Final Report

"Modelling spatial patterns in koala density on Kangaroo Island, South Australia, to inform sterilisation targets for population control"

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June 29, 2019

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Contents

1 Executive Summary

- We used a multinomial-Poisson model to jointly estimate the detectability and density of koalas from island-wide long-term monitoring data collected by the Kangaroo Island Koala Management Program (KIKMP). The models were constructed to include nonlinear patterns in spatially-varying environmental covariates that explained variation in koala density. These models provided a snapshot of spatial patterns of koala density, as well as starting values (including uncertainties) for the spatial population model.

- Detectability of koalas in monitoring surveys was generally higher for more experienced observers, highlighting the importance of the core monitoring staff of the KIKMP.

- We assessed the congruence of an "historical" map of the extent of suitable koala habitat (based on aerial survey mapping of koala food trees) and mapped locations where koalas were actually captured for sterilisation as part of the KIKMP. A large proportion of captures occurred outside the historical habitat extent.

- To further evaluate where koalas occurred, we modelled the spatial point pattern of koala captures from the KIKMP sterilisation program (n = 14439) to estimate spatial variation in the intensity of captures associated with environmental covariates. Model predictions show that there are areas beyond the historical habitat map to have a high intensity of captures.

- Using spatial population simulations, we tested different sterilisation strategies and intensities, and provide recommendations for the target number of female koalas to be sterilised each year for the next 10 years. Simulation modelling indicated that sterilisation targets of 400 to 500 female koalas per year should be sufficient to achieve a relatively stable population, and to limit the area of habitat impacted by koala densities greater than 0.75 individuals per hectare. These results assume that subcatchments where koala density is high are prioritised by the management programme.

- Spatially-targeted sterilisation strategies were more effective at controlling koalas below threshold densities. Targeting high-density subcatchments each year performed substantially better than random sterilisation strategies, as did a more realistic strategy of rotating effort through important subcatchments every 5 years. Under these targeted strategies, sterilisation effort was concentrated in a few subcatchments within the Cygnet River, Eleanor-Timber Creek, and South Coast management units.

- In simulations that assumed high starting densities of koalas in blue-gum plantations, koalas emigrated from plantations and increased the population density in native vegetation. Consequently, a higher sterilisation effort was required, concentrated in the South-West management unit.

- Key knowledge gaps include the paucity of information on current female sterilisation rates, and the potential impact of high koala densities in blue-gum plantations. More precise estimates of the proportion of females sterilised across the island would inform

the parameterisation of population models, and also provide valuable information on the effectiveness of the koala sterilisation program. Similarly, better information on the density of koalas in blue-gum plantation, and the current rates of dispersal between plantation habitat and adjacent native vegetation, would assist with targeting sterilisation effort appropriately, and with evaluating the impact of displacing koalas once harvesting commences in the blue-gum plantations.

- There is an urgent need to re-evaluate the extent of suitable koala habitat on Kangaroo Island, particularly because the input starting abundances of koalas used for the spatial population model are dependent on this extent, and so affect the sterilisation targets.

2 Introduction

Population (or 'demographic') models can be used to simulate the population dynamics of a given wildlife species over time, and to evaluate different management alternatives. Previously, a non-spatial population model was developed to simulate the effect of different annual sterilisation targets on the population trajectory of koalas within discrete Kangaroo Island management units, over a 10-year management time frame (Delean et al. 2014, 2016). The current project improves on this past approach by developing a spatial population model for koalas that includes spatial variation in koala density and the dispersal of koalas across the landscape. Therefore, this new model provides a more realistic simulation that accounts for immigration into regions where sterilisation effort has been invested and also the influence of unmanaged 'refuge' populations (e.g., blue-gum plantations) that are (presumably) made of up of unsterilized koalas. The spatial population model can be used to test different 'scenarios' that represent different intervention options available to managers and their expected impact on the Kangaroo Island koala population in space and time. In particular, different sterilisation targets and scenarios can be evaluated with regard to a number of metrics, including their impact on the probability of achieving stable or declining koala densities, or their ability to control koalas to threshold densities below desirable levels. In the future, the spatial model could be used to evaluate additional management scenarios, including the impact of harvesting blue-gum plantations and spatially-targeted sterilisation regimes.

The values of the parameters used in a spatial population model must be informed by real-world estimates of the dynamics of the koala population on Kangaroo Island. Therefore, there are two stages in the analysis of the population model. The first is to use the existing long-term koala monitoring data to build spatial models of: (i) koala density, and (ii) of the proportion of females sterilised. In the second stage, these estimates, and measures of their uncertainty, are used as inputs to the spatial population model. The upper bounds of estimated koala density across the four "census" monitoring surveys of koalas on kangaroo Island (in years 2000, 2006, 2010, and 2015) were then used to determine a spatial layer of population carrying capacity to inform the population model. We also used a combination of information from the long-term monitoring survey, as well as koala capture records from the sterilisation program, to derive estimates of the proportion of females sterilised in the population.

The specific aims of the population modelling were to:

1. To develop a spatial population model that incorporated spatial variation in koala density, and explicitly accounted for the dispersal of koalas across the Kangaroo Island landscape;
2. To simulate Kangaroo Island koala population trajectories under different spatial approaches to sterilisation; and
3. To evaluate the performance of different sterilisation strategies to limit the area of habitat impacted by koalas above threshold densities.

In this Report, we firstly summarise the results of a series of statistical analyses used to derive koala densities and sterilisation rates from the long-term monitoring data, and then present the results of multiple scenarios using the spatial population model to identify target sterilisation rates. We present in detail the approaches used for all analyses in the Methods section, and further detail about the sampling design and methods of the long-term koala monitoring program can be found in Delean et al (2014, 2016).

3 Methods

3.1 Koala density estimated from double-observer monitoring data

We used a multinomial-Poisson model to jointly estimate the detectability and density of koalas for each Kangaroo Island Koala Management Program (KIKMP) management unit in the four "census" survey years (2000, 2006, 2010, and 2015) from double-observer counts across a set of 131 monitoring sites. We used "census" survey years because they sampled the majority of monitoring sites in the survey period within a single year. For example, the 2015 "census" survey sampled at 101 of the 131 monitoring sites (Fig. 1).

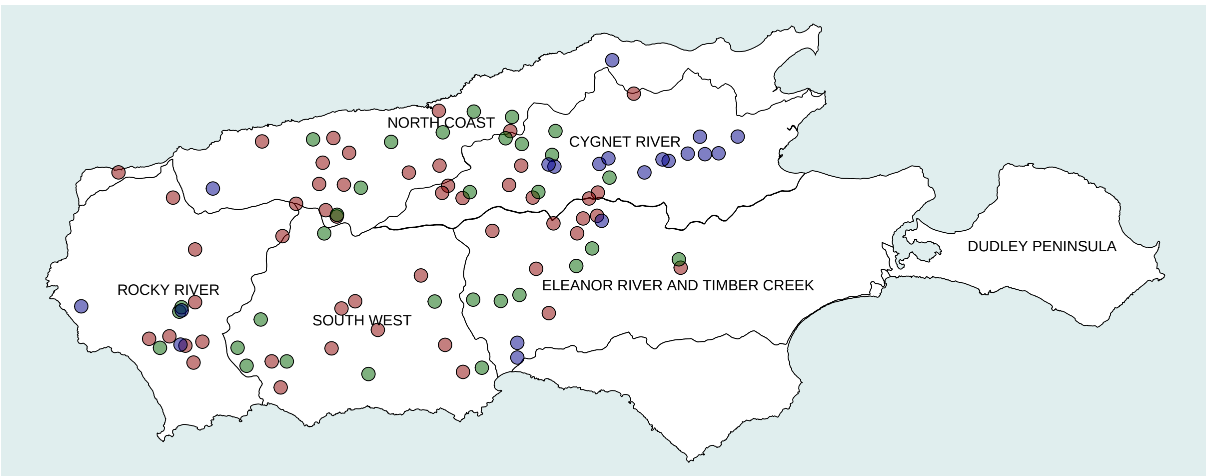

Figure 1. Monitoring sites (n = 101) surveyed in the 2015 census in low (red points), medium (green) and high (blue) quality habitat classes (based on "historical" vegetation mapping of koala food trees from aerial photographs) across the management units on Kangaroo Island.

We modelled detectability to vary between observers as this had been shown previously to explain variation in detection of koalas (Delean et al 2016) likely associated with observer experience. There was no evidence for spatial variation in detectability, and so this was not considered in any of the final model evaluations.

The models were constructed to include different spatially-varying environmental covariates that could explain variation in koala density. Exploratory analysis showed that there were non-linear relationships between koala density and environmental and spatial predictors. Therefore, we constructed smooth terms using penalized thin plate regression splines (splines are piecewise polynomials joined together at knot points) to estimate nonlinear spatial patterns in koala density (which included the possibility of threshold relationships that can not be accounted for when using global polynomial relationships). We used thin plate smoothers as they can be used in 2-dimensions to represent a bendable surface (for example, in geographic space), give optimal performance in terms of mean squared error, and are isotropic (independent of rotations of the geographic coordinates).

Methods are not available to estimate the optimal amount of smoothness directly using a penalized approach with a multinomial-Poisson model. Instead, we re-fit the models for a range of knots representing high to low smoothness (i.e., increasing "wiggliness"). We then used a model selection criterion (Akaike's information criterion corrected for finite sample sizes, AIC_c; Hurvich and Tsai 1989) to identify the optimal smoothness, as well as the contribution of other (environmental) predictors of koala density (see below). We estimated these relationships whilst controlling for observer differences in the detection of koalas and variation in the size of the monitored area of each site. We included an offset term for area (log transformed) in all the models for density to account for the proportional relationship between koala density and survey site area (i.e., model estimates were therefore on the scale of koala density hectare^{-1}). The highest ranked models based on AIC_c were then used for inference.

The candidate model set included all combinations of the following: (a) detectability was modelled as varying between observers or as constant; and (b) density was modelled as varying spatially as a nonlinear 2-dimensional smooth surface, as a continuous relationship with elevation, topographic wetness index, and rainfall. Relationships with continuous univariate covariates were modelled as flexible nonlinear functions using natural splines (where increasing degrees of freedom available to the spline increases the "wiggliness" of the fitted relationships). The bivariate thin plate spline basis functions were constructed for an island-wide spatial extent to facilitate prediction of koala density outside the spatial extent of observed long-term monitoring sites.

Model results were summarised visually with plots of estimated mean koala densities, and 95% confidence intervals, associated with the range of univariate covariate values observed. Density estimates (and their precision using standard errors) were predicted across the island on spatial grids to visualise spatial patterns in density.

3.1.1 Spatial layers of environmental data

We collated spatial layers of environmental variables from multiple sources, and these included both shape files and raster layers. Combining these data for analysis involved projecting different layers to have the same coordinate system, resolution, and extent. This data management included writing R functions to convert shape files to rasters with standardised backgrounds.

Layers included landcover vegetation classes (2010-2015 period; these are model-based estimates of the cover of vegetation classes, specifically the ”native vegetation” class for this report), elevation, topographic wetness index, and mean total annual rainfall (Fig, 2). We also collated layers for the sampling area of model projections, and for the Kangaroo Island management zones and historical vegetation classifications.

In addition, we sourced shapefiles of the road netowrk and the coastline of Kangaroo Island. These layers were used to calculate ”distance to nearest road” and ”distance to coast” variables that represent potential biases in the sampling to capture koalas for the sterilisation program (see below).

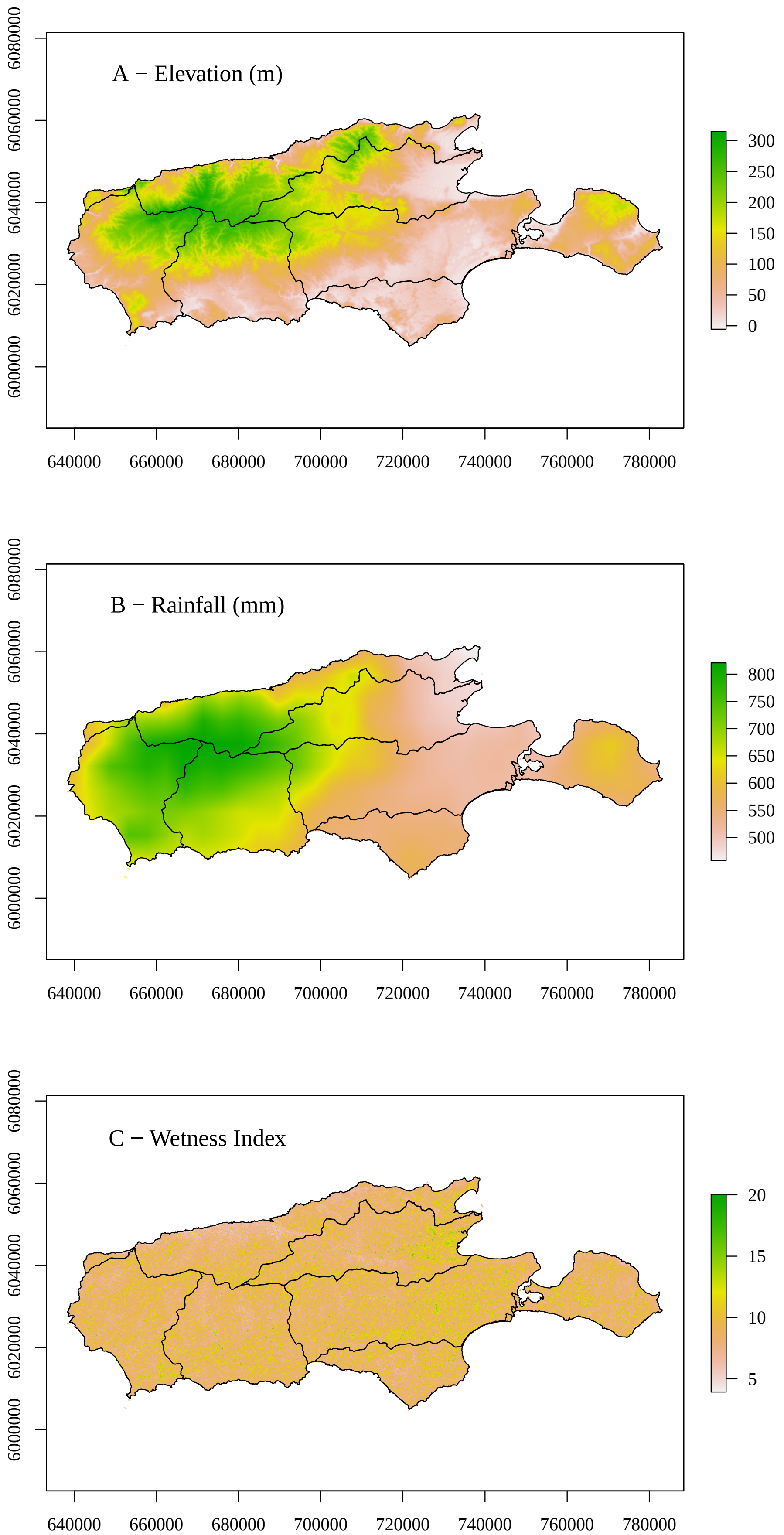

Figure 2. Environmental predictor variables on Kangaroo Island. Black lines identify the boundaries of the Kangaroo Island management units for reference.

3.2 Areas of suitable koala habitat

We required starting population abundances to initialise the spatial population model, which can be calculated based on extrapolation from koala density estimates for a given area. Previous population models have used abundance estimates based on average densities in each management unit scaled up its area (Delean et al. 2014, 2016). The scaled densities are known to be overestimates due to the unrealistic assumption that koalas occur at average density across the entire management unit area. Several approaches have been used to minimise the bias by restricting the area of a management unit to only include ”suitable habitat”. Generally, habitat suitability has been based on an ”historical” vegetation layer that represents the extent of ”food tree” habitats digitised from areial photographs. These historical data classify habitat according to koala food tree preferences (low/medium/high quality habitat).

For this Report, we also investigated the use of newly available, model-based, landcover vegetation layers with goal of using model-based predictions of suitable habitat from more recent data than the ”historical” food tree habitat layer. We extracted the ”native vegetation” class from these landcover layers as the lowest resolution classification of potential koala habitat. A comparison of the extent of ”suitable habitat” from each of these sources is shown in Fig. 3.

The model-based landcover spatial vegetation layer estimates native vegetation to cover about 3.5 times greater area of Kangaroo Island than the historical vegetation data (Fig. 3). It is clear from the extent of the landcover layer that it includes other native vegetation types that are not suitable koala food tree habitat, so this was not a useful alternative representation of ”suitable habitat”.

However, there is historical evidence that koalas utilise ”non-preferred” habitat on Kangaroo Island (Carney 2010). In order to investigate the extent of suitable koala habitat further, we used the occurrence data on koala captures from the sterilisation program to model the areas where koala are recorded (Supplementary Material Figs. 23, 24, 25). We focused on the recent captures data from 2007 until 2017 (n = 14439) because over this period we also had access to the data on occurrences of koalas that were not sterilised (i.e., they were recaptures that had previously been sterilised, or were identified as males and therefore not captured as pat of the sterilisation program). The vast majority of the ”observed but not captured” records were not uniquely identified individuals (i.e., they were clearly tagged, and therefore known to be sterilised, but the tag number was not seen or recorded). Therefore, these data are not suitable for a mark-recapture analysis that requires individual identification. Additionally, we do not have data on search effort, or the spatial extent of search area, in each sterilisation year that could be used to calculate ”catch per unit effort” or similar measures.

Our assessment of the congruence of the ”historical” food tree habitat extent with the areas where koalas are actually captured for sterilisation found that approximately half of captures occurred outside the historical food tree habitat extent. It is worth noting that this estimate of the proportion of captures ”inside versus outside” the food tree habitat layer will vary depending on how large a ”buffer” is used around each capture record when classifying habitat. However, our results were robust for buffers up to 300m. An analysis of captures occuring within (i.e., ”inside”) and outside of the historical food tree habitat layer showed that this was not systematically related to particular tree species in which the koalas were captured (Fig. 4). That is to say, there is no evidence that koala are showing a ”differential preference” for any tree species outside of their preferred habitat relative to those used inside the habitat layer. These results show that suitable koala habitat does extend beyond the historical food tree layer, and that we currently lack information about the full extent of available habitat.

Regarding the suitability of blue-gum habitat, there has only been a small amount of previous sampling of koalas undertaken in blue-gum plantations on Kangaroo Island, which have been mature trees and potential koala habitat since 2008 and collectively cover approximately 13000 hectares. Initial estimates based on ground surveys using the same sampling approach as for the long-term monitoring surveys indicated that koala densities were well above target densities (1.8 koalas hectare^{-1}, 95% CI = 1.3, 2.3; Molsher 2017). Further surveys during 2016-2017 using drone technology yielded slightly higher density estimates of 1.9 koalas hectare^{-1} (95% CI = 1.3, 2.4; Pin Koh and Hennekam (2017)). Therefore, koala density was set at two koalas hectare^{-1} in blue-gum plantations for one of the approaches we took for spatial population model simulations to reflect the most recent estimates (see Section 3.4.5).

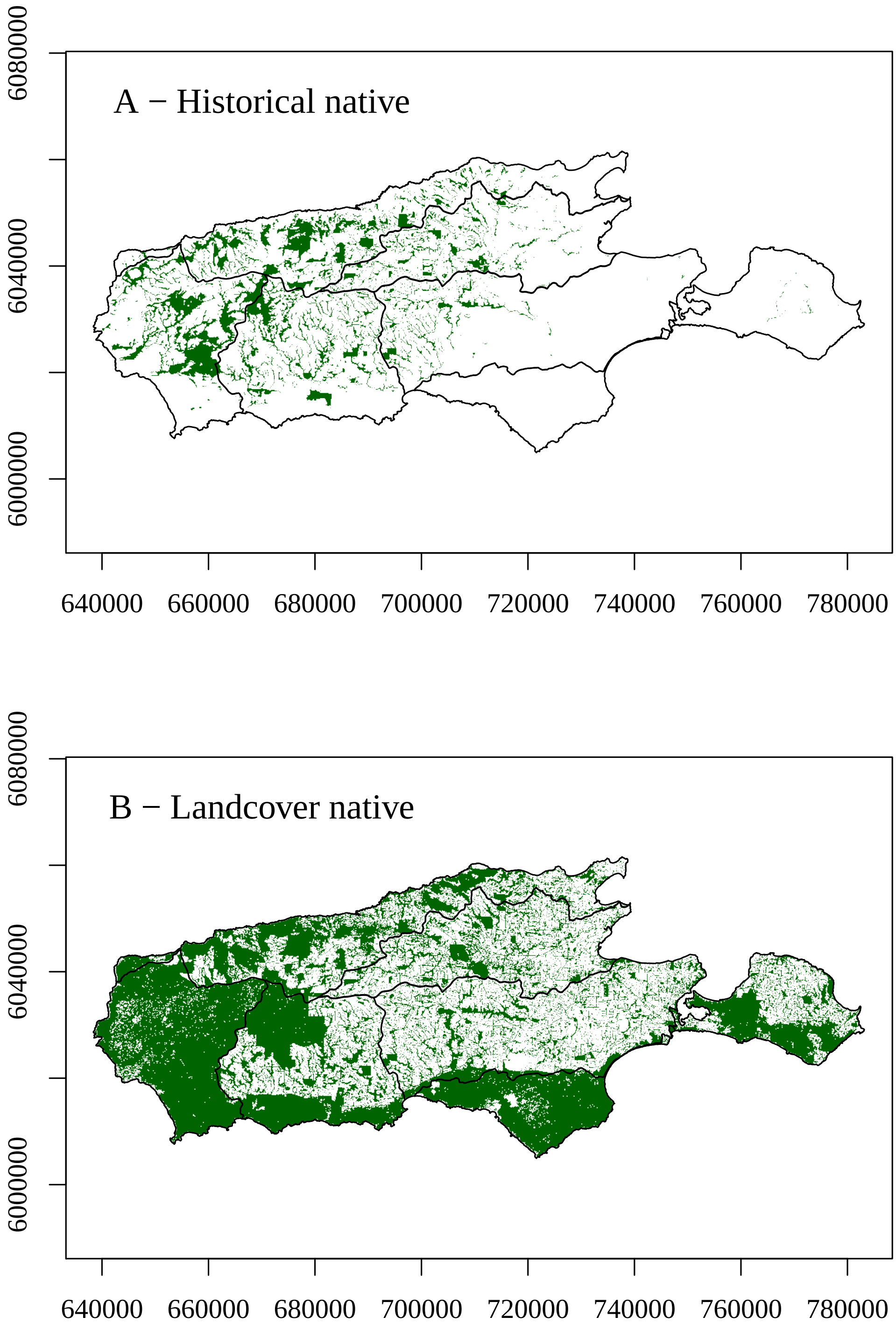

Figure 3. Areas with native vegetation on Kangaroo Island based on (A) historical food tree habitat based on aerial photographs, and (B) model-based landcover estimates of native vegetation. The Dudley Peninsula management unit and south-central region have been excluded from model predictions. Black lines identify the boundaries of the Kangaroo Island management units for reference.

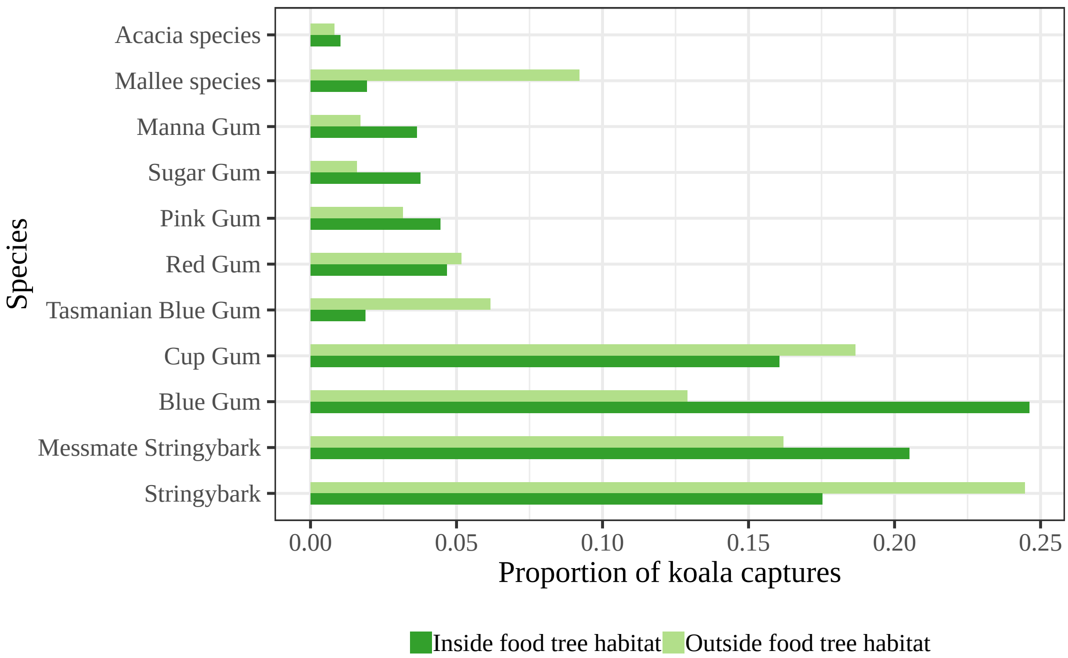

Figure 4. The proportion of koala captures that occurred in each tree species classified by whether the captures occurred inside or outside of the historical ”food tree” habitat area.

3.3 Koala sterilisation program capture data

Despite the koala sterilisation capture data not being suitable for mark-recapture analysis, these data do afford a spatially-varying measure of the intensity of koala captures. This can be considered as a representation of the combined effect of suitability of koala habitat and spatial variation in capture effort.

We modelled the spatial point pattern of koala captures (n = 14439) to estimate the intensity of captures. Essentially, this was a model of the mean number of captures per unit area for the aggregated capture occurrences over 2007-2017. We used the same set of spatial environemntal predictors as used for the koala density models (i.e., elevation, topographic wetness index, and mean annual rainfall). In addition, we included measures of the distance to nearest road (Supplementary Material Fig. 26), and distance to coast, to account for potential sampling bias in the koala capture locations.

Our approach involved sampling random locations from a background of locations on a spatial grid (100m resolution) where there were no koala captures. We assessed the optimal spatial resolution for the background sampling using methods for point process models. We re-fit the models using MaxEnt (Phillips et al. 2006) to examine the relationships between the intensity of captures and the covariates in environmental space. Subsequently, we predicted the spatial pattern of relative intensity of captures of koalas across the island from the environemntal varaibles. The spatial intensity estimates are predicted controlling for the sampling bias of distance to roads (i.e., assuming all areas are equally accessible and adjacent to roads). We use a different colour scheme when plotting these results to indicate that these are estimates of the spatial intensities of captures (i.e., spatial effort), and are <u>not</u> koala density estimates.

3.4 Spatial model of koala population dynamics

3.4.1 Model Overview

We developed a spatial, cohort-based, population model to simulate the consequences of different sterilisation strategies on Kangaroo Island koala population trajectories over time and space. The population model was developed across a lattice of 1 km2 grid cells representing suitable koala habitat. Within each cell, the total area of suitable koala habitat was calculated from a map of historical native food tree habitat available for Kangaroo Island. Starting koala density for each grid cell, used to initiate the model, was the predicted density from the spatial model of the monitoring data from the 2015 ”census”. The carrying capacity for each grid cell was taken as the maximum historical predicted koala density across all census years; the distribution of carrying capacity values from across the island is shown in Fig. 5.

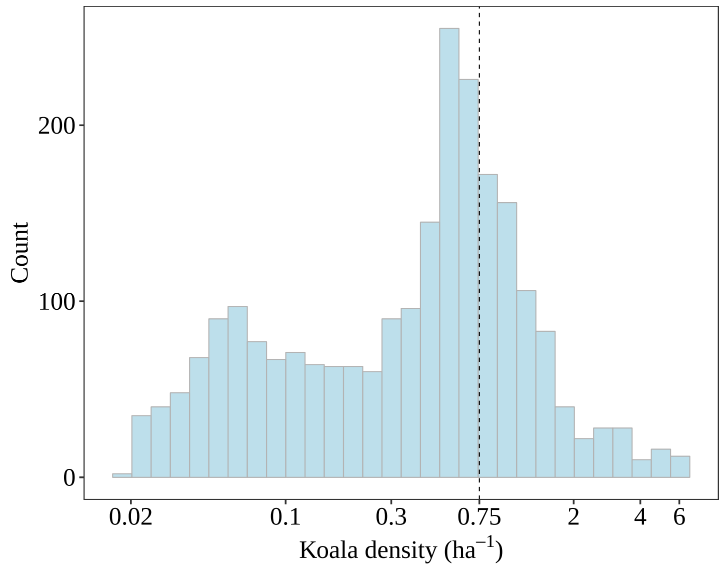

Figure 5. Frequency histogram showing the distribution of koala carrying capacity from across Kangaroo Island. The x-axis is on the log scale, with values showing the raw koala densities. The dashed line shows the management target threshold of 0.75 koalas hectare^{-1}.

Grid cells were labelled according to the ”subcatchment” in which they occurred. Subcatchments were derived from a spatial layer to represent spatial water catchment regions that were on a scale relevant to the targeted management of koala sterilisation by the KIKMP (Fig. 6). The Flinders Chase National Park management unit was treated as a single catchment as no other data were available.

The model was structured by age and sex; at each cell, the model tracked the simulated numbers of males and females of different age classes (0-1, 1-2, 2-3, and > 3 years) over time. This allowed differences in fertility rates between female age classes to be considered, and also female-only sterilisation regimes to be simulated. The model assumed a discrete-time, pre-breeding census design (Caswell 2001) and an annual time-step, with the following events occurring each year: reproduction, sterilisation, mortality, dispersal, ageing, and a population census. The simulation also assumed density-dependence in koala vital (survival and fertility) rates, which were improved when the population was reduced to low density.

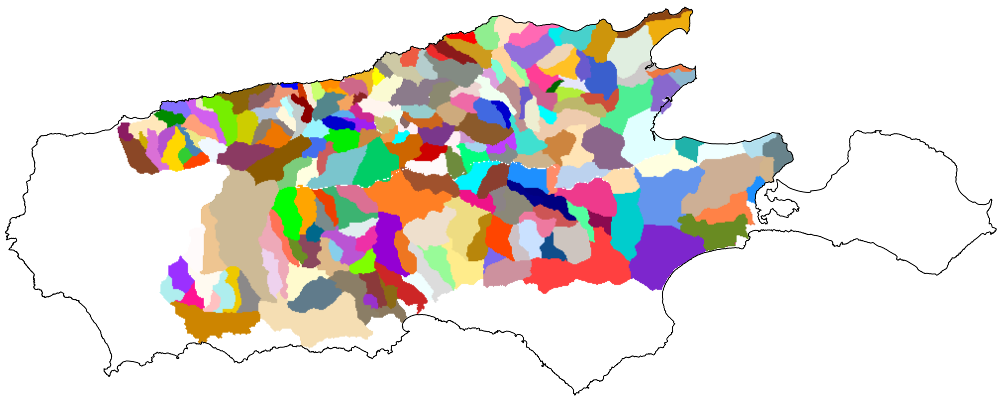

Figure 6. Geographic boundaries for subcatchments on Kangaroo Island. Colours identify the 246 subcatchments.

A density-dependent population growth rate for koalas assumes increased female survival and fertility when koalas are at lower densities. The density-dependent function used in the simulation model depended primarily on two parameters - the maximum population growth rate (r_{max}), and the carrying capacity of the environment for koalas (K). We assumed r_{max} = 0.11 based on a previous population model for koalas on Kangaroo Island (Delean et al. 2014), and on a range of estimates for koala populations in southern Australia (McLean 2003). Although there is some suggestion that r_{max} could be as high as 0.2 for koalas in favourable habitats (e.g., McLean 2003), we consider r_{max} = 0.11 to be a reasonable estimate for Kangaroo Island, where the availability of high-quality koala habitat (e.g., manna gum) is very limited. Further, we previously tested values of r_{max} up to 0.15 (Delean et al. 2014) using a non-spatial population model which did not have a substantial impact on model outcomes. For the first scenario modelled using the spatial population model in this report (see Section 3.4.5), we used a spatially-varying carrying capacity which was set using model-based estimates of the maximum historical koala density across the island. This yielded carrying capacities for each grid cell which ranged from 0.02 to 6.50 koalas ha^{-1} (Fig. 5).

Sterilisation regimes simulated in the model affected the net reproductive rate and hence the population growth rate. The sterilisation effort simulated could be distributed randomly across the landscape or in a spatially-targeted manner. The model included variation in the simulation population trajectory due to chance differences in the survival and reproductive rates among individuals in the population (termed *demographic stochasticity*). Therefore, the model was run many times for each management scenario to generate estimates of the mean and variance of the simulated population trajectory. Full details of the demographic parameters used are found in Table 1. We coded the model using the R computing environment (R Core Team 2018).

3.4.2 Reproduction

We assumed female koalas reached reproductive maturity by 3 or 4 years of age, and also assumed an equal sex ratio at birth and density-dependent fertility rates. Based on data from the scientific literature, we assigned per-capita probabilities of reproduction at carrying capacity of 0.25 and 0.75 for females aged 3 and ≥ 4 years, respectively. To allow for improvements in reproductive rate at low koala densities, we assumed maximum probabilities of reproduction of 0.5 and 1.0 for these two groups. Each year, probabilities of reproduction for each reproductive age class were then calculated assuming a theta-logistic function, which adjusted probabilities of reproduction in each grid cell as a function of the ratio of the number of koalas inhabiting the cell and the carrying capacity of that cell. To incorporate the effects of demographic stochasticity (i.e., variation in the population growth rate that occurs even if the mean demographic rates remain constant), we modelled the outcome of all reproduction probabilities with binomial distributions.

3.4.3 Survival

For simplicity, we used age-structured survival rates that were common to both sexes but differed between juveniles (0-1 year) and subadults/adults (> 1 year). For cells at carrying capacity, we assumed annual survival probabilities of 0.65 and 0.85 for these age classes, respectively, which produced a population growth rate (r) of zero when matched with the corresponding probabilities of reproduction. To allow for improvements in survival rates at low koala densities, we adjusting these initial values upwards until the maximum annual population growth rate matched that estimated for the species (r_{max} = 0.11), which resulted in maximum survival probabilities of 0.70 and 0.91 for these age classes, respectively. Again, we assumed a theta-logistic form of density dependence to calculate the survival probabilities in each cell each year, and modelled survival as a stochastic process using binomial distributions.

3.4.4 Dispersal

Movement of koalas dispersing across the landscape will impact appropriate sterilisation targets. Given empirical evidence that koalas on Kangaroo Island form relatively small home ranges (Carney 2010), we parameterised a distance-based dispersal function which assumed the probability of a koala dispersing more than 5 km in a year was 2.5%. We assumed a negative exponential dispersal function, such that the probability of moving from one grid cell to another declined exponentially as the distance between the two cells increased. Stochastic dispersal from each cell was simulated using multinomial distributions.

3.4.5 Starting values to initiate the model

Spatial estimates of koala density and carrying capacity across Kangaroo Island, calculated at a 100 × 100 m resolution, were first cropped to a habitat area deemed suitable for koalas. To achieve this, we generated a native woodland mask from a GIS polygon layer representing the historical extent of native food tree classes on the island. We also tested the influence of two different approaches to defining the initial density and carrying capacity of koalas in bluegum plantations: (1) both variables were set using estimates derived from the spatial models of koala density as described in Section 3.4.1; or (2) as for (1) except both initial koala density

Table 1. Details of the parameters governing koala demography and dispersal used for the spatial population modelling.

Parameter	Value
Koala Demography	
Age at 1st reproduction for females (years)	3.00
Female fertility (offspring per year)	1.00
Sex ratio at birth (% males)	50.00
Mean % females that breed each year (for a grid cell at carrying capacity)	
3 years	25.00
4+ years	75.00
Mean % females that breed each year (for a grid cell close to zero koala density)	
3 years	50.00
4+ years	100.00
Annual mortality (%, for a grid cell at carrying capacity)	
0-1 years	65.00
1+ years	85.00
Annual mortality (%, for a grid cell close to zero koala density)	
0-1 years	0.70
1+ years	0.91
Maximum population growth rate (rmax)	0.11
Theta (curvature parameter for theta-logistic density-dependent population growth)	2.00
Koala Dispersal	
Exponent for negative exponential dispersal function (set so that the probability of a koala dispersing more than 5 km in a year was 2.5%)	-0.92

and carrying capacity in blue-gum plantations was assumed to be 2 koalas ha^{-1} (Pin Koh and Hennekam 2017).

We conducted simulations using the second approach, in which the starting density and carrying capacity of plantations was set to 2 koalas ha^{-1}, to account for the possibility of unusually high koala densities in blue-gum habitat (relative to native habitat). This was deemed necessary because the spatial models of koala density used koala count data from census years at fixed monitoring sites, none of which were located within plantation habitat. Therefore, these data do not inform koala density in the plantations. Importantly, simulation results for this scenario should be taken as indicative only, since further surveys within blue-gum plantations across time and space would be required to generate empirical estimates of these parameters. In this second simulation approach, the low dispersal rate (as defined in Section 3.4.4) was sufficient to see large increases in koala densities adjacent to plantations. Only additional koala surveys near plantations could determine whether this simulated outcome is also reflected by koala densities on the island.

On this basis, koalas of different age and sex classes were allocated to each 1 km2 grid cell simulated by the population model, assuming an equal sex ratio and according to the stable age distribution that would be achieved for a population at carrying capacity. In the absence of detailed spatial data on current sterilisation rates, we estimated the proportion of females sterilised at the level of different management units using data from the 2015 census, and initiated the model with a population of sterilised females by applying those proportions to every cell within a unit (equally across all female age groups).

3.4.6 Sterilisation strategies

We tested the following sterilisation strategies:

(i) Random - Cells were randomly selected for sterilisation each year until the sterilisation target was met. This strategy was regarded as a reference scenario.

(ii) Target subcatchments - Each year, subcatchments were ordered by koala density, and those with the highest density were targeted for sterilisation first.

(iii) Target subcatchments (5-year rotation) - As for (ii) except subcatchments that were selected for sterilisation could not be considered for management for another 5 years. This is the most realistic scenario based on feedback from managers.

Note that no sterilisation was implemented within blue-gum plantations in the simulation, because sterilisation has not occurred with plantations historically.

3.4.7 Outputs

For each scenario tested, we ran 500 stochastic iterations of the model so that summary statistics could be computed. Over a 10-year management time frame, the model was configured to produce a number of outputs including the mean population size, the mean final population size, the probability of a population decline, and the expected minimum abundance. The model was also used to output and compare the expected area of native vegetation in which koalas exceed some threshold density (in this report, thresholds of 0.75 and 1.5 koalas ha^{-1} were tested).

4 Results

4.1 Spatial model of koala density

We used a multinomial-Poisson model to jointly estimate spatial and environmental patterns in the density and detectability of koalas, and to make predictions of koala density across Kangaroo Island in the four ”census” years based on double-observer counts from the long-term monitoring sites.

Elevation and a 2-dimensional smooth geographic surface were the best predictors of koala density (Fig. 7); these relationships were both nonlinear on the modelled (i.e., log density hectare^{-1}) scale and were back-transformed to the raw koala density scale for display. The spatial patterns in koala density varied among ”census” years, and the highest densities were observed in the high quality manna gum habitat areas in 2000 (Fig. 8). There were consistent declines in density, particularly in the higher quality habitat areas, through 2006 and 2010, and a subsequent small increase in density in 2015, particularly in the higher density areas in the Cygnet River, Eleanor-Timber Creek, and South-West management units (Fig. 8; Delean et al. 2014, 2016). Uncertainty in the density estimates, measured as the standard error of the predictions, were also mapped to visualise geographic areas where predictions have higher or lower confidence (Fig. 9).

To simplify the interpretation of the spatial patterns in density, we mapped areas with an estimated density greater than 0.75 koalas hectare^{-1}, which is the target density below which there is expected to be no over-browsing or loss of tree condition (Delean et al. 2014, 2016). Once again, we see a reduction of the area with density above the threshold from 23% in 2000, through 13% and 6% in 2006 and 2010, respectively, and an increase to 10% in 2015 (Fig. 10).

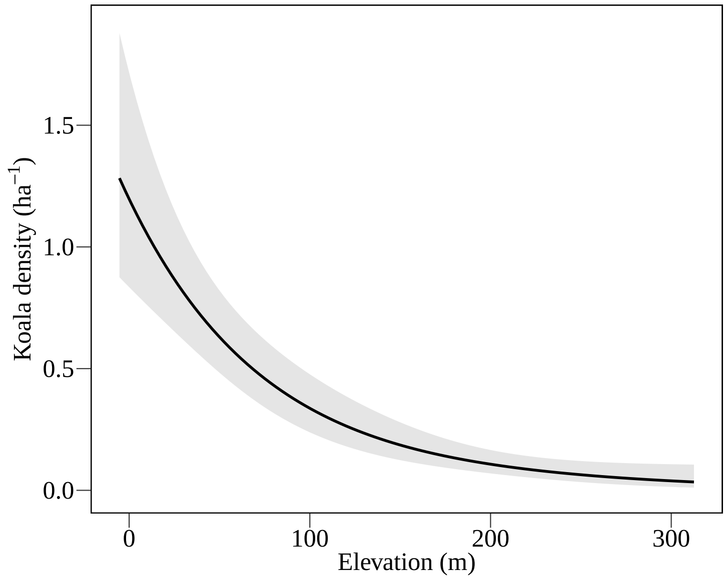

Figure 7. Relationship between estimated koala density (hectare^{-1}) and elevation based on the 2015 island-wide census. Solid black lines identify the average predictions; grey shading shows 95% confidence intervals for the fitted relationship. Estimates are partial effects conditional on other model terms (i.e., the 2-dimensional spatial smooth) being held constant at their median values.

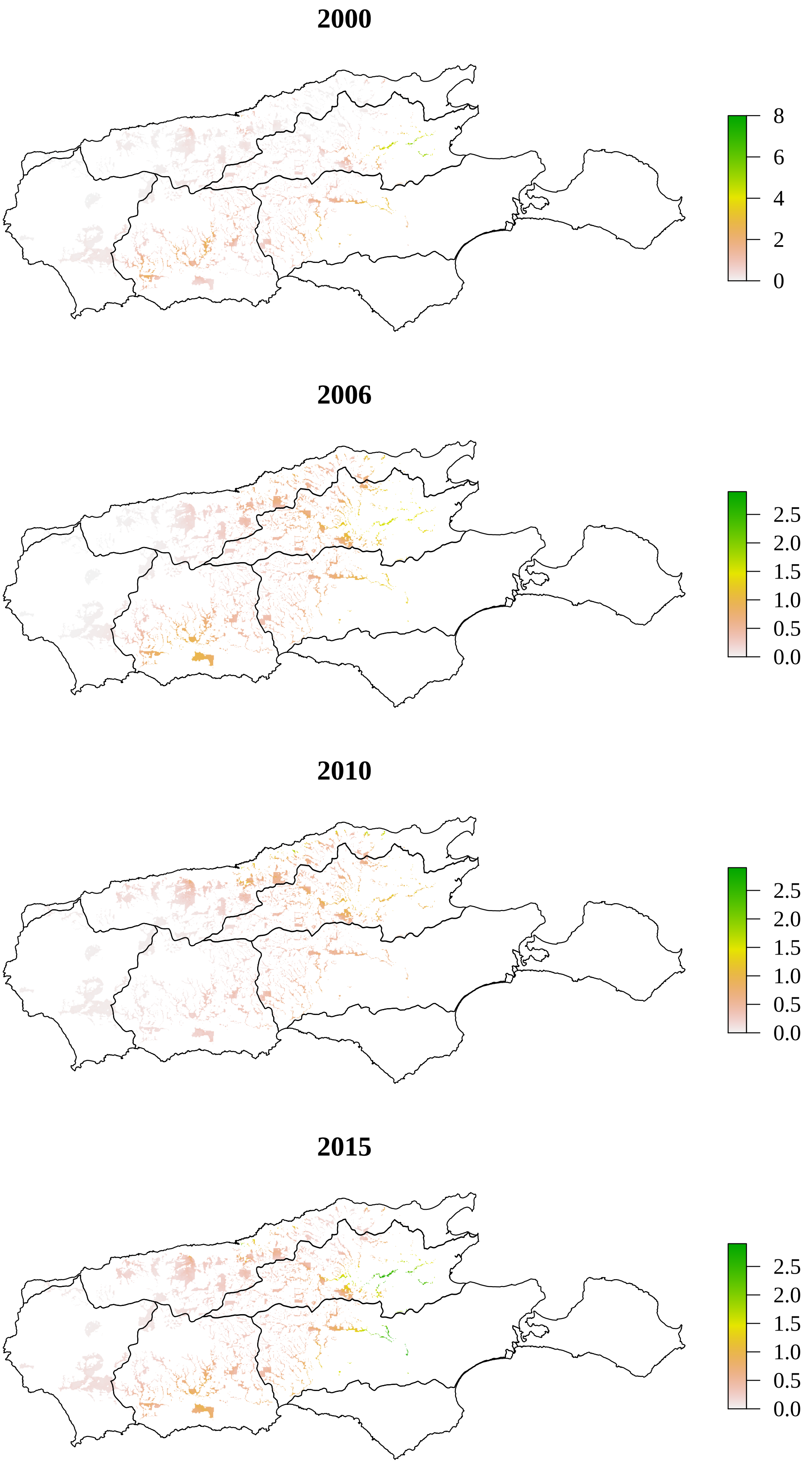

Figure 8. Predicted koala density (hectare^{-1}) across Kangaroo Island based on the island-wide census data. The Dudley Peninsula management unit and south-central region have been excluded from model predictions. Black lines identify the boundaries of the Kangaroo Island management units for reference. Note the scale differences between panels.

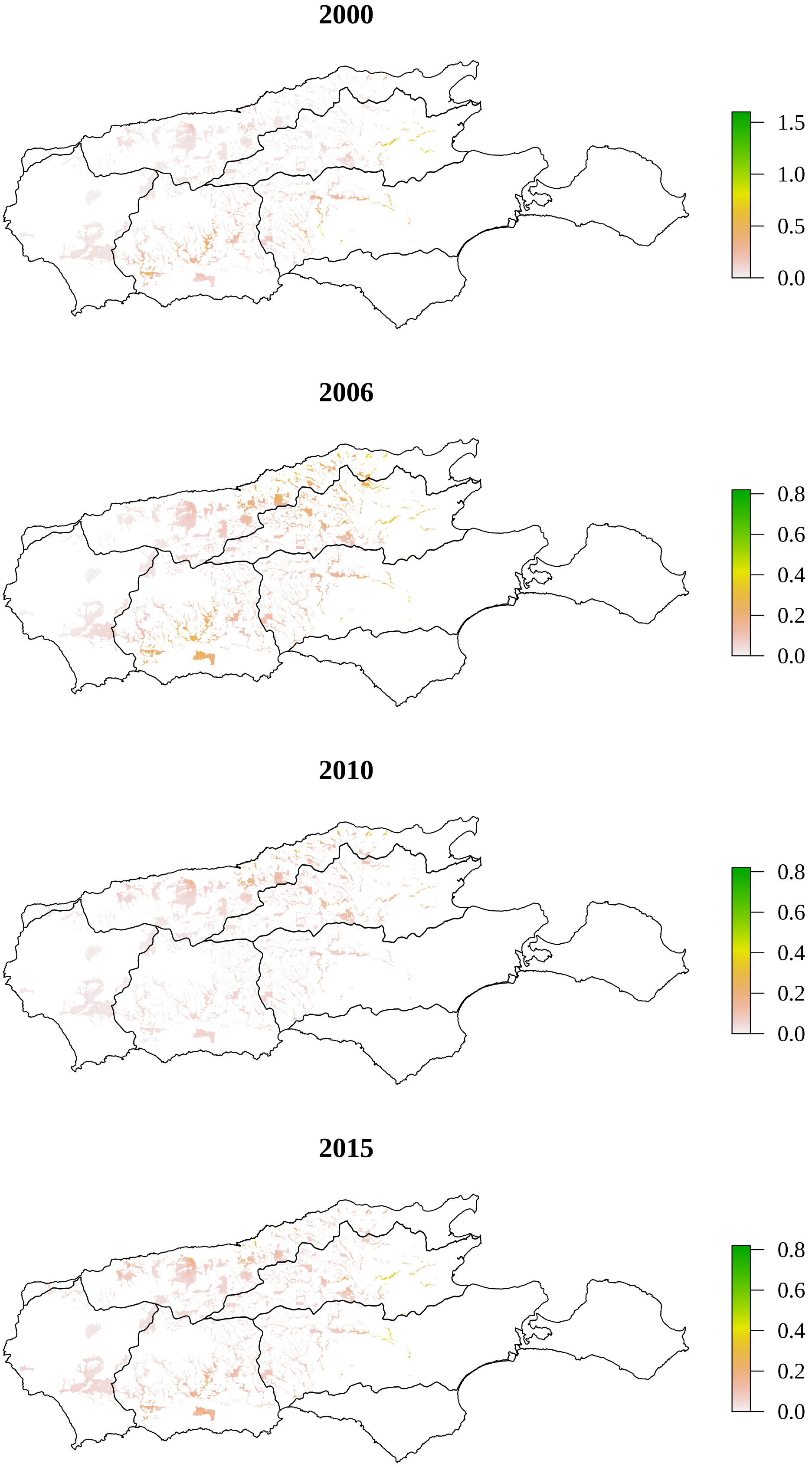

Figure 9. Standard errors showing uncertainty in predicted koala density (hectare^{-1}) across Kangaroo Island based on the island-wide census data. The Dudley Peninsula management unit and south-central region have been excluded from model predictions. Black lines identify the boundaries of the Kangaroo Island management units for reference.

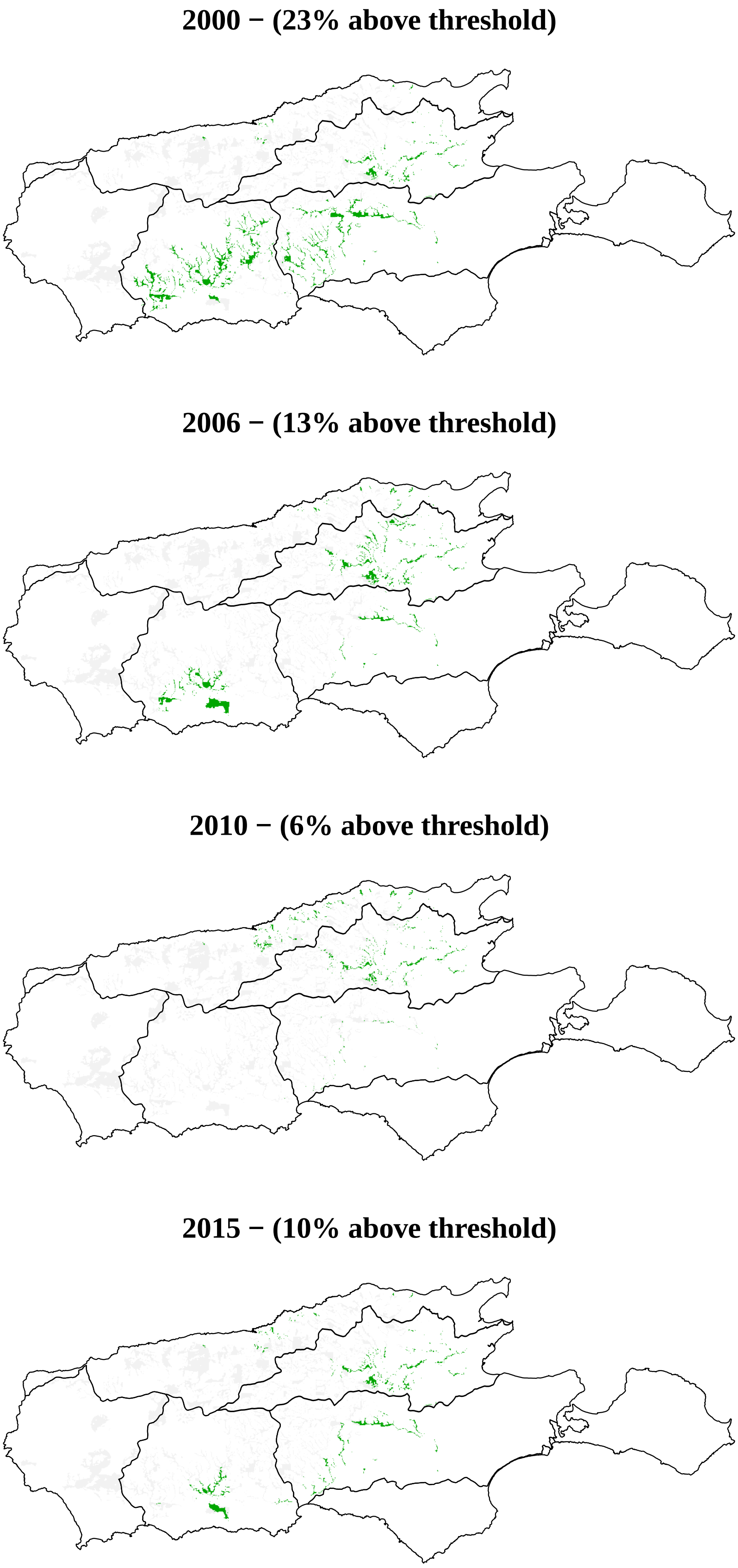

Figure 10. Areas with predicted koala density greater than 0.75 koalas hectare^{-1} across Kangaroo Island based on the island-wide census data. The Dudley Peninsula management unit and south-central region have been excluded from model predictions. Black lines identify the boundaries of the Kangaroo Island management units for reference.

4.2 Spatial model of the intensity of koala captures for sterilisation

The vast majority of koala captures for sterilisation between 2007-2017 occur in the Cygnet River and Eleanor-Timber Creek management units, but there is also good coverage across the North Coast and South-West units (Fig. 11). Flinders Chase National Park receives the least attention in the sterilisation program, since 2007 at least.

Koala captures are relatively more likely at very low and at the higher elevations, in areas with mid-range average annual rainfall, and areas with a higher topographic wetness index (Fig. 12). Captures also occur at lower intensity close to the coast, and there is strong evidence for sampling bias associated with access to roads with capture intensity declining linearly up to 2km from roads (Fig. 12).

Spatial predictions of capture intensity show a substantial increase from the North Coast and Flinders Chase National Park units toward the South-West, Cygnet River, and Eleanor-Timber Creek units. The highest intensities coincide with the areas of high estimated koala density from the monitoring surveys in Cygnet River and Eleanor-Timber Creek (Fig. 13).

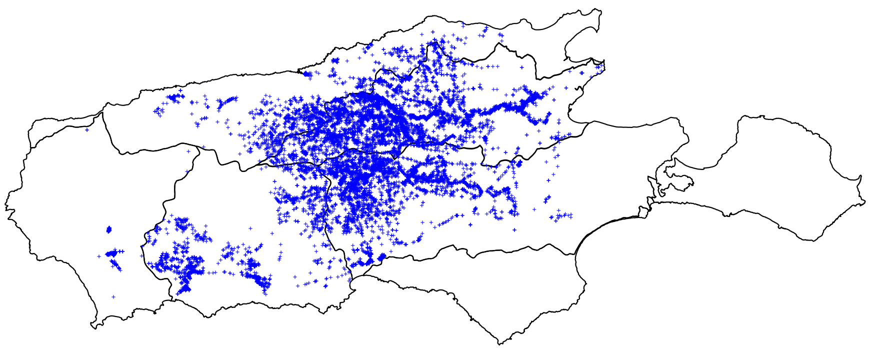

Figure 11. Geographic locations of all koala captures for the sterilisation program between 2007 and 2017. "Captures" includes individuals captured and sterilised, as well as all individuals observed but not captured (e.g., previously sterilised, males not sterilised, etc.).

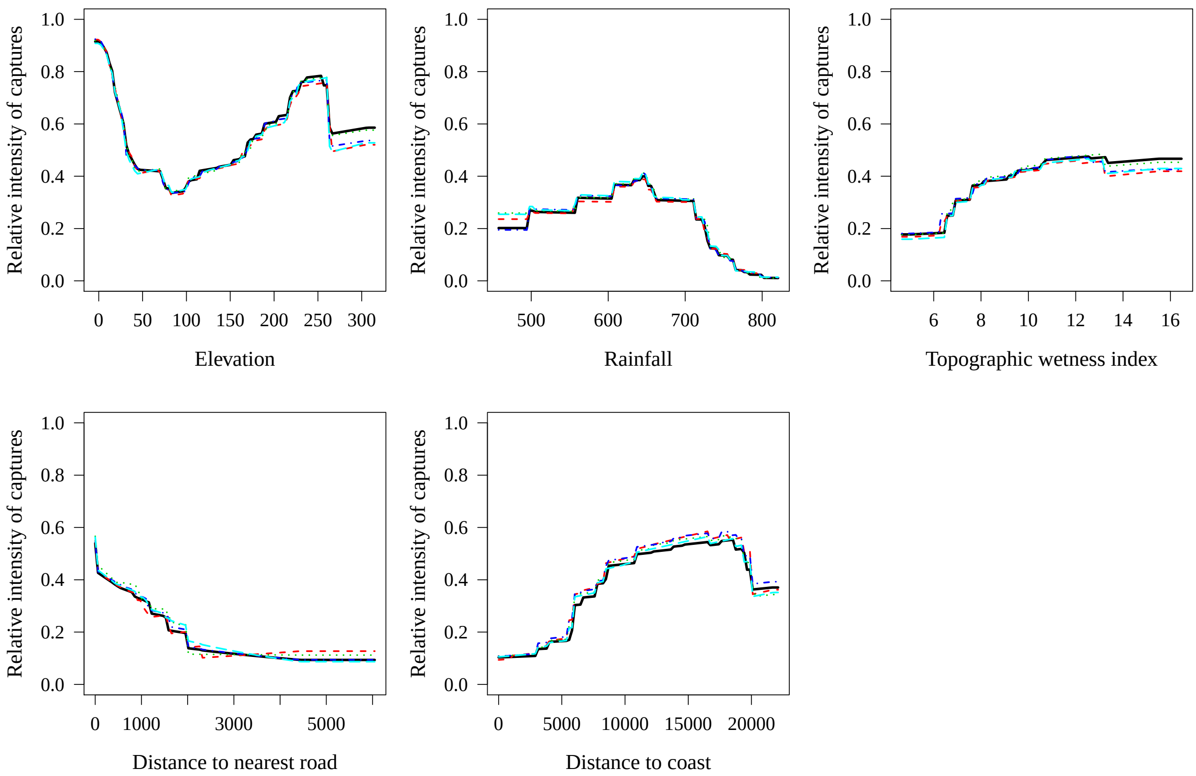

Figure 12. Partial effects of the environmental variables and sampling constraints on the relative intensity of captures of koalas estimated from point process models. Units are Elevation (m), Rainfall (mm), and the "Distance to" varaibles (m). Multiple coloured lines in each panel represent estimated effects from five random cross-validation subsets used for training the models (similarity of the lines indicates consistent estimates of the fitted relationships).

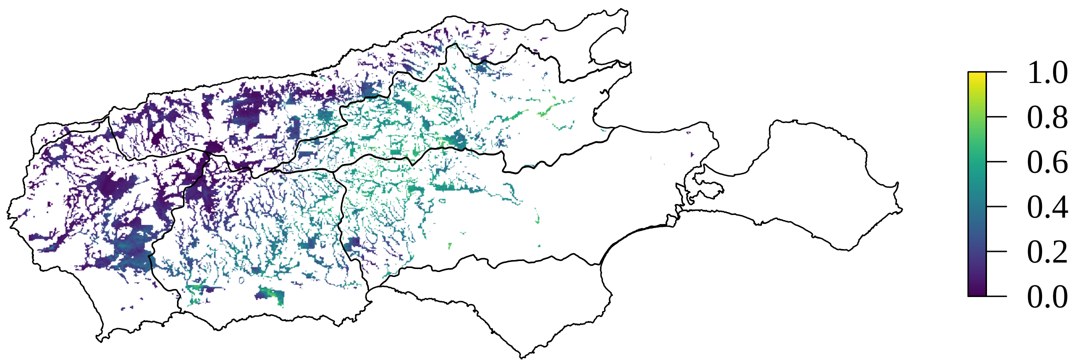

Figure 13. Spatial pattern of relative intensity of captures of koalas for the sterilisation program between 2007 and 2017 predicted from environmental variables. Note that the estimates are predicted controlling for the sampling bias of distance to roads (i.e., assuming all areas are equally accessible and adjacent to roads). We use a different colour scheme to indicate that these are estimates of the spatial intensities of captures (i.e., spatial effort), and are not koala density estimates.

4.3 Simulations assuming koala density in blue-gum plantations are set by the abundance model

In the absence of sterilisation, the simulated koala population in native vegetation (i.e., excluding plantation) grew from just under 17,000 to approximately 21,500 individuals over a 10-year time frame (Fig. 14). Across all three sterilisation strategies tested, a target of 400 to 500 females sterilised annually was sufficient to maintain a relatively stable population over this period (Fig. 14). Similarly, 400 females sterilised per year was sufficient to produce a moderate increase in the proportion of sterilised females over time (Fig. 14). Higher sterilisation targets were able to achieve a substantial population decline; for example, sterilising 800 females annually controlled the simulated population to fewer than 15,000 koalas within 10 years (Figs. 14 & 15). There was little difference between sterilisation scenarios in terms of the final population size, the final proportion of females sterilised, and the probability of achieving a population decline.

However, spatially-targeted sterilisation strategies were more effective at controlling koalas below threshold densities (Fig. 16). Using a threshold of 0.75 koalas ha-1, 6.5 % of koala habitat exceeded this density at initialisation (year 0). The spatially-targeted sterilisation of 500 female koalas per year was sufficient to prevent this area from increasing over a 10-year period (Fig. 16a). Using a threshold of 1.5 koalas ha-1, sterilisation strategies that targeted high-density subcatchments performed substantially better than random sterilisation strategies (Fig. 16b). Rotating effort through important subcatchments every 5 years (a realistic strategy to ensure unsterilized females are readily located) did slightly increase the final area of habitat above 1.5 koalas ha-1, but still performed far better than random sterilisation (Fig. 16b).

Under spatially-targeted sterilisation regimes, sterilisation effort was concentrated in a few subcatchments within the Cygnet River, Eleanor-Timber Creek, and South Coast management units (Fig. 17a). Spatially targeted sterilisation of just 400 females per year was sufficient to achieve a relative high proportion of females sterilised (> 0.3) across those important subcatchments with high koala densities (Fig . 17b). In contrast, little sterilisation effort was invested in the North Coast or Flinders Chase management units, where the carrying capacity for koalas is generally low (Fig. 17a).

Relative to a no-management scenario, targeted sterilisation naturally yielded the greatest benefits in the Cygnet River, Eleanor-Timber Creek, and South Coast management units, where substantial effort was invested in the simulation model (Fig. 18). In particular, local densities initially exceeding 3 koalas ha-1 were reduced effectively by sterilising at least 400 female koalas per year. From a management perspective, sterilisation effort could be planned at the subcatchment scale (Fig. 19).

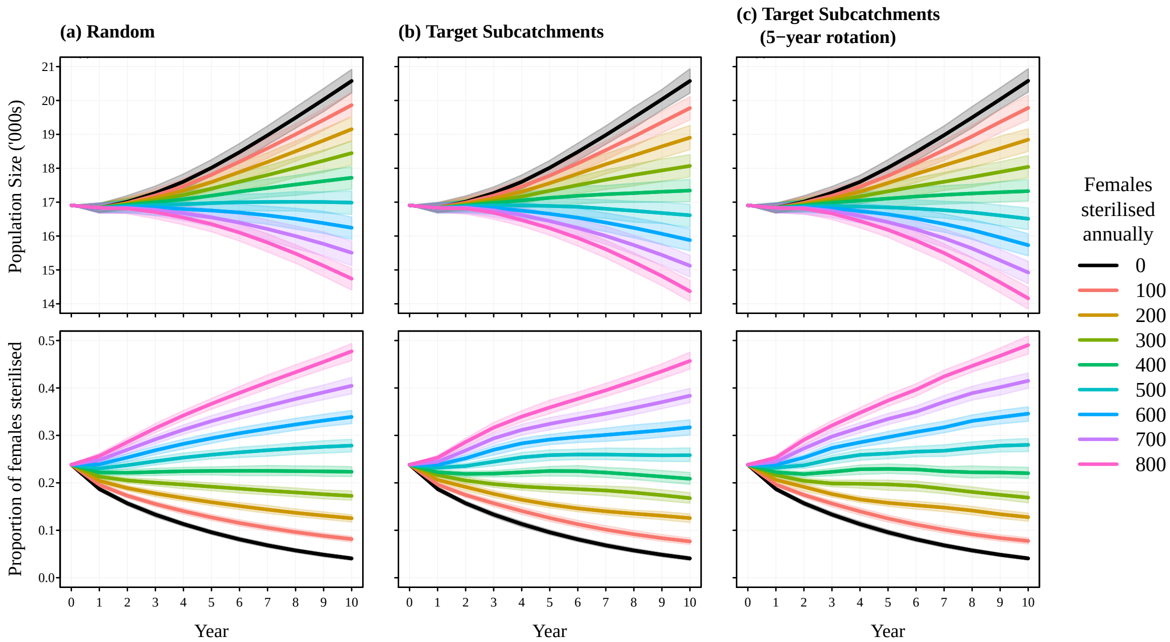

Figure 14. Simulation results assuming different annual sterilisation targets and three different spatial sterilisation scenarios: (a) Random; (b) Target Subcatchments; and (c) Target Subcatchments with a 5-year rotation. Rows represent results for: (i) total population size; and (ii) the proportion of females sterilised. Each line represents the mean from 500 iterations for each scenario, and ribbons represent 95% confidence intervals. These simulations assume an area of suitable koala habitat defined by the historical native vegetation layer, and that koala densities in blue-gum plantation are set by the abundance model.

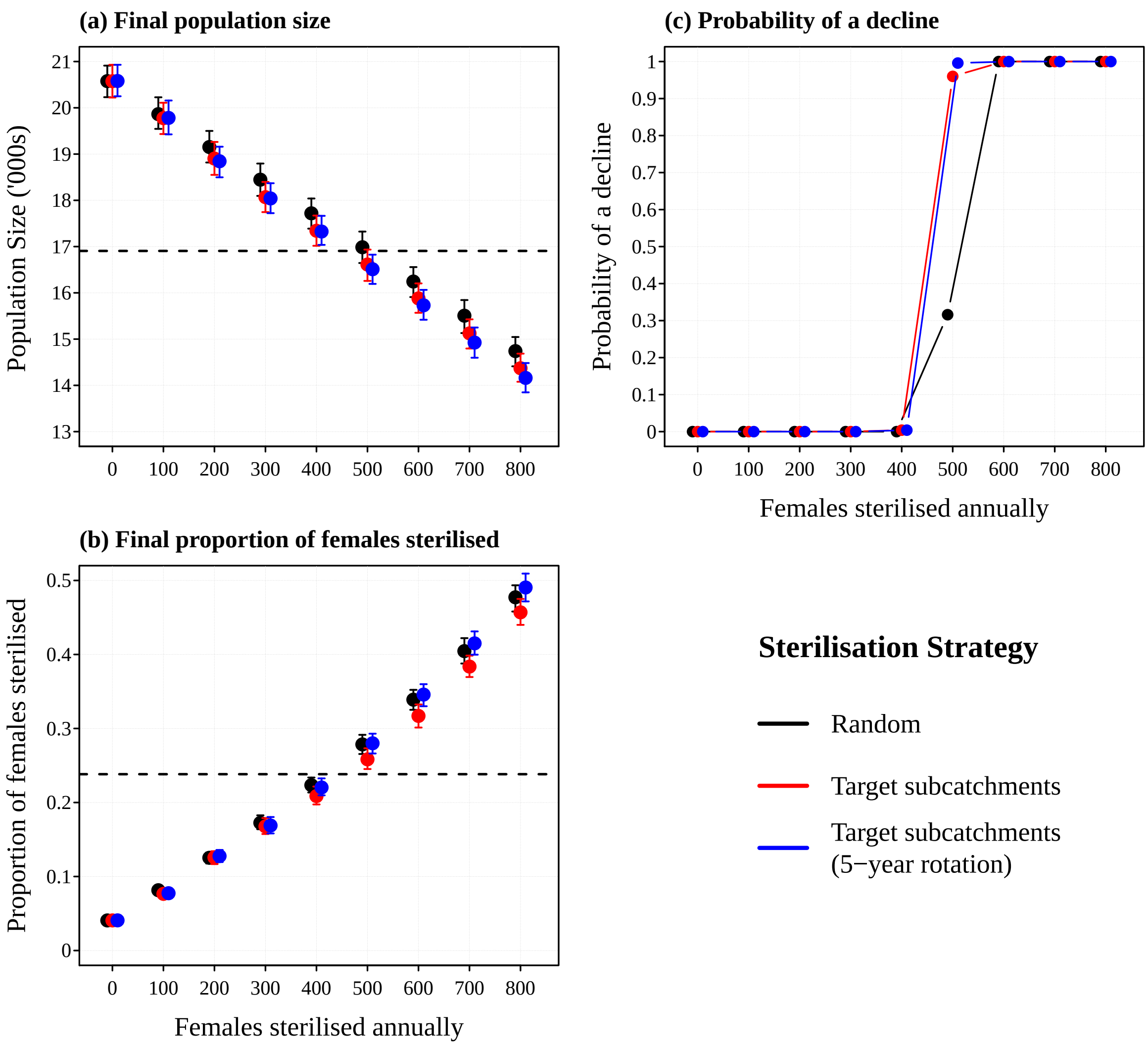

Figure 15. (a) Mean final population size; (b) mean final proportion of female koalas sterilised; and (c) the probability of achieving a simulated population decline, for different sterilisation strategies. Each point is calculated from data from 500 stochastic iterations, and error bars represent 95% confidence intervals. Dashed horizontal lines in (a) and (b) indicate the initial values used for the population size and the proportion of females sterilised, respectively. These simulations assume an area of suitable koala habitat defined by the historical native vegetation layer, and that koala densities in blue-gum plantation are set by the abundance model.

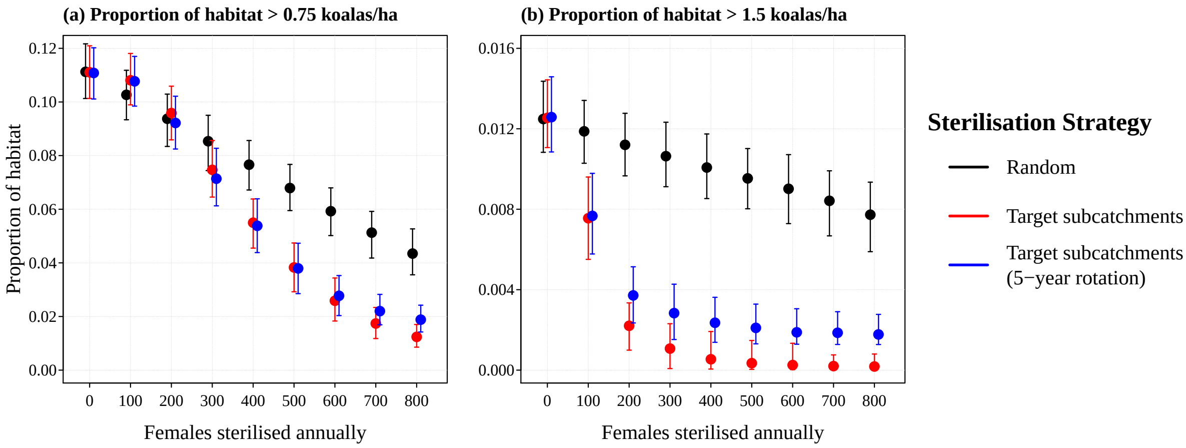

Figure 16. The final proportion of suitable koala habitat within which koala density exceeds: (a) 0.75 koalas ha-1; and (b) 1.5 koalas ha-1. Error bars represent 95% confidence intervals. Dashed horizontal lines in (a) and (b) indicate the proportion of habitat in which koala density exceeded the threshold density at the start of each simulation run. These simulations assume an area of suitable koala habitat defined by the historical native vegetation layer, and that koala densities in blue-gum plantation are set by the abundance model.

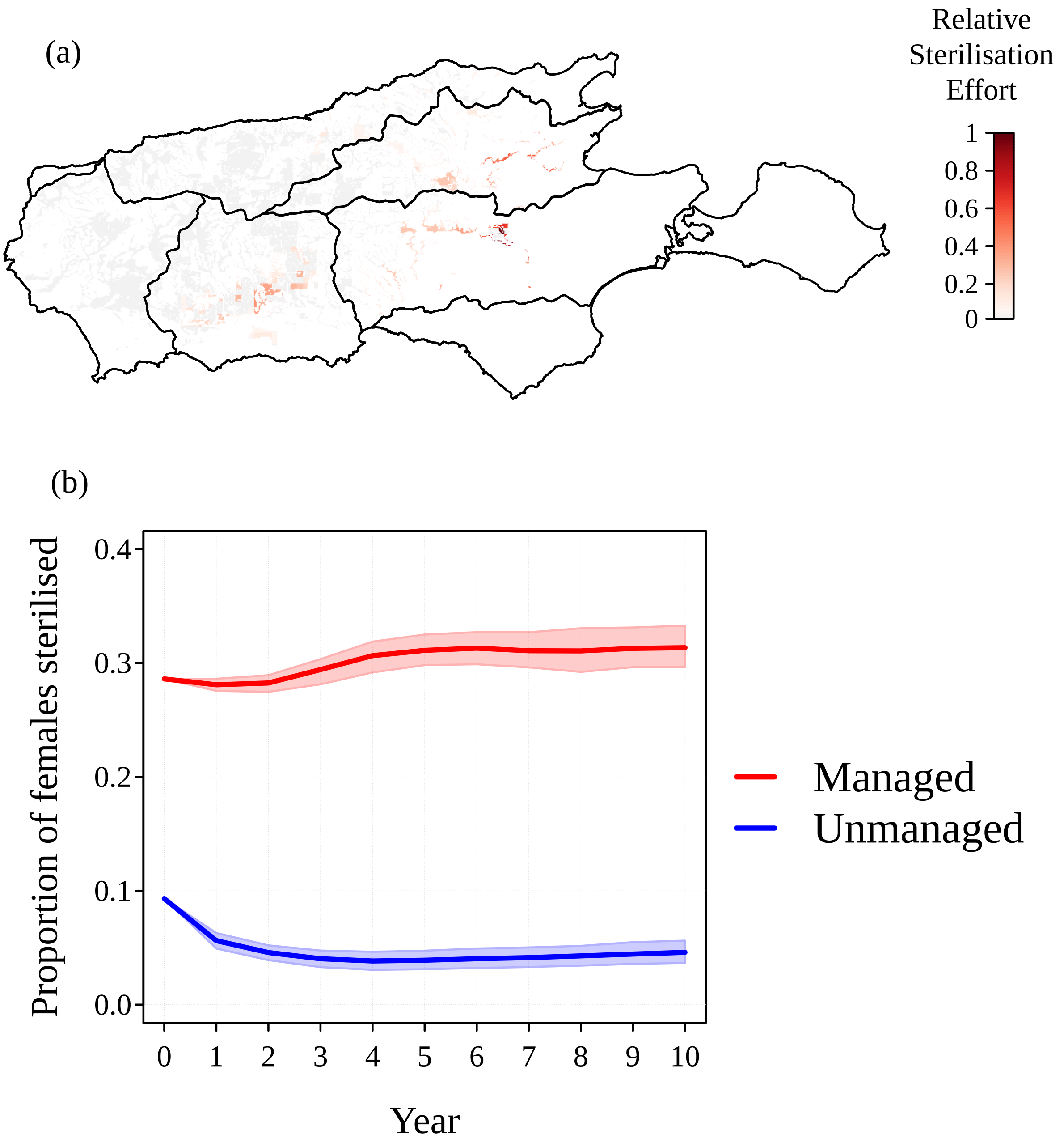

Figure 17. Simulation results assuming 400 female koalas sterilised per year and a sterilisation strategy targeting high-density subcatchments with a 5-year rotation. (a) Map of Kangaroo Island, showing relative sterilisation effort simulated across the grid of cells representing suitable habitat. White areas contain no suitable habitat for koalas, while grey cells contain some suitable habitat but were not selected for management by sterilisation in the simulations. (b) The proportion of females sterilised in managed and unmanaged subcatchments, showing targeting sterilisation can maintain sterilisation rates across important subcatchments with high koala densities.

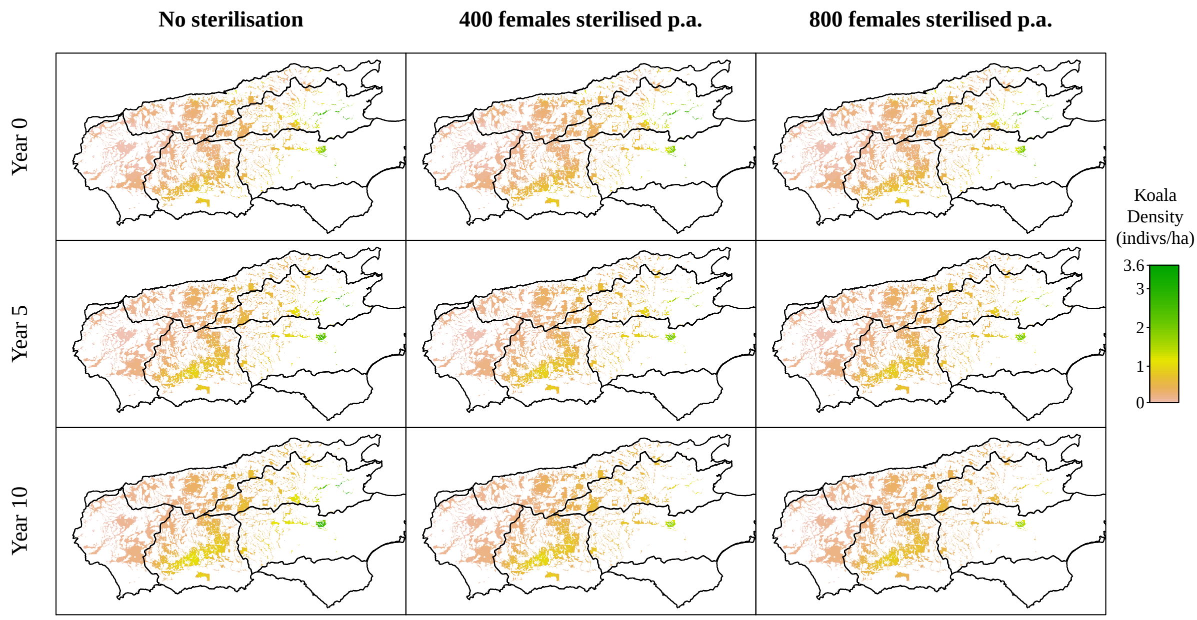

Figure 18. Simulated mean koala density on Kangaroo Island at years 0 (initialisation), 5 and 10. Results are shown for a sterilisation strategy targeting high-density subcatchments (with a 5-year rotation), and assuming 0, 400, and 800 female koalas sterilised annually. These maps include koala density simulated in blue-gum plantations.

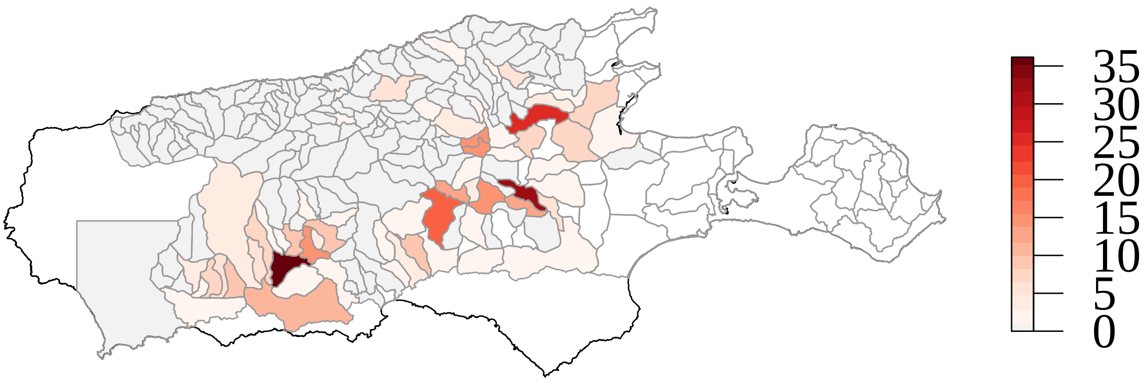

Figure 19. Annual sterilisation targets to show which subcatchments are priorities for intervention. Subcatchments targets sum to 400 across the island.

4.4 Simulations assuming koala density in blue-gum plantations of 2 koalas ha^{-1}

Simulation outcomes were substantially different if a high starting koala density (2 koalas ha-1) was assumed for blue-gum plantations. Under this scenario, some koalas emigrated from plantation and increased the size of the population inhabiting native vegetation on the island (Fig. 20). There was a corresponding increase in the sterilisation effort required to stabilise the island-wide koala population (Fig. 20). Under spatially targeted sterilisation regimes, sterilisation effort was now concentrated in subcatchments within the South Coast management unit, which contains the bulk of the plantation habitat (Fig. 21). However, even substantial sterilisation effort failed to control koala density adjacent to blue-gum plantations effectively (Fig. 22).

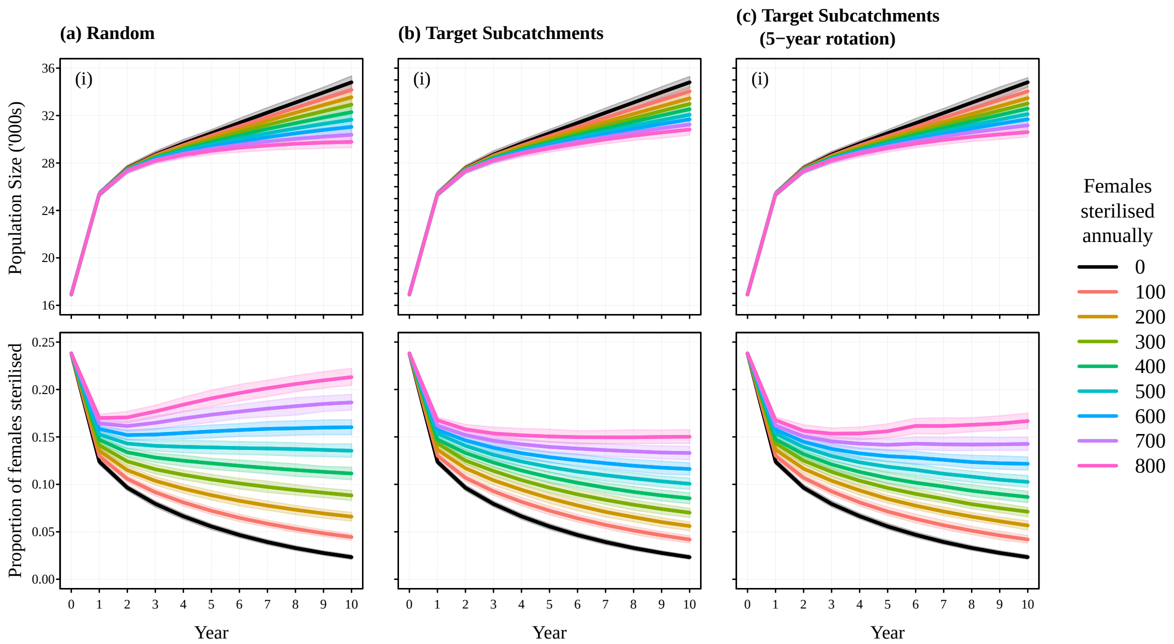

Figure 20. Simulation results assuming a starting density of 2 koalas ha-1 in blue-gum-plantation, different annual sterilisation targets and three different spatial sterilisation scenarios: (a) Random; (b) Target Subcatchments; and (c) Target Subcatchments with a 5-year rotation. Rows represent results for: (i) total population size; and (ii) the proportion of females sterilised. Each line represents the mean from 500 iterations for each scenario, and ribbons represent 95% confidence intervals.

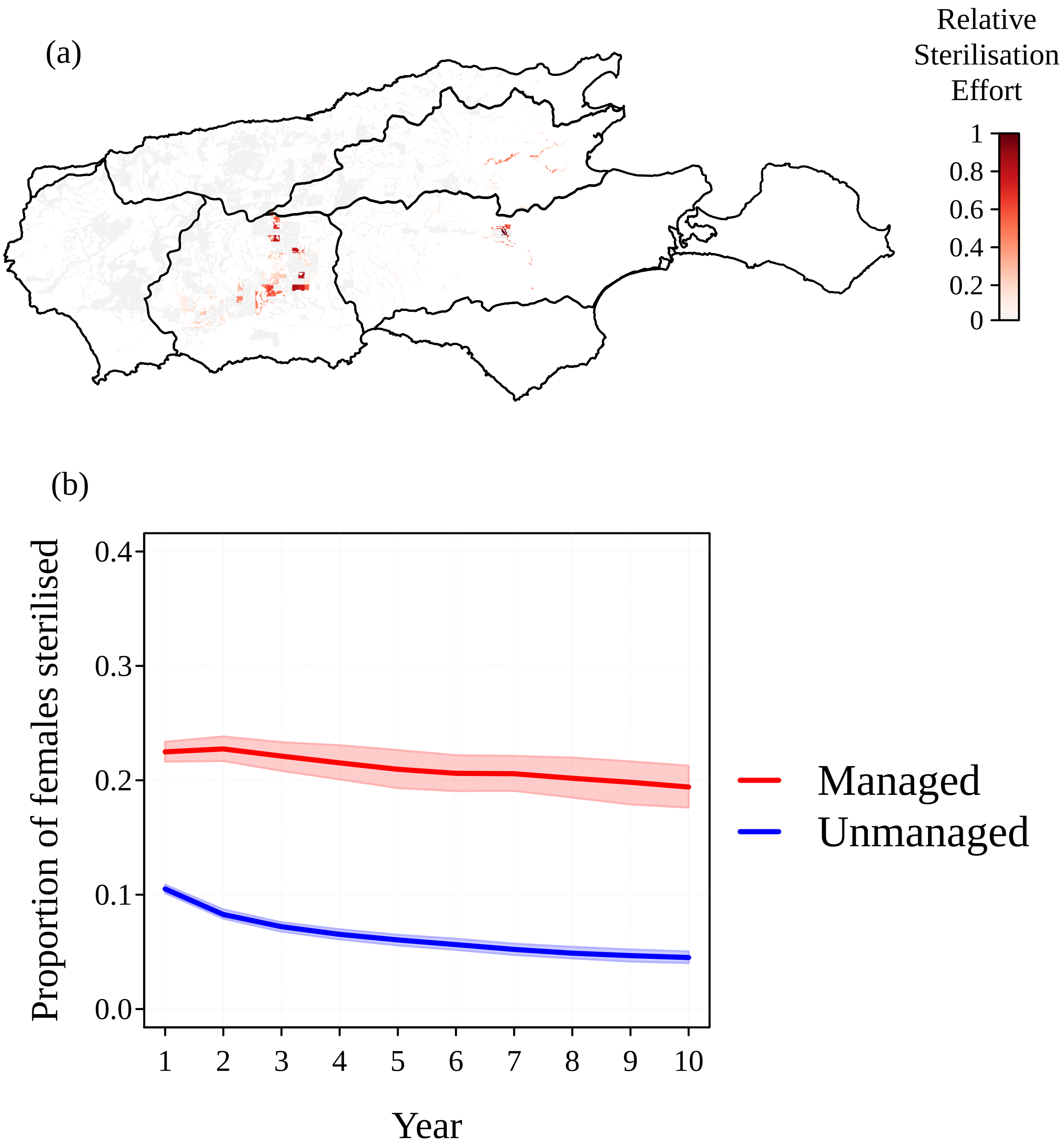

Figure 21. Simulation results assuming a starting density of 2 koalas ha-1 in blue-gum-plantation, 400 female koalas sterilised per year, and a sterilisation strategy targeting high-density subcatchments with a 5-year rotation. (a) Map of Kangaroo Island, showing relative sterilisation effort simulated across the grid of cells representing suitable habitat. White areas contain no suitable habitat for koalas, while grey cells contain some suitable habitat but were not selected for management by sterilisation in the simulations. (b) The proportion of females sterilised in managed and unmanaged subcatchments, showing targeting sterilisation fails to maintain high sterilisation rates across important subcatchments if substantial emigration of koalas from blue-gum plantations is assumed.

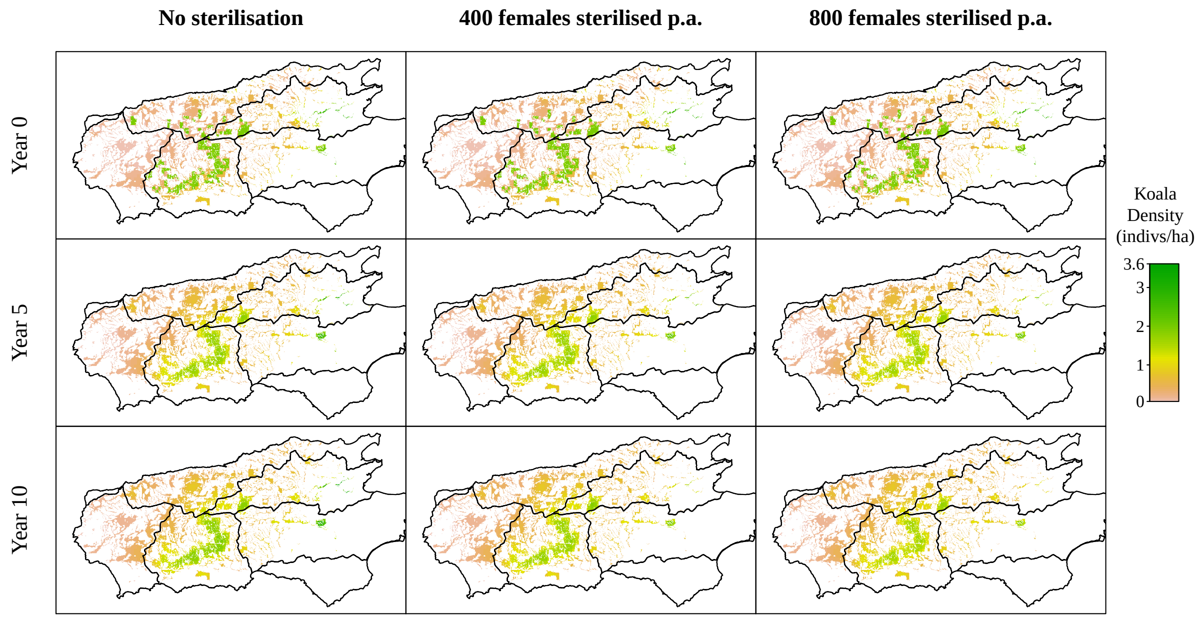

Figure 22. Simulated mean koala density on Kangaroo Island at years 0 (initialisation), 5 and 10. Results are shown assuming a starting density of 2 koalas ha-1 in blue-gum-plantation, a sterilisation strategy targeting high-density subcatchments (with a 5-year rotation), and 0, 400, and 800 female koalas sterilised annually. Note the prevalence of blue-gum plantation in the South Coast management unit, and the increased koala densities adjacent to plantation over the course of the simulation.

5 Discussion

There was substantial spatial variation in the density of koalas across Kangaroo Island. These abundance models showed clear evidence for koala density hotspots that occurred in areas with high habitat quality. Models fitted for the time slices representing "census" monitoring years reflected known trends of declining densities from the earliest survey years, but also show spatial variation in those trends and are probably influenced by changes in locations of sterilisation efforts through time. Mapping the locations with estimated densities above the target threshold of 0.75 koalas hectare^{-1} helps to identify these changes, and highlights the importance of the ongoing monitoring surveys to evaluate the impacts of sterilisation efforts and to identify areas where management efforts should be focused in future years. These findings are also reflected in the outcomes of the simulated sterilisation strategies from the population models that are discussed below.

An assessment of the congruence of an "historical" map of the extent of koala habitat (based on aerial survey mapping of koala food trees) and mapped locations where koalas were actually captured for sterilisation as part of the KIKMP showed that a large proportion of captures occurred outside the historical habitat extent. There was no qualitative evidence to suggest a preference for any specific vegetation type relative to availability, either inside or outside the historical habitat extent. This suggests that suitable koala habitat may extend beyond the boundaries of the historical map of suitable habitat.

To further evaluate where koalas occurred, we modelled the spatial point pattern of koala captures from the KIKMP sterilisation program (n = 14439) to estimate spatial variation in the intensity of captures associated with environmental covariates. We included measures of the distance to nearest road, and distance to coast, in the models to account for potential sampling bias in the koala capture locations. We found a strong overlap between the historical habitat distribution and areas where the the model predicted the intensity of koala captures to be higher (representing higher capture effort). However, the model also predicts areas beyond the historical habitat map to have a high intensity of captures. This result highlights an urgent need to re-evaluate the extent of suitable koala habitat on Kangaroo Island, particularly because the input starting abundances of koalas used for the spatial population model are dependent on this extent, and so affect estimates of suitable sterilisation targets.

Simulations indicate that the koala population on Kangaroo Island in native vegetation is expected to grow substantially in the absence of sterilisation control measures. However, a rather modest target of 400 to 500 females sterilised annually was sufficient to maintain a stable population over this period, and to produce a moderate increase in the proportion of sterilised females. But real gains can be made by implementing sterilisation strategies that target areas of known higher density (informed by the ongoing monitoring surveys). Rotating density-targeted sterilisation efforts at the scale of subcatchments over a five-year cycle produced equivalent results to the density-targeted strategy, however this approach has the obvious benefits of a greater spatial coverage of sterilisation efforts through time and would help prevent surges in density in areas with slightly lower densities that would otherwise receive delayed attention.

Assuming koala density in blue-gum plantations are set by the abundance model, our population modellings suggests that the spatially targeted sterilisation of 400-500 female koalas per year is sufficient to maintain a stable Kangaroo Island population, and to control the area of habitat impacted by koalas at high densities. These results contrast with those from our previous non-spatial modelling, which indicated 600-700 females must be sterilised per year to control the koala population. The primary reason for this difference is that the spatial population model uses spatially explicit starting densities and estimates of carrying capacity across a grid of cells representing suitable koala habitat. Consequently, areas with low carrying capacity for koalas (e.g., within the Flinders Chase National Park) experienced little or no population growth within the spatial model, and therefore sterilisation effort was not required in these regions. Further, the spatial model highlights that targeted management in high-risk subcatchments can be effective at controlling the area of habitat impacted by koalas above threshold densities of 0.75 or 1.5 individuals ha-1 (Fig. 15).

When the starting density (and carrying capacity) in blue-gum plantation was increased to 2 koalas/ha, more sterilisation was required to control the koala population in native vegetation. This result reflects the fact that the model allowed koalas to disperse from plantation to nearby native vegetation, which increased koala density in those areas (Fig. 22). As a result, more sterilisation was required overall, and more simulated sterilisation effort was invested near the blue-gum plantations, particularly in the South Coast management unit (Fig. 21). This result highlights the gap in our understanding of how koalas use blue-gum plantation, and how this affects koala density in adjacent native vegetation. Future empirical work could tag koalas with GPS devices, both inside and outside plantations, to quantify movement between these two habitats. This information would be particularly useful to inform spatial modelling that included the displacement of koalas due to blue-gum harvesting, and their possible impacts on native vegetation as a result.

5.1 Statistical software

All analyses were conducted using the statistical programming platform R (R Core Team, 2018; `http://cran.r-project.org/`). The multinomial-Poisson model used the functions in the R package `unmarked` (Fiske and Chandler, 2011), and we used `mgcv` (Wood, 2003) for thin plate regression splines. We also used packages `spatstat` (Baddeley et al. 2015), `ppmlasso` (Renner and Warton 2012), and `sdm` (Naimi and Araujo 2016) for fitting and interpreting point process models.

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7 Supplementary Material

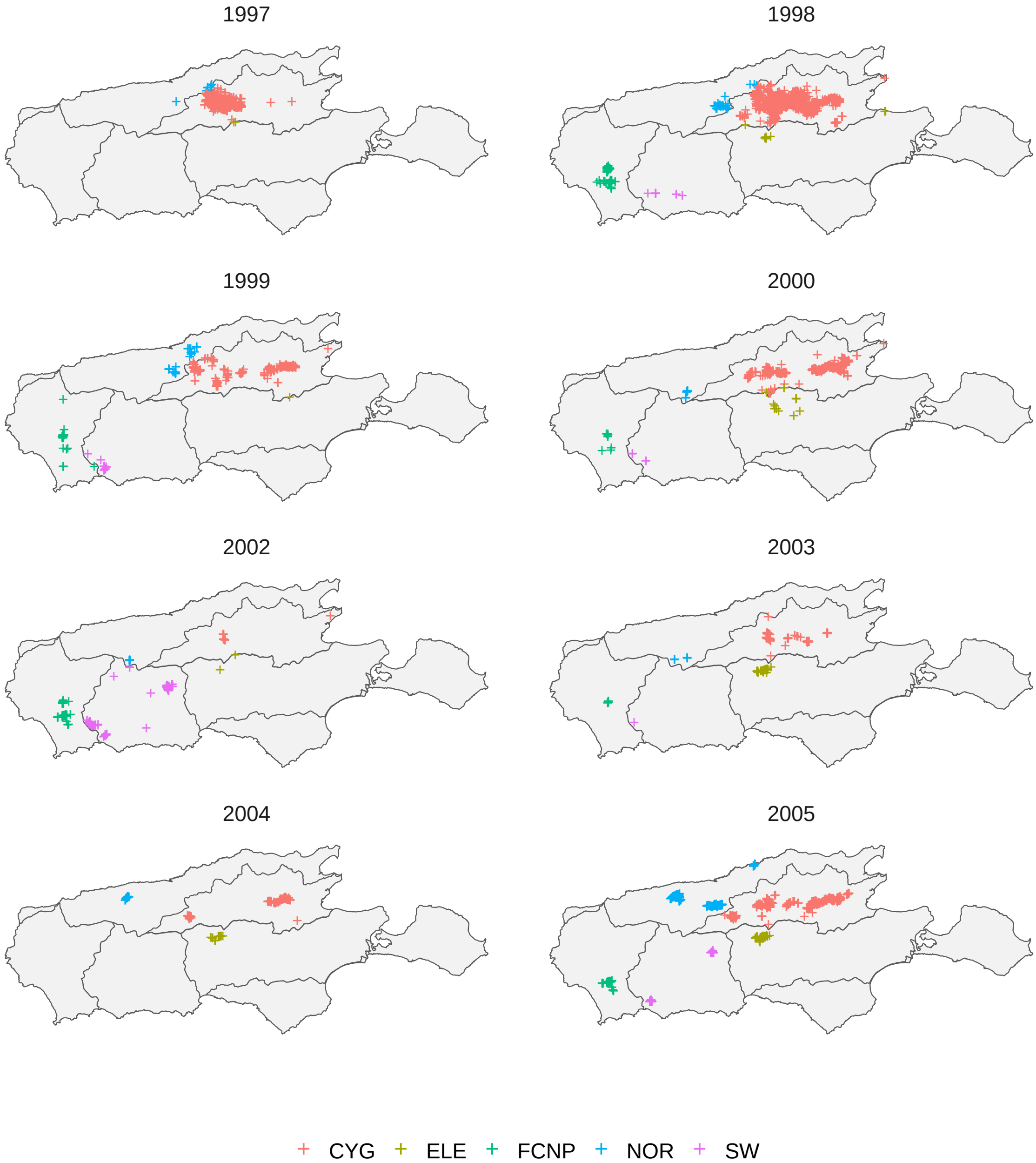

Figure 23. Locations of koalas captured for sterilisation over the period 1997-2005. "CYG", Cygnet River; "ELE", Eleanor-Timber Creek; "FCNP", Flinders Chase National Park; "NOR" North Coast; and "SW", South-West management units.

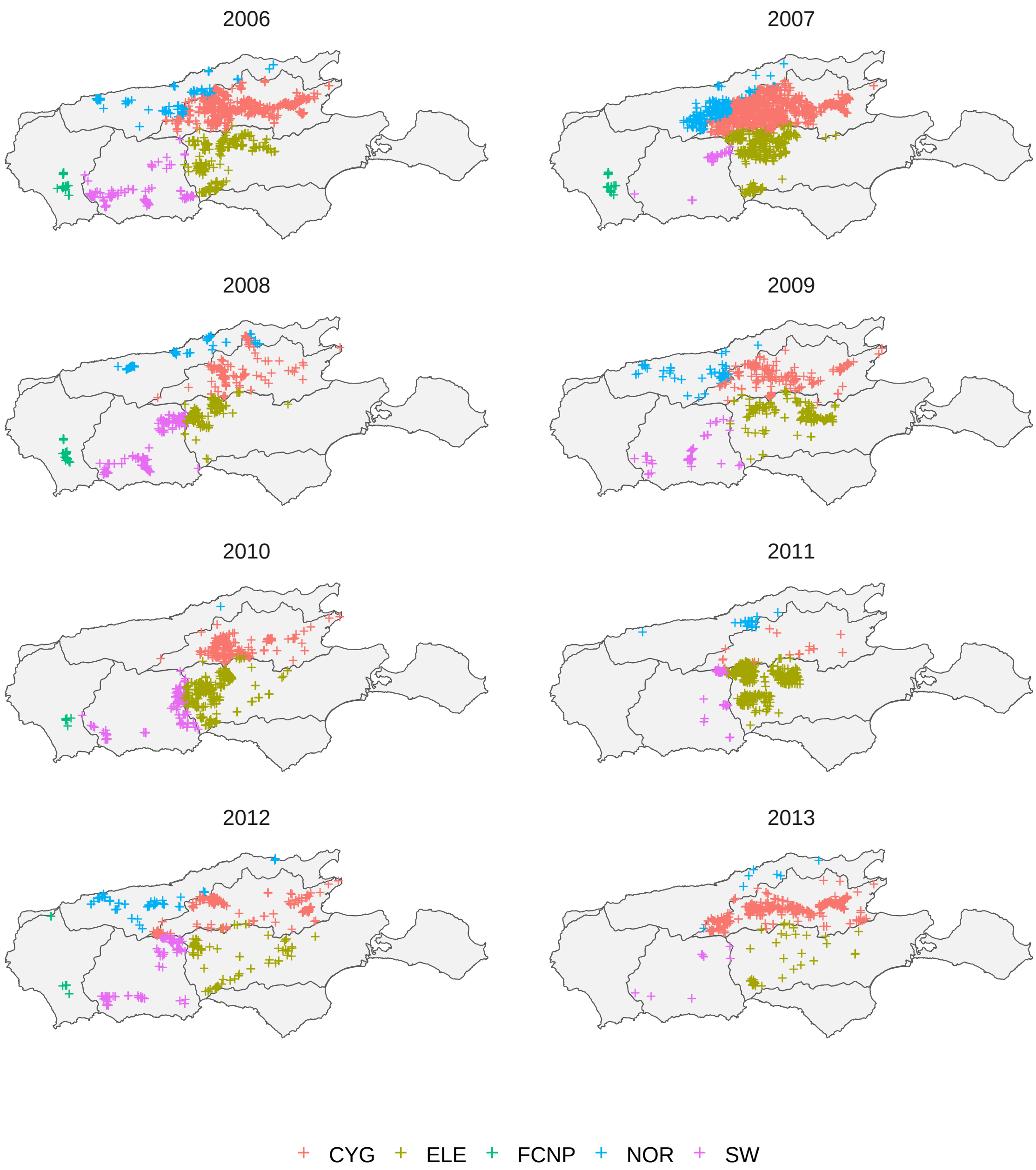

Figure 24. Locations of koalas captured for sterilisation over the period 2006-2013. "CYG", Cygnet River; "ELE", Eleanor-Timber Creek; "FCNP", Flinders Chase National Park; "NOR" North Coast; and "SW", South-West management units.

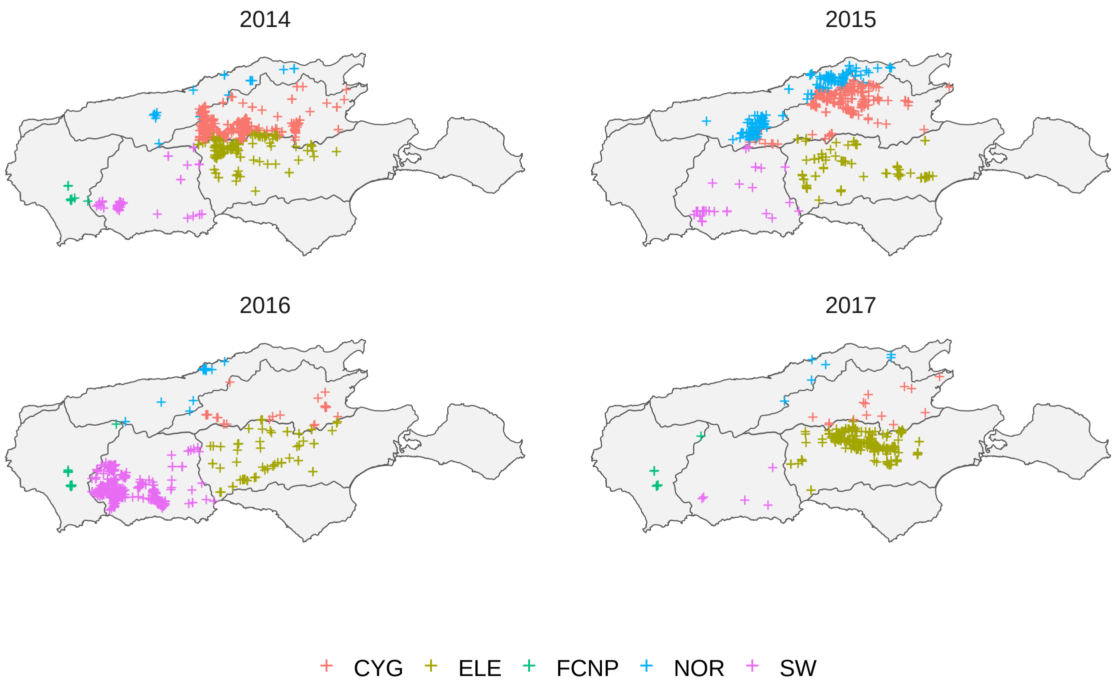

Figure 25. Locations of koalas captured for sterilisation over the period 2014-2017. "CYG", Cygnet River; "ELE", Eleanor-Timber Creek; "FCNP", Flinders Chase National Park; "NOR" North Coast; and "SW", South-West management units.

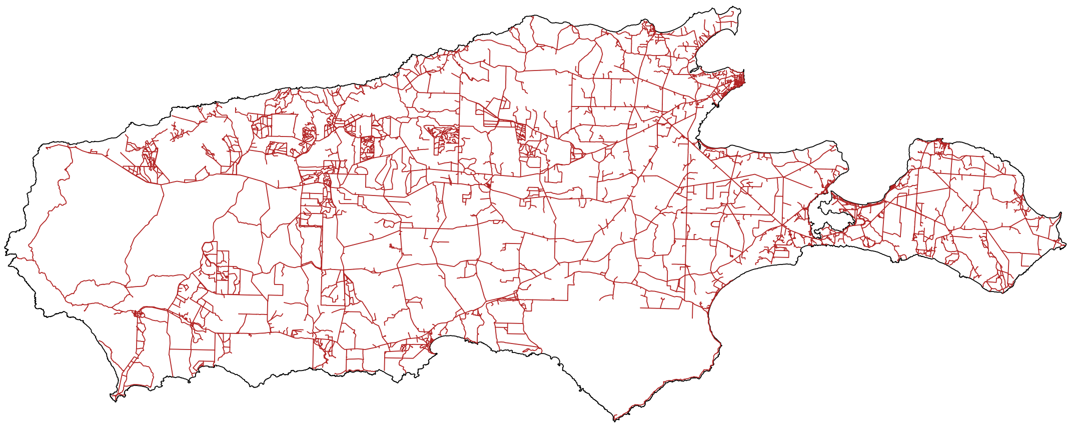

Figure 26. Road network on Kangaroo Island. These data were used to calculate distance from nearest road for each koala capture from the sterilisation program between 2007 and 2017.

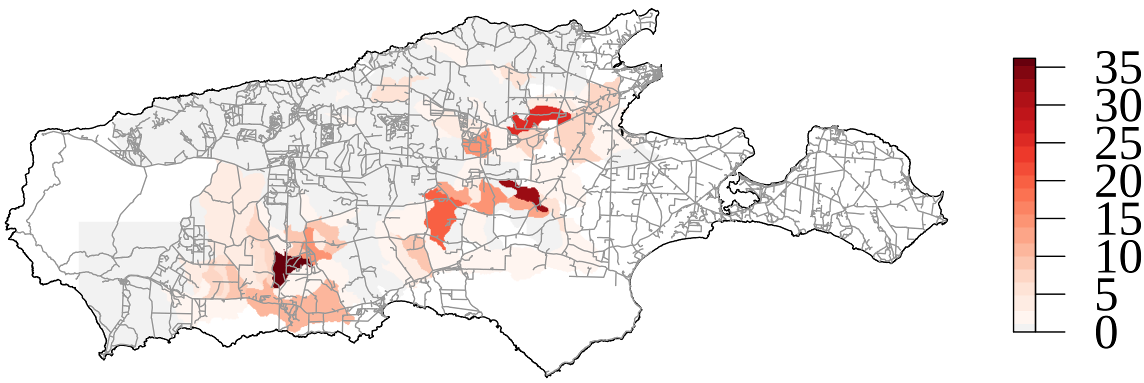

Figure 27. Annual sterilisation targets for each subcatchment show which subcatchments are priorities for intervention. Subcatchments targets sum to 400 across the island. Here we also overlay the road network to help managers to locate the subcatchments.

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