S + M + H	5	-212.2	434.5	34.2	0.00	456.5	25.4	0.00	434.4	34.2	0.00	31.1
	~ RS + S + M + GEN	7	-193.1	400.3	0.0	1.00	431.1	0.0	0.99	400.2	0.0	1.00	37.4
	~ RS + S + M + C3	5	-204.7	419.4	19.1	0.00	441.5	10.3	0.01	451.9	51.7	0.00	33.6
123 pres : 494 abs	~ RS + S + M + SC	7	-205.6	425.3	25.0	0.00	456.1	25.0	0.00	425.3	25.0	0.00	33.3
prevalence 0.20	~ RS + S + M + VL	6	-214.6	441.3	41.0	0.00	467.7	36.6	0.00	441.1	40.9	0.00	30.4

Appendix X Explanatory strength of the null and *a priori* boosted regression tree models, where 'occupied sites' are represented by survey sites within 150 m, 500 m and 1000 m of a known animal location. Shown are the optimal tree complexity (number of nodes) and learning rate (number of trees added to the model) used to apply the BRT model, the resultant number of trees required and the per cent deviance explained (% DE). Model composition follows that listed in Table 1, p13.

	150 m							500 m							1 000 m						
	M 1	M 2	M 3	M 4	M 5	M6	M7	M 1	M 2	M 3	M 4	M 5	M6	M7	M 1	M 2	M 3	M 4	M 5	M6	M7
a I. o. obesulus																					
Tree complexity	1	2	1	1	1	-	-	2	3	3	2	1	-	-	2	3	3	2	1	-	-
Learning rate	0.005	0.005	0.005	0.005	0.005	-	-	0.010	0.005	0.001	0.005	0.005	-	-	0.010	0.005	0.005	0.010	0.010	-	-
No. trees	2200	550	1900	1000	800	-	-	1200	1200	1800	1600	1500	-	-	1200	1450	800	1200	1550	-	-
% DE	27.5	26.8	26.8	25.9	25.6	-	-	33.3	26.6	26.5	26.7	22.1	-	-	35.9	28.8	26.1	27.6	25.2	-	-
b A. f. flavipes																					
Tree complexity	2	2	2	4	2	-	-	2	2	3	2	2	-	-	2	2	3	2	2	-	-
Learning rate	0.010	0.005	0.005	0.005	0.005	-	-	0.010	0.005	0.005	0.005	0.005	-	-	0.010	0.005	0.005	0.005	0.005	-	-
No. trees	1600	1350	2950	700	850	-	-	1400	1050	1200	1000	1450	-	-	800	1500	1100	1600	1000	-	-
% DE	45.6	39.7	47.6	38.9	38.5	-	-	47.4	41.7	45.8	41.1	43.3	-	-	46.4	42.4	47.5	42.9	42.3	-	-
c. R. f. greyi																					
Tree complexity	2	4	3	5	4	-	-	2	3	4	3	4	-	-	2	3	4	3	4	-	-
Learning rate	0.010	0.005	0.005	0.005	0.005	-	-	0.010	0.005	0.005	0.005	0.005	-	-	0.010	0.005	0.010	0.005	0.005	-	-
No. trees	2100	950	1050	1050	850	-	-	2650	2050	1800	1350	1200	-	-	1800	1600	1150	1650	1250	-	-
% DE	32.4	23.6	23.5	24.7	24.9	-	-	35.4	25.2	27.3	24.2	25.9	-	-	33.2	23.3	25.3	24.0	24.9	-	-
d. R. l. lutreolus																					
Tree complexity	2	3	2	3	3	2	4	2	3	4	3	4	3	3	2	4	4	3	4	3	4
Learning rate	0.010	0.010	0.005	0.005	0.005	0.005	0.005	0.010	0.010	0.005	0.005	0.005	0.005	0.005	0.010	0.010	0.005	0.005	0.005	0.005	0.005
No. trees	1950	1450	1050	800	1000	800	900	3200	1600	1350	1300	1300	1350	1050	4750	1300	800	2000	1000	1300	1250
% DE	27.2	28.9	29.5	39.3	30.3	32.8	29.1	35.7	32.6	35.5	41.8	37.3	34.9	30.8	38.6	36.0	33.7	42.2	35.0	33.1	33.5

Appendix XI Explanatory strength of each variable represented by the percentage deviance explained (% DE) when added to the null model, divided by the degrees of freedom used by the variable (as per Garnett and Brook 2007).

		Deviance explained (%)			
Variable	*k*	150 m	500 m	1 000 m	Difference†
a. I. o. obesulus					
~ MT	1	3.4	2.4	1.7	-1.7
~ RS	1	25.2	20.2	17.8	-7.4
~ WC	1	2.2	2	2.4	na
~ H	1	10.2	7.6	6.1	-4.1
~ GEN	3	2.1	1.4	1	-1.1
~ CAT3	1	0.3	0	0.7	na
~ SC	4	1.3	1.8	2.4	1.1
b. A. f. flavipes					
~ MT	1	1.7	1.6	1.5	-0.2
~ RS	1	35	37.2	36.9	na
~ WC	1	9	10	10.9	1.9
~ H	1	10	10.7	11.1	1.1
~ GEN	3	8.5	9	8.6	na
~ C3	1	0.3	0.3	0.3	0
~ SC	4	1.6	2.4	2	na
c. R. f. greyi					
~ MT	1	1.5	1.5	1	-0.5
~ RS	1	17.2	17.1	14.9	-2.3
~ S	1	0.5	0.3	0.9	na
~ H	1	1.5	1	0.9	-0.6
~ M	1	4.8	4.6	3.5	-1.3
~ GEN	4	0.8	1	0.7	na
~ C3	1	0.1	0.3	0.6	0.5
~ SC	4	0.4	0.2	0.2	-0.2

(cont.)

(cont.) **Appendix XI**

d. R. l. lutreolus					
~ MT	1	4.9	4.6	4.4	-0.5
~ RS	1	12.4	15.2	16.7	4.3
~ S	1	4	3.4	2.7	-1.3
~ lWC	1	1.9	0.2	0.1	-1.8
~ H	1	1.6	0.6	1.2	na
~ M	1	10.5	14.9	16	5.5
~ GEN	4	19.7	16.5	14.4	-5.3
~ C3	1	7.7	7.4	5.1	-2.6
~ SC	4	11.5	6.1	5.1	-6.4
~ VL	3	1.6	1.2	1.6	na

†Calculated as the percentage deviance explained (% DE) at 1 000 m minus that calculated at 150 m. Where values increase or decrease inconsistently, across the 1 000 m, 500 m and 150 m, a ‘na’ has been inserted. This could indicate variables with more complex relationships between species, or be an artefact of the small differences in % DE, so these variables were not included in Fig. 4, p34.

Appendix XII Demographic parameters applied in the coupled niche-population models using RAMAS-GIS. This process requires a habitat suitability map generated using a species distribution model. Once a threshold value is applied, the map represents unsuitable and suitable habitat (0 and 1, respectively) and habitat pixels combined into patches using the neighbourhood distance. These patches then form the basis of the population demographic model. Where two parameters are presented, the left and right values were applied to the 100 m^2 and 1000 m^2 models, respectively. Sources of the population demographic perameters are also indicated.

	A. f. flavipes	*I. o. obesulus*	*R. f. greyi*	*R. l. lutreolus*
Species biology				
Family	Dasyuridae	Peramelidae	Muridae	Muridae
Status	VU (Sth Aust.)	EN (Aust.)	No listing	Rare (Sth Aust.)
Weight (g)	21 - 79	400 - 1850	40 - 225	50 - 200
Habitat preference	structurally complex	dense and low vegetation	dense and low vegetation	tall grass and sedge
Diet	insectivorous and carnivorous	omnivorous	omnivorous	herbivorous
Shelter	tree hollows, *Xanthorrhoea* spp.	mounds of leaf litter, dense shrubs	burrows	burrows
Habitat suitability index				
Number of records^{b}	80:390 or 293	209:426 or 317	198:344 or 260	52:446 or 338
Regions of occurrence included in models^{c}	FP, SE	FP, KI, SE	EP, FP, KI, SE	FP, SE
Threshold (MSS)	0.15^{a}, 0.17^{a}	0.39 ^{a}, 0.43^{a}	0.565 ^{a}, 0.61^{a}	0.07, 0.115
Neighbourhood distance	2.5, 1.5	1.5, 1.5	1.5, 1.5	1.5, 1.5
Population demographic parameters				
Life history table / stage matrix				
• No. stages	3 (≤ 2 yr)^{R1}	4 (≤ 3 yr)^{R5,6}	3 (≤ 2 yr)^{R12}	4 (≤ 3 yr)^{R19}
• Age at first breeding	1	1	1	1
• Fertility (/yr) (young*litters/♀)	(8*1)/2 = 4^{R2}	(3.1*3)/2 = 4.62 Don't breed in 4th breeding season^{R5,7}	(5*3.5)/2 = 8.75 Don't breed in 2nd breeding season^{R12,14}	(5*2)/2 = 5 Don't breed in 3rd breeding season^{R12}
SD	± 33.75 %	± 36 %	± 30 %	± 30 %
Survival rates (%)	24.7 (0 – 1) 1.72 (1 yr)^{R1}	10.5 (0 – 1) 65 (1+ yr)^{R5,8}	11.2 (0 – 1) 2.53 (1+ yr)^{R14}	12.47 (0 – 1) 60.1 (1+ yr)^{R12}
SD	± 5 %	± 5 %	± 5 %	± 5 %
Rmax	1.574 (biol.)	1.72 (biol.)	2. 075 (oregan vole; biol. 2.25)	1.243 (ave. watervole muskrat; biol. 1.78)
Initial abundance & carrying capacity (K)	2 ha^{-1}, 200 km^{-1} ^{R1}	3 ha^{-}1, 300 km^{-1} ^{R9,10}	10 ha^{-1}, 1000 km^{-1} ^{R15}	7 ha^{-1}, 700 km^{-1} ^{R15}

(cont.)

(cont.) **Appendix XII**

	A. f. flavipes	*I. o. obesulus*	*R. f. greyi*	*R. l. lutreolus*
Dispersal function, Mij = a.exp(-Dij$^{c/b}$), where D is the distance from patch i to j	0.8.exp(-Dij$^{0.6/0.24}$)[R3]	0.5.exp(-Dij$^{0.95/0.1}$)	0.5.exp(-Dij$^{0.6/0.2}$)	0.5.exp(-Dij$^{0.9/0.1}$)R\
Max. dispersal (Dmax)	1.55 km[R4]	0.6 km[R11]	0.75 km[R16,17,18]	0.45 km[R15]

[a] Threshold used to convert probabilities into suitable and unsuitable habitat.

[b] The limited number of presences available was retained at both scales by manually inserting missing environmental data no longer represented at 100 m^2 or 1000 m^2 resolution before the species distribution models were created.

[c] Region codes represent Eyre Peninsula (EP), Fleurieu Peninsula (FP) Kangaroo Island (KI) and South East (SE).

[R1] Marchesan D, Carthew S (2004) Autoecology of the yellow-footed antechinus (*Antechinus flavipes*) in a fragmented landscape in southern Australia. Wildl Res 31:273-282.

[R2] Smith G (1984) The biology of the yellow-footed antechinus *Antechinus flavipes* (Marsupialia: Dasyuridae), I a swamp forest on Kinaba Island, Cooloola, Quensland. Aust Wild Res 11:465-480.

[R3] Marchesan D, Carthew SM (2008) Use of space by the yellow-footed antechinus, *Antechinus flavipes*, I a fragmented landscape in South Australia. Landscape Ecol 23:741-752.

[R4] Van der Ree R (2003) The occurrence of the yellow-footed antechinus *Antechinus flavipes* in remnanr linear habitats in north-eastern Victoria. Aust Mammal 25:97-100.

[R5] Lobert B, Lee AK (1990) Reproduction and life history of *Isoodon obesulus* in Victorian heathland. In Bandicoots and Bilbies (eds Seebeck JH, Brown PR, Wallis RL, Kemper CM) Surrey Beatty & Sons (Australia) p311-318

[R6] Paull DJ (2008) Southern Brown Bandicoot, *Isoodon obesulus* (Shaw, 1797). In The Mammals of Australia (3rd Edition) (eds van Dyck S, Strahan R) New Holland Publishers (Australia) p180-182.

[R7] Paull D (1992) *The distribution, ecology and conservation of the southern brown bandicoot (Isoodon obesulus obesulus) in South Australia*. Masters Thesis. University of Adelaide, Adelaide.

[R8] Heinsohn GE (1966) Ecology and reproduction of the Tasmanian bandicoots (*Perameles gunni* and *Isoodon obesulus*). U Calif Publ Zool 80:1–96.

[R9] Stoddart DM, Braithwaite RW (1979) A strategy for utilization of regenerating heathland habitat by the brown bandicoot (*Isoodon obesulus*; Marsupialia, Peramelidae). J Animal Ecol 48:165–179.

[R10] Lobert B (1990) Home range and activity period of the Southern Brown Bandicoot (*Isoodon obesulus*) in a Victorian heathland. In Bandicoots and Bilbies (eds Seebeck JH, Brown PR, Wallis RL, Kemper CM) Surrey Beatty & Sons (Australia) p319-325

[R11] Friend G (1990) Breeding and population dynamics of *Isoodon macrourus* (Marsupialia: Peramelidae): studies from the wet-dry tropics of northern Australia. In Bandicoots and Bilbies (eds Seebeck JH, Brown PR, Wallis RL, Kemper CM) Surrey Beatty & Sons (Australia) p357-365

[R12] Braithwaite RW, Lee AK (1979) The ecology of *Rattus lutreolus* I. A Victorian heathland population. Australian Journal of Wildlife Research 6:173-189.

[R13] Taylor JM, Calaby JH (1988) *Rattus fuscipes*. Mammalian species 298:1-8.

[R14] Robinson AC (1987) The ecology of the bush rat, *Rattus fuscipes* (Rodentia: Muridae), in Sherbrooke Forest, Victoria. Aust Mammal 11:35-49.

[R15] Wilson BA, Bourne AR, Jessop RE (1986) Ecology of small mammals in coastal heathland at Anglesea, Victoria. Aust Wildl Res 13:397-406.

[R16] Warneke RM (1971) Field study of the bush rat (*Rattus fuscipes*). Wildl Contrib 14:1-115.

[R17] Bentley JM (2008) Role of movement, interremnant dispersal and edge effects in determining sensitivity to habitat fragmentation in two forest-dependent rodents. Austral Ecol 33:184-196.

[R18] Peakall R, Ruibal M, Lindenmayer DB (2003) Spatial autocorrelation analysis offers new insights into gene flow in the Australian bush rat, *Rattus fuscipes*. Evolution 57:1182-1195.

[R19] Braithwaite RW (1980) The ecology of *Rattus lutreolus* III. The rise and fall of a commensal population. Aust Wildl Res 7:199-215.

Appendix XIII Evaluation of species distribution models.

Regardless of the spatial scale employed, SDMs better explained the occupancy of the more mobile woodland generalist and insectivore (*A. f. flavipes*), compared to the wet-heath specialist (*R. l. lutreolus*), and two understorey preferring species (*I. o. obesulus* and *R. f. greyi*) (50.1 - 25.6 % DE; Table 2a). Rainfall parameters were the most important predictors of species distribution in all cases. Distance to watercourse and root zone water holding capacity were also important predictors of *R. l. lutreolus* and *A. f. flavipes* occurrence (Appendix 2b). Elevation, soil acidity and average minimum temperature during summer were most strongly correlated with the occurrence of the insectivore *A. f. flavipes* and omnivore *I. o. obesulus*.

A suitable threshold to convert probability values into suitable and unsuitable habitat was determined by comparing the predicted probability with the actual occurrence of the model data. As all data were used, validation statistics provide an optimistic indication of the 'best case' performance of these models may be obtained when used to predict the original species occurrence. These models predictive performances were relatively good (AUC values: 0.82-0.94 Kappa values: 0.53-0.66; Table 2a), which were lower than expected probably as a result of small datasets.

Appendix XIIIa. Explanatory strength of null and *a priori* generalised linear models constructed using a) 100 m^2, and b) 1000 m^2 resolution environmental data. Shown are the number of parameters (*k*), minimised negative log-likelihood (-LL) and the per cent deviance explained by the model relative to the null (% DE) for each species. Also shown is validation statistics derived from the model being predicted back onto the original dataset. These statistics include the area under the curve (AUC) and when the Maximum Sensitivity and Specificity threshold is used to convert the probability of occurrence into present, or absent, the Kappa, Sensitivity (Sens) and Specificity (Spec). Note: Where the resampling of environmental data caused missing values for presence records, values were manually substituted from the original environmental data layers.

Species	Model variables	*k*	-LL	% DE	AUC (SD)	Kappa (SD)	Sens (SD)	Spec (SD)
a. 0.01 km^2								
I. o. obesulus	~ MT+RS+RW+E+lWC+H+GEN	10	-279.0	30.6	0.85 (0.02)	0.53 (0.04)	0.76 (0.03)	0.79 (0.02)
A. f. flavipes	~ MT+RS+RW+E+lWC+M+H+GEN	11	-109.8	48.8	0.93 (0.01)	0.60 (0.04)	0.93 (0.03)	0.84 (0.02)
R. f. greyi	~ MT+RS+RW+E+lWC+GEN	9	-257.1	27.7	0.83 (0.02)	0.58 (0.04)	0.64 (0.03)	0.92 (0.02)
R. l. lutreolus	~ RS+E+lWC+GEN+M+H	9	-89.5	46.3	0.94 (0.01)	0.61[a] (0.05)	0.79[a] (0.06)	0.93[a] (0.01)

(cont.)

(cont.) **Appendix XIIIa.**

Species	Model variables	*k*	-LL	% DE	AUC (SD)	Kappa (SD)	Sens (SD)	Spec (SD)
b. 1 km^2								
I. o. obesulus	~ MT+RS+RW+E+lWC+H+GEN	10	-245.3	30.6	0.85 (0.02)	0.56 (0.04)	0.78 (0.03)	0.79 (0.02)
A. f. flavipes	~ MT+RS+RW+E+lWC+M+H+GEN	11	-96.8	50.1	0.93 (0.02)	0.66 (0.04)	0.95 (0.02)	0.84 (0.02)
R. f. greyi	~ MT+RS+RW+E+lWC+GEN	9	-230.2	25.6	0.82 (0.02)	0.57 (0.04)	0.64 (0.03)	0.91 (0.02)
R. l. lutreolus	~ RS+E+lWC+GEN+M+H	9	-85.9	43.9	0.94 (0.01)	0.62[a] (0.06)	0.75[a] (0.06)	0.93[a] (0.01)

[a] Derived using a threshold to maximise the Kappa statistic (MaxKappa) due to the very low prevalence of presence records.

Appendix XIIIb. Explanatory strength of each variable calculated using generalised linear modelling (GLM), derived by combining the % deviance explained when a variable is deleted from the saturated model with the % deviance explained when adding that variable to the null model, divided by the number of degrees of freedom (as per Garnett and Brook 2007). Note: Where the resampling of environmental data caused missing values for presence records, values were manually substituted from the original environmental data layers.

		I. o. obesulus		*A. f. flavipes*		*R. f. greyi*		*R. l. lutreolus*	
Variable	df	0.01 km^2	1.0 km^2	0.01 km^2	1.0 km^2	0.01 km^2	1.0 km^2	0.01 km^2	1.0 km^2
MT	1	3.9	4.2	5.7	8.0	0.5	0.3		
RS	1	17.8	19.7	32.0	35.5	15.1	15.9	23.4	24.9
RW	1	26.2	26.8	34.2	34.5	26.7	25.6		
E	1	14.0	14.7	25.2	25.9	3.2	3.4	6.2	5.2
lnWC	1	5.4	4.1	8.6	10.9	3.1	4.0	20.8	12.5
M	1			10.1	12.3			17.3	14.2
H	1	11.5	10.5	11.2	15.1			2.6	1.8
GEN	3	1.3	1.4	3.0	2.1	0.6	0.4	7.4	9.1

MT, average minimum temperature in winter (Jun - Aug); RS / RW, average monthly rainfall during summer (Nov-Jan) and winter; E, elevation; lnWC, distance from nearest water course or body transformed using the natural logarithm; M, root zone water holding capacity; H, soil acidity; GEN, broad vegetation community.

Appendix XIV Change in distribution and extent of available habitat, number of populations and species abundance predicted over 40 years of climate change, over 1000 iterations, for the species' range on the a) Fleurieu Peninsula and b) South East. No changes in the parameters below were reported over the burn-in period.

	I. o. obesulus		*A. f. flavipes*		*R. f. greyi*		*R. l. lutreolus*	
Resolution (km^2)	0.01	1.0	0.01	1.0	0.01	1.0	0.01	1.0
a. Fleurieu Peninsula								
Initial area of habitat (km^2)	198	221	317	306	227	255	28	15
Initial no. patches	1182	82	1292	113	947	76	1069	15
Ave. initial no.	1011	82	1198	113	935	76	626	15
populations (SD)[1]	(0.0)	(0.03)	(0.0)	(0.1)	(0.0)	(0.06)	(0.0)	(0.0)
Max no. patches within dispersal dist.	35	0	137	0	47	0	8	0
and when Dmax = 5 km (SA1 and 3)	168	11	323	14	156	11	96	3
Changes following 40 years of climate change:								
Habitat area (%)	-74	-60	-37	-3	-94	-86	-62	-40
Population no. (%)	-65	-52	-15	-4	-87	-69	-9	-22
No. new populations created	748	14	1095	21	975	22	157	1
Ave. abund. animals yr^{-1}	-694	-3523	-135	-4364	-4364	-6538	-123	-508
(SE)	(37)	(1481)	(28)	(124)	(124)	(1693)	(7)	(58)
r^2 (p value)	0.90**	0.74**	0.37**	0.14	0.97**	0.96**	0.89**	0.93**
No. occupied popns	-13.4	-0.8	-1.3	-0.1	-19.7	-1.5	-2.3	-0.1
yr^{-1} (SE)	(1.0)	(0.1)	(0.7)	(0.0)	(0.7)	(0.1)	(0.3)	(0.0)
r^2 (p value)	0.80**	0.74**	0.08	0.14	0.96**	0.96**	0.56**	0.93**
Expected minimum abundance (%)	24	40	58	85	8	14	57	57

(cont.)

(cont.) **Appendix XIV**

	I. o. obesulus		*A. f. flavipes*		*R. f. greyi*		*R. l. lutreolus*	
Resolution (m^2)	0.01	1.0	0.01	1.0	0.01	1.0	0.01	1.0
b. South East								
Initial area of habitat (km^2)	82	92	66	101	212	269	523	514
Initial no. patches	260	34	237	49	613	91	2567	217
Ave. initial no.	223	34	213.4	49	604.9	91	2108	217
populations (SD)[1]	(2.18)	(0)	(1.1)	(0.1)	(0)	(0.1)	(0)	(0)
Max no. patches within dispersal dist.	13	0	13	0	28	0	15	0
and when Dmax = 5 km (SA1 and 3)	42	4	35	5	102	10	99	9
Changes following 40 years of climate change:								
Habitat area (%)	-35	-15	-24	2	-61	-40	-20	-10
Population no. (%)	-21	-15	-20	0	-56	-47	-3	3
No. new populations created	74	1	162	10	255	5	180	16
Ave. abund. animals yr^{-1}	-223	-89	-97	14	-2052	-2742	-1217	-400
(SE)	(22)	(7)	(13)	(4)	(58)	(48)	(113)	(76)
r^2 (p value)	0.73**	0.80**	0.58**	0.28**	0.97*	0.99**	0.77**	0.45**
No. occupied popns	-1.5	-0.1	-1.4	-0.0	-11.3	-1.2	-4.3	0.12
yr^{-1} (SE)	(0.1)	(0.0)	(0.2)	(0.0)	(0.6)	(0.0)	(0.9)	(0.03)
r^2 (p value)	0.75**	0.61**	0.65**	0.10*	0.91**	0.99**	0.38**	0.30**
Expected minimum abundance (%)	65	80	68	89	44	56	78	88

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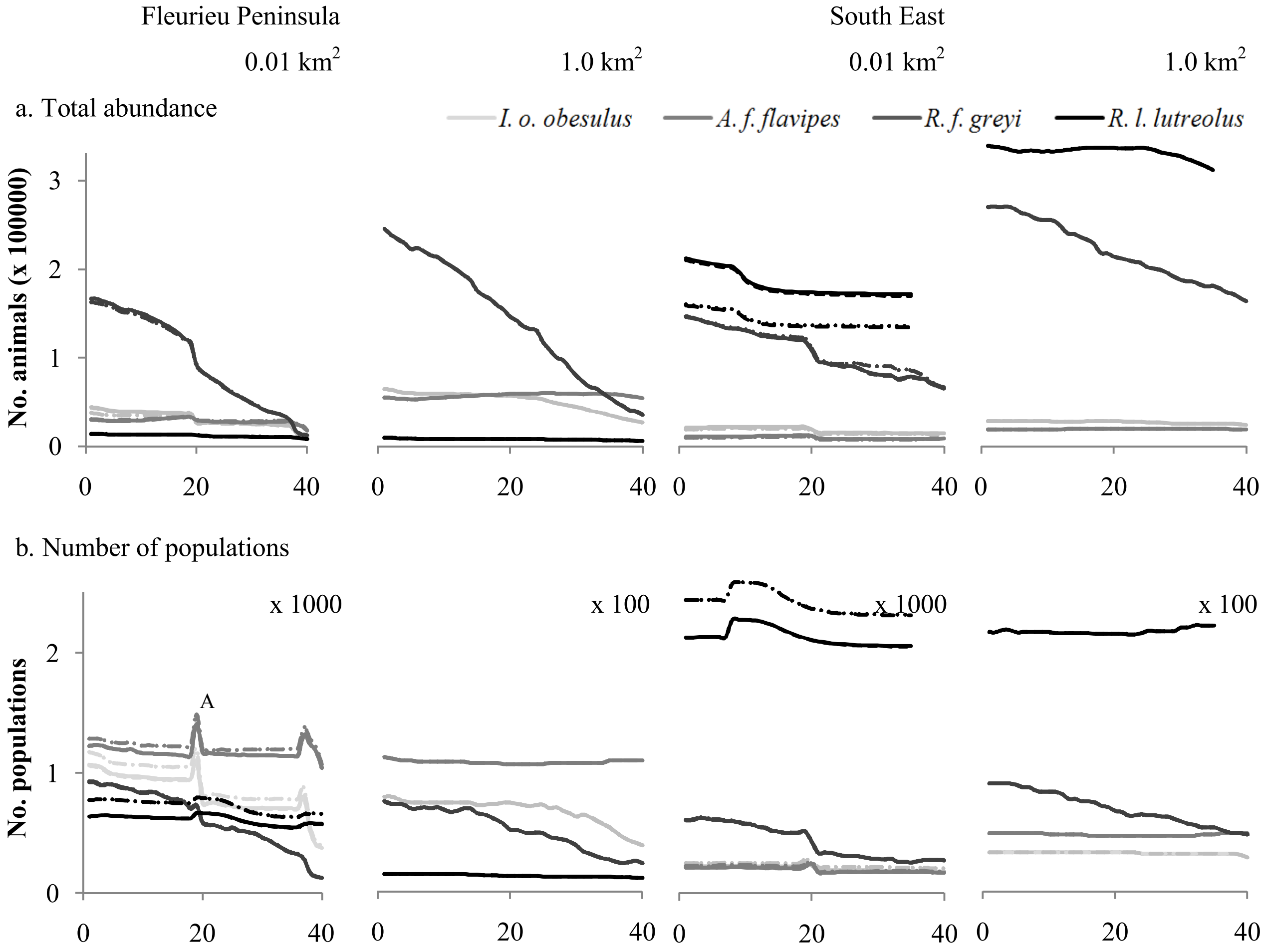
[1] Average number of populations at the last time step of the 20 years of stable climate from 1000 iterations

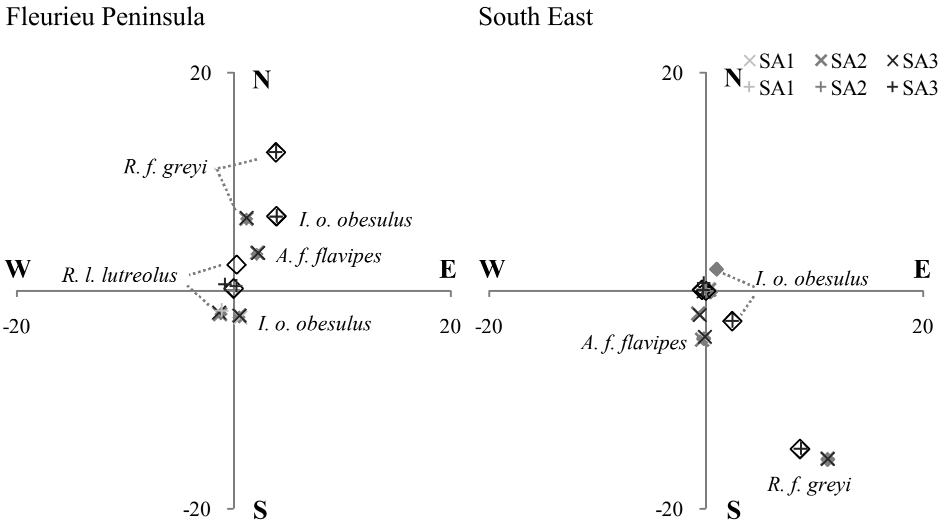
*p value < 0.05, ** p value < 0.001

[a] Negative values indicate an overall range expansion, rather than contraction

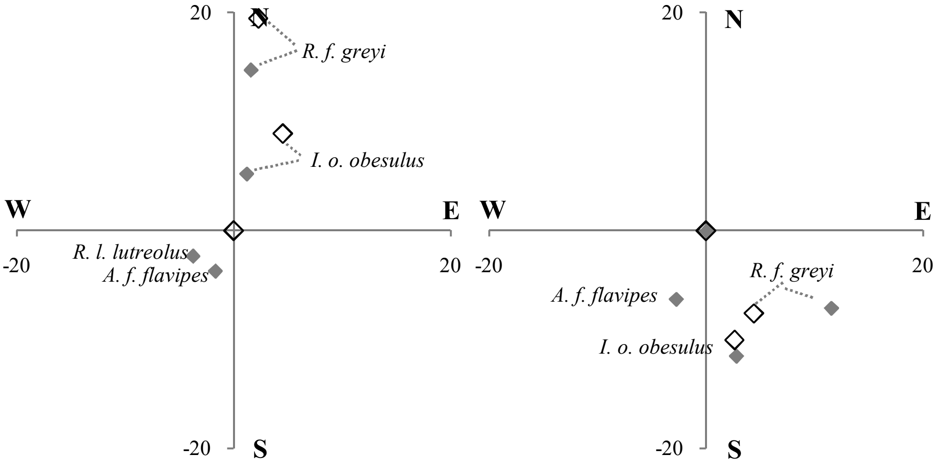


Appendix XV Total number of animals (a) and populations (b) over 40 years of simulated climate change, represented at two scales of resolution (0.01 and 1.0 m^2). Results for the sensitivity analyses are also shown, including increasing potential habitat connectivity by increasing max dispersal to 5 km given environmental data are limited (SA1, dotted line), increasing the SD of mortality to 10 % (SA2, square dotted line), and a combination of both (SA3, dashed line). Temporary peaks (e.g. A) indicate time steps where habitat suitability of many pixels falls below threshold, leading to a substantial alteration in the area and spatial configuration of available habitat and increase in translocated populations that perish in the subsequent time step.

a. Occupied habitat



b. Available habitat

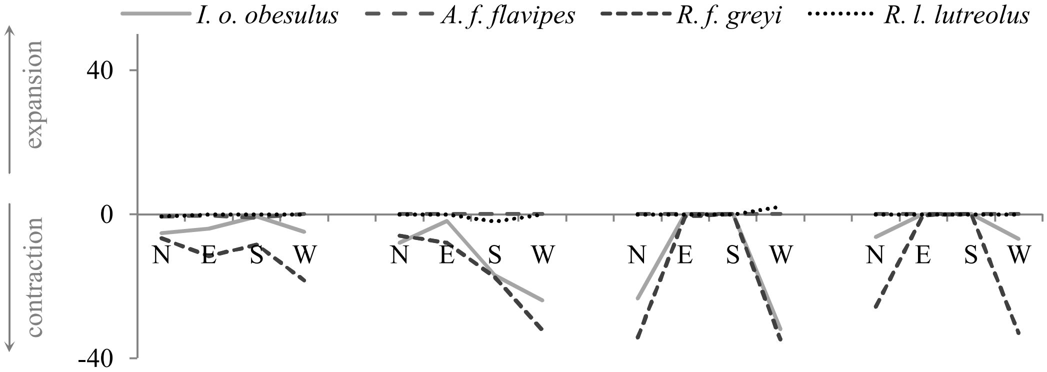


Appendix XVI Shift in the centre-point of occupied (a) and available (b) habitat at 0.01 and 1.0 km^2 resolution (solid or hollow symbols, respectively), in the Fleurieu Peninsula and South East. The centre points calculated during each of the sensitivity analyses performed on the metapopulation model are also shown, included increasing potential habitat connectivity by increasing maximum dispersal to 5 km given environmental data are limited (SA1, light grey), increasing the SD of mortality to 10 % (SA2, medium grey), and a combination of both (SA3, dark grey).

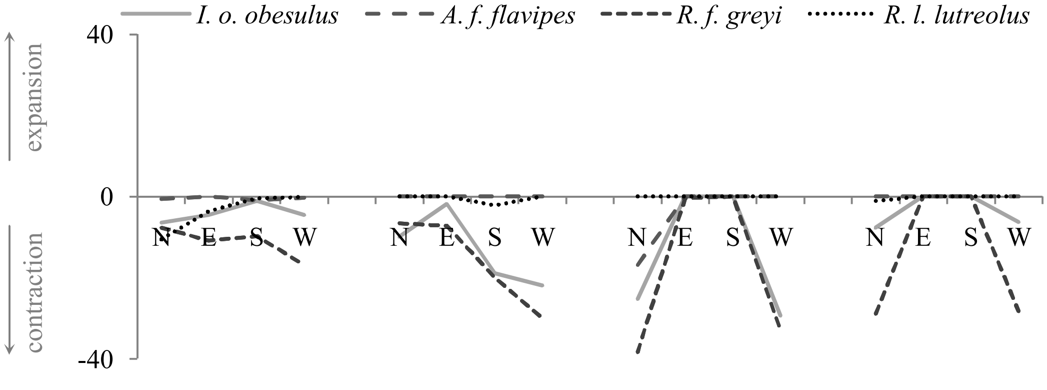
Fleurieu Peninsula South East

0.01 km^2 1.0 km^2 0.01 km^2 1.0 km^2

a. Occupied habitat



b. Available habitat



Appendix XVII Contractions in the extent of occupied (a) and available (b) habitat at 0.01 and 1.0 km^2 resolution, within the Fleurieu Peninsula, and South East. In the South East, expansion in the south-easterly direction is constrained by the coast (south) and this investigation being constrained by a state boundary (east).

Appendix XVIII Landscape and vegetation characteristics of the Interim Biogeographic Regionalisation for Australia (IBRA) v6.1 subregions spanning the study area. All subregions fall within the Channel Country region, which experiences dry, hot summers and unpredictable rainfall (http://www.anra.gov.au/topics/rangelands/overview/nt/ibra-chc.html).

Appendix XIX Brief review of the ecology relevant to the five species targeted in this investigation.

Kowari, Dasyuroides byrnei (vulnerable, Environment Protection and Biodiversity Conservation Act 1999)

Dasyuroides byrnei is a top marsupial carnivore (Lim 1992), weighing 100-170 g (Woolley 1971) that preys on a range of native vertebrates and invertebrates (Watts 1972, Ehman 2005; Lim 2008). Within a restricted distribution (Lim 2008), covering gibber plains that occur between dunes and river channels (Watts and Aslin 1974; Lim 1992), *Dasyuroides byrnei* occupies low, very open shrubland or scrubland, woodland and hummock grassland (Brandle 1998). The species prefers areas with less than 25 % shrub and ground cover (Lim 2008) that produce abundant prey (Lim 1992; Letnic and Dickman 2010). The species is terrestrial, nocturnal, fossorial (i.e. burrows), solitary and nomadic (Woolley 1971; Lim 1992; Lim 2008). The species is capable of maintaining a higher body temperature than smaller species (e.g. *N. cervinus*; Dawson and Dawson 1982) and enters torpor less often and for shorter periods than smaller dasyurids (e.g. *S. macroura*; Geiser and Baudinette 1987).

Kultarr, Antechinomys laniger (endangered, NSW Threatened Species Conservation Act 1995)

Antechinomys laniger is a small insectivorous dasyurid, capable of preying on other small vertebrates (e.g. *Mus musculus*; Watts 1972; Valente 2008) and weighs 20 – 30 g (Woolley 1984). Within a contracting range (Smith and Medlin 1982; Dickman et al. 1993) this naturally rare, but once widespread species (Wood-Jones 1923; Kemper 1990) occupies low shrubland and low very open shrubland and scrubland, tussock grassland, on stony plains, flood plains and hill slope (Morton 1982; Brandle 1998). Within this environment, *A. laniger* nests opportunistically under logs, beneath saltbush and Spinifex tussocks, in deep cracks, at the base of *Acacia* spp. and *Eremophilla* spp. and in burrows constructed by other species (including *N. cervinus*) or in its own shallow burrows (Watts and Aslin 1974; Valente 2008). Species abundance fluctuates seasonally and is highest in April to October (Ayres et al. 1996; Owens 1997; Valente 2008). Heavy rainfall can cause numbers to fall as a result of drowning and decreased food supply (Woolley 1984). This species is nocturnal, terrestrial and solitary and can enter torpor to conserve energy and water (Watts 1972; Ayres et al.1996; Valente 2008).

Stripe-faced dunnart, Sminthopsis macroura (vulnerable, NSW Threatened Species Conservation Act 1995)

Sminthopsis macroura is also an insectivorous dasyurid (Watts 1972; Morton et al. 1983), that occasionally preys on mammals and lizards (Morton and Dickman 2008) and weighs approximately 20 g (Woolley 1982). This species has a widespread, although sparse, distribution across central Australia (Ayres et al. 1996), which has not changed since the arrival of Europeans (Morton and Dickman 2008). *Sminthopsis macroura* occupies a variety of habitats, including low very open shrub, scrubland, low shrubland, shrubland, woodland and hummock grassland on stony plains, drainage lines, hill slopes, rocky outcrops, dunes, sand plains and flood plains (Cole and Gibson 1991; Ayres et al.1996; Brandle 1998). Within this range of habitats, *S. macroura* prefers ungrazed tussock grasslands and dense shrubland often found in creek beds and gullies and recently flooded areas (Watts and Aslin 1974; Morton 1978; Woolley 1982; Morton and Dickman 2008). *Sminthopsis macroura* nests in cracks, under rocks and logs and in burrows constructed by other species' (Brown 1974; Morton and Dickman 2008) and burrows constructed by itself in suitable sandy substrates (Wood-Jones 1923; Watts 1972; Denny 1975). This species is also nocturnal, solitary and fossorial (Watts 1972; Woolley 1982; Morton and Dickman 2008).

Forrest's mouse, Leggadina forresti (vulnerable, Threatened Species Conservation Act 1995)

Leggadina forresti is a small rodent (13 - 30 g; Reid 2008) with an omnivorous or granivorous diet, depending on the degree to which invertebrates supplement its seeds and green vegetation-based diet (Watts 1979; Read 1984; Murray et al. 1999; Moro and Bradshaw 2002). This species has a sparse distribution throughout central and north eastern arid Australia (Watts and Aslin 1981; Breed and Ford 2007), which has not changed since European arrival (Reid 2008). *Leggadina forresti* occupies a variety of vegetation communities, but most often captured in low and low very open shrubland and scrubland, followed by woodland, hummock grassland and shrubland on stony plains and flood plains, followed by drainage lines, hill slopes and dunes and sand plains (Philpott and Smyth 1967; Ayres et al. 1996; Brandle 1998). The species prefers plains and tussock grasslands (Read 1984; Ayres et al. 1996; Reid 2008) and numbers increase following rain and an increase in ephemeral cover (Owens 1997; Moro and Morris 2000). Individuals nest predominantly in shallow burrows under or near *Atriplex rhagodiodes*, dug after rain (Philpott and Smyth 1967) and in soil cracks and at the base of Spinifex tussocks (Finlayson 1941; Denny 1975). This species is nocturnal, terrestrial, solitary and nomadic (Philpott and Smyth 1967; Dickman 1993; Reid 2008).

Fawn hopping-mouse, Notomys cervinus (endangered, Territory Parks and Wildlife Conservation Act 2006; vulnerable National Parks and Wildlife Act 1972)

Notomys cervinus is also a small rodent (30-50 g; Breed 2008) with a predominantly granivorous diet of seed, green plant material and invertebrates (Watts 1970; Murray et al. 1999). This species has a sparse and restricted distribution (Ellis 1993; Robinson et al. 2000; Breed 2008). *Notomys cervinus* occupies low shrubland and tussock grasslands in stony plains and clay pans (Watts and Aslin 1981). Rain increases grass seed production and subsequently animal abundance (especially during the breeding season April – Dec; Philpott and Smyth 1967). During flooding *N. cervinus* occupy high ground with vegetation of variable density above river channels (Dickman 1993). *Notomys cervinus* nests in deep, relatively simple burrows, compared to other *Notomys spp.* (possibly due to the substrate being penetrable shortly after rain only; Watts and Aslin 1981). This species nocturnal (Dickman 1993) and solitary, but can live in small groups (Watts and Aslin 1974; Watts and Aslin 1981).

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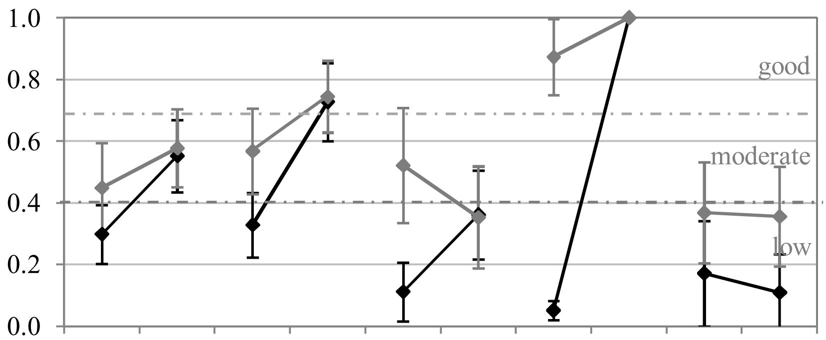
Appendix XX Original species occurrence data from the Biological Databases of South Australia (BDBSA, extracted April 2011, Department of Environment and Natural Resources). Fewer records were available for analysis due to gaps in environmental data or sub-setting data for validation (e.g. GEN).

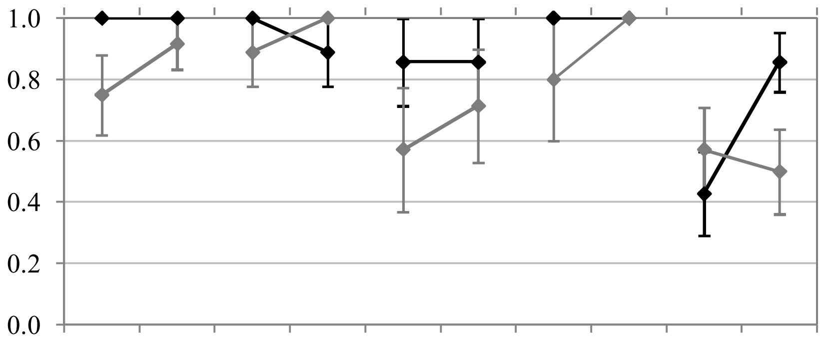
	A. laniger	*D. byrnei*	*L. forresti*	*N. cervinus*	*S. macroura*
Year range	1987 - 2008	1992 – 2008	1983 – 2008	1995 -2009	1993 - 2008
Filters	≤ 100 m location accuracy, single observation per location				
Sampling method					
• Cage trap		1			
• Elliott trap	44	20	7	4	24
• Pit trap			41	1	91
• Captured (by hand)		1		1	
• Observed (incl. spotlighting)	11	4	3	19	2
• Sign-diggings		1			
• Sign-dropping		1			
• Unknown / unspecified	6	1	9	5	27
Total	61	29	60	30	144

Appendix XXI Parameters applied to the *a priori* boosted regression trees (BRT) for candidate model set 1 (a) and 2 (b). Shown are the optimal tree complexity (Tc: number of nodes), learning rate (lr: the shrinkage applied to each tree) and the resultant number of trees (#) used in each BRT model. Variables are defined in Table 1, p62.

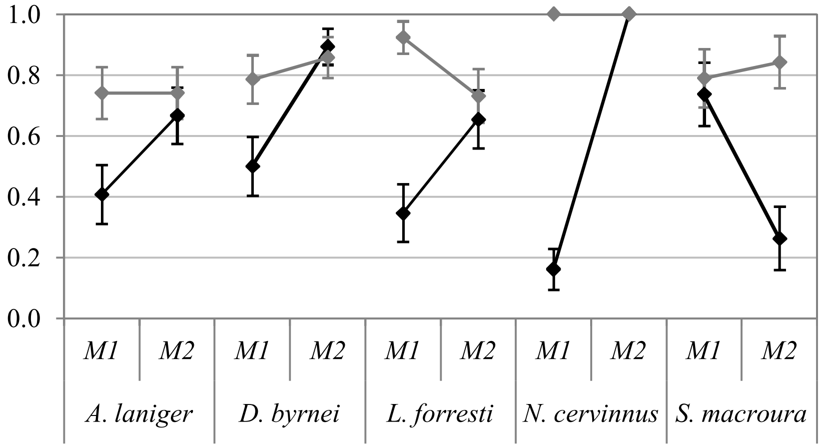
	A. laniger			*D. byrnei*			*L. forresti*			*N. cervinus*			*S. macroura*		
	tc	lr	#	tc	lr	#	tc	lr	#	tc	lr	#	tc	lr	#
a. candidate model set 1: M1, spp ~ RS + RW; M2, spp ~ RS + RW + E + lnWC + GEN + PAWHC															
M1	2	0.005	1500	2	0.005	850	2	0.005	600	2	0.005	450	2	0.001	800
M2	2	0.005	950	1	0.005	1150	2	0.001	1750	2	0.005	450	2	0.001	1250
b. candidate model set 1: M1, spp ~ RS + RW; M2, spp ~ RS + lnWC + PAWHC; M3, spp ~ RS + lnWC + C2; M4, spp ~ RS + GEN; M5, spp ~ RS + SD; Sat; spp ~ RS + RW + lnWC + PAWHC + C2 + GEN + SD															
M1	1	0.001	2400	-	-	-	1	0.005	1100	-	-	-	2	0.001	1800
M2	2	0.001	3200	-	-	-	2	0.001	1800	-	-	-	2	0.001	1250
M3	2	0.001	4900	-	-	-	3	0.001	4450	-	-	-	2	0.001	1900
M4	2	0.005	2000	2	0.005	1800	2	0.005	2300	2	0.01	1250	1	0.001	3950
M5	2	0.001	8550	2	0.005	2250	2	0.005	2250	2	0.001	4600	3	0.001	1700
Sat	2	0.001	2250	2	0.001	2200	2	0.001	2550	-	-	-	2	0.001	2850



a. Kappa

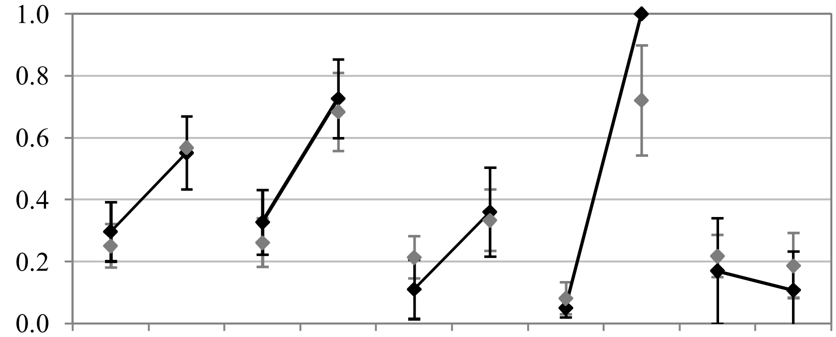


b. Sensitivity

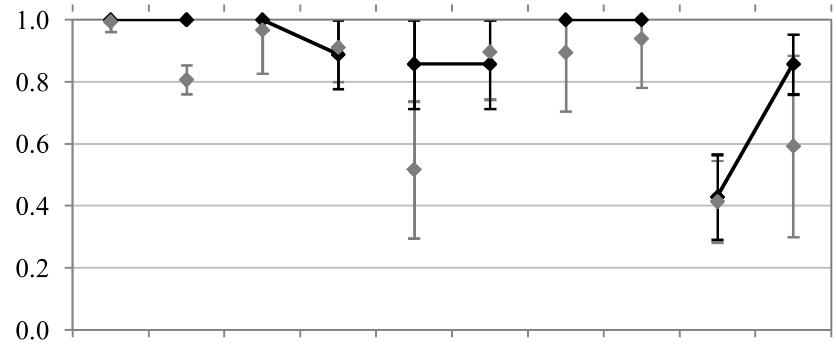


c. Specificity

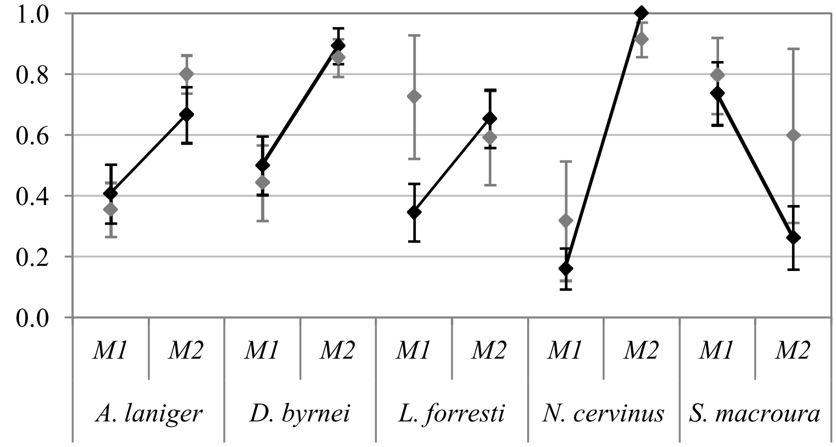
Appendix XXII Out-of-region predictive performance, illustrated using three measures of agreement: Kappa, sensitivity and specificity statistics (Fielding and Bell 1997). These metrics were derived from probability estimates using the Maximum Sensitivity and Specificity threshold (MSS) for each model (generalised linear modelling, black line and boosted regression tree modelling, grey line) and species where *A. laniger*, *D. byrnei*, *L. forresti, N. cervinus* and *S. macroura* have 0.31, 0.24, 0.21, 0.14 and 0.42 prevalence in the predict dataset, respectively. Error bars are calculated as standard deviation.



a. Kappa



b. Sensitivity



c. Specificity

Appendix XXIII Illustration of model bias using average generalised linear modelling-generated statistics, based on 1 000 boot-strap samples (black diamonds), and the initial predict values (grey diamonds and lines) calculated using the Maximum Sensitivity and Specificity threshold (MSS) for each model. Error bars are calculated as standard deviation.

Appendix XXIV Coefficients estimated for each parameter of the more complex generalised linear model for each species (M2: Species ~ RS + RW + E + lnWC + GEN + PAWHC), standard error (SE), z score and the associated p-value and levels of significance to: * <0.05; ** < 0.01; *** < 0.001. Variables are defined in Table 1, p62.

	Coefficient	SE	z score	Pr(>|z|)	
a. *A. laniger*					
(Intercept)	0.00	1.00	0.50	0.730	
RS	0.42	0.53	0.06	0.502	**
RW	0.70	0.63	0.82	0.533	
E	0.49	0.51	0.18	0.533	
lnWC	0.77	0.58	0.98	0.500	***
GEN2	0.16	1.00	0.50	0.731	
GEN3	1.00	1.00	0.50	0.730	
GEN4	1.00	1.00	0.50	0.730	
PAWHC	0.49	0.50	0.09	0.505	*
b. *D. byrnei*					
(Intercept)	0.00	1.00	0.50	0.730	
RS	0.59	0.56	0.83	0.528	
RW	0.66	0.64	0.76	0.561	
E	0.50	0.51	0.44	0.695	
lnWC	0.78	0.60	0.96	0.500	**
GEN2	0.28	1.00	0.50	0.731	
GEN3	1.00	1.00	0.50	0.730	
GEN4	1.00	1.00	0.50	0.730	
PAWHC	0.49	0.50	0.15	0.520	.
c. *L. forresti*					
(Intercept)	0.02	0.98	0.26	0.574	
RS	0.52	0.52	0.72	0.585	
RW	0.50	0.56	0.50	0.729	
E	0.50	0.50	0.39	0.660	
lnWC	0.46	0.54	0.26	0.575	
GEN2	0.15	0.77	0.19	0.539	
GEN3	0.82	0.70	0.86	0.517	.
GEN4	0.80	0.70	0.83	0.528	
PAWHC	0.50	0.50	0.90	0.507	*

(cont.)

(cont.) **Appendix XXIV**

	Coefficient	SE	z score	Pr(>|z|)	
d. *N. cervinus*					
(Intercept)	0.00	1.00	0.50	0.729	
RS	0.58	0.59	0.71	0.593	
RW	0.70	0.71	0.72	0.585	
E	0.49	0.51	0.35	0.628	
lnWC	0.88	0.64	0.97	0.500	***
GEN2	0.24	1.00	0.50	0.731	
GEN3	1.00	1.00	0.50	0.730	
GEN4	1.00	1.00	0.50	0.730	
PAWHC	0.50	0.50	0.55	0.697	
d. *S. macroura*					
(Intercept)	0.00	0.97	0.17	0.527	
RS	0.53	0.52	0.85	0.521	.
RW	0.54	0.56	0.67	0.620	
E	0.50	0.50	0.27	0.579	
lnWC	0.50	0.54	0.50	0.730	
GEN2	0.48	0.69	0.48	0.717	
GEN3	0.55	0.69	0.56	0.692	
GEN4	0.79	0.68	0.85	0.522	.
PAWHC	0.50	0.50	0.71	0.593	

Appendix XXV Explanatory strength of the null and *a priori* generalised linear models, where 'occupied sites' are represented by survey sites within 150 m, 500 m, 1000 m, 5 000 m and 10 000 m of a known record. Shown are the number of parameters (*d.f.),* minimised negative log-likelihood (-LL), Akaike's information criterion corrected for small sample sizes (AIC_c), Bayesian Inference Criterion (BIC), difference from the highest-ranking model (ΔAIC_c, ΔBIC), weight scaled to a sum of 1($w\text{AIC}_c$, *w*BIC), and the per cent deviance explained (% DE) by the model relative to the null. Variables are defined in Table 1, p62.

a. A. laniger

Model	*d.f.*	-LL	AIC_c	ΔAIC_c	$w\text{AIC}_c$	BIC	ΔBIC	*w*BIC	%DE
150 m (17 presence : 150 absence sites) (prevalence 0.11)									
~ 1	1	-54.9	111.9	28.8	0.00	115.0	19.6	0.00	
~ RS + RW	3	-48.2	102.5	19.4	0.00	111.7	16.4	0.00	12.3
~ RS + lnWC + PAWHC	4	-37.4	83.1	0.0	0.97	95.4	0.0	0.97	31.8
~ RS + lnWC + Cat2	4	-41.1	90.4	7.2	0.03	102.6	7.2	0.03	25.3
~ RS + GEN	5	-42.8	96.1	12.9	0.00	111.3	15.9	0.00	22.0
~ RS + SD	5	-45.5	101.4	18.2	0.00	116.6	21.2	0.00	17.2
500 m (20 presence : 147 absence sites) (prevalence 0.12)									
~ 1	1	-61.2	124.4	37.5	0.00	127.5	28.4	0.00	
~ RS + RW	3	-55.4	116.9	30.0	0.00	126.1	27.0	0.00	9.5
~ RS + lnWC + PAWHC	4	-39.3	86.9	0.0	0.98	99.1	0.0	0.98	35.7
~ RS + lnWC + Cat2	4	-43.1	94.5	7.6	0.02	106.8	7.6	0.02	29.5
~ RS + GEN	5	-47.8	106.1	19.2	0.00	121.3	22.2	0.00	21.8
~ RS + SD	5	-51.5	113.5	26.6	0.00	128.7	29.6	0.00	15.8
1 000 m (24 presence : 143 absence sites) (prevalence 0.14)									
~ 1	1	-68.7	139.5	52.7	0.00	142.6	43.5	0.00	
~ RS + RW	3	-61.3	128.7	41.8	0.00	137.9	38.8	0.00	10.9
~ RS + lnWC + PAWHC	4	-39.3	86.9	0.0	1.00	99.1	0.0	1.00	42.8
~ RS + lnWC + Cat2	4	-45.5	99.3	12.4	0.00	111.5	12.4	0.00	33.8
~ RS + GEN	5	-52.2	114.8	27.9	0.00	130.0	30.9	0.00	24.1
~ RS + SD	5	-57.4	125.2	38.3	0.00	140.4	41.3	0.00	16.5
5 000 m (44 presence : 123 absence sites) (prevalence 0.26)									
~ 1	1	-96.3	194.6	82.4	0.00	197.7	73.3	0.00	
~ RS + RW	3	-75.7	157.6	45.4	0.00	166.8	42.4	0.00	21.4
~ RS + lnWC + PAWHC	4	-52.0	112.2	0.0	1.00	124.4	0.0	1.00	46.0
~ RS + lnWC + Cat2	4	-65.5	139.3	27.1	0.00	151.5	27.1	0.00	32.0
~ RS + GEN	5	-60.3	131.0	18.8	0.00	146.2	21.8	0.00	37.4
~ RS + SD	5	-74.3	159.0	46.8	0.00	174.2	49.8	0.00	22.8
10 000 m (61 presence : 106 absence sites) (prevalence 0.37)									
~ 1	1	-109.6	221.3	117.2	0.00	224.4	108.1	0.00	
~ RS + RW	3	-84.8	175.8	71.7	0.00	185.0	68.7	0.00	22.6
~ RS + lnWC + PAWHC	4	-47.9	104.1	0.0	1.00	116.3	0.0	1.00	56.3
~ RS + lnWC + Cat2	4	-66.5	141.2	37.1	0.00	153.4	37.1	0.00	39.4
~ RS + GEN	5	-60.6	131.5	27.4	0.00	146.7	30.4	0.00	44.7
~ RS + SD	5	-83.2	176.7	72.6	0.00	191.9	75.6	0.00	24.1

(cont.)

(cont.) **Appendix XXV**

b. D. byrnei

Model	*d.f.*	-LL	AIC$_c$	ΔAIC$_c$	*w*AIC$_c$	BIC	ΔBIC	*w*BIC	%DE
150 m (11 presence : 156 absence sites) (prevalence 0.07)									
~ 1	1	-40.6	83.1	26.4	0.00	86.2	17.3	0.00	
~ RS + RW	3	-36.3	78.7	22.0	0.00	87.9	19.0	0.00	10.5
~ RS + lnWC + PAWHC	4	-24.2	56.7	0.0	0.89	69.0	0.0	0.89	40.2
~ RS + lnWC + Cat2	4	-26.3	60.9	4.2	0.11	73.2	4.2	0.11	35.0
~ RS + GEN	5	-31.4	73.1	16.4	0.00	88.3	19.3	0.00	22.7
~ RS + SD	5	-36.7	83.7	26.9	0.00	98.9	29.9	0.00	9.6
500 m (14 presence : 153 absence sites) (prevalence 0.11)									
~ 1	1	-48.1	98.2	36.3	0.00	101.3	27.2	0.00	
~ RS + RW	3	-45.4	96.9	34.9	0.00	106.1	31.9	0.00	5.7
~ RS + lnWC + PAWHC	4	-26.8	61.9	0.0	0.90	74.2	0.0	0.90	44.2
~ RS + lnWC + Cat2	4	-29.0	66.3	4.3	0.10	78.5	4.3	0.10	39.7
~ RS + GEN	5	-37.0	84.3	22.4	0.00	99.5	25.4	0.00	23.1
~ RS + SD	5	-43.9	98.1	36.2	0.00	113.4	39.2	0.00	8.8
1 000 m (15 presence : 152 absence sites) (prevalence 0.09)									
~ 1	1	-50.5	102.9	42.5	0.00	106.0	33.4	0.00	
~ RS + RW	3	-47.5	101.1	40.7	0.00	110.3	37.7	0.00	5.9
~ RS + lnWC + PAWHC	4	-26.1	60.4	0.0	0.96	72.7	0.0	0.96	48.3
~ RS + lnWC + Cat2	4	-29.3	66.8	6.3	0.04	79.0	6.3	0.04	42.0
~ RS + GEN	5	-38.3	87.0	26.6	0.00	102.2	29.6	0.00	24.1
~ RS + SD	5	-45.8	102.1	41.6	0.00	117.3	44.6	0.00	9.1
5 000 m (27 presence : 140 absence sites) (prevalence 0.16)									
~ 1	1	-73.9	149.8	81.9	0.00	152.9	72.8	0.00	
~ RS + RW	3	-66.0	138.2	70.4	0.00	147.4	67.3	0.00	10.6
~ RS + lnWC + PAWHC	4	-29.8	67.9	0.0	1.00	80.1	0.0	1.00	59.7
~ RS + lnWC + Cat2	4	-41.9	92.1	24.3	0.00	104.4	24.3	0.00	43.2
~ RS + GEN	5	-55.9	122.2	54.3	0.00	137.4	57.3	0.00	24.3
~ RS + SD	5	-66.7	143.8	75.9	0.00	159.0	78.9	0.00	9.7
10 000 m (40 presence : 127 absence sites) (prevalence 0.24)									
~ 1	1	-91.9	185.9	60.6	0.00	189.0	51.4	0.00	
~ RS + RW	3	-75.8	157.7	32.3	0.00	166.9	29.3	0.00	17.6
~ RS + lnWC + PAWHC	4	-58.5	125.3	0.0	1.00	137.6	0.0	1.00	36.3
~ RS + lnWC + Cat2	4	-65.9	140.1	14.8	0.00	152.3	14.8	0.00	28.3
~ RS + GEN	5	-71.2	152.8	27.5	0.00	168.0	30.5	0.00	22.5
~ RS + SD	5	-77.6	165.7	40.3	0.00	180.9	43.3	0.00	15.5

(cont.)

(cont.) **Appendix XXV**

c. L. forresti

Model	*d.f.*	-LL	AIC$_c$	ΔAIC$_c$	wAIC$_c$	BIC	ΔBIC	wBIC	%DE
150 m (27 presence : 140 absence sites) (prevalence 0.16)									
~ 1	1	-73.9	149.8	3.9	0.07	152.9	0.0	0.90	
~ RS + RW	3	-71.6	149.3	3.4	0.09	158.5	5.6	0.05	3.1
~ RS + lnWC + PAWHC	4	-70.0	148.2	2.4	0.16	160.5	7.6	0.02	5.3
~ RS + lnWC + Cat2	4	-71.1	150.5	4.6	0.05	162.7	9.8	0.01	3.8
~ RS + GEN	5	-67.7	145.9	0.0	0.52	161.1	8.2	0.02	8.3
~ RS + SD	5	-69.3	149.0	3.1	0.11	164.2	11.3	0.00	6.2
500 m (28 presence : 139 absence sites) (prevalence 0.17)									
~ 1	1	-75.5	153.0	5.2	0.05	156.1	0.0	0.90	
~ RS + RW	3	-73.2	152.6	4.8	0.07	161.8	5.7	0.05	3.0
~ RS + lnWC + PAWHC	4	-72.0	152.2	4.4	0.08	164.4	8.3	0.01	4.7
~ RS + lnWC + Cat2	4	-72.8	153.8	6.0	0.04	166.1	9.9	0.01	3.6
~ RS + GEN	5	-68.7	147.8	0.0	0.71	163.0	6.9	0.03	9.0
~ RS + SD	5	-71.3	153.0	5.1	0.05	168.2	12.0	0.00	5.6
1 000 m (30 presence : 137 absence sites) (prevalence 0.18)									
~ 1	1	-78.6	159.3	6.5	0.03	162.4	0.0	0.85	
~ RS + RW	3	-76.2	158.6	5.8	0.04	167.8	5.4	0.06	3.1
~ RS + lnWC + PAWHC	4	-74.5	157.3	4.6	0.08	169.5	7.2	0.02	5.2
~ RS + lnWC + Cat2	4	-75.8	159.7	7.0	0.02	172.0	9.6	0.01	3.7
~ RS + GEN	5	-71.2	152.7	0.0	0.76	168.0	5.6	0.05	9.5
~ RS + SD	5	-73.7	157.7	4.9	0.06	172.9	10.5	0.00	6.3
5 000 m (49 presence : 118 absence sites) (prevalence 0.29)									
~ 1	1	-101.1	204.2	9.8	0.01	207.2	0.0	0.69	
~ RS + RW	3	-98.2	202.6	8.3	0.01	211.8	4.6	0.07	2.8
~ RS + lnWC + PAWHC	4	-97.7	203.7	9.3	0.01	215.9	8.7	0.01	3.3
~ RS + lnWC + Cat2	4	-98.3	204.9	10.5	0.00	217.1	9.8	0.01	2.7
~ RS + GEN	5	-95.7	201.8	7.5	0.02	217.0	9.8	0.01	5.3
~ RS + SD	5	-92.0	194.3	0.0	0.94	209.6	2.3	0.22	9.0
10 000 m (72 presence : 95 absence sites) (prevalence 0.43)									
~ 1	1	-114.2	230.4	13.7	0.00	233.5	1.6	0.19	
~ RS + RW	3	-109.0	224.1	7.5	0.02	233.3	1.5	0.20	4.5
~ RS + lnWC + PAWHC	4	-112.2	232.6	15.9	0.00	244.8	13.0	0.00	1.8
~ RS + lnWC + Cat2	4	-109.5	227.2	10.6	0.00	239.5	7.6	0.01	4.1
~ RS + GEN	5	-103.1	216.6	0.0	0.70	231.8	0.0	0.42	9.7
~ RS + SD	5	-104.0	218.4	1.8	0.28	233.6	1.8	0.17	8.9

(cont.)

(cont.) **Appendix XXV**

d. N. cervinus

Model	*d.f.*	-LL	AIC$_c$	ΔAIC$_c$	*w*AIC$_c$	BIC	ΔBIC	*w*BIC	%DE
150 m (2 presence : 165 absence sites) (prevalence 0.01)									
~ 1	1	-10.8	23.7	2.8	0.11	26.8	0.0	0.91	
~ RS + RW	3	-9.9	26.0	5.1	0.03	35.2	8.4	0.01	8.3
~ RS + lnWC + PAWHC	4	-6.4	21.0	0.0	0.42	33.2	6.4	0.04	41.3
~ RS + lnWC + Cat2	4	-6.3	20.9	0.0	0.43	33.2	6.4	0.04	41.5
~ RS + GEN	5	-9.0	28.4	7.4	0.01	43.6	16.8	0.00	17.0
~ RS + SD	5	-10.0	30.4	9.5	0.00	45.6	18.8	0.00	7.6
500 m (4 presence:163 absence sites) (prevalence 0.02)									
~ 1	1	-18.9	39.8	11.8	0.00	42.9	2.6	0.14	
~ RS + RW	3	-18.7	43.6	15.6	0.00	52.8	12.5	0.00	0.9
~ RS + lnWC + PAWHC	4	-10.3	28.9	0.9	0.38	41.2	0.9	0.33	45.2
~ RS + lnWC + Cat2	4	-9.9	28.0	0.0	0.61	40.2	0.0	0.53	47.7
~ RS + GEN	5	-15.4	41.3	13.3	0.00	56.5	16.3	0.00	18.2
~ RS + SD	5	-17.5	45.3	17.3	0.00	60.5	20.3	0.00	7.4
1 000 m (4 presence : 163 absence sites) (prevalence 0.02)									
~ 1	1	-18.9	39.8	11.8	0.00	42.9	2.6	0.14	
~ RS + RW	3	-18.7	43.6	15.6	0.00	52.8	12.5	0.00	0.9
~ RS + lnWC + PAWHC	4	-10.3	28.9	0.9	0.38	41.2	0.9	0.33	45.2
~ RS + lnWC + Cat2	4	-9.9	28.0	0.0	0.61	40.2	0.0	0.53	47.7
~ RS + GEN	5	-15.4	41.3	13.3	0.00	56.5	16.3	0.00	18.2
~ RS + SD	5	-17.5	45.3	17.3	0.00	60.5	20.3	0.00	7.4
5 000 m (5 presence:162 absence sites) (prevalence 0.03)									
~ 1	1	-22.47	46.96	18.28	0.000	50.05	9.15	0.01	
~ RS + RW	3	-22.41	50.96	22.28	0.000	60.16	19.26	0.00	0.3
~ RS + lnWC + PAWHC	4	-10.82	29.88	1.21	0.353	42.11	1.21	0.35	51.9
~ RS + lnWC + Cat2	4	-10.21	28.67	0.00	0.647	40.90	0.00	0.64	54.5
~ RS + GEN	5	-18.19	46.75	18.07	0.000	61.97	21.07	0.00	19.0
~ RS + SD	5	-20.74	51.85	23.18	0.000	67.07	26.17	0.00	7.7
10 000 m (16 presence : 151 absence sites) (prevalence 0.10)									
~ 1	1	-52.7	107.5	54.9	0.00	110.6	45.8	0.00	
~ RS + RW	3	-52.1	110.3	57.7	0.00	119.5	54.7	0.00	1.3
~ RS + lnWC + PAWHC	4	-22.2	52.7	0.1	0.49	64.9	0.1	0.49	57.9
~ RS + lnWC + Cat2	4	-22.2	52.6	0.0	0.51	64.8	0.0	0.51	58.0
~ RS + GEN	5	-44.8	100.1	47.5	0.00	115.3	50.5	0.00	15.0
~ RS + SD	5	-50.4	111.2	58.6	0.00	126.4	61.6	0.00	4.4

(cont.)

(cont.) **Appendix XXV**

e. S. macroura

Model	*d.f.*	-LL	AIC$_c$	ΔAIC$_c$	*w*AIC$_c$	BIC	ΔBIC	*w*BIC	%DE
150 m (50 presence : 117 absence sites) (prevalence 0.30)									
~ 1	1	-101.9	205.9	1.7	0.23	209.0	0.0	0.97	
~ RS + RW	3	-100.5	207.2	3.0	0.12	216.4	7.4	0.02	1.4
~ RS + lnWC + PAWHC	4	-100.4	209.1	4.9	0.05	221.3	12.3	0.00	1.5
~ RS + lnWC + Cat2	4	-100.6	209.5	5.4	0.04	221.7	12.8	0.00	1.3
~ RS + GEN	5	-99.7	209.8	5.6	0.03	225.0	16.0	0.00	2.2
~ RS + SD	5	-96.9	204.1	0.0	0.54	219.4	10.4	0.01	5.0
500 m (52 presence:115 absence sites) (prevalence 0.31)									
~ 1	1	-103.6	209.2	1.2	0.26	212.3	0.0	0.97	
~ RS + RW	3	-102.2	210.5	2.5	0.13	219.7	7.4	0.02	1.3
~ RS + lnWC + PAWHC	4	-102.1	212.4	4.3	0.05	224.6	12.3	0.00	1.5
~ RS + lnWC + Cat2	4	-102.2	212.7	4.6	0.05	224.9	12.6	0.00	1.3
~ RS + GEN	5	-101.1	212.6	4.6	0.05	227.8	15.6	0.00	2.4
~ RS + SD	5	-98.82	208.0	0.0	0.46	223.2	11.0	0.00	4.6
1 000 m (58 presence : 109 absence sites) (prevalence 0.35)									
~ 1	1	-107.8	217.7	7.4	0.02	220.8	0.0	0.85	
~ RS + RW	3	-105.4	217.0	6.7	0.03	226.2	5.4	0.06	2.2
~ RS + lnWC + PAWHC	4	-104.8	217.8	7.4	0.02	230.0	9.2	0.01	2.9
~ RS + lnWC + Cat2	4	-105.7	219.6	9.2	0.01	231.8	11.0	0.00	2.0
~ RS + GEN	5	-104.8	219.9	9.6	0.01	235.2	14.4	0.00	2.8
~ RS + SD	5	-100.0	210.4	0.0	0.91	225.6	4.8	0.08	7.3
5 000 m (92 presence:75 absence sites) (prevalence 0.55)									
~ 1	1	-114.9	231.8	2.5	0.17	234.9	0.0	0.95	
~ RS + RW	3	-113.1	232.3	3.0	0.13	241.5	6.6	0.04	1.6
~ RS + lnWC + PAWHC	4	-113.4	235.0	5.8	0.03	247.2	12.3	0.00	1.3
~ RS + lnWC + Cat2	4	-113.9	236.1	6.9	0.02	248.3	13.4	0.00	0.8
~ RS + GEN	5	-111.9	234.1	4.8	0.05	249.3	14.4	0.00	2.6
~ RS + SD	5	-109.4	229.3	0.0	0.60	244.5	9.6	0.01	4.7
10 000 m (92 presence : 75 absence sites) (prevalence 0.55)									
~ 1	1	-114.9	231.8	2.5	0.17	234.9	0.0	0.95	
~ RS + RW	3	-113.1	232.3	3.0	0.13	241.5	6.6	0.04	1.6
~ RS + lnWC + PAWHC	4	-113.4	235.0	5.8	0.03	247.2	12.3	0.00	1.3
~ RS + lnWC + Cat2	4	-113.9	236.1	6.9	0.02	248.3	13.4	0.00	0.8
~ RS + GEN	5	-111.9	234.1	4.8	0.05	249.3	14.4	0.00	2.6
~ RS + SD	5	-109.4	229.3	0.0	0.60	244.5	9.6	0.01	4.7

Publications arising from this thesis

Manuscripts - published

- Haby, N.A., Delean, S and Brook, BW. 2011. Specialist resources are key to improving small mammal distribution models. Austral Ecology (early view, doi: 10.1111/j.1442-9993.2011.02267.x)

Manuscripts – in review

- Haby, N.A., Foulkes, J. & Brook, B.W. How well do existing evaluations of climate change impacts on range dynamics represent Australian small mammls?
- Haby, N.A., Delean, S. & Brook, B.W. Improving performance and transferability of small-mammal distribution models.
- Haby N.A., Prowse T.A.A., Gregory S.D., Watts M.J., Delean S., Fordham D.A., Foulkes J. & Brook B.W. Scale dependency of metapopulation models used to predict climate change impacts on small mammals
- Haby, N.A., Foulkes, J. & Brook, B.W. Lessons from the arid zone: using climate variables to predict small mammal occurrence in hot, dry environments.
- Haby, N.A., Foulkes, J. & Brook, B.W. Ecosystem dynamics, evolution and dependency of higher trophic organisms on resource gradients.

Conference presentations

- Haby, N.A. 2011. Better use of ecological information in modelling climate change impacts on the distribution of small mammal populations. ICCB, Aukland (oral)
- Haby, N.A. 2011. Using multiple-scale environmental data to model small mammal distributions in arid Australia. Ecological Society of Australia, Hobart (oral)
- Haby, N.A., Delean, S. and Brook, B.W. 2010. Ecologically relevant information is required to improve climate change forecast for small mammals. Ecological Society of Australia, Canberra (oral).
- Haby, N.A., Delean, S. and Brook, B.W. 2010. Effect of multiple-scale environmental variables on coastal small mammal distribution models. Ecological Society of Australia, Canberra (poster)
- Haby, N.A., Delean, S. and Brook, B.W. 2009. Effect of multiple-scale environmental variables on coastal small mammal distribution models. Intercol, Brisbane (oral)

Symposia presentations

- Haby, N.A. 2011. Ecologically relevant information is required to improve climate change forecasts for small mammals. Dept of Environment and Natural Resources, Adelaide (oral)

Newsletter articles

- Haby, N. 2011. Bringing small mammals into focus. Terrestrial Research E-bulletin 7, 2 [http://nccarf.jcu.edu.au/terrestrialbiodiversity/index.php/Home.html]