

Scale dependency of metapopulation models used to predict climate change impacts on small mammals

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To investigate potential range shifts in a changing climate it is becoming increasingly common to develop models that account for demographic processes. Metapopulation models incorporate the spatial configuration of occupied habitat (i.e. arrangement, size and quality), population demographics, 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 realistically represent the spatial configuration of suitable habitat, including stepping stones and refugia. We aimed to determine whether relatively fine-scale environmental information influenced predictions of metapopulation persistence and range shift. Species distribution models were constructed for four small terrestrial mammals from southern Australia using environmental predictors measured at 0.1×0.1 km (0.01 km²) or 1.0×1.0 km (1 km²) resolution, and combined with demographic information to parameterise coupled niche-population models. These models were used to simulate population dynamics projected over 40-yr under a stable and changing climate. Initial estimates of the area of available habitat were similar at both spatial scales. However, at the fine-scale, habitat configuration comprised a greater number of patches (ca 12 times), that were more irregular in shape (ca 8 times the perimeter:area), and separated by a tenth of the distance than at the coarse-scale. While small patches were not more prone to extinction, populations generally declined at a higher rate and were associated with a lower expected minimum abundance. Despite increased species vulnerability at the fine-scale, greater range shifts were measured at the coarse-scale (for species illustrating a shift at both scales). These results highlight the potential for range shifts and species vulnerability information to be misrepresented if advanced modelling techniques incorporating species demographics and dispersal inadequately represent the scale at which these processes occur.

Anthropogenic climate change is forecast to reduce the range of many species of mammals (Levinsky et al. 2007). These changes will depend on the capacity of a species to track a suitable climate envelope within a landscape, which reflects not just climatic suitability, but also the configuration of suitable habitat and demographic and dispersal dynamics within and between habitat 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 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 (Kotliar 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 (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 (Brito and da Fonseca 2007), including the potential effects of development and management programs on small mammal persistence (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 km² (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-yr of simulated climate change. These models integrated SDMs built with environmental information sampled at 0.1 × 0.1 km (0.01 km²) and 1.0 × 1.0 km (1.0 km²) resolution. The 1.0 km² 'coarse' resolution represents a scale often reported in SDM investigations (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 km² '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 (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: 1) rate of change in abundance, 2) expected minimum abundance (McCarthy and Thompson 2001), and 3) 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). Habitat loss and fragmentation for agricultural production has contributed to the southern brown bandicoot (Peramelidae, *Isodon 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 expected to represent gradients that define the fundamental niche were used to generate a species distribution model (SDM) of the potential distribution of 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 (Supplementary material Appendix 1). These spatial layers were resampled to 0.1 × 0.1 km (0.01 km²) or 1.0 × 1.0 km (1.0 km²) pixel resolution using ArcInfo 9.3 (ESRI 2009). Variable range was similar between

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 km² and 1.0 km² models, respectively.

	<i>A. f. flavipes</i>	<i>I. o. obesulus</i>	<i>R. f. greyi</i>	<i>R. f. lutreolus</i>
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, <i>Xanthorrhoea</i> 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 incl. 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 (cells)	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 \times litters/females)	(8×1)/2 = 4	(3.1×3)/2 = 4.62	(5×3.5)/2 = 8.75	(5×2)/2 = 5
		don't breed in their 4th breeding season	don't breed in their 2nd breeding season	don't breed in their 3rd breeding season
SD	$\pm 33.75\%$	$\pm 36\%$	$\pm 30\%$	$\pm 30\%$
Survival rates (%)	24.7 (0–1)	10.5 (0–1)	11.2 (0–1)	12.47 (0–1)
	1.72 (1 yr)	65 (1 + yr)	2.53 (1 + yr)	60.1 (1 + yr)
SD	$\pm 5\%$	$\pm 5\%$	$\pm 5\%$	$\pm 5\%$
Rmax	1.574 (biol.)	1.72 (biol.)	2.075 (oregan vole; biol. 2.25)	1.243 (ave. watervole and muskrat; biol. 1.78)
Initial abundance and carrying capacity (K)	2 ha ⁻¹ , 200 km ⁻²	3 ha ⁻¹ , 300 km ⁻²	10 ha ⁻¹ , 1000 km ⁻²	7 ha ⁻¹ , 700 km ⁻²
Dispersal function, $M_{ij} = a \times \exp(-D_{ij}^{c/b})$, where D is the distance from patch i to j	$0.8 \times \exp(-D_{ij}^{0.60/24})$	$0.5 \times \exp(-D_{ij}^{0.93/0.1})$	$0.5 \times \exp(-D_{ij}^{0.60/2})$	$0.5 \times \exp(-D_{ij}^{0.90/1})$
Max. dispersal (Dmax)	1.55 km	0.6 km	0.75 km	0.45 km

^aThreshold used to convert probabilities into suitable and unsuitable habitat.

^bThe limited number of presences available was retained at both scales by manually inserting missing environmental data no longer represented at 0.01 km² or 1.0 km² resolution before the species distribution models were created.

^cRegion codes represent Eyre Peninsula (EP), Fleurieu Peninsula (FP), Kangaroo Island (KI) and South East (SE).

resolutions, however, marked differences occurred in the spatial arrangement of fine resolution vector layers resampled to the coarse resolution. While some correlation occurred between layers at each scale, each layer had potential to be correlated with or represent physiological limits and 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 and patch structure

SDMs were constructed using all available occurrence data and environmental variables considered important for species survival and reproduction based on known species' ecology. The adequacy of available environmental data to represent gradients of the fundamental niche was previously demonstrated by improved model robustness verified using out-of-region validation (Haby et al. unpubl.). In this investigation, generalised linear models (GLM) were used with a binomial error distribution and logit link function were fitted in R ver. 2.13.1 (R Core Development Team 2011; <www.r-project.org>). The model structure goodness-of-fit was reported as the percent deviance explained relative to the null model (% DE) and performance statistics calculated (area under the receiver curve (AUC), Kappa, sensitivity and specificity, using the MSS threshold). The performance of each of these SDMs is evaluated in Supplementary material Appendix 2.

Each SDM was then predicted across 0.01 km² and 1.0 km² 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).

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 (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 was set to 0 at the first time step for models built at the fine-scale. The occupancy of these patches was driven by immigration during a 20-yr burn-in period of stable climate preceding each simulation (see 'Simulation' below). Over-estimating patch occupancy and animal abundance was 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, effecting 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. 2012).

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 used in a negative exponential dispersal function 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-yr of climate change based on a no-climate-policy reference (no stabilization) scenario (MiniCAM Ref.; Clarke et al. 2007). Maggicc/Scengen ver. 5 (Fordham et al. 2012) was used to generate multi-model climate averaged 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-yr burn-in period over a stable climate (held constant at 2001 level), followed by 40-yr climate change (time step = 1 yr) 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 yr climate change due to limitations in program capacity when modelling populations at the 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 increased variability in survival were chosen for the sensitivity analyses to indirectly represent missing habitat (e.g. remnant roadside vegetation) that would facilitate dispersal in a fragmented landscape and a key vital rate governing 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 between the two scales through their effect on range extents and landscape metrics associated with the distribution of habitat. 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). 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.

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 accounted for time dependent data and the 40-yr, right-censored data. The overall model structure goodness

of fit was reported as the percent 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

Overall, habitat area estimated according to fine-scale SDMs was similar to that estimated at the coarse-scale (Table 2a). 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; Supplementary material Appendix 3). 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 2a).

Available habitat was more irregularly shaped at the fine-scale than at the coarse-scale, based on the greater perimeter-to-area ratios (Table 2a) and lower correlation between patch area and perimeter-to-area ratio (mean Pearson's r -0.36 and -0.66, respectively). These habitat patches were configured in a way that increased connectivity between populations (Table 2a), enabling greater opportunities for dispersal between neighbouring patches. In contrast there was no dispersal possible at the coarse-scale where the distance between patches exceeded maximum dispersal capacity (Table 2a).

At the fine-scale, environmental stochasticity drove local extinctions in the stable population demographic models within the 40-yr 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 ('stable' climate; Fig. 2). The strength of this correlation was weaker during the climate change scenario, illustrating an indiscriminate effect of climate change on population persistence at a regional scale ('climate change'; Fig. 2).

Table 2. Summary of the a) initial habitat and population, and b) changes over 40-yr 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 Supplementary material Appendix 3.

Resolution	Fleurieu Peninsula		South East	
	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 yr of climate change:				
Patch no. (%)	–55 (30)	–41 (28)	–23 (22)	11 (88)
Habitat area (%)	–67 (24)	–47 (35)	–35 (18)	–16 (18)
Ave. abund. animals yr ^{–1}	–1329 (2041)	–3733 (2497)	–897 (918)	–804 (1304)
Population no. (%)	–44 (38)	–37 (29)	–25 (22)	–15 (23)
No. new populations created	744 (417)	15 (10)	168 (74)	8 (6)
Total available habitat that is occupied (%)	78 (27)	92 (4)	73 (14)	92 (4)
No. occupied popns yr ^{–1}	–9 (9)	–1 (1)	–5 (5)	0 (1)
Expected minimum abundance (%)	37 (25)	49 (30)	64 (14)	78 (15)

¹Averaged from 1000 simulations over the burn-in period.

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

Over 40-yr 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 Fleurieu Peninsula; Table 2b, Supplementary material Appendix 3), but was associated with greater population loss and lower median expected minimum abundance after 40-yr of simulated climate change (Table 2b). Higher rates of population

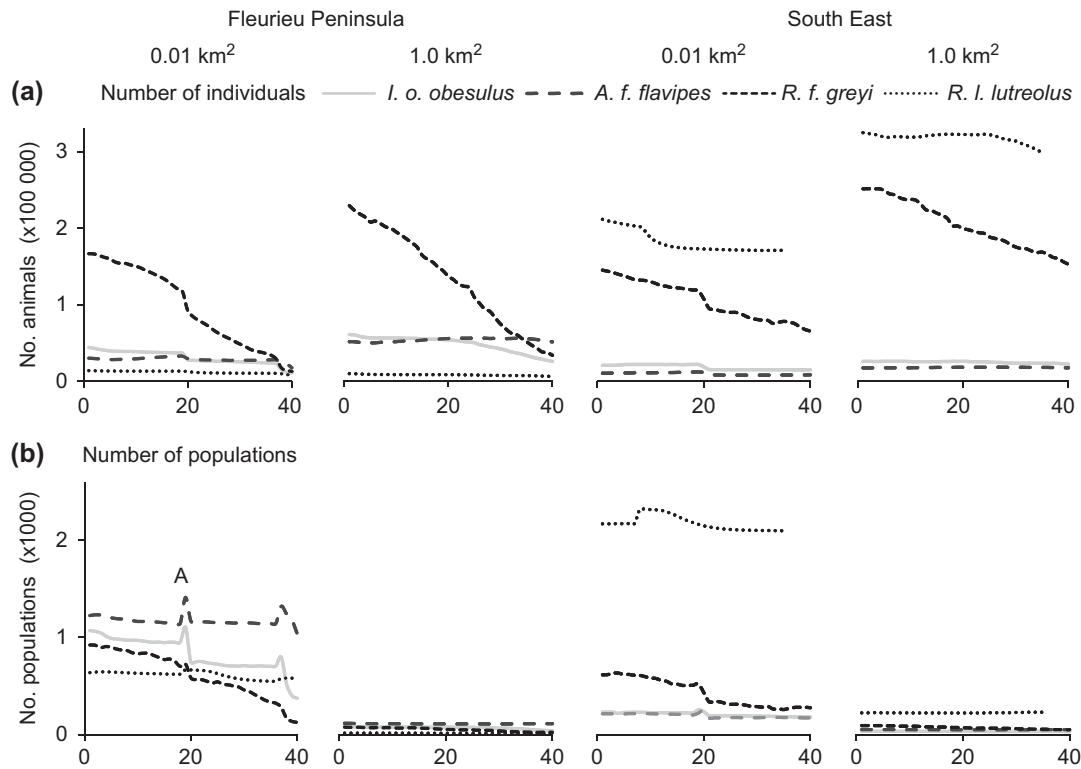


Figure 1. Number of (a) individuals, and (b) populations simulated over 40-yr of projected climate change using coupled niche-population models built using environmental information at two scales of spatial resolution (0.01 km² and 1.0 km²). Temporary peaks (e.g. A) indicate time steps where habitat suitability of many pixels fall below threshold, leading to a substantial alteration in the configuration of available habitat and temporarily increase in the number of transitional populations. Unsustainable populations perish in the subsequent time steps. The absence of these peaks from trends at the coarse resolution are an additional reflection of low metapopulation function (i.e. dispersal into new habitats).

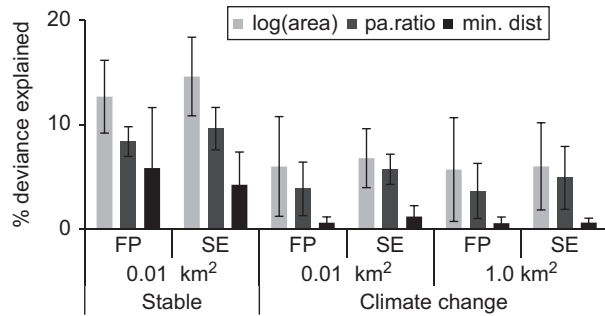


Figure 2. Average (SD) strength of each landscape variable in explaining occupancy duration for the original patches of habitat predicted during the stable climate ('stable') and 40 yr of projected climate change ('changing climate') at 0.01 km² and 1.0 km² resolution (there was insufficient environmental variability to cause local extinctions at 1.0 km² in the 'stable' climate scenario). Variables include the natural log of patch area (log(area)), perimeter-to-area ratio (pa.ratio) and minimum distance between patches (min. dist). These variables were uncorrelated at 0.01 km², but correlated at 1.0 km² (mean Pearson's r -0.36 and -0.66 , respectively). Patch metrics from transitional populations over the course of the simulation are not included.

loss were obtained despite more frequent movement of animals into available patches generated through fragmentation of occupied habitat, unsuitable habitat becoming suitable within dispersal distance of extant populations, or recolonisation of suitable habitat where the local population had gone extinct (Fig. 1b, Table 2b; Supplementary material Appendix 4). The greater decline in populations was not solely due to increased loss of small populations (Supplementary material Appendix 5).

Range shift to track habitat availability

The largest shifts in the range centroid (a parameter 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. 3). 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. 3). These patterns were also reflected in the centroid of available habitat, which in most cases, shifted NE or SE at a faster rate than occupied patches (Supplementary material Appendix 6b). Results obtained from the sensitivity analyses generally agreed with these values (Supplementary material Appendix 6).

Range shifts in both regions coincided with contracting SW or NW range edges, especially for *I. o. obesulus* and *R. f. greyi* (Fig. 4, Supplementary material Appendix 7a). At the fine-scale, contractions were lower than illustrated at the coarse-scale in the Fleurieu Peninsula. 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; Supplementary material Appendix 7b).

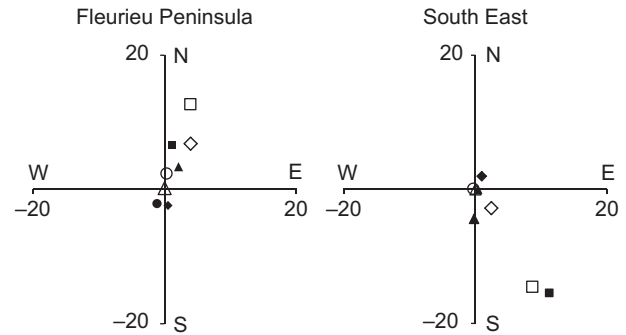


Figure 3. Shift in the centroid of occupied habitat at 0.01 km² and 1.0 km² resolution (solid or hollow symbols, respectively), in the two study areas: Fleurieu Peninsula and South East. Range shift is greater at the coarse resolution for species illustrating a shift at both scales, contrary to evidence supporting increased patch connectivity to facilitate dispersing populations at the fine-scale (i.e. reflecting greater number, variability in shape and connectivity of patches at the fine scale). Species are represented by diamonds (*I. o. obesulus*), triangles (*A. f. flavipes*), squares (*R. f. greyi*) or circles (*R. l. lutreolus*).

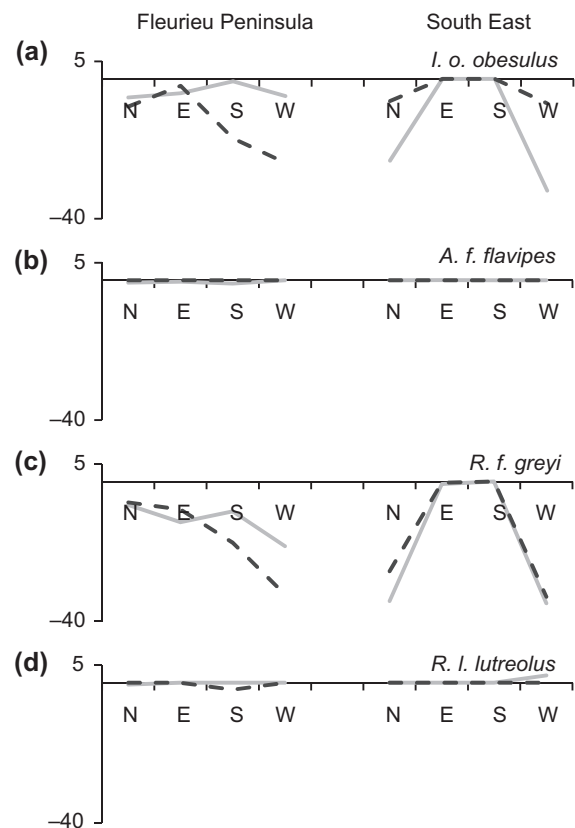


Figure 4. Contractions in the extent of habitat predicted to be occupied by four mammals (a-d), at 0.01 km² (grey solid line) and 1.0 km² resolution (dark grey dashed line), within the Fleurieu Peninsula, and South East. Contrary to expectations greater contractions were detected at the coarse-scale 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 relating small changes in a landscape, populated by fewer populations with limited inter-patch dispersal, to greater estimated rates of decline in the number of individuals and range shift (when detected), using coarse-scale environmental information. Initial estimates of the average total area of available habitat and maximum patch size were similar at both scales (Table 2a). However, patches of available habitat defined at the fine-scale were 1) much greater in number (ca 12 times) and included small patches that may act as stepping stones for shifting populations, 2) more irregularly shaped (greater range of perimeter-to-area values), 3) had a greater core area (max perimeter-to-area 0.04 at a fine-scale; 0.004 coarse-scale), and 4) 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 and had a lower expected minimum abundance (Table 2b). 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 Humphrey 1999). However, a greater rate of loss of small populations relative to habitat fragmentation was not supported in this investigation (Supplementary material Appendix 5). 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 2b), 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 1) 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'), 2) a greater number of transitional populations (Supplementary material Appendix 3), 3) increased rates of fragmentation (Fig. 4), and 4) increased occupation of available habitat in response to increased dispersal capacity in the sensitivity analyses (i.e. SA 1 and 3; Supplementary material Appendix 5).

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. 3). In these cases, greater range shifts at the coarse-scale supports the assertion that using coarse environmental data risks overestimating species' extinction risk (Austin and van Niel 2011b).

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 shift in range centroids, Fig. 3; and contractions of range edge, Fig. 4). This ranking reflected species SDMs influenced more by climate variables than additional environmental variables (e.g. topographic, soil and vegetation variables for the wet-heath specialist, *R. l. lutreolus* and *A. f. flavipes*; Supplementary material Appendix 2, Table A2). The importance of fine-scale, non-climatic landscape information in representing habitat geometry and quality and subsequently population demography and dispersal potential has support from empirical investigations across a variety of additional taxa (Bradford et al. 2003, Löbel et al. 2006, Arthington et al. 2010, Hokit et al. 2010, Baguette et al. 2011, Uezu and Metzger 2011).

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 (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).

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.

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Supplementary material (Appendix E7749 at <www.oikosoffice.lu.se/appendix>). Appendix 1–7.