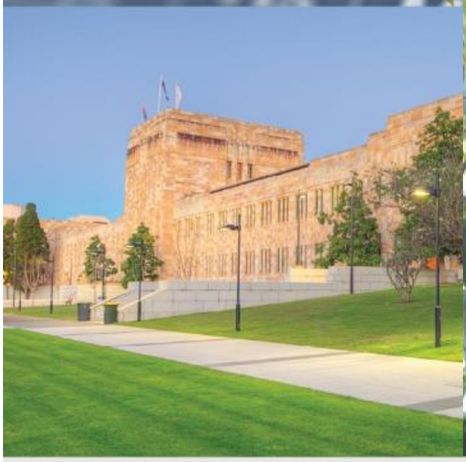

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Title

South East Queensland Koala Population Modelling Study

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South East Queensland Koala Population Modelling Study

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1. EXECUTIVE SUMMARY

This study was commissioned by the Queensland Department of Environment and Heritage Protection (EHP) to analyse data from the South East Queensland (SEQ) Koala Monitoring Program and to receive an independent assessment of the conservation status of the koala in the seven Local Government Areas (LGAs) that make up the 'Koala Coast' – Moreton Bay Regional Council, Noosa Shire Council, Ipswich City Council, Brisbane City Council, Redland City Council, Logan City Council and Gold Coast City Council. The primary aims of the project were to:

1) develop a model of relative koala density (here defined as the number of koalas per hectare) that could be used to predict koala densities across the seven LGAs in South East Queensland and to identify key correlates with koala density;
2) develop a model of trend in koala populations where possible and to identify any correlates with trend; and
3) provide any recommendations on the monitoring program.

Using survey data between 1996 and 2015, we developed spatial models of koala density for the seven LGAs and models of trends in koala density for the Koala Coast and Pine Rivers survey regions, where there was sufficient replication through time to estimate trends. We used Bayesian state-space statistical models that explicitly account for detection errors incurred through the survey process. This was particularly important because the data were collected using multiple survey methods and because estimating detection error was likely to be critical for obtaining unbiased estimates of koala density. In addition, our trend models were explicit about the dynamics of koala populations through time in the Koala Coast and Pine Rivers regions, leading to more nuanced insights into the status of these koala populations than standard regression models. We used *V*-fold cross validation to validate and compare alternative models and also to quantify model adequacy.

The spatial models were then used to map koala densities (and 95% credible intervals) across the LGAs. Although it may be possible to estimate koala numbers (i.e. the number of koalas across the region) from the spatial maps of koala density, we guard against doing so without careful consideration and possibly the use of ancillary data. This is because substantial biases could arise from the extrapolating across such a large area using a model derived from data collected from a limited area only. Therefore, here we focus on reporting on relative densities and trends which are likely to be much more robust and within the scope of the project.

The spatial models predicted the highest koala densities occurring along the coastal regions of SEQ, but particularly in the central and southern coastal regions, but with average densities across the region estimated as being relatively low at 0.04 koalas/ha.

There were also some unexpected areas of high density predicted in western regions, although these were areas where surveys have not been conducted and uncertainty in the density estimates was high. Overall, across the region, the primary factors associated with the broad-scale distribution of koala densities were climatic factors (temperature and rainfall). However, there was also some suggestion that koala densities may be highest at intermediate levels of forest cover (foliage projective cover [FPC]) and road density. These patterns may arise because the *Eucalypt* habitats that koalas prefer occur at intermediate levels of FPC and human settlement patterns are largely coincident with where the best koala habitat occurs along the coast (although high road density ultimately leads to a decline in koala densities). There was also evidence that koala densities increased with reduced amounts of forest cover around sites. This may be due to the crowding of koalas in sites when local habitat loss occurs and where low amounts of habitat are present in the surrounding landscape, although this would be expected to be a transient effect ultimately.

There was strong evidence for a rapid decline in population densities between 1996 and 2014 in the Koala Coast and Pine Rivers populations, with an estimated 80.3% (95% credible interval: 70.8% to 86.2%) decline in the Koala Coast sites and an estimated 54.3% (95% credible interval: 20.1% to 74.4%) decline in the Pine Rivers sites. There was also evidence that the rates of decline have increased over time. However, apart from a strong seasonal effect, with declines occurring primarily in the periods between summer and winter, rather than the periods between winter and summer, there were few strong correlates with the rate of decline. Given the rapid declines in the Koala Coast and Pine Rivers, a key priority for policy development is to understand whether this is a more widespread phenomenon across the region, or restricted to these areas.

Finally, a number of key additional recommendations for the monitoring program arise from this study, including:

- use the estimated spatial distributions of koala density and measures of uncertainty to prioritise locations for future surveys to improve the effectiveness of the monitoring program and maximise improvement in density predictions over time,
- design future survey locations and temporal replication with clear monitoring objectives in mind, with the understanding that no single monitoring design, of realistic size, is likely to be effective at simultaneously measuring spatial distributions and trends,
- design survey methods to explicitly deal with, and estimate, observation error better, and
- adopt a formal database structure that ensures data is recorded in a consistent manner, that no important data are missing from survey records, and that allows the dataset to be easily transformed into a format that facilitates statistical analysis.

2. INTRODUCTION

The koala (*Phascolarctos cinereus*) is an Australian endemic, Queensland's faunal emblem and one of the world's most iconic mammals. Koalas have a broad but patchy distribution restricted to the eucalypt forests and woodlands of eastern Australia, extending from north Queensland to South Australia (Melzer et al. 2000, Lunney et al. 2009, Adams-Hosking et al. 2011a, Santika et al. 2014). Although koala populations in Victoria and South Australia face issues of overabundance (Masters et al. 2004, Lunney et al. 2007a), in New South Wales and Queensland, koala populations are threatened by habitat loss, dog attacks, vehicle collisions, climate change and disease (Dique et al. 2003d, Lunney et al. 2007b, Rhodes et al. 2011, Seabrook et al. 2011, Lunney et al. 2014, Santika et al. 2014). In South East Queensland, koala populations appear to have suffered declines due to a range of threats associated with habitat loss/urbanisation and disease (Rhodes et al. 2011), with the Koala Coast population estimated to have declined by 68% between 1996/1999 and 2010 (Department of Environment and Resource Management 2012).

In response to the increasing pressures on koalas in South East Queensland, in 2004 the species was listed as vulnerable in the South East Queensland Bioregion under the Queensland *Nature Conservation Act 1992*. Then, in 2012, the koala was recognised as a threatened species in Queensland, New South Wales and the Australian Capital Territory under the *Environmental Protection Biodiversity Conservation Act 1999* (EPBC). The Victorian and South Australian populations were not listed because they were considered abundant and mostly stable or increasing. As a consequence of the national listing of koalas, the conservation status of the koala in Queensland is being reviewed, with the likely outcome being that koalas will be listed as vulnerable across the state (statements.qld.gov.au/Statement/2015/5/31/queenslands-koalas-to-be-listed-as-vulnerable).

Since 1996 the Queensland Government has made significant investments in baseline and monitoring surveys of koalas in South East Queensland with the aim of understanding koala distribution, abundance, ecology and population dynamics (Department of Environment and Resource Management 2012). Initial monitoring surveys were constrained to the Koala Coast and Pine Rivers Shire areas, but were recently extended to other Local Government Areas in South East Queensland. This is one of the most extensive data sets on koala populations in Australia and provides unique opportunity to quantify and understand the drivers of koala population trends and distribution. However, an integrated analysis of the entire data set to understand koala population trends and distributions has not yet been undertaken. This report addresses this gap and presents a statistical analysis of the data to:

1) understand the key factors related to koala density;
2) map predicted distributions across the region; and
3) quantify population trends in the Koala Coast and Pine Rivers.

3. OVERVIEW OF KOALA POPULATION DYNAMICS

The distribution and density of koalas is influenced by numerous factors affecting habitat extent, habitat quality and population dynamics. Koalas are habitat specialists and feed almost exclusively on eucalyptus leaves (McKay 1988, Melzer and Houston 2001), which have low nutritional value (minerals, protein and non-structural carbohydrate) and are high in indigestible or toxic materials (cellulose, lignin and plant secondary metabolites). Consequently, to meet their energy and water requirements, koalas are selective about which tree species and leaves they consume and the nutritional value of leaves varies among Eucalypt species and along geophysical gradients (Moore et al. 2010). In general, soils with higher fertility and moisture holding capacity produce better quality, more palatable browse with higher nutrients, which support higher koala densities (Cork 1986, Lawler et al. 1998, Moore and Foley 2000 Wallis, 2003 #439). In South East Queensland, for example, soil substrate and tree species have been found to be important in determining the occurrence of koalas in Noosa Shire (McAlpine et al. 2006a, McAlpine et al. 2008).

Koala home range sizes are variable and influenced by habitat quality, season, koala density and sex, with females usually having smaller home ranges than males. Home range areas of 1–135have been described in southern and central Queensland (White and Kunst 1990, Melzer 1995, Ellis et al. 2002, Thompson 2006). Dispersal and exploratory movements by koalas have been shown to average approximately 3.5km in South East Queensland, with less frequent long-range dispersal of up to 10km (Dique et al. 2003c). Dispersal is usually undertaken by sub-adult koalas in the pre-mating and early mating period of the breeding season from June to December, with high mortality rates reported for koalas in urban and peri-urban areas (Dique et al. 2003c, Rhodes et al. 2011).

Koalas move across the ground (rather than through the canopy) to forage, find mates, or disperse to new habitats outside their home range (Martin and Handasyde 1999), but this is also when they are risk of mortality from threats such as dog attacks and vehicle collisions. Therefore, habitat loss and fragmentation may have the combined effect of reducing the amount of habitat, but also increasing the amount of time koalas must spend moving on the ground at risk from a range of threats. Therefore, the structure and permeability of the landscape appears to be an important driver of koala occurrence (McAlpine et al. 2006b, Rhodes et al. 2006, McAlpine et al. 2008, Rhodes et al. 2008) and movement (Dudaniec et al. 2013).

The population dynamics of koalas are also impacted by disease and can make up a major component of overall mortality (Rhodes et al. 2011). Of particular concern is persistent chlamydial infection, which is often prevalent at high levels in koala populations and can cause irreversible infertility in females (Polkinghorne et al. 2013). The health consequences of other pathogens known to infect koalas, including koala retrovirus (Hanger et al. 2000) and trypanosomes (McInnes et al. 2009, McInnes et al. 2011a, McInnes et al. 2011b) are not well understood.

4. PROJECT SCOPE

4.1 Project commissioning

This project was commissioned by the Queensland Department of Environment and Heritage Protection (EHP) to analyse data from the South East Queensland (SEQ) Koala Survey Program and to receive an independent assessment of the conservation status of the koala in the seven Local Government Areas (LGAs) of Moreton Bay Regional Council, Noosa Shire Council, Ipswich City Council, Brisbane City Council, Redland City Council, Logan City Council and Gold Coast City Council.

A team from The University of Queensland (UQ), led by Associate Professor Jonathan Rhodes from the School of Geography, Planning and Environmental Management (GPEM), was awarded the contract for the analysis (Request for Quotation #EHP1418). The project commenced on 27 October 2014.

4.2 Aims and objectives

The aim of this project was to determine the conservation status of the koala populations in seven eastern LGAs of SEQ, comprising Moreton Bay Regional Council, Noosa Shire Council, Ipswich City Council, Brisbane City Council, Redland City Council, Logan City Council and Gold Coast City Council. At the time of the commissioning of the project, no survey data were available for the Sunshine Coast Regional Council.

The primary activities to be conducted to address the aims were to develop:

1) a spatial model of koala relative densities across the eastern LGAs of SEQ; and
2) models of koala trends where time series data were available.

The specific objectives related to the deliverables were:

- Information on relative density (potentially including detection error and occupancy) using the Queensland Government koala survey data, and appropriate data for covariates;
- Information on trends in populations using the Queensland Government koala survey data, and appropriate data for covariates;
- Appropriate model validation;
- Maps of predicted relative density (with 95% confidence interval estimates) across each of the LGAs;
- A report that includes appropriate descriptions of relationships with density, trends, data, models and maps; and

- If applicable, any recommended changes or improvements to the Queensland Government koala survey program, and any data or analyses produced in undertaking the project.

4.3 Tasks and deliverables

The project requirements specified by EHP identified the following tasks and deliverables.

Tasks to be performed

The tasks to be performed included:

- Identify suitable models that are proven in the literature to provide robust estimates of population parameters and trend;
- Develop information on relative density (potentially including detection error and occupancy) and trends in population using the Queensland Government koala survey data, and appropriate remote sensing data;
- Perform appropriate model validation; and
- The development of maps and reporting on predicted density/likelihood across each of the LGAs and population trends in two LGAs.

Deliverables

The deliverables of the projects were:

- Information on relative density (potentially including detection error and occupancy) using the Queensland Government koala survey data, and appropriate data for covariates;
- Information on trends in populations using Queensland Government koala survey data, and appropriate data for covariates;
- Appropriate validation;
- Maps of predicted relative density/likelihood across each of the LGAs;
- A report including appropriate descriptions of relationships with density, trends, data, models and maps; and
- If applicable, any recommended changes or improvements to the Queensland Government koala survey program, and any data or analyses produced in undertaking the project.

A major task identified at the commencement of the project was the need to compile, clean and organise the Queensland Government koala survey data to facilitate statistical analysis. This necessitated developing a completely new relational database from the source data which were supplied in several Excel worksheets together with access to the raw field data sheets.

5. STUDY AREA

The study area was the eastern portion of the South East Queensland planning region and is comprised of eight LGAs. However, because no koala survey data were available for the Sunshine Coast Regional Council area, the modelling was conducted using data from only seven LGAs: Moreton Bay Regional Council, Noosa Shire Council, Ipswich City Council, Brisbane City Council, Redland City Council, Logan City Council and Gold Coast City Council.

The study region (Figure 1) covers an area of almost one million hectares (9,700km^2) and contains one of the largest and most significant koala populations in Australia (Melzer et al. 2000). High fertility lowland alluvials, deep red soils and consolidated sediment in the east give way to the low fertility, shallow metamorphic soils of the D'Aguilar mountain range on the western boundary of the study region (Young and Dillewaard 1999). Approximately 35% of the region is remnant vegetation dominated by eucalypt woodlands and open forests, with moist forests and rainforests in higher rainfall areas with heaths and melaleuca communities near the coast. The major remnant regional ecosystems include:

- 12.11.5 *Corymbia citriodora* subsp. *variegata*, *Eucalyptus siderophloia*, *E. major* open forest on metamorphics +/- interbedded volcanics (47,000ha);
- 12.11.3 *Eucalyptus siderophloia*, *E. propinqua* +/- *E. microcorys*, *Lophostemon confertus, Corymbia intermedia*, *E. acmenoides* open forest on metamorphics +/- interbedded volcanics (42,000ha);
- 12.9-10.2 *Corymbia citriodora* subsp. *variegata* +/- *Eucalyptus crebra* open forest on sedimentary rocks (22,000ha);
- 12.12.15 *Corymbia intermedia* +/- *Eucalyptus propinqua*, *E. siderophloia*, *E. microcorys*, *Lophostemon confertus* open forest on Mesozoic to Proterozoic igneous rocks (22,000ha).

The mountain ranges in the west extend to elevations of 750 m and are heavily forested with rainforest that is not suitable habitat for koalas and forms an ecological barrier that has reduced gene flow between koala populations on either side of this range (Lee et al. 2010). The southern boundary is the watershed that forms the border with New South Wales on the edge of the ancient Tweed shield volcano.

In contrast to the forested mountain ranges to the west and south, the coastline to the east is fringed by densely populated urban centres. These areas are experiencing rapid human population growth associated with increased urbanisation and the process of development has resulted in the loss and fragmentation of koala habitat (Seabrook et al. 2003, Queensland Government 2009, Department of Science Information Technology Innovation and the Arts 2014). Many koala populations also face high levels of mortality associated with disease, vehicle collisions and dog attacks (Dique et al. 2003d, Rhodes et al. 2011). Lack of a clear quantitative understanding of the consequences of these pressures on koala populations highlights the need to be able to map koala distributions relative to the key threats, quantify any trends in koala populations over time, and identify the determinants of koala distributions and trends.

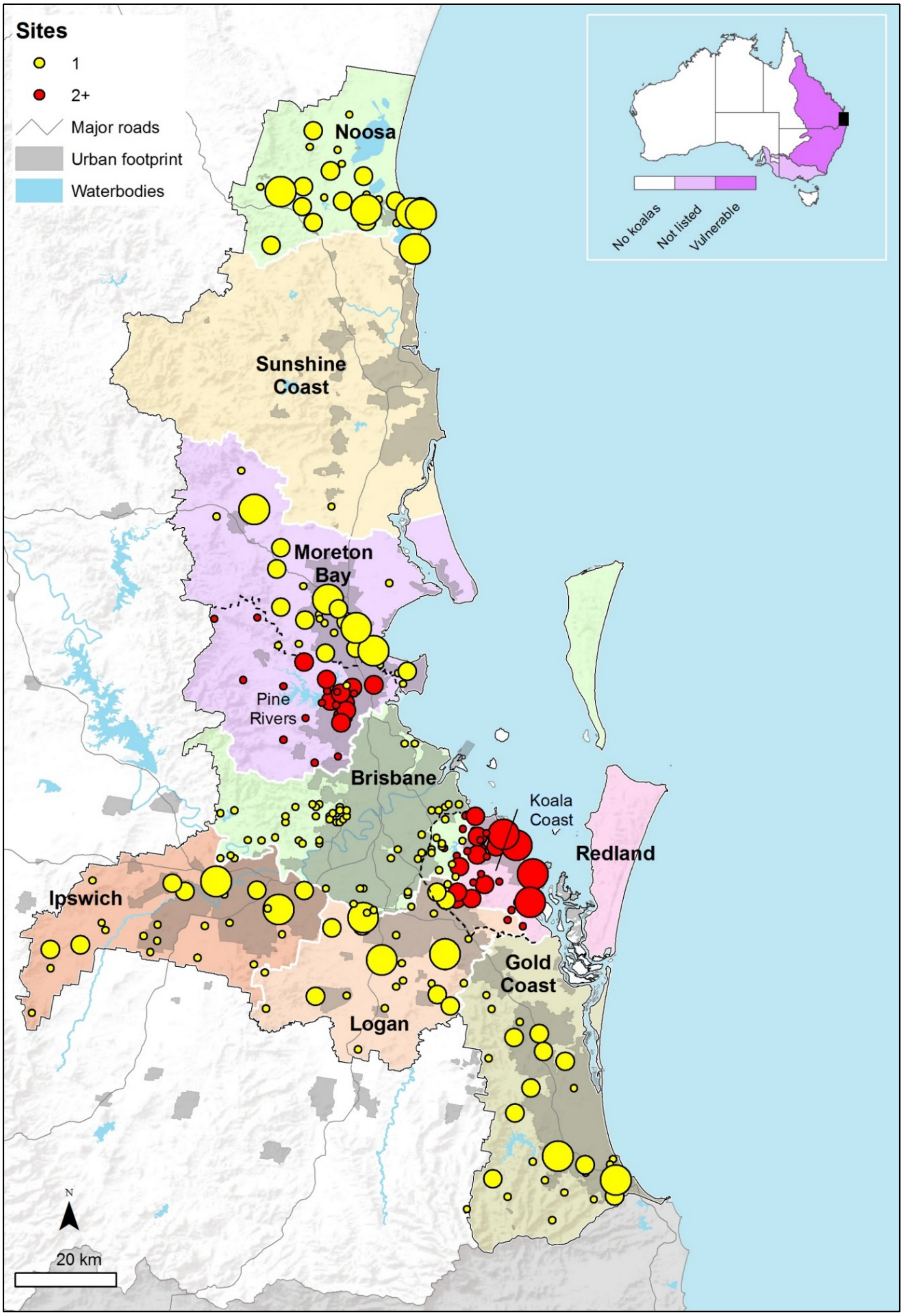


Figure 1. Survey site locations (circles) colour coded by the number of surveys (single survey or more than one survey). The sizes of the circles are proportional to the average survey effort (i.e. area surveyed) per survey (1996–2015).

6. SOUTH EAST QUEENSLAND KOALA MONITORING DATA

The Queensland Government has been monitoring koalas in South East Queensland for around 20 years and in this time has amassed considerable data on koala distribution, density and demographic parameters (Dique 2004, Thompson 2006, Preece 2007, de Villiers 2015). The first regional surveys of koalas were conducted in the "Koala Coast" region (portions of Redland City Council, Brisbane City Council and Logan City Council LGAs) between 1996 and 1999 (Dique 2004). Subsequent major surveys occurred in 2005–2006, 2008, 2010, and 2012, to monitor trends in koala numbers. Minor surveys of three sites in the Koala Coast were conducted nearly every year between 1996 and 2013. In 2001, with funding support from Pine Rivers Shire Council, surveys were expanded to include the then Pine Rivers Shire Council, now a district within Moreton Bay Regional Council (Dique et al. 2003a, Dique et al. 2003b). Follow-up surveys in Pine Rivers were conducted in 2011 and 2013 by EHP to monitor trends in the koala population.

In December 2008, the Queensland Government announced a Koala Response Strategy to recover koala populations in South East Queensland and in August 2010 the koala surveys were expanded to a five year program encompassing the eastern LGAs of South East Queensland. As part of this commitment, the Threatened Species Unit, EHP has been surveying populations of koalas to establish information about the distribution, population size, and long term trends of koala populations in eight LGAs: Moreton Bay Regional Council, Sunshine Coast Regional Council, Noosa Shire Council, Ipswich City Council, Brisbane City Council, Redland City Council, Logan City Council and Gold Coast City Council.

6.1 Koala survey sites and survey methods

A major component of this project was compiling, checking, correcting, and formatting the koala survey data and associated spatial data to ensure adequacy for modelling. Koala count data from the systematic surveys were originally supplied in several Excel worksheets and had to be pre-processed to: resolve discrepancies in and remove duplicate records, correct errors and enter some data (often by referencing raw field data sheets), and to collate and organise the data into a relational format prior to analysis. Spatial representations of the survey transects also had to be generated from GPS coordinates.

<u>Site selection</u>

The site selection process varied over time with three different approaches implemented at different times and in different regions. The first approach used between 1996 and 2011 for the Koala Coast was based on satellite land cover classification and potential koala habitat strata as outlined by Dique et al. (2004).

The second approach used primarily between 2012 and 2013 for Moreton Bay Regional Council, Noosa Shire Council, Ipswich City Council, Logan City Council and the Gold Coast City Council was a modification of the Dique et al. (2004) approach that could be undertaken without the use of a classified satellite image. The third approach used between 2014 and 2015 for Brisbane City Council adopted a new methodology based on randomly sampling mapped koala habitat.

In the initial Dique et al. (2004) approach, potential koala habitat strata were derived from a Landsat image classification that discriminated forest, urban and grass land cover classes for the Koala Coast. Subsequently, in the absence of a classified image for other areas, the approach was modified to use a visual assessment of forest and urban land cover using GIS data (including Google Earth, etc.). These approaches enabled the study area to be stratified into four broad koala habitat strata consisting of:

1) Bushland habitat – forest land cover patches larger than 100ha in the non-urban zone;
2) Remnant bushland habitat – smaller isolated forest land cover patches, generally10–100 ha, in the urban zone;
3) Urban habitat – suburban small-lot development and some small forest patches (usually less than 10ha); and
4) Non-habitat – areas where koalas are generally not present, such as grass, rainforest and impervious surfaces (industrial, high development density urban areas, roads, parking areas, etc.).

Sites were then located in each of these potential habitat strata, but no sites were located in the non-habitat stratum. Site size varied depending on the stratum and the size of the forest patches, with the mean size being approximately 50ha (range 7–900ha). Usually the smaller sites were located in the urban areas and the larger sites were protected areas of forest, such as national parks.

In the approach used for the Brisbane surveys between 2014 and 2015, koala survey sites were randomly selected from six of the nine habitat classes delineated in the “South East Queensland Koala Habitat Assessment and Mapping Project” (www.ehp.qld.gov.au/wildlife/koalas/mapping). This mapping was completed in May 2009 by private consultants GHD, on behalf of the Queensland Government and contained a total of nine habitat classes, comprising three habitat value rankings (high, medium, and low) for each of three habitat categories:

1) Bushland - forested or woodland areas where koalas occur, or have the potential to occur, and regarded as the most important habitat for koalas;
2) Suitable for rehabilitation - generally cleared land that lacks closed canopy forest or woodland, that if rehabilitated would have the potential to provide important habitat for koalas;

3) Other areas of value - generally urban landscapes where koalas occur, or have the potential to occur and may include fragmented patches of bushland, parklands, schools and suburban backyards.

After dividing Brisbane into 36ha grid squares (600m by 600m) a total of 58 sites (each 36ha in size) were randomly selected from the six ‘Bushland high/medium/low’ and ‘Other Areas of value high/medium/low’ classes. No sites were located in the ‘Suitable for rehabilitation high/medium/low’ classes. Generally, half the site (18ha) was searched using strip transects, although some total counts were conducted in urban areas. Some sites overlapped previously established sites in the Brisbane portion of the Koala Coast.

Survey methods

Koala surveys were conducted using one of three methods: strip transects, total counts (all of area searches), and line transects. Strip transects were long narrow plots of known area with the aim of counting all koalas seen within the boundary. Total counts (all of area searches) consisted of counting all individuals seen in a known area (of non-specific shape). Line transects involved walking along a line and recording the perpendicular distance from the line to each animal sighted (Buckland et al. 2001). We describe each of these survey methods below.

Strip transects

Strip transects, with fixed boundaries were established in bushland areas to sample a diversity of vegetation types across the landscape. Boundaries were fixed using survey pegs with locations established using differential GPS. Each strip transect was typically 60m wide with five trained observers spaced 15m apart walking a fixed bearing (using a sighting compass) and searching all trees for koalas with the aid of binoculars. All koalas observed were recorded, but koalas detected outside the boundary of transects were not included in the analysis. Transects varied in length depending on the site and terrain but were typically 400m long.

The first transect at a survey site was randomly located between 1m and 60m from the edge of the site. Each subsequent transect was spaced parallel to the initial transect at intervals corresponding to multiples of 60m, with the objective of uniformly sampling approximately 30% of each site in order to maintain precision (Dique et al. 2001). Sampling intensity was generally higher for smaller sites, typically those sites less than 40ha in size. Sampling intensity was also higher for higher density sites in order to optimise precision as determined by Dique et al. (2001).

Total counts (all of area searches)

Urban sites, typically 90ha in size, were systematically searched using teams of up to 16 observers. When volunteers were used, care was taken to ensure that each volunteer was paired with an experienced observer. Searches were undertaken of individual trees in yards and small areas of parkland or small patches of bushland (less than 10ha in size) within the urban matrix of the site. Access to individual properties was made (with the owner's permission) where possible, otherwise searching was done from the street using binoculars (Dique 2004). All koalas observed were recorded.

Line transects

Line transects were established at bushland sites across the Moreton Bay region (Dique et al. 2003b). The first line within each site was located at a random starting point, but in a direction aimed to sample a variety of vegetation communities and topography within the landscape. Each additional line was located parallel to the first line with a 150 m "spacer" transect at right angles separating each line, typically resulting in "U-shaped" transects. The 150 m spacer distance was used to minimise the potential for double counting from adjacent lines and was based on a pilot survey that showed most koalas were sighted within 50m of the transect line. Searching the spacers maximised the use of time spent in the field but also meant that the search intensity varied slightly where a transect met a spacer (i.e., intensity was slightly higher for a short distance, less than 50m, on the inside and slightly lower on the outside edge). This would be expected to have minimal effect on the density calculations because care was taken to ensure that no koala was double counted. The length of the line transects varied according to the site characteristics, such as the patch size, shape, forest structure and terrain, but were typically 800m long.

Each line transect was walked by two experienced observers using binoculars to assist in searching. One observer (the navigator) used a compass to navigate the line, while the second observer was free to move a few metres either side of the line to optimise koala detection and avoid obscuring vegetation. Care was taken to thoroughly search trees on or close to the transect line to ensure that the detection probability along the line was as close to one as possible (Buckland et al. 2001). The second observer rarely moved more than a few metres from the line to ensure that the detectability of koalas further away was not increased.

When a koala was detected, it was recorded and the perpendicular distance from the line was measured to the point vertically below the koala with a 50m measuring tape. Additional information relating to the GPS location, tree, and koala were also recorded.

<u>Timing of surveys</u>

Koala surveys (counts) were initially planned to take place twice per year, commencing in February and six months later commencing in August. The survey timing in August was important because at that time of the year koala joeys were still dependent, with their mothers as either back young or pouch young, and large enough to be detected by observers from the ground using binoculars if necessary. The presence of observable young made it possible to estimate the proportion of adult females breeding and to monitor trends in breeding rates over time (although this data was not used in this report). In 2010, when the survey program was expanded to include sites outside the

Koala Coast and Pine Rivers, it became necessary to conduct surveys in all months of the year in order to fully utilise staff resources.

However, to maintain consistency with previous years, surveys in the Koala Coast and Pine Rivers were scheduled to be undertaken during the same months as in previous surveys, although this did not always occur. Overall, surveys were conducted in most months of the year, with 65% conducted from August to December and 17% in February to March.

6.2 Data summary

A total of 249 sites were systematically surveyed across the seven LGAs, with a total transect area of 23,262ha (assuming an effective strip width of approximately 70m (Dique et al. 2003a)) and 3,426 independent adult koalas detected across all years (Table 1). In the Koala Coast and Pine Rivers, 61 sites were systematically surveyed with a total transect area of 15,761 ha and 3,262 independent adult koalas were detected (Table 2).

Table 1. Summary of koala surveys conducted within each local government area.

Local Government Area (LGA)	Number of Sites	Transect Area (ha)	Number of Koalas* Detected
Brisbane	66	3216	639
Gold Coast	26	1275	50
Ipswich	25	1078	36
Logan	29	2234	272
Moreton Bay	52	3816	339
Noosa	26	1535	7
Redland	25	10107	2083
Total	249	23262	3426

**Independent adult koalas excludes pouch young and dependent juveniles*

Table 2. Summary of koala surveys conducted within the Koala Coast and Pine Rivers.

Survey Region	Number of Sites	Transect Area (ha)	Number of Koalas* Detected
Koala Coast	37	13336	2963
Pine Rivers	24	2425	299
Total	61	15761	3262

**Independent adult koalas excludes pouch young and dependent juveniles*

Some sites in the Koala Coast and Pine Rivers were surveyed multiple times over 19 years with five major surveys in the Koala Coast (1996–1999, 2005–2006, 2008, 2010 and 2012) and three major surveys in Pine Rivers (2001, 2011, and 2013). Minor surveys of three sites in the Koala Coast (Ney Road, Gravel Reserve, and Burbank) were conducted nearly every year. However, overall, a small proportion of 249 sites were surveyed in multiple years over this time, with only baseline (single) surveys conducted at the majority of sites within SEQ (Figure 1, Appendix A).

7. STATISTICAL METHODS

We aimed to develop statistical regression models that were capable of:

1) predicting relative koala density spatially across the study area; and
2) quantifying trends in relative koala density over time in the Koala Coast and Pine Rivers.

In doing so, there were some unique challenges in the data that had to be overcome, including:

1) the use of multiple survey methods (i.e. strip transects, all of areas searches and line transects) and multiple observers;
2) irregularly spaced sampling through time; and
3) the presence of detection error (i.e. the probability of failing to observe a koala that is present).

Dealing with these issues appropriately requires advanced statistical techniques that are explicit about observation processes (i.e. the process of observing koalas) and ecological processes (i.e. the factors that determine koala abundance).

All field survey data of animal populations contain errors. These errors arise from two main sources, namely, process error and observation error (Ahrestani et al. 2013). Process error describes random variation in animal abundance driven by ecological factors such as variation in habitat, weather/climate, and animal movement. Observation error, on the other hand, describes the imperfect measurement of animal abundance through field surveys because the true abundance of a species at a site is rarely directly observed. An example of observation error is the failure to detect an animal that is actually present at a site because it is simply missed by chance (known as a false negative). Importantly, observation error can depend on a range of factors, including the type of habitat and the skill and experience of the observers. Given these two distinct sources of error, obtaining unbiased estimates of abundance depends critically on being able to represent each source explicitly in statistical models developed using survey data (Tyre et al. 2003).

Models known as state-space models are currently the state-of-the-art statistical approach for dealing with this and explicitly representing both observation and process error (Buckland et al. 2004, Clark and Bjornstad 2004, Royle 2004, Dennis et al. 2006, Royle and Dorazio 2008, Dail and Madsen 2011, Knape and De Valpine 2012, Hostetler and Chandler 2015). These models can be formulated to allow for multiple survey methods and observers and to allow for missing data. They are therefore ideally suited for addressing the major challenges of multiple survey methods, multiple observers and missing data that are inherent in the koala monitoring data.

First, we developed a model to predict the spatial distribution of koala densities using the entire koala monitoring data set. Then we developed a model of trends in koala densities for the sites situated in the Koala Coast and Pine Rivers. We were unable to develop a trend model for the entire region because outside of the Koala Coast and Pine Rivers there was insufficient replication through time. Below we describe the structure of each of these two models, the data that the models were fit to, including the response variables and covariates, the procedures used to fit each model to the data to estimate the parameters and how we conducted model selection and validation.

7.1 Response data

The response data for our regression models were the koala count data for each site. Prior to analysis, for each site, we arranged the counts of koalas into the discrete surveys and allocated each survey to six monthly intervals between 1996 and 2015. We chose six-monthly time-steps so that they broadly coincided with the koala summer breeding season (October–March) and the winter non-breeding season (April–September). The aim here was to account for any seasonal differences in abundance that may be present. There were 39 six-monthly time intervals between summer 1996 and summer 2015. We also associated, with each survey, the area surveyed (in hectares) for the strip transect and total count surveys and the transect length (in metres) for the line transect surveys. Finally, we linked the perpendicular distances with the line transect surveys they were recorded from.

7.2 Covariate data

Prior to model development an extensive process of compiling spatial covariates was undertaken. Covariates were selected to represent the characteristics within sites and the characteristics of the areas within buffers surrounding sites (see Table 3 for a list of the covariates and the rationale for their choice). Covariates were chosen based on their hypothesised links with koala density and to represent biophysical, habitat and threat drivers of koala density. However, covariate data were also chosen based on their ability to be mapped consistently across the entire study region (to allow spatial predictions to be made) and likely to be available in the future (to allow the analysis to be updateable in the future as more monitoring data becomes available). Where possible we acquired year-specific datasets. All covariate data sets were prepared using a combination of ArcGIS (ESRI, Redlands, CA, USA) and the Geospatial Modelling Environment (GME) software (http://www.spatialecology.com/gme).

For each site we calculated covariate values either within the site (to represent site scale processes) or within buffers surrounding the site (to represent broader landscape scale processes), or both. For the calculation of covariates within buffers surrounding each site we used a buffer size of 2.5km. This was chosen to be close to the median dispersal distance of around 2km recorded for koalas in South East Queensland (Dique et al. 2003c).

However, we found that covariates calculated within 1km and 5km buffers were highly correlated with covariates calculated at 2.5km, so we expect model results to be insensitive to the exact choice of buffer size. Although we did not specifically include measures of fragmentation (e.g., patch density, isolation, etc.) in our set of covariates, metrics of habitat amount tend to be highly correlated with measures of fragmentation (Fahrig 2003). Therefore, our covariates that were related to habitat amount calculated within the buffers around sites were also designed to reflect fragmentation effects.

Table 3. Model covariates for site level and context variables.

Variable Category	Variable	Site/Buffer	Description	Source data	Rationale
Physical	Temperature†	Site	Annual maximum temperature (°C) for each year between 1996 and 2015.	Australian Water Availability Project (AWAP), 5km raster.	High maximum summer temperatures have been found to be important determinants of koala mortalities and distributions (Lunney et al. 2012, Lunney et al. 2014, Santika et al. 2014). Hence maximum temperature may be a good indicator of where koalas occur in higher densities.
Physical	Rainfall†	Site	Annual precipitation (mm/year) for each year between 1996 and 2015.	Australian Water Availability Project (AWAP), 5km raster.	Rainfall is important for koalas as they are sensitive to drought (Seabrook et al. 2011). Drought affects the leaf moisture content and the nutrition of eucalypt leaves that are important for koala habitat quality (Moore et al. 2004).
Physical	Elevation	Site	Mean altitude (m).	DEM v1.0 Geoscience Australia, Commonwealth of Australia, 1 second (~30m) raster.	Low altitude areas area associated with some depositional flood plains and coastal lowlands that have higher fertility soils linked to higher koala densities (Crowther et al. 2009). Elevation is also lined to temperature and rainfall.
Physical	Topographic Wetness	Site	Mean Topographic Wetness Index (TWI). This estimates the relative wetness within catchments.	Australian Soil Resource Information System (ASRIS), 250m raster.	Topographic wetness is an indicator of soil moisture available to eucalypt trees and influences the leaf moisture content available to koalas (Moore et al. 2010). This covariate was used instead of the more commonly used distance to water measure, which is likely to be a relatively crude measure of moisture availability.
Physical	Slope	Site	Mean slope (0-90 degrees).	DEM v1.0 Geoscience Australia, Commonwealth of Australia, 1 second (~30m) raster.	Slope has an important indirect influence on koala occurrence and density because steeply sloping areas tend to have lower soil fertility and lower soil moisture (Crowther et al. 2009).
Soil	Soil clay	Site	Mean soil clay content (%).	Australian Soil Resource Information System (ASRIS), 250m raster.	High clay content is linked to increased water holding capacity and increased soil fertility which in turn influence foliar moisture and foliar nutrients (Moore and Foley 2005).

Variable Category	Variable	Site/Buffer	Description	Source data	Rationale
Soil	Soil water	Site	Mean plant available water capacity of soil (mm).	Australian Soil Resource Information System (ASRIS), 250m raster.	The health of the tree canopy and foliar moisture and nutrients is dependent on available soil moisture. In dry seasons, koalas are dependent on leaf moisture content where they do not have access to free-standing water (Gordon et al. 1988, Ellis et al. 2010). Water holding capacity is the total amount of water a soil can hold at field capacity and therefore related to the available soil moisture.
Soil	Soil bulk density	Site	Mean soil bulk density (mg/m^3).	Australian Soil Resource Information System (ASRIS), 250m raster.	Bulk density is the weight of soil in a given volume. Soils with a bulk density higher than 1.6 g/cm^3 tend to restrict root growth and therefore may affect the nutritional quality of leaves for koalas.
Soil	Soil nitrogen	Site	Mean mass fraction of total nitrogen in the soil by weight (%).	Australian Soil Resource Information System (ASRIS), 250m raster.	Total nitrogen content of soils is the mass fraction of total nitrogen in the soil by weight and is a key soil attribute influencing the nutrient content of eucalypt trees (Cork 1986).
Soil	Soil phosphorus	Site	Mean mass fraction of total phosphorus in the soil by weight (%).	Australian Soil Resource Information System (ASRIS), 250m raster.	Phosphorous is critical for the overall health of eucalypts, including the development of roots, stems, flowers and seeds and is vital for photosynthesis. Ullrey et al. (1981) found koalas preferred browse with higher phosphorus and potassium.
Habitat	Foliage projective cover (FPC) †	Site & buffer	Mean Foliage projective cover (FPC) calculated within sites and within 2.5km buffers around each site (%) for years 1999, 2001, and 2004 - 2013. FPC is the percentage of ground area occupied by the vertical projection of foliage and is a measure of canopy closure.	SLATS program, DNRM 30m raster.	Koala populations occupying habitats with high Foliage Projective Cover have been shown to have a lower risk of extinction in NSW (Santika et al. 2014).
Habitat	Remnant	Site & buffer	For each 1:1,000,000	Version 8.0 regional	The proportion of the landscape occupied by eucalypt and

Variable Category	Variable	Site/Buffer	Description	Source data	Rationale
	vegetation[†]		Broad Vegetation Group (BVG) (Neldner et al. 2014) containing eucalypt or melaleuca remnant vegetation, the percentage of each site and each 2.5km buffer around each site (%) covered by the BVG. Calculated for years 1997, 1999, 2000, 2001, 2003, 2005, 2006, 2007, 2009, and 2011. See Appendix B.	ecosystems (RE), DSITIA. The positional accuracy of RE data, mapped at a scale of 1:100,000, is 100 metres. The map scale of 1:50,000 applies to part of South-eastern Queensland.	melaleuca forests and woodlands has been shown to be an important determinant of koala occurrence in Noosa Shire Council (McAlpine et al. 2006a) and elsewhere across its geographic range (McAlpine et al. 2008).
Threat	Lot density[†]	Buffer	Density of property parcels within a 2.5km buffer around each site (lots/ha) for years 1997, 2002, 2003, 2004, 2006, 2007, 2010, 2012, and 2013.	Department of Natural Resources and Mines (DNRM) digital cadastre (DCDB) (vector).	Lot density is a measure of urban density, especially housing density. Habitats in high-density urban areas are highly transformed and have limited habitat resources for koalas. This covariate was only calculated within buffers to reflect the broader landscape-scale effects of urban density not captured by the habitat variables measured at the site scale.
Threat	Road density[†]	Buffer	Percentage of a 2.5km buffer around each site that is road (%) for years 1997, 2002, 2003, 2004, 2006, 2007, 2010, 2012, and 2013.	Department of Natural Resources and Mines (DNRM) digital cadastre (DCDB) (vector).	Road density has been shown to negatively influence koala occurrence in Noosa Shire, South East Queensland (McAlpine et al. 2005) and is also associated with increased road mortality (Dique et al. 2003d, Preece 2007). This covariate was only calculated within buffers to reflect the broader landscape-scale effects of roads not captured by the habitat variables measured at the site scale.
Other	Season[†]	-	Two seasons. Breeding = Summer (Oct – Mar). Non-breeding = winter (Apr – Sept).	-	Seasonal variation in koala numbers has been reported by Dique et al. (2001) in the Koala Coast associated with changes in habitat utilization. In addition, there may be higher rates of koala mortality in winter months possibly linked to dispersal patterns (Dique et al. 2003c). Seasonal variation also linked to changes in fodder quality in some areas (Gordon et al. 1990, White and Kunst 1990, Melzer

Variable Category	Variable	Site/Buffer	Description	Source data	Rationale
					1995).
Other	Year†	-	Time series variable from 1996 – 2015.	-	Year was used as a variable to model change through time.

† *Covariate represented by a time series.*

7.3 Statistical models

We developed two statistical models of koala density. The first model (the spatial model) was based on the entire koala monitoring data set that aimed to model the spatial distribution of koala density across the study area. The second model (the trend model) was based on the data from the Koala Coast and Pine Rivers only and aimed to model trends in koala density for those areas. The robust estimation of trends was possible only for the Koala Coast and Pine Rivers because these were the only areas where the data provided sufficient temporal replication. The two models are described in detail below.

Spatial model

The basis for the spatial model was a Bayesian state-space model with a process component describing the dynamics of the true koala densities (i.e., accounting for process error) and an observation component (i.e., accounting for observation error) that models the chance of missing koalas during searches based on an *N*-mixture model for the strip transect and total count surveys (Royle 2004, Dail and Madsen 2011, Hostetler and Chandler 2015) and based on Distance Sampling for the line transect surveys (Buckland et al. 2001, Gimenez et al. 2009).

For the process model, true koala densities at each site and each 6-monthly interval (i.e., time-step) were modelled as a function of spatial covariates such that

$$\mathrm{E}\left(D_{i,t}\right) = \exp\left(\beta^T X_{i,t} + \eta_i\right), \tag{1}$$

where $\mathrm{E}\left(D_{i,t}\right)$ is the expected density of koalas at site *i* at time-step *t*, β is a vector of coefficients, $X_{i,t}$ is a vector of covariates for site *i* at time-step *t*, and η_i is a normally distributed random-effect for site *i* (where $\eta_i \sim \mathrm{Normal}\left(0, \sigma_d^2\right)$, with ~ signifying “distributed as”). Here the site level random-effect was included to account for the non-independence of repeat surveys within the same site (Rhodes et al. 2009). Then, stochastic variation in koala densities was allowed for by assuming that the actual (unobserved) koala densities, $D_{i,t}$, followed a gamma distribution, such that

$$D_{i,t} \sim \mathrm{Gamma}\left(a_{\lfloor (t-1)/10 \rfloor + 1}, a_{\lfloor (t-1)/10 \rfloor + 1} \middle/ E\left(D_{i,t}\right)\right), \tag{2}$$

where $a_{\lfloor (t-1)/10 \rfloor + 1}$ ($\lfloor \; \rfloor$ is the floor operator) is the shape parameter for each five year block $\lfloor (t-1)/10 \rfloor + 1$ (note that we divide by 10 here instead of five to get a five year interval because the time-steps are six months in length rather than 12 months) and $a_{\lfloor (t-1)/10 \rfloor + 1} \big/ E\left(D_{i,t}\right)$ is the scale parameter for the gamma distribution. This parameterisation of the Gamma distribution ensures that the expectation of this distribution is $E\left(D_{i,t}\right)$. Here we allow the shape parameter to vary among five year blocks of time to account for any change in the distribution of densities over time.

More specifically we assumed that the shape parameter is described by a log-normally distributed random-effect where $a_{\lfloor (t-1)/10 \rfloor+1} \sim \text{Log-normal}\left(\theta, \sigma_a^2\right)$.

The observation model for the strip transect and total count surveys accounted for the chance of failing to detect koalas based on information contained in repeat observations at the same sites (sensu Hostetler and Chandler 2015), and was as defined as follows

$$N_{i,t,r} \sim \text{Binomial}\left(p, \left\| D_{i,t} A_{i,t,r} \right\|\right), \tag{3}$$

where $N_{i,t,r}$ is the number of koalas observed at site *i* in time-step *t* during strip transect/total count survey *r*, $A_{i,t,r}$ is the area (in hectares) searched at site *i* in time-step *t* during survey *r*, and *p* is the probability of detecting a koala, given it is present at a site. Here, although there is likely to be variation in the probability of detecting a koala given it is present at a site, *p*, among observers and habitat types, a lack of replication across these factors limited the extent to which we could estimate these effects. Therefore we assumed that *p* was constant.

For the line transects, the observation model used a model based on Distance Sampling to estimate a detection function from the recorded perpendicular distances and then applied this to estimate density at each site (Buckland et al. 2001, Gimenez et al. 2009). We evaluated six competing detection function models: the half-normal, uniform and hazard functions, each with and without cosine adjustment. The half-normal and hazard functions with no cosine adjustment were the top ranked models and performed similarly (a difference in AIC < 2). On the basis of parsimony we selected the half-normal distribution as it required one less parameter than the two parameter hazard function (Appendix C). Based on this we assumed that the perpendicular distances are distributed such that

$$S_i \sim \text{Half-normal}\left(0, \tau\right), \tag{4}$$

where S_i is the perpendicular distance for observation *i* in metres, and τ is the precision for the half-normal distribution. Then we assumed that the number of koalas observed at site *i* in time-step *t* during line transect survey *r*, $N_{i,t,r}$, was Poisson distribution such that

$$N_{i,t,r} \sim \text{Poisson}\left(\frac{2L_{i,t,r}D_{i,t}}{10000 f\left(0\right)}\right), \tag{5}$$

where $L_{i,t,r}$ is the distance surveyed at site *i* in time-step *t* during line transect survey *r* in metres and $f\left(0\right) = \sqrt{2\tau/\pi}$. We divide by 10000 here to convert from units of m^2 to hectares. In this case, the detection information is contained in $f\left(0\right)$ that is estimated from the perpendicular distances, with $1/f\left(0\right)$ being the effective strip width (Buckland et al. 2001). As for *p*, we assumed that detection is constant across habitats and observers due to limited replication across these.

Trend model

The trend model for the Koala Coast and Pine Rivers sites was essentially the same basic structure as the spatial model, but we explicitly modelled the temporal dynamics of the population at each site. This meant that the process model differed from the spatial model, but the observation model was identical. We describe the process model below.

First of all, we assumed that the initial koala densities at each site in time-step 1 (i.e., summer 1996) followed a random-effect such that

$$\mathrm{E}\left(D_{i,1}\right) = \exp\left(\eta_i\right), \tag{6}$$

where $\mathrm{E}\left(D_{i,1}\right)$ is the expected density of koalas at site *i* at time-step 1 and η_i is a normally distributed random-effect for site *i* (where $\eta_i \sim \mathrm{Normal}\left(0, \sigma_d^2\right)$). Here we do not include covariates for the initial density because we only want to control for the initial density (by simply estimating the initial density for each site) in the estimation of trends, rather than explaining the spatial distribution of abundances in time-step 1.

However, where the model differs from the spatial model is that the expected densities in subsequent time-steps were assumed to be the result of exponential population growth (or decline), such that

$$E\left(D_{i,t}\right) = D_{i,t-1} r_{i,t-1}, \tag{7}$$

where $r_{i,t-1}$ is the per time step population growth rate for site *i* at time-step *t* - 1. We ignored density dependence because most populations are expected to be well below carrying capacity (Rhodes et al. 2011). Then, $r_{i,t-1}$ was assumed to depend on covariates such that

$$r_{i,t-1} = \exp\left(\gamma^T Y_{i,t-1}\right), \tag{8}$$

where γ is a vector of coefficients, and $Y_{i,t-1}$ is a vector of covariates for site *i* related to time step *t* – 1.

As for the spatial model, stochastic variation in koala densities was allowed for by assuming that the true koala densities, $D_{i,t}$, followed a gamma distribution, such that

$$D_{i,t} \sim \mathrm{Gamma}\left(a_{\lfloor (t-1)/10 \rfloor + 1}, a_{\lfloor (t-1)/10 \rfloor + 1} \big/ E\left(D_{i,t}\right)\right), \tag{9}$$

where $a_{\lfloor (t-1)/10 \rfloor + 1}$ is the shape parameter for each five year block $\lfloor (t-1)/10 \rfloor + 1$ and $a_{\lfloor (t-1)/10 \rfloor + 1} \big/ E\left(D_{i,t}\right)$ is the scale parameter for the gamma distribution. Again, we assumed that the shape parameter is described by a log-normally distributed random-effect where

$$a_{\lfloor (t-1)/10 \rfloor + 1} \sim \text{Log-normal}\left(\theta, \sigma_a^2\right).$$

7.4 Model fitting

Prior to model fitting, we arranged the count data into their separate surveys and then into the seasonal time-steps for each site (249 sites and 39 time-steps between summer 1996 and summer 2015). Where there were no surveys within a time step for a site we coded that as missing data to be estimated from the model. We also arranged the areas searched for the strip transect and total count surveys and the transect lengths for the line transect surveys so that they were associated with each survey. We also arranged the perpendicular distances into a vector, but did not associate these with specific surveys for the analysis.

Next we arranged the covariate data so that each covariate had a value associated with each of the 39 six monthly time-steps for each site (in so doing we assumed that the period October – December was associated with covariates for the following year). For the temperature, rainfall, lot density, road density, FPC, and remnant vegetation covariates that varied through time (Table 3), we extracted the covariate value associated with each year for each site and associated those values with the relevant site and time-step combination. For years where we did not have data, we used the value associated with the closest year where we did have data. Then, for those covariates we averaged the covariate values across all years for each site and used these average values to characterise the covariate values for each site. Although we could have matched time-specific covariate values to each time-step, possibly with lags (e.g. Clark and Bjornstad 2004), given the sparseness of the surveys through time, even for the most frequently surveyed sites, and the unknown lags in the system, the most parsimonious approach was instead to characterise sites by their average covariate values over the whole survey period. However, this means that the covariates essentially represent spatial variation among sites rather than their temporal trends. For the soil and topographic covariates, which do not vary through time, we assigned the covariate value associated with each site to each site and time-step combination. Season (which we coded as summer = 0 and winter = 1) and year covariates were associated with each six monthly time-step.

For the remnant vegetation covariate, because there was insufficient survey replication across individual Broad Vegetation Groups, we grouped Broad Vegetation Groups in two different ways, which we then included as two alternative representations in the models. First, we grouped all Broad Vegetation Groups that contained eucalypt or melaleuca remnant vegetation into a single category (Appendix B).

We subsequently refer to this as the “remnant vegetation (habitat)” covariate. Second we grouped Broad Vegetation Groups into ordinal ranks of habitat suitability based on the tree species present in each Broad Vegetation Group (Appendix B). This resulted in three ordinal categories of habitat suitability (high suitability, suitable, and low suitability) and the rationale for the classification is explained in Appendix B. We subsequently refer to this as the "remnant vegetation (habitat suitability)" covariate.

Prior to model fitting, collinearity between all continuous covariates was assessed using Spearman's rank correlation and, when the correlation between two covariates was greater than 0.6 or less than -0.6, either one covariate was removed, or one covariate was regressed on the other and the residuals used for one of the covariates to remove collinearity (Trzcinski et al. 1999, Rhodes et al. 2009). All remaining covariates, except for the categorical season covariate, were standardised to have a mean of zero and standard deviation of one.

Models were fit to the data using Markov Chain Monte Carlo (MCMC) in JAGS (http://mcmc-jags.sourceforge.net/) using the *runjags* package in R (www.r-project.org). The advantages of this approach are that it allows for the straightforward construction of the non-standard models developed here and naturally deals with the problem of missing data, specifically the unobserved true koala densities and missing data in time-steps where surveys were not conducted (McCarthy 2007). We assumed Normal (0,0.001) priors for the β and γ coefficients and θ, a Gamma (0.001,0.001) prior for τ, Uniform (0,10) priors for the variance components σ_d and σ_a, and a Uniform (0,1) prior for *p*. These were chosen to be largely uninformative priors. We simulated three MCMC chains using over-dispersed starting values and a burn-in of 40,000 iterations and then retained 100,000 iterations per chain. Convergence was assessed using the Gelman and Rubin convergence statistic (R-hat) (Gelman and Rubin 1992). See Appendix D for the JAGS code for both the spatial and trend models.

7.5 Model selection

The Deviance Information Criterion (DIC) is widely used for model selection for complex Bayesian models fitted using MCMC (Spiegelhalter et al. 2002, Celeux et al. 2006). However, for state-space models the use of DIC may be problematic unless DIC can be calculated using the marginal likelihood with the latent (unobserved) variables integrated out (Millar 2009). Due to the complexity of calculating the marginal likelihood for our models and because the purpose of these models is primarily prediction, we instead used *V*-fold cross validation for model selection (Arlot and Celisse 2010). In conducting the *V*-fold cross validation we evaluated observed koala counts against the mean predicted counts across 100 replicates for the spatial model and 50 replicates for the trend model (fewer replicates for the trend model due to computational constraints) and leaving out approximately 20% of the data in each replicate (110 surveys for the spatial model and 71 surveys for the trend model).

We used a loss function, which increases in value as predictive performance declines, defined as the square root of the mean squared differences between the observed koala counts and the mean predicted counts and identified the model with the smallest loss as the best model. Cross-validation was conducted using the *drop.k* function in the *runjags* package in R, using a target Gelman and Rubin convergence statistic (R-hat) of 1.1 to determine convergence.

For the spatial model we found collinearity between:

1) FPC and buffer FPC;
2) FPC and remnant vegetation (habitat);
3) FPC and remnant vegetation (habitat suitability) - low suitability class;
4) buffer FPC and buffer remnant vegetation (habitat);
5) elevation, slope and topographic wetness index;
6) soil bulk density and soil clay content; and
7) lot density and road density.

Consequently, we removed buffer remnant vegetation, slope, topographic wetness index, soil bulk density and lot density to deal with collinarity in these variables. To deal with collinarity in the other variables but to still retain them, logit(buffer FPC + 0.01) was regressed on FPC, logit(remnant vegetation (habitat) + 0.01) was regressed on FPC, and logit(remnant vegetation (habitat suitability) - low suitability class + 0.01) was regressed on FPC with the residuals used instead of buffer FPC, remnant vegetation (habitat), and remnant vegetation (habitat suitability) - low suitability class, respectively (Trzcinski et al. 1999).

For the trend model, collinearity among variables was similar, but we found high levels of collinearity between:

1) soil clay and soil phosphorous;
2) temperature and rainfall; and
3) soil water availability and road density.

To deal with this, in addition to the measures taken for the spatial model, we removed soil phosphorous and temperature, and logit (road density + 0.01) was regressed on soil water with the resulting residuals used instead of road density.

For both models we first considered a model with all covariates included as predictors (and including the remnant vegetation (habitat suitability) classification, rather than remnant vegetation (habitat) classification), plus quadratic terms for FPC and road density to allow for possible non-linear effects in those variables. We then classified covariates into physical variables, soil variables, habitat variables, and threat variables (Table 3).

Based on this, we then constructed simplified models based on reducing the number of variables within the physical, soil and habitat classes. For the physical class, simplification consisted of only including elevation which is likely to be a good proxy for physical drivers of koala density. For the soil class, simplification consisted of only including soil water and soil nitrogen based on the likely importance of these two variables for koalas (Table 3).

For the habitat class, simplification consisted of including the remnant vegetation (habitat) classification rather than the more complex remnant vegetation (habitat suitability) classification. Alternative models were constructed based on all combinations of the above simplification strategies (eight models in total) and the best model identified based on the *V*-fold cross-validation. Then the quadratic terms for FPC and road density were removed from the best model and that model was then evaluated using the *V*-fold cross-validation to examine whether the quadratic terms improved model performance. Season and year were included in all models. Based on this strategy we evaluated nine alternative model structures for the spatial and trend models.

7.6 Model adequacy and validation

We assessed model adequacy and validated the models using a number of strategies. First, we plotted spatial spline correlograms (Bjørnstad and Falck 2001) on the model residuals to test for the presence of any spatial autocorrelation that may invalidate statistical tests. Spline correlograms were constructed using the package *ncf* in R (www.r-project.org). Second, quantile-quantile plots were constructed to examine departures from the distributional assumptions of the model, including any zero-inflation that may be present (Landwehr et al. 1984, Rhodes 2015). Third, we conducted posterior predictive checks to check for significantly poor model fit based on the Pearson χ^2 statistic as a measure of fit (Gelman et al. 2004). Finally, we compared predictions obtained from the *V*-fold cross-validation with the actual survey data to validate the predictive performance of the models.

7.7 Model predictions

We generated spatial predictions of the expected koala density based on the spatial model at a resolution of 50ha hexagonal grid cells across the study region. We chose a resolution of 50ha because this is the approximate mean size of the surveyed sites and we wanted to match the resolution of the spatial predictions with the resolution of the data. However, model selection based on cross-validation can favour models that are over-fit (i.e., complex models that are fit too closely to error in the data and have low ability to predict outside of the range of the data used to fit the models) (Zhang 1993). Therefore, to ensure that predictions were not made for grid cells with covariate values well outside the range of the covariate values at the survey sites, we only made predictions for grid cells with covariate values within the range of covariate values for the survey sites for elevation, FPC, FPC buffer, and road density. We also made predictions for the expected change in the average density of koalas at the survey sites in Pine Rivers and the Koala Coast based on the trend model.

8. RESULTS

8.1 Spatial model

MCMC chain convergence for the spatial models was good (R-hat < 1.05) for all model fits (Gelman and Rubin 1992). The best model out of the initial eight models, based on the cross-validation performance, was the model with simplified soil and habitat variables (Table 4). Removing the quadratic term for FPC and road density resulted in a slight loss of model performance, but the resulting model was still the second best performing mode (Table 4). For the best model, the agreement between the predicted and observed koala counts was high, with a Pearson's correlation coefficient of around 0.88 (Table 4 and Figure 2). Further, in only 5% of the surveys did the 95% credible intervals of the cross-validation predictions not include the true koala count in more than 20% of the cross-validation replicates. Therefore cross-validated model performance was very good. Examination of the quantile-quantile plots revealed relatively good agreement between the distributional assumptions of the model and the data, although there was some sign of under-dispersion in the data relative to the model (Appendix D). Nonetheless, there was no sign of significant lack of fit based on the posterior predictive checks (p = 0.84). Therefore, model fit was reasonably good.

Table 4. Competing spatial model comparisons based on the *V*-fold cross validation. "Pearson's correlation" is the Pearson's correlation coefficient between the predicted and observed koala counts and "Loss score" is the mean squared difference between the predicted and observed koala counts. The two best models are highlighted in bold.

Model	Pearson's correlation	Loss score
(1) rainfall + temperature + elevation + soil water + soil clay + soil nitrogen + soil phosphorous + FPC + buffer FPC + remnant vegetation (habitat suitability) + road density + FPC^2 + road density^2 + season + year	0.87	21.84
(2) elevation + soil water + soil clay + soil nitrogen + soil phosphorous + FPC + buffer FPC + remnant vegetation (habitat suitability) + road density + FPC^2 + road density^2 + season + year	0.86	24.79
(3) rainfall + temperature + elevation + soil water + soil nitrogen + FPC + buffer FPC + remnant vegetation (habitat suitability) + road density + FPC^2 + road density^2 + season + year	0.87	21.74
(4) rainfall + temperature + elevation + soil water + soil clay + soil nitrogen + soil phosphorous + FPC + buffer FPC + remnant vegetation (habitat) + road density + FPC^2 + road density^2 + season + year	0.88	21.20
(5) elevation + soil water + soil nitrogen + FPC + buffer FPC + remnant vegetation (habitat suitability) + road density + FPC^2 + road density^2 + season + year	0.87	21.93
(6) rainfall + temperature + elevation + soil water + soil nitrogen + FPC + buffer FPC + remnant vegetation (habitat) + road density + FPC^2 + road density^2 + season + year	**0.88**	**20.07**
(7) elevation + + soil water + soil clay + soil nitrogen + soil phosphorous + FPC + buffer FPC + remnant vegetation (habitat) + road density + FPC^2 + road density^2 + season + year	0.86	23.73
(8) elevation + soil water + soil nitrogen + FPC + buffer FPC + remnant vegetation (habitat) + road density + FPC^2 + road density^2 + season + year	0.88	21.57
(9) rainfall + temperature + elevation + soil water + soil nitrogen + FPC + buffer FPC + remnant vegetation (habitat) + road density + season + year	**0.88**	**20.28**

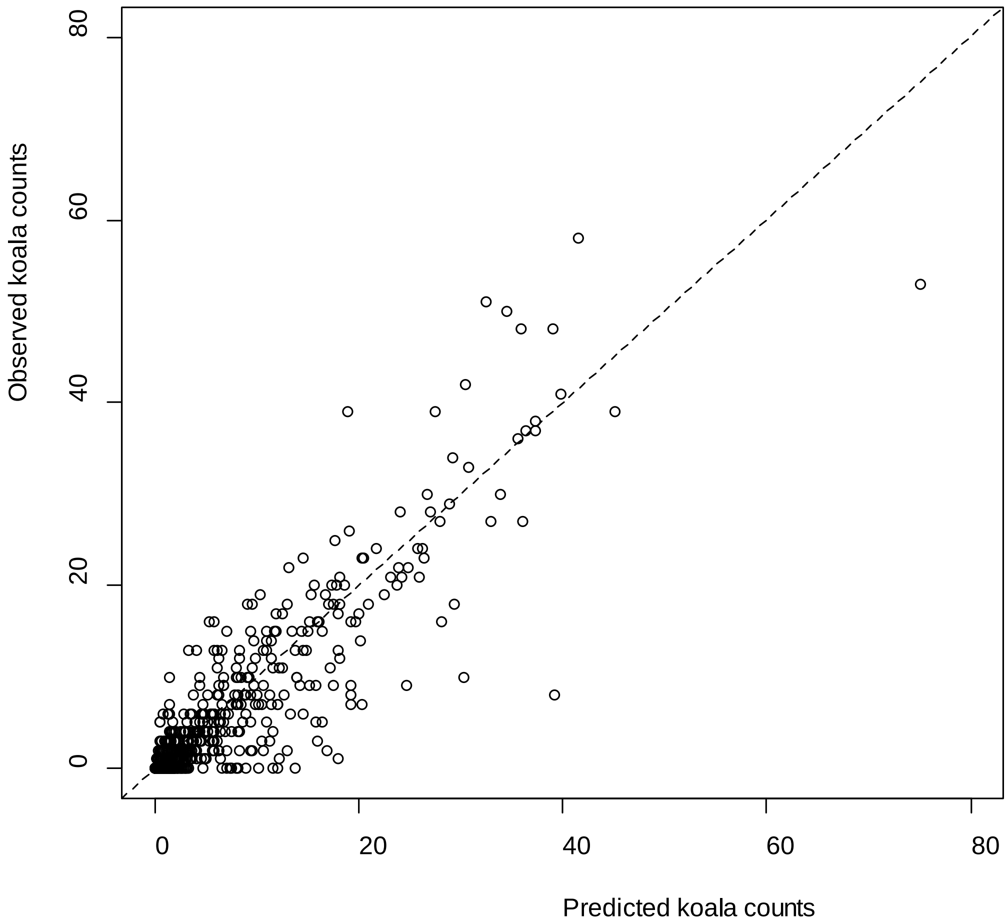


Figure 2. Relationship between the predicted koala counts derived from the *V*-fold cross validation and the observed koala counts for the best spatial model (model 6). The dotted line shows the 1:1 relationship.

In terms of the effects of each of the covariates on koala density derived from the best spatial model, many of the effects (i.e. the model coefficients) for the covariates were not significantly different from zero (Table 5). The coefficients that were significantly different from zero were rainfall (negative), temperature (negative), FPC buffer residuals (negative), and year (negative). These indicate significant negative relationships between koala density and rainfall, temperature, and FPC buffer (after accounting for the relationship with FPC at the site scale), and a significant decline in density over time. The coefficients for FPC and remnant vegetation showed a positive association with koala density, but were not significantly different from zero.

Surprisingly, the coefficient for road density was positive, although again not significantly different from zero, providing some suggestion of higher koala densities in areas with high road densities compared to areas with low road densities. However, because the quadratic terms for FPC and road density are negative, the highest koala densities are estimated to occur at intermediate levels of FPC and road density. The probability of detecting a koala, given that it is present at a site, was estimated to be 0.67 (Table 5).

Table 5. Parameter estimates for the best spatial model (model 6).

Parameter	Estimate (95% credible interval)
Intercept	-2.99 (-3.34, -2.67)
Rainfall	-0.66 (-1.05, -0.26)
Temperature	-1.18 (-1.57, -0.78)
Elevation	-0.43 (-0.87, 0.02)
Soil water	0.11 (-0.10, 0.31)
Soil nitrogen	-0.22 (-0.60, 0.20)
FPC	1.17 (-0.50, 2.81)
FPC buffer residuals	-0.74 (-1.03, -0.47)
Remnant vegetation residuals (habitat)	0.19 (-0.06, 0.46)
Road density	0.35 (-0.63, 1.32)
FPC^2	-0.89 (-2.64, 0.83)
Road $density^2$	-0.24 (-1.17, 0.68)
Season	-0.05 (-0.16, 0.07)
Year	-0.44 (-0.51, -0.38)
Distance sampling parameter (τ)	1.36×10^{-3} (1.09×10^{-3}, 1.64×10^{-3})
Standard deviation of site random-effect (σ_d)	1.15 (0.91, 1.40)
Detection probability (*p*)	0.67 (0.54, 0.80)

The predicted distribution of high koala density based on the best spatial model was concentrated in the coastal regions of South East Queensland from Moreton Bay southwards, but with some patches of high density predicted in the western parts of Moreton Bay Regional Council, Sunshine Coast Regional Council and Gold Coast City Council (Figure 3). However these areas of high density in the western regions had high levels of uncertainty associated with them, as indicated by their high coefficients of variation (Figure 3; also see Appendix F for the 95% credible intervals for the spatial distribution of koala densities).

The highest densities of koala were predicted for Redland City Council, Moreton Bay Regional Council, the eastern part of Logan City Council, and Gold Coast City Council. Koala densities in Noosa Shire Council were generally predicted to be low. The predicted spatial patterns based on the second best spatial model were very similar (Appendix G).

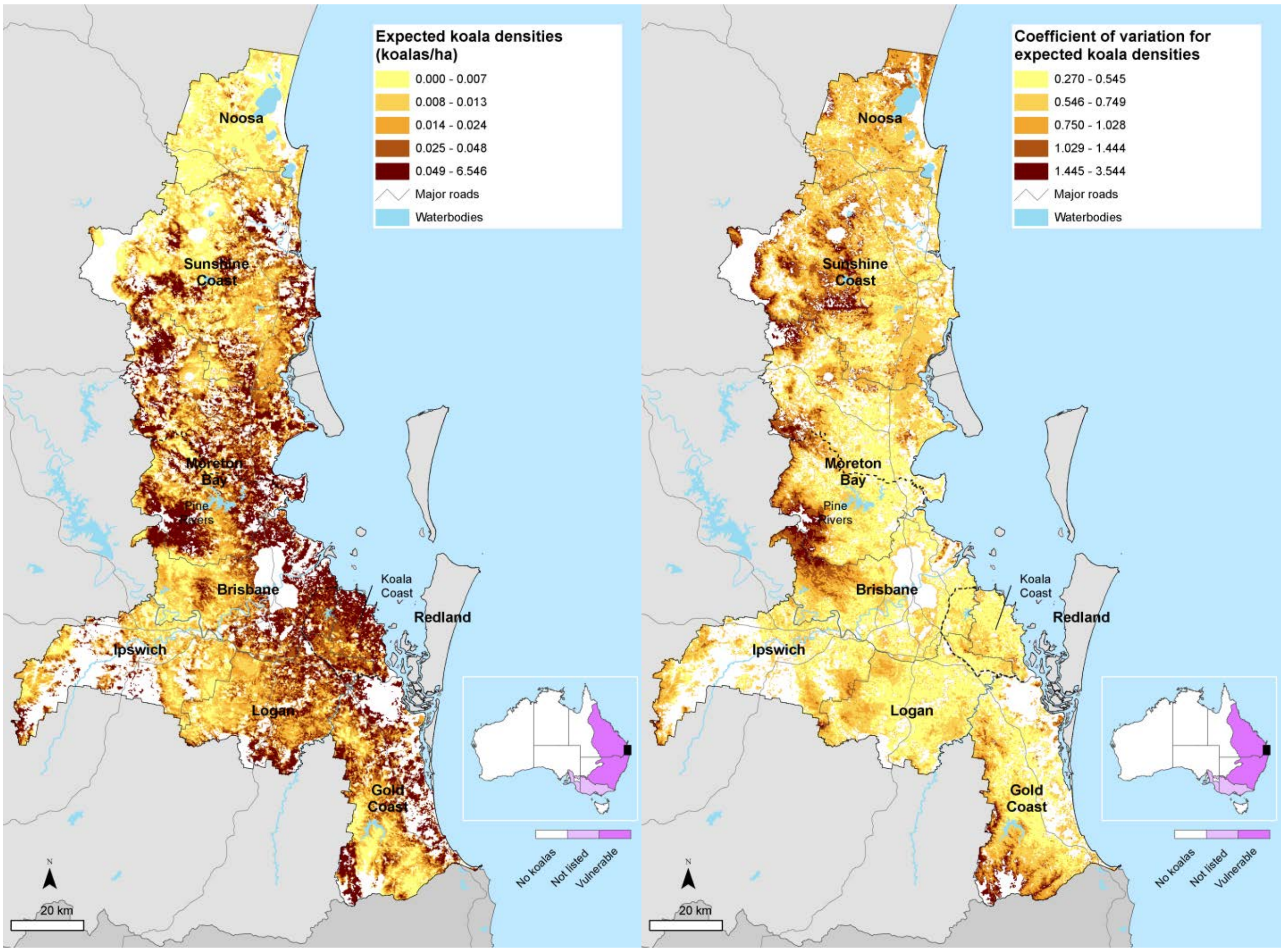


Figure 3. The spatial distribution of expected koala densities based on the best spatial model (model 6) and the coefficient of variation for those densities. Maps were constructed at a resolution of 50ha, but excluding areas that were outside the range of covariate values at the surveyed sites for elevation, FPC, FPC buffer, and road density. See Appendix F for the 95% credible intervals for the spatial predictions.

8.2 Trend model

MCMC chain convergence for the trend models was good (R-hat < 1.05) for all model fits (Gelman and Rubin 1992). The best model out of the initial eight models, based on the cross-validation performance, was the full model containing all variables (Table 6). Removing the quadratic term for FPC and road density resulted in a slight loss of model performance suggesting that the quadratic terms are important predictors (Table 6). The second best model was the model with simplified physical and soil variables (Table 6). However, overall there was less distinction among models than there was for the spatial model (i.e. lower variation in loss scores).

For the best model, the agreement between the predicted and observed koala counts was high, with a Pearson's correlation coefficient of around 0.92 (Table 6 and Figure 4). Further, in only 9% of the surveys did the 95% credible intervals of the cross-validation predictions not include the true koala count in more than 20% of the cross-validation replicates.

Therefore, cross-validated model performance was very good. Examination of the quantile-quantile plots revealed relatively good agreement between the distributional assumptions of the model and the data, although there was some sign of under-dispersion in the data relative to the model (Appendix D). Nonetheless, there was no sign of significant lack of fit based on the posterior predictive checks (p = 0.16). Therefore, model fit was reasonably good.

Table 6. Competing trend model comparisons based on the *V*-fold cross validation. "Pearson's correlation" is the Pearson's correlation coefficient between the predicted and observed koala counts and "Loss score" is the mean squared difference between the predicted and observed koala counts. The two best models are highlighted in bold.

Model	Pearson's correlation	Loss score
(1) rainfall + temperature + elevation + soil water + soil clay + soil nitrogen + soil phosphorous + FPC + buffer FPC + remnant vegetation (habitat suitability) + road density + FPC^2 + road density^2 + season + year	**0.92**	**16.36**
(2) elevation + soil water + soil clay + soil nitrogen + soil phosphorous + FPC + buffer FPC + remnant vegetation (habitat suitability) + road density + FPC^2 + road density^2 + season + year	0.91	18.45
(3) rainfall + temperature + elevation + soil water + soil nitrogen + FPC + buffer FPC + remnant vegetation (habitat suitability) + road density + FPC^2 + road density^2 + season + year	0.91	18.19
(4) rainfall + temperature + elevation + soil water + soil clay + soil nitrogen + soil phosphorous + FPC + buffer FPC + remnant vegetation (habitat) + road density + FPC^2 + road density^2 + season + year	0.91	19.77
(5) elevation + soil water + soil nitrogen + FPC + buffer FPC + remnant vegetation (habitat suitability) + road density + FPC^2 + road density^2 + season + year	**0.92**	**17.58**
(6) rainfall + temperature + elevation + soil water + soil nitrogen + FPC + buffer FPC + remnant vegetation (habitat) + road density + FPC^2 + road density^2 + season + year	0.91	19.05
(7) elevation + + soil water + soil clay + soil nitrogen + soil phosphorous + FPC + buffer FPC + remnant vegetation (habitat) + road density + FPC^2 + road density^2 + season + year	0.91	19.28
(8) elevation + soil water + soil nitrogen + FPC + buffer FPC + remnant vegetation (habitat) + road density + FPC^2 + road density^2 + season + year	0.91	18.66
(9) rainfall + temperature + elevation + soil water + soil nitrogen + FPC + buffer FPC + remnant vegetation (habitat) + road density + season + year	0.91	19.14

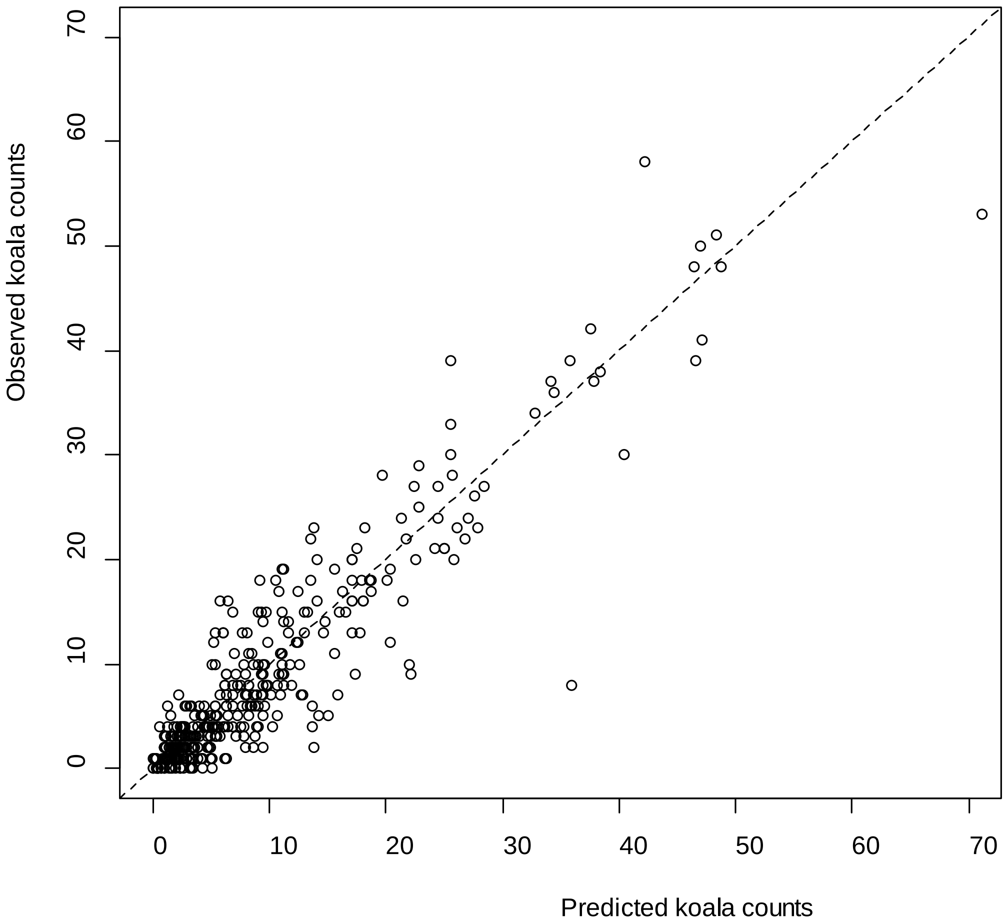


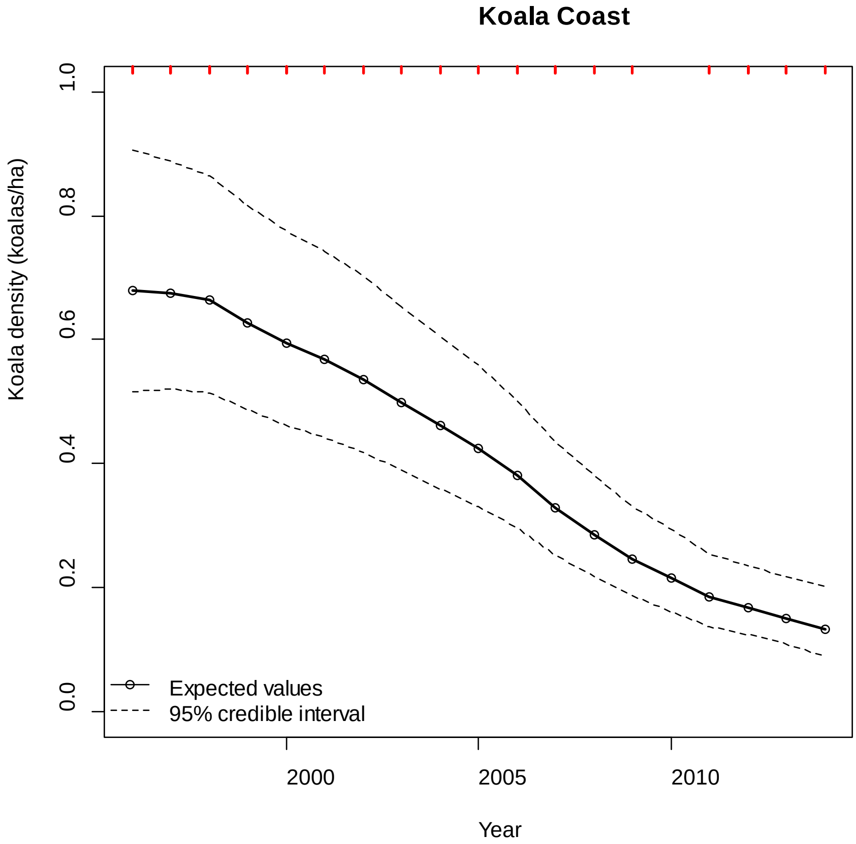
Figure 4. Relationship between the predicted koala counts derived from the *V*-fold cross validation and the observed koala counts for the best trend model (model 1). The dotted line shows the 1:1 relationship.

In terms of the effects of each of the covariates on the growth rate of koalas derived from the best trend model, many of the effects (i.e. the model coefficients) for the covariates were, again, not significantly different from zero (Table 7). In fact, there were only three variables that were significantly different from zero: rainfall (negative), season (positive) and year (negative). This suggests that growth rates decline with increasing rainfall and also that growth rates have also declined over time. The strong seasonal effect implies that the growth rate between summer and winter was generally much lower than the growth rate between winter and summer.

Table 7. Parameter estimates for the best trend model (model 1).

Parameter	Estimate (95% credible interval)
Intercept	-0.112 (-0.184, -0.038)
Rainfall	-0.015 (-0.027, -0.002)
Elevation	-0.014 (-0.039, 0.010)
Soil water	-0.011 (-0.022, 0.001)
Soil clay	0.012 (-0.002, 0.026)
Soil nitrogen	-0.006 (-0.024, 0.013)
FPC	0.024 (-0.054, 0.111)
FPC buffer residuals	-0.005 (-0.017, 0.008)
Remnant vegetation (habitat) – high suitability	-0.001 (-0.014, 0.012)
Remnant vegetation (habitat) – suitable	0.004 (-0.028, 0.036)
Remnant vegetation residuals (habitat) – low suitability	-0.013 (-0.058, 0.030)
Road density residuals	0.001 (-0.013, 0.015)
FPC^2	-0.019 (-0.104, 0.067)
Road density residuals^2	-0.002 (-0.013, 0.010)
Season	0.146 (0.002, 0.282)
Year	-0.020 (-0.038, -0.002)
Distance sampling parameter (τ)	1.29×10^{-3} (1.03×10^{-3}, 1.58×10^{-3})
Standard deviation of site random-effect (σ_d)	0.89 (0.63, 1.16)
Detection probability (*p*)	0.49 (0.38, 0.60)

Overall, koala densities at the survey sites in the Koala Coast and Pine Rivers declined between 1996 and 2014, with the greatest declines occurring at the Koala Coast sites (Figure 5). The estimated mean decline in koala density at the Koala Coast sites between 1996 and 2014 was -80.25% (95% credible interval: -86.19% to -70.81%). On the other hand, the estimated mean decline in koala density at the Pine Rivers sites between 1996 and 2014 was -54.28% (95% credible interval: -74.42% to -20.10%). The estimated annual rate of change in density in the Koala Coast in 1996 was -1.93% (95% credible interval: -6.84% to +3.26%), but in 2014 it was -13.26% (95% credible interval: -19.44% to -6.49%), while in Pine Rivers, the estimated annual rate of change in the density in 1996 was +0.87% (95% credible interval: -5.77% to +8.01%) and -10.81% (95% credible interval: -16.53% to -4.52%) in 2014 (Figure 6). This illustrates a likely acceleration in the rate of decline over time.



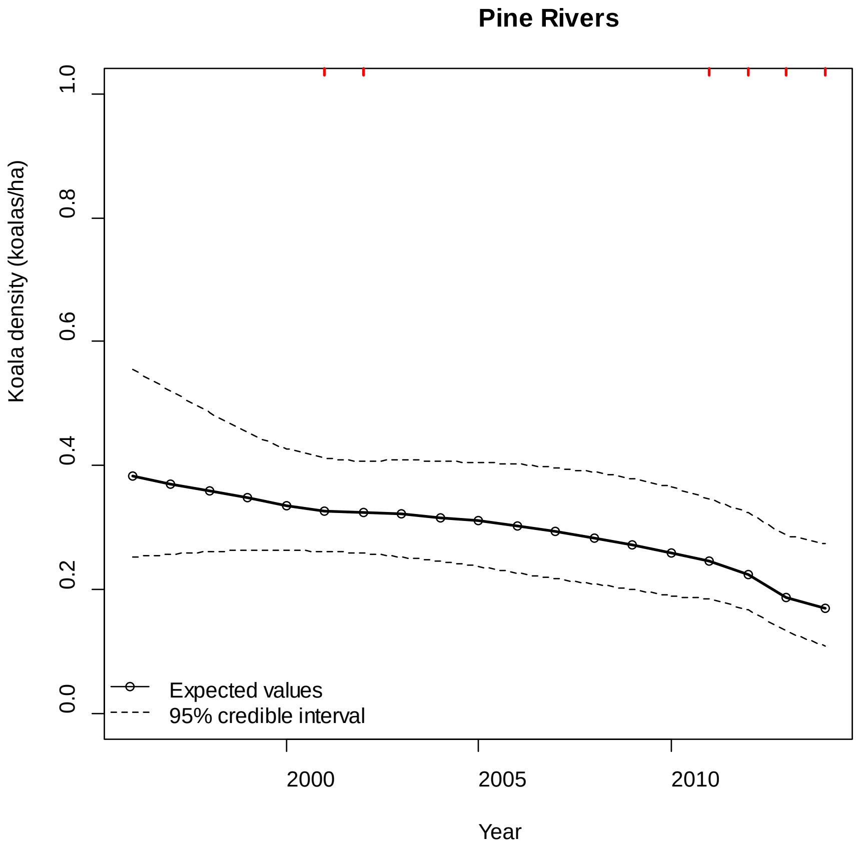
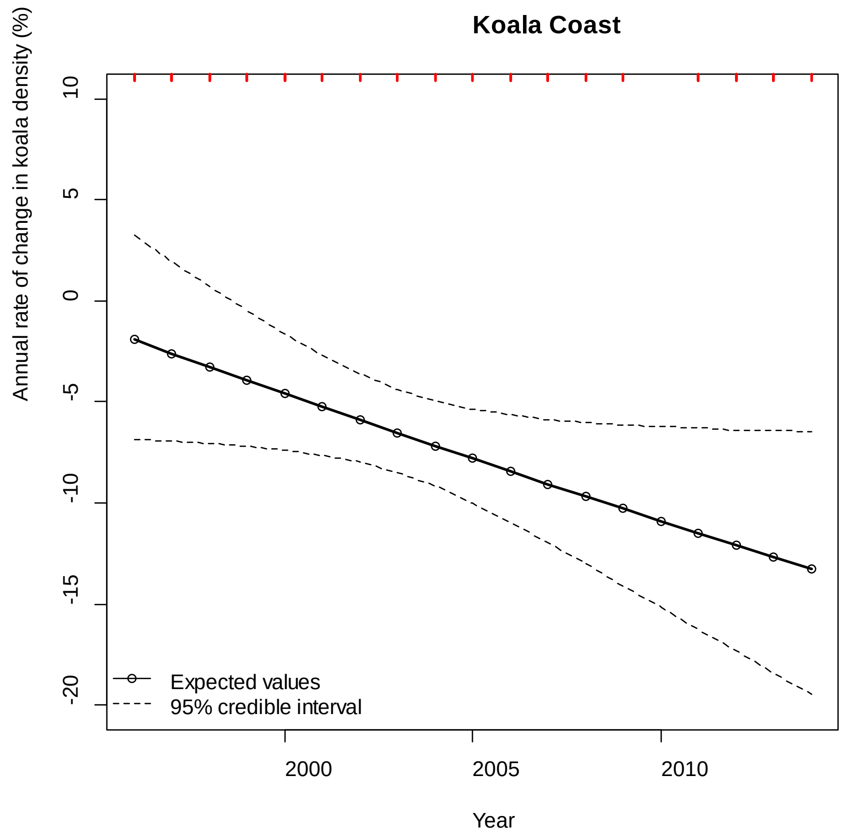


Figure 5. Estimated mean koala densities at the Koala Coast and Pine Rivers sites between 1996 and 2014. Red ticks at the tops of the graphs indicate years when surveys occurred.



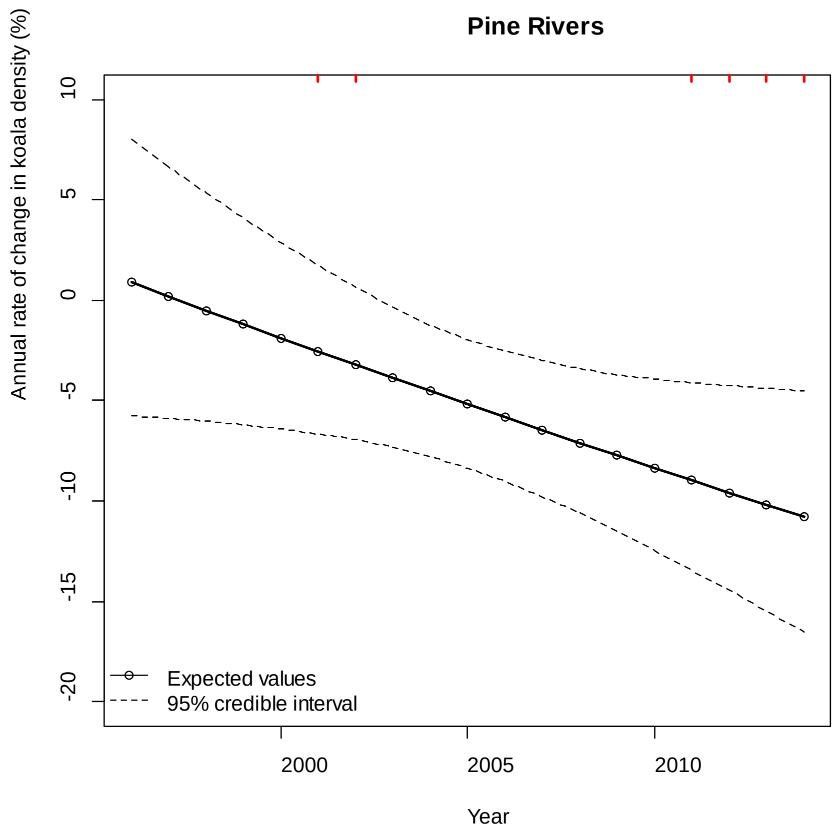


Figure 6. Estimated mean annual percentage change in koala density at the Koala Coast and Pine Rivers sites between 1996 and 2015. Red ticks at the tops of the graphs indicate years when surveys occurred.

9. DISCUSSION

This study draws together a unique long-term data set of koala counts to estimate koala densities and trends across South East Queensland for the first time. The models developed predict that the highest koala densities currently occur along the coastal regions of South East Queensland, and particularly in the central and southern coastal regions (Figure 3). There was strong evidence for a rapid decline in population densities between 1996 and 2014 in the Koala Coast (-80%) and Pine Rivers (-54%) and that the rate of decline has been increasing over time. Although it was not possible to estimate population trends for the whole of the region these population declines may well be indicative of patterns of population decline more broadly.

Overall, across the region, the primary factors associated with the broad-scale distribution of koala densities appear to be climatic factors (temperature and rainfall). However, there is some suggestion that koala densities may be highest at intermediate levels of forest cover (FPC) and road density and clearer evidence that koala densities depend upon the amount of forest cover around sites. There were also some unexpected areas of predicted high density in western regions, but these were areas where surveys have not been conducted and uncertainty in the density estimates was high (Fig. 3). Therefore, the reliability of the predictions in those western areas may be low.

9.1 Koala densities and spatial distributions

Across the region, the average koala density was estimated to be 0.04 koalas/ha (ranging from 0 to 6.54 koalas/ha). Although the predicted densities for areas at the top of the range of densities are unlikely to be realistic predictions, the vast majority of areas are predicted to have low population densities. This suggests that koalas in South East Queensland may be relatively widely distributed, but of low density in most areas. The focus of this project was on estimating koala densities (defined as the number of koalas per unit area) and this is distinct from population numbers (the total number of koalas in an area).

In theory, population numbers could be estimated from the densities estimates, by multiplying densities by area, but we guard against doing this without considerable care and further analysis. The spatial density predictions are an extrapolation based on a model fitted to data from only a small portion of the study region and this could introduce considerable error into an estimate of population numbers. We also excluded some areas from the spatial predictions to limit the extent to which extrapolations were made outside the range of the data used to develop the model, so we do not know what koala densities are in these regions. The power of the spatial model developed here is to provide estimates of the distribution of koalas across the region and, although it may ultimately be possible to estimate population numbers from this model, this would need considerable thought and care to be able to do so with confidence.

The negative relationship between temperature and koala densities that we found is consistent with other studies elsewhere (Adams-Hosking et al. 2011b, Lunney et al. 2014, Santika et al. 2014) and seems to be associated with low koala densities in Ipswich City Council and Noosa Shire Council, where temperatures are relatively high. However, the negative relationship with rainfall appears contradictory with studies elsewhere (Seabrook et al. 2011, Santika et al. 2014), although these studies have typically been conducted in areas where rainfall is likely to be a much greater limiting factor. Elevation was not a statistically significant predictor of koala densities, but it did have a negative coefficient indicating lower koala densities at high elevations. Although most of the remaining covariates were not statistically significant (apart from FPC buffer), there was some indication that koala densities are highest at intermediate levels of FPC and road density. It is likely that areas of intermediate road density, reflecting intermediate human population densities, coincide with areas of good koala habitat because these are the most productive and fertile soils, with these patterns having been demonstrated for biodiversity in general (Luck 2007). However, once road densities get too high, threats from high density urban development are likely to increase substantially, resulting in koala density declines. The relationship between FPC and koala density is likely to be a reflection of the fact that their preferred *Eucalypt* habitat types tend to occur at intermediate levels of FPC. We also note, however, that interpretation of individual coefficients associated with the spatial covariates is difficult as the value of any one predictor can be masked by correlations (even weak correlations) with multiple other variables.

The strong negative relationship between koala density and the FPC buffer variable may appear contradictory. However, the variable used was the residuals after accounting for the FPC at the site in a regression, thus some of the effect of FPC buffer variable is reflected in the FPC coefficient. Therefore, when the FPC buffer variable is low this means that there is lower forest cover around a site than would be expected based on the level of forest cover at the site. In this case, a lack of forest cover around a site could result in crowding of populations at the site (which would not necessarily have low levels of forest cover), resulting in a higher than expected density. Similar patterns have been observed at Ney Road in the Koala Coast as habitat at and around the site was cleared (Harriet Preece, personal observation), although such patterns will usually be transient and the population will eventually decline, as was observed at Ney Road.

9.2 Koala Trends

The estimated declines in koala density in the Koala Coast and Pine Rivers are very rapid and there is evidence that the rate at which these populations are declining is actually increasing. Our estimates of decline are broadly consistent with previous estimates of trends in the Koala Coast (Department of Environment and Resource Management 2012) and Pine Rivers (GHD 2008), but changes in the rate of decline had not previously been explored. We did not find any particularly strong spatial predictors of declines in density, apart from year, and a strong seasonal effect, but the rate of decline for the Koala Coast was estimated to be more rapid than in Pine Rivers, possibly reflecting the different histories of development.

For an animal that already occurs at relatively low densities, annual population declines of the order of magnitude estimated here are likely to result in local extinctions for some populations within a small number of generations. The koala survey data suggests that there are already a number of areas in which koalas may become locally extinct or are at such low densities that they are effectively extinct (i.e., they are at high risk of stochastic events eliminating the population and have inadequate recruitment rates to sustain the population). For example, in the 1996 major survey of the Koala Coast there were two sites (of 17) in which zero or one koalas were detected, and no sites (of 21) in the 1997 major survey with detections of zero or one koalas. However, in the 2010 and 2012 major surveys, there were seven and eight (of 20) sites, respectively, with zero or one koalas detected, and large reductions in densities at the remaining sites. Overall, it appears that the loss of koalas from many sites in the Koala Coast is imminent, and Pine Rivers sites appear to be following a similar trajectory. These types of patterns are common across coastal eastern Australia where development and koala habitat coincide (Lunney et al. 2002, Lunney et al. 2007b, Santika et al. 2014).

9.3 The modelling approach

This is the first attempt to explicitly model the dynamics and spatial distribution of koala density across South East Queensland. In doing so, we used state-of-the art statistical methods that are explicit about the temporal dynamics of koala populations and observation processes (Hostetler and Chandler 2015). The benefit of such an approach is that it reduces bias in parameter estimates, such as trends and the effect of spatial covariates, and allows for the explicit quantification of the drivers of the dynamics of the koala populations (at least for those populations with sufficient surveys through time) (Dail and Madsen 2011). This is a significant advance in methods for modelling koala survey data and provides a new framework which can be used to update estimates of spatial distributions and trends as new data is collected.

9.4 Limitations

There are a number of issues that must be considered when making inferences from these analyses. In the case of the strip transects and total counts, detection probability, p, can only be estimated if there are repeated surveys of sites within a short enough time interval that it is reasonable to assume density has not changed (this is known as the closure assumption) (Royle 2004, Rota et al. 2009, Dail and Madsen 2011). In this analysis we capitalise on repeated surveys within a season to estimate the detection probability, under the assumption that density at sites does not change over a six month period. Clearly that is rather a strong assumption because koalas may enter or leave a survey site during that time, or may die.

However, repeated surveys did often yield fairly consistent counts within a time period, although there were some counts that were more variable. Thus, the detection probability parameter likely reflects more than simply detection probability and should be interpreted cautiously. This is because, if the detection parameter has been underestimated, then koala densities will be overestimates and vice versa if detection probability is overestimated. Further, failure to meet the closure assumption is likely to result in increased uncertainty in the detection probability parameter that is propagated through the analysis and contributes to the uncertainty in all other parameter estimates.

One major limitation was potential sampling bias in the survey site locations. Sampling bias in survey site selection is problematic for generating spatial predictions of density (Buckland et al. 2001, Rogerson 2010) and this was a particular problem because approaches to site selection varied over the span of the koala survey data. In the early years, survey sites were preferentially located in what was deemed to be suitable habitat for koalas and was accessible to survey teams (primarily this was public land, although permission was granted to access some private lands). This does not constitute a representative spatial sample of environmental conditions across South East Queensland, or even within an area such as Pine Rivers or the Koala Coast. In the latter years a stratified and randomised sampling approach was developed. These survey designs reflect different objectives motivating data collection.

The sampling design in the Koala Coast and Pine Rivers is suitable for quantifying trends at particular sites, while more recent survey designs are better suited to quantifying spatial variation in koala densities across a wider range of environmental conditions. Further, some regions of environmental space are sampled much more intensively than others. For example, there is relatively little empirical data that can be used to estimate koala densities in highly urbanised areas and in rainforest areas. The ability to predict in these areas, where little or no sampling has occurred and where koala densities are likely to be low or zero, is therefore limited. This is a general problem of extrapolation outside the range of environmental conditions within which data were collected and has important implications for future monitoring survey design (see recommendations below).

The dynamics of koala densities at sites is complex and driven by a suite of processes that operate at different spatial and temporal scales. Time lags between changes in environmental conditions and the effects on animal populations often make it difficult to relate dynamic covariates (e.g., temperature, rainfall, habitat clearing, etc.) to population dynamics (Clark and Bjornstad 2004). Although some environmental conditions may have obvious and immediate effects (e.g., large mortality events arising from extreme weather), many environmental conditions affect populations through multiple, complex pathways over a variety of time scales (e.g., fire may have immediate detrimental effects, but longer term beneficial effects on koala populations). In our models, dynamic covariates were represented as averaged values across all years because of the difficulty of representing lags between changes in covariate values and effects on koala density. Further complexity arises when environmental change in the areas surrounding koala habitat is considered.

For example, building roads near a survey site will not be accounted for in any site-specific covariates, but may still have important long-term effects on population viability if mortality rates of animals moving around the area increase. Quantifying covariates within distance buffers around each site goes some way to addressing this problem, but does not resolve the issue of lag effects associated with those variables. This is an issue that will need future work to examine the implications of not being able to account for these complexities in our models.

9.5 Recommendations

The rapid declines in koala densities in the Koala Coast and Pine Rivers indicate populations in considerable danger and there is a risk that it may be too late to stabilise or recover these populations. A key question, however, is whether the declines in koala densities in the Koala Coast and Pine Rivers are representative of declines elsewhere in the study region, or whether they are unique to these regions. The data are currently insufficient to answer this question because of the absence of repeated koala surveys over multiple years at sites outside of these two regions. As such, a monitoring strategy to identify remaining areas of relatively high koala density and to evaluate trends more broadly is critical for developing conservation policy for koalas in South East Queensland. If there are areas that are not suffering declines to the same extent as those in the Koala Coast and Pine Rivers then these may be areas where koalas could still be conserved with adequate protection and management. Identifying these areas with a carefully designed monitoring program would appear to be a priority.

Similarly, there were some areas where spatial predictions were highly uncertain or deemed to be too far outside of the range of sampled data to make reasonable predictions about koala density. Future additional surveys could be targeted in these areas to improve the accuracy and extent of the spatial predictions. More generally, the spatial predictions presented here could be used to help design future survey strategies in order to improve the efficiency of survey effort and the expected benefit of data acquired to our understanding of koala distribution and population dynamics. The benefits of using models of the distribution of species combined with techniques for optimising survey effort has been shown to be highly effective in other systems (e.g., Hauser and McCarthy 2009) and could provide a practical way forward for prioritising future surveys.

The current survey data suffers from three key limitations that should be addressed in future decisions about survey design in addition to the two recommendations highlighted above. First, the usefulness of the data suffers from a strategy that was initially designed to estimate trends in a few sites, to a later design aimed primarily at obtaining data on the spatial distribution of koalas. Appropriate strategies to address these different questions will tend to be quite different and there is a need to be clear about what the objectives of the monitoring program are. Ultimately, because a single survey design is unlikely to be able to adequately address both trend and spatial distribution questions effectively, separate strategies for estimating trends and distributions may be required.

Second, the design of many of the surveys makes the estimation of detection error difficult. The estimation of detection error, so that unbiased density estimates can be obtained should form a central component of future survey design, either through appropriate replication of surveys or Distance Sampling (Buckland et al. 2001, Royle 2004, MacKenzie et al. 2006).

Third, the design of the database within which the monitoring data were held was inappropriate for effective analysis of the data. In addition to the models presented in this report, this project has also delivered a new database structure for the monitoring data that enable efficient retrieval of data for analysis. In order to cost-effectively update the analysis presented here as new monitoring data becomes available, we strongly recommend that a formal database structure should be adopted that ensures data is recorded in a consistent manner, that no important data are missing from survey records, and that allows the dataset to be easily transformed into a format that facilitates statistical analysis.

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12. APPENDICES

12.1 Appendix A. Summary of koala monitoring data

Table A1. Number of systematic surveys conducted within each LGA between 1996 and 2015.

Year	Brisbane	Gold Coast	Ipswich	Logan	Moreton Bay	Noosa	Redland	Total
1996	10			6			25	**41**
1997	10			5			27	**42**
1998	2						23	**25**
1999	6			3			18	**27**
2000	1						1	**2**
2001	1				24		2	**27**
2002	1						3	**4**
2003	1						2	**3**
2004	1						1	**2**
2005	5			3			17	**25**
2006	1						10	**11**
2007	1						2	**3**
2008	6			3			21	**30**
2009								
2010	5			3			21	**29**
2011	4		21	2	50		4	**81**
2012	6	4	4	26	1		23	**64**
2013	1	22			22	18	2	**65**
2014	56					8		**64**
2015	2							**2**
Total	**120**	**26**	**25**	**51**	**97**	**26**	**202**	**547**

Table A2. Number of systematic surveys conducted within the Koala Coast and Pine Rivers between 1996 and 2015.

Year	Koala Coast	Pine Rivers	Total
1996	41		**41**
1997	42		**42**
1998	25		**25**
1999	27		**27**
2000	2		**2**
2001	3	24	**27**
2002	4		**4**
2003	3		**3**
2004	2		**2**
2005	25		**25**
2006	11		**11**
2007	3		**3**
2008	30		**30**
2009			
2010	29		**29**
2011	8	23	**31**
2012	32		**32**
2013	3	22	**25**
2014			
2015			
Total	**290**	**69**	**359**

Table A3. Number of independent koalas* detected within each LGA between 1996 and 2015.

Year	Brisbane	Gold Coast	Ipswich	Logan	Moreton Bay	Noosa	Redland	Total
1996	56			57			254	367
1997	125			77			478	680
1998	50						385	435
1999	83			42			260	385
2000	30						15	45
2001	42				138		27	207
2002	25						45	70
2003	21						28	49
2004	18						6	24
2005	50			29			165	244
2006	26						89	115
2007	20						14	34
2008	28			16			131	175
2009								
2010	18			15			84	117
2011	16		29	0	145		11	201
2012	17	6	7	36	0		88	154
2013	7	44			56	7	3	117
2014	7					0		7
2015	0							0
Total	**639**	**50**	**36**	**272**	**339**	**7**	**2083**	**3426**

**Independent adult koalas excludes pouch young and dependent juveniles.*

Table A4. Number of independent koalas* detected within the Koala Coast and Pine Rivers between 1996 and 2015.

Year	Koala Coast	Pine Rivers	Total
1996	367		**367**
1997	680		**680**
1998	435		**435**
1999	385		**385**
2000	45		**45**
2001	69	138	**207**
2002	70		**70**
2003	49		**49**
2004	24		**24**
2005	244		**244**
2006	115		**115**
2007	34		**34**
2008	175		**175**
2009			
2010	117		**117**
2011	27	105	**132**
2012	117		**117**
2013	10	56	**66**
2014			
2015			
Total	**2963**	**299**	**3262**

**Independent adult koalas excludes pouch young and dependent juveniles.*

Table A5. Area surveyed (ha) within each LGA between 1996 and 2015.

Year	Brisbane	Gold Coast	Ipswich	Logan	Moreton Bay	Noosa	Redland	Total
1996	244			231			773	**1247**
1997	416			284			1094	**1794**
1998	71						1203	**1274**
1999	204			130			666	**1000**
2000	51						22	**73**
2001	56				813		61	**929**
2002	34						87	**122**
2003	37						81	**119**
2004	30						20	**50**
2005	140			130			880	**1150**
2006	51						458	**509**
2007	51						80	**131**
2008	170			149			1584	**1903**
2009								
2010	148			149			1195	**1492**
2011	111		971	52	2218		363	**3715**
2012	151	129	107	1109	12		1458	**2966**
2013	56	1146			773	1182	81	**3238**
2014	1160					353		**1514**
2015	35							**35**
Total	**3216**	**1275**	**1078**	**2234**	**3816**	**1535**	**10107**	**23262**

Table A6. Area surveyed (ha) within the Koala Coast and Pine Rivers between 1996 and 2015.

Year	Koala Coast	Pine Rivers	Total
1996	1247		1247
1997	1794		1794
1998	1274		1274
1999	1000		1000
2000	73		73
2001	116	813	929
2002	122		122
2003	119		119
2004	50		50
2005	1150		1150
2006	509		509
2007	131		131
2008	1903		1903
2009			
2010	1492		1492
2011	475	839	1314
2012	1743		1743
2013	137	773	911
2014			
2015			
Total	**13336**	**2425**	**15761**

12.2 Appendix B. Broad Vegetation Group classifications

Table B1. Broad Vegetation Groups (BVGs) at the scale of 1:5 million (5M), 1:2 million (2M), and 1:1 million (1M) and the classifications for the "remnant vegetation (habitat)" and "remnant vegetation (habitat suitability)" covariates.

5M BVG	DESCRIPTION	2M BVG	DESCRIPTION	1M BVG	DESCRIPTION	"Habitat" Classes	"Habitat Suitability" Classes
1	Rainforests, scrubs	2	Complex to simple, semi-deciduous mesophyll to notophyll vine forest, sometimes with Araucaria cunninghamii.	2a	Complex evergreen notophyll vine forest frequently with Araucaria cunninghamii (hoop pine) from foothills to ranges. (land zones 11, 12, 8)	Other	Other
		3	Notophyll vine forest/ thicket (sometimes with sclerophyll and/or Araucarian emergents) on coastal dunes and sand-masses.	3a	Evergreen to semi-deciduous, notophyll to microphyll vine forest/ thicket on beach ridges and coastal dunes, occasionally Araucaria cunninghamii (hoop pine) microphyll vine forest on dunes. Pisonia grandis on coral cays. (land zone 2, [5])	Other	Other
		4	Notophyll and notophyll feather palm or fan palm vine forest on alluvia, along streamlines and in swamps on ranges.	4a	Notophyll and mesophyll vine forest with feather or fan palms in alluvia and in swampy situations on ranges or within coastal sand-masses. (land zones 3, 11, 12, 2)	Other	Other
				4b	Evergreen to semi-deciduous mesophyll to notophyll vine forest, frequently with Archontophoenix spp. (palms) fringing streams. (land zones 3, [10])	Other	Other
		5	Notophyll to microphyll vine forests, frequently with Araucaria spp. or Agathis spp.	5a	Araucarian notophyll/microphyll and microphyll vine forests of southern coastal bioregions. (land zones 8, 11, 5, 9)	Other	Other

		6	Notophyll vine forest and microphyll fern forest to thicket on high peaks and plateaus.	6a	Notophyll vine forest and microphyll fern forest to thicket on high peaks and plateaus of southern Queensland. (land zone 8) (SEQ)	Other	Other
		7	Semi-evergreen to deciduous microphyll vine thicket.	7a	Semi-evergreen vine thickets on wide range of substrates. (land zones 8, 9, 11, 12, 5, 4, 3, 10, [7])	Other	Other
2	Wet eucalypt open-forests	8	Wet eucalypt tall open-forest on uplands and alluvia.	8a	Wet tall open forest dominated by species such as Eucalyptus grandis (flooded gum) or E. saligna, E. resinifera (red mahogany), Lophostemon confertus (brush box), Syncarpia glomulifera (turpentine), E. laevopinea (silvertop stringybark). Contains a well-developed understorey of rainforest components, including ferns and palms, or the understorey may be dominated by sclerophyll shrubs. (land zones 12, 8, 10, 11, 3, 5, 9)	Euc/Mel	Suitable
				8b	Moist open forests to tall open forests mostly dominated by Eucalyptus pilularis (blackbutt) on coastal sands, sub-coastal sandstones and basalt ranges. Also includes tall open forests dominated by E. montivaga, E. obliqua (messmate stringybark) and E. campanulata (New England ash). (land zones 12, 2, 9, 11, 5, 8)	Euc/Mel	Low suitability

3	Eastern eucalypt woodlands to open-forests	9	Moist to dry eucalypt open-forests to woodlands usually on coastal lowlands and ranges.	9a	Moist to dry eucalypt open forests to woodlands, dominated by a variety of species including Eucalyptus acmenoides (narrow-leaved white stringybark), E. carnea (broad-leaved white mahogany), E. propinqua (small-fruited grey gum), E. siderophloia (red ironbark), E. tindaliae (Queensland white stringybark), E. racemosa, Corymbia intermedia (pink bloodwood), C. trachyphloia (yellow bloodwood), E. planchoniana (Planchon's stringybark), E. baileyana (Bailey's stringybark), E. moluccana (gum-topped box) and Angophora leiocarpa (rusty gum). (land zones 11, 9-10, 8, 12, 5, 3)	Euc/Mel	High suitability
				9f	Woodlands dominated by Corymbia spp. e.g.: C. intermedia (pink bloodwood), C. tessellaris (Moreton Bay ash) and/or Eucalyptus spp. (E. racemosa, E. tereticornis (blue gum)), frequently with Banksia spp., Acacia spp. and Callitris columellaris (white cypress pine) on coastal dunes and beach ridges. (land zone 2)	Euc/Mel	Suitable
				9g	Moist woodlands dominated by Eucalyptus tindaliae (Queensland white stringybark) or E. racemosa or E. tereticornis (blue gum) and Corymbia intermedia (pink bloodwood) on remnant Tertiary surfaces. (land zone 5)	Euc/Mel	Suitable

			9h	Dry woodlands dominated by species such as Eucalyptus acmenoides (narrow-leaved white stringybark) (or E. portuensis), E. tereticornis (blue gum), Angophora leiocarpa (rusty gum), Corymbia trachyphloia (yellow bloodwood) or C. intermedia (pink bloodwood), and often ironbarks including E. crebra (narrow-leaved red ironbark) or E. fibrosa (dusky-leaved ironbark). A heathy shrub layer is frequently present. On undulating to hilly terrain. (land zones 12, 11, [5])	Euc/Mel	Suitable
	10	Corymbia citriodora dominated open-forests to woodlands on undulating to hilly terrain.	10b	Moist open forests to woodlands dominated by Corymbia citriodora (spotted gum). (land zones 12, 11, 9, 5, 8)	Euc/Mel	Low suitability
	11	Moist to dry eucalypt open-forests to woodlands mainly on basalt areas (land zone 8).	11a	Moist to dry open forests to woodlands dominated by Eucalyptus orgadophila (mountain coolibah). Some areas dominated by E. tereticornis (blue gum), E. melliodora (yellow box), E. albens (white box), E. crebra (narrow-leaved red ironbark) or E. melanophloia (silver-leaved ironbark). (land zones 8, 11, 4, [3])	Euc/Mel	High suitability

	12	Dry eucalypt woodlands to open-woodlands, mostly on shallow soils in hilly terrain (mainly on sandstone and weathered rocks, land zones 7 and 10).	12a	Dry woodlands to open woodlands dominated by ironbarks such as Eucalyptus decorticans (gum-topped ironbark), E. fibrosa subsp. nubila (blue-leaved ironbark), or E. crebra (narrow-leaved red ironbark) and/or bloodwoods such as Corymbia trachyphloia (yellow bloodwood), C. leichhardtii (rustyjacket), C. watsoniana (Watson's yellow bloodwood), C. lamprophylla, C. peltata (yellowjacket). Occasionally E. thozetiana (mountain yapunyah), E. cloeziana (Gympie messmate) or E. mediocris are dominant. Mostly on sub-coastal/inland hills with shallow soils. (land zones 10, 7, 9)	Euc/Mel	Low suitability
	13	Dry to moist eucalypt woodlands and open forests, mainly on undulating to hilly terrain of mainly metamorphic and acid igneous rocks, Land zones 11 and 12).	13c	Woodlands of Eucalyptus crebra (sens. lat.) (narrow-leaved red ironbark), E. drepanophylla (grey ironbark), E. fibrosa (dusky-leaved ironbark), E. shirleyi (shirley's silver-leaved ironbark) on granitic and metamorphic ranges (land zones 12, 11, 9, [5])	Euc/Mel	Suitable
			13d	Woodlands dominated by Eucalyptus moluccana (gum-topped box) (or E. microcarpa (inland grey box)) on a range of substrates. (land zone 5, 9, 3, 11, 12)	Euc/Mel	High suitability

4	Eucalypt open-forests to woodlands on floodplains	16	Eucalyptus spp. dominated open-forest and woodlands drainage lines and alluvial plains.	16a	Open forest and woodlands dominated by Eucalyptus camaldulensis (river red gum) (or E. tereticornis (blue gum)) and/or E. coolabah (coolabah) (or E. microtheca (coolabah)) fringing drainage lines. Associated species may include Melaleuca spp., Corymbia tessellaris (carbeen), Angophora spp., Casuarina cunninghamiana (riveroak). Does not include alluvial areas dominated by herb and grasslands or alluvial plains that are not flooded. (land zone 3)	Euc/Mel	High suitability
				16c	Woodlands and open woodlands dominated by Eucalyptus coolabah (coolabah) or E. microtheca (coolabah) or E. largiflorens (black box) or E. tereticornis (blue gum) or E. chlorophylla on floodplains. Does not include alluvial areas dominated by herb and grasslands or alluvial plains that are not flooded. (land zone 3)	Euc/Mel	High suitability
				16d	River beds, open water or sand, or rock, frequently unvegetated. (land zone 3)	Other	Other
5	Eucalypt dry woodlands on inland depositional plains	17	Eucalyptus populnea or E. melanophloia (or E. whitei) dry woodlands to open-woodlands on sandplains or depositional plains.	17b	Woodlands to open woodlands dominated by Eucalyptus melanophloia (silver-leaved ironbark) (or E. shirleyi (shirley's silver-leaved ironbark)) on sand plains and foot-slopes of hills and ranges. (land zones 5, 12, 3, 11, 9, 7)	Euc/Mel	Low suitability

		18	Dry eucalypt woodlands to open-woodlands primarily on sandplains or depositional plains.	18b	Woodlands dominated Eucalyptus crebra (sens. lat.) (narrow-leaved red ironbark) frequently with Corymbia spp. or Callitris spp. on flat to undulating plains. (land zones 5, 3)	Euc/Mel	Low suitability
8	Melaleuca open-woodlands on depositional plains	21	Melaleuca spp. dry woodlands to open-woodlands on sandplains or depositional plains.	21b	Low open woodlands and tall shrub-lands of Melaleuca citrolens or M. stenostachya or other Melaleuca spp. (land zones 5, 3, 7, 10, 11, 12)	Euc/Mel	Low suitability
		22	Melaleuca spp. on seasonally inundated open-forests and woodlands of lowland coastal swamps and fringing lines. (palustine wetlands).	22a	Open forests and woodlands dominated by Melaleuca quinquenervia (swamp paperbark) in seasonally inundated lowland coastal areas and swamps. (land zones 3, 2, 1, [11])	Euc/Mel	High suitability
				22c	Open forests dominated by Melaleuca spp. (M. argentea (silver tea-tree), M. leucadendra (broad-leaved tea-tree), M. dealbata (swamp tea-tree) or M. fluviatilis), fringing major streams with Melaleuca saligna or M. bracteata (black tea-tree) in minor streams. (land zone 3)	Euc/Mel	Low suitability
10	Other acacia dominated open-forests, woodlands and shrublands	25	Acacia harpophylla sometimes with Casuarina cristata open-forests to woodlands on heavy clay soils.	25a	Open forests to woodlands dominated by Acacia harpophylla (brigalow) sometimes with Casuarina cristata (belah) on heavy clay soils. Includes areas co-dominated with A. cambagei (gidgee) and/or emergent eucalypts (land zones 4, 9, 3, 11, 7, 12, [5, 8])	Other	Other

12	Other coastal communities or heaths	28	Open-forests to open-woodlands in coastal locations. Dominant species such as Casuarina spp., Corymbia spp., Allocasuarina spp., Acacia spp., Lophostemon suaveolens, Asteromyrtus spp., Neofabricia myrtifolia.	28a	Complex of open shrub-land to closed shrub-land, grassland, low woodland and open forest, on strand and foredunes. Includes pure stands of Casuarina equisetifolia (coastal sheoak). (land zones 2, 1)	Other	Other
				28d	Sand blows to closed herblands of Lepturus repens (stalky grass) and herbs on sand cays and shingle cays. (land zone 2)	Other	Other
				28e	Low open forest to woodlands dominated by Lophostemon suaveolens (swamp box) (or L. confertus (brush box)) or Syncarpia glomulifera (turpentine) frequently with Allocasuarina spp. on rocky hill slopes. (land zones 12, 9, 3, 11, [10, 8])	Euc/Mel	Low suitability
		29	Heathlands and associated scrubs and shrub-lands on coastal dune-fields and inland/ montane locations.	29a	Open heaths and dwarf open heaths on coastal dune-fields, sandplains and headlands. (land zones 5, 2, 3, [7, 10, 12, 11])	Other	Other
				29b	Open shrub-lands to open heaths in montane frequently rocky locations. (land zones 7, 12, 11, 5, 8, 10)	Other	Other
13	Tussock grasslands, forblands	30	Astrebla spp., Dichanthium spp. tussock grasslands.	30b	Tussock grasslands dominated by Astrebla spp. (Mitchell grass) or Dichanthium spp. (bluegrass) often with Iseilema spp. on undulating downs or clay plains. (land zones 9, 3, 4, 8, [5])	Other	Other
15	Wetlands (swamps and lakes)	34	Wetlands associated with permanent lakes and swamps, as well as ephemeral lakes, clay-pans and swamps. Includes fringing woodlands and shrub-lands.	34a	Lacustrine wetlands. Lakes, ephemeral to permanent, fresh to brackish; water bodies with ground water connectivity. Includes fringing woodlands and sedgelands. (land zones 3, 2, [1])	Other	Other

				34c	Palustrine wetlands. Freshwater swamps on coastal floodplains dominated by sedges and grasses such as Oryza spp., Eleocharis spp. (spikerush) or Baloskion spp. (cord rush) / Leptocarpus tenax / Gahnia sieberiana (sword grass) / Lepironia spp. (land zones 3, 2, [1])	Other	Other
				34d	Palustrine wetlands. Freshwater swamps/springs/billabongs on floodplains ranging from permanent and semi-permanent to ephemeral. (land zone 3)	Other	Other
				34f	Palustrine wetlands. Sedgelands/grasslands on seeps and soaks on wet peaks, coastal dunes and other non-floodplain features. (land zones 3, 9, 12, [11])	Other	Other
16	Mangroves and tidal saltmarshes	35	Mangroves and tidal saltmarshes.	35a	Closed forests and low closed forests dominated by mangroves. (land zone 1)	Other	Other
				35b	Bare saltpans ± areas of Tecticornia spp. (samphire) sparse forbland and/or Xerochloa imberbis or Sporobolus virginicus (sand couch) tussock grassland. (land zone 1)	Other	Other

Rationale for "habitat suitability" classification

The Queensland Herbarium's Broad Vegetation Groups (BVGs) occurring in the Southeast Queensland region were classified in three koala habitat suitability classes based on their dominant and sub-dominant tree species composition and the underlying geological substrate. The *Eucalyptus* genus (consisting of eucalypt, corymbia and angophora species) has consistently been shown to provide the principal nutritional resources for koalas, and hence we maintain that they constitute the major limiting resources that influence habitat quality. There is a large body of evidence that koalas often use a relatively small number of the Eucalyptus species in South East Queensland. We used this information to classify BVGs into three habitat suitability classes: high suitability, suitable and low suitability.

High suitability class.

BVGs 9a, 13d, 16a, 16c and 22a were categorised as high suitability koala habitat. This class is able to support moderate to high densities of koalas, especially where mortality from key threatening processes has not caused "empty habitat'. The key criteria for this ranking were the dominance or sub-dominance of Queensland blue gum (*Eucalyptus tereticornis*), small-fruited grey gum (*E. propinqua*), tallowwood (*E. microcorys),* gum-top box (*E. moluccana*) and swamp mahogany (*E. robusta*), within the BVG. There is strong empirical evidence across South East Queensland that koalas regularly use *E. tereticornis* for forage (Hasegawa 1995, McAlpine et al. 2006a, McAlpine et al. 2006b, Callaghan et al. 2011, Waller 2012, Rymer 2014). This species is widely distributed in South East Queensland and occurs on fertile alluvial soils and coastal lowlands. Hasegawa (1995) found that *E. tereticornis* constituted greater than 80% of cuticle fragments from pellet samples over a 12-month period in Victoria Point, Redland Bay. Similarly, *E. tereticornis* was identified as the highest ranked eucalypt species for Noosa Shire for a 1996-97 and 2001-02 survey periods (Callaghan et al. 2011). Koalas are also known to regularly use *E. propinqua, E. microcorys* and *E. acmenoides* associated with the wetter eucalypt forests in the Sunshine Coast hinterland (McAlpine et al. 2006a, McAlpine et al. 2006b, Callaghan et al. 2011) and the Gold Coast hinterland (J. Callaghan personal communication).

Suitable class.

BVGs in this class are generally of low-moderate habitat suitability. Key eucalypt species in the tall wet BVGs include flooded gum (*E. grandis*), Sydney blue gum (*E. saligna*), red stringbark (*E. resinifera*) and white mahogany (*E. acmenoides*). Suitable habitats in the drier BVG woodlands and open forests are dominated by *E. acmenoides,* narrow-leaved ironbark (*E. crebra*), broad-leaved ironbark (*E. fibrosa*) and silver-leaved ironbark (*E. melanophloia*) and coastal forests dominated by scribbly-gum (*E. racemosa*) with narrow-leaved grey gum (*E. seeana*) and *E. tereticornis* often a sub-dominant species.

Angophora and Corymbia species such as rusty-gum (*Angophora leiocarpa*), yellow bloodwood (*Corymbia trachyphloia*), pink bloodwood (*C. intermedia*) and Moreton-Bay Ash (*C. tesselaris*) are also common. With the exception *of E. tereticornis*, these species have a lower rate of usage as a food resource by koalas, and so tend to support lower koala densities.

Low suitability class.

BVGs in this class are generally of low habitat suitability. Woodland to open woodlands dominated by spotted gum (*Corymbia citriodora subsp. variegate, C. citriodora subsp. citriodora*) and *E. melanophloia* on poorer soils are of low habitat suitability for koalas. Similarly tall blackbutt forests *(E. pilurlaris*) have a low rate of usage by koalas. These BVGs occur mainly on low fertility soils.

12.3 Appendix C. Detection function fit

The half-normal distribution provided a reasonable fit to the observed distribution of perpendicular distances of koala sighting from the transect line (Figure C1).

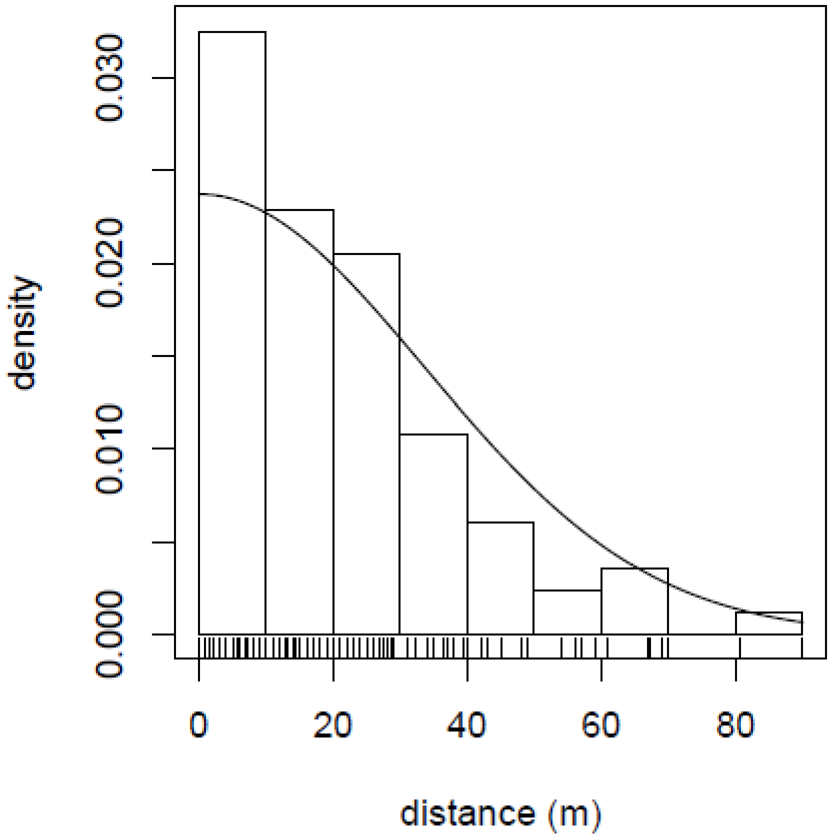

Figure C1. Histogram of the observed perpendicular distances of koala sightings and the fitted half-normal curve that we used to approximate the distribution.

12.4 Appendix D. JAGS code

<u>Spatial model</u>

```
model {

# process model

#random-effect for a - loop through years
for (i in 1:4)
{
	a[i] ~ dlnorm(amean,tau1)
}

# loop through sites
for (i in 1:NSites)
{
	#intercept random-effect
	intmean[i] <- sum(Y[i,1,] * alpha)
	int[i] ~ dnorm(intmean[i],tau2)

	# sample density for first time step
	Lambda[i,1] <- exp(int[i] + sum(X[i,1,] * beta))
	# D[i,j] is density
	# mean of dgamma(a, b) is a/b, so if Lambda[i] = a/b, we sample a and
	# calculate b deterministically using Lambda
	b[i,1] <- a[trunc((Year[i,1] - 1995)/5.1) + 1]/Lambda[i,1]
	D[i,1] ~ dgamma(a[trunc((Year[i,1] - 1995)/5.1) + 1],b[i,1])
	# simulate for model adequacy checks
	#D.sim[i,1] ~ dgamma(a[trunc((Year[i,1] - 1995)/5.1) + 1],b[i,1])

	# loop through remaining time steps
	for (j in 2:NSteps)
	{
		# sample density for remaining time step
		Lambda[i,j] <- exp(int[i] + sum(X[i,j,] * beta))
		# D[i,j] is density
		# mean of dgamma(a, b) is a/b, so if Lambda[i] = a/b, we sample a and
```

```
                # calculate b deterministically using Lambda
                b[i,j] <- a[trunc((Year[i,j] - 1995)/5.1) + 1]/Lambda[i,j]
                D[i,j] ~ dgamma(a[trunc((Year[i,j] - 1995)/5.1) + 1],b[i,j])
                # simulate for model adequacy checks (uncomment to use)
                #D.sim[i,j] ~ dgamma(a[trunc((Year[i,j] - 1995)/5.1) + 1],b[i,j])
        }
}

# observation model - strip transects
# count data
for (i in 1:NStrips)
{
        #sample observed counts
        SNTrue[i] <- ifelse((round(D[SIndex[i,1],SIndex[i,2]] * Area[i]) - (D[SIndex[i,1],SIndex[i,2]] *
        Area[i])) <= 0.5,round(D[SIndex[i,1],SIndex[i,2]] * Area[i]),trunc(D[SIndex[i,1],SIndex[i,2]] *
        Area[i]))
        NAll[i] ~ dbin(p,SNTrue[i])

        #goodness-of-fit & model adequacy (uncomment to use)
        #compute discrepancy statistics for observed data
        #expect[i] <- p * Lambda[SIndex[i,1],SIndex[i,2]] * Area[i]
        #res.obs[i] <- NAll[i] - expect[i]
        #R.obs[i] <- pow((NAll[i] - expect[i]),2) / expect[i]
        #compute discrepancy statistics for simulated data
        #SNT.sim[i] <- ifelse((round(D.sim[SIndex[i,1],SIndex[i,2]] * Area[i]) -
        (D.sim[SIndex[i,1],SIndex[i,2]] * Area[i])) <= 0.5,round(D.sim[SIndex[i,1],SIndex[i,2]] *
        #Area[i]),trunc(D.sim[SIndex[i,1],SIndex[i,2]] * Area[i]))
        #y.sim[i] ~ dbin(p,SNT.sim[i])
        #res.sim[i] <- y.sim[i] - expect[i]
        #R.sim[i] <- pow((y.sim[i] - expect[i]),2) / expect[i]
}

# observation model - line transects
# perpendicular distance data
# Distance Sampling (estimate f0) - this is separate from the density estimate
# because this should not be applied to any records with 0 observations, whereas
# the density estimate is applied to all line transects
for (i in 1:NDists)
```

```
{
	#likelihood function for half-normal
	zeros[i] ~ dpois(phi[i])
	phi[i] <- -(log(2 * DistLambda / 3.141593) / 2 - DistLambda * pow(PDist[i],2) / 2)
}
f0 <- sqrt(2 * DistLambda / 3.141593)
# count data
for (i in 1:NLines)
{
	#sample observed counts
	NAll[NStrips + i] ~ dpois((D[LIndex[i,1],LIndex[i,2]] * 2 * LL[i]) / (f0 * 10000))

	#goodness-of-fit
	#compute discrepancy statistics for observed data
	#expect[NStrips + i] <- (Lambda[LIndex[i,1],LIndex[i,2]] * 2 * LL[i]) / (f0 * 10000)
	#res.obs[NStrips + i] <- NAll[NStrips + i] - expect[NStrips + i]
	#R.obs[NStrips + i] <- pow((NAll[NStrips + i] - expect[NStrips + i]),2) / expect[NStrips + i]
	#compute discrepancy statistics for simulated data
	#y.sim[NStrips + i] ~ dpois((D.sim[LIndex[i,1],LIndex[i,2]] * 2 * LL[i]) / (f0 * 10000))
	#res.sim[NStrips + i] <- y.sim[NStrips + i] - expect[NStrips + i]
	#R.sim[NStrips + i] <- pow((y.sim[NStrips + i] - expect[NStrips + i]),2) / expect[NStrips + i]
}

#calculate goodness-of-fit statistics (uncomment to use)
#fit.obs <- sum(R.obs[])
#fit.sim <- sum(R.sim[])
#fit.test <- fit.obs - fit.sim

# priors
amean ~ dnorm(0,0.001)
tau1 <- sig1^-2
sig1 ~  dunif(0,10)
tau2 <- sig2^-2
sig2 ~  dunif(0,10)
for (i in 1:Ny)
{
	alpha[i] ~ dnorm(0,0.001)
}
```

```
for (i in 1:Nx)
{
        beta[i] ~ dnorm(0,0.001)
}
p ~ dunif(0,1)
DistLambda ~ dgamma(0.001,0.001)

}
```

<u>Trend model</u>

```
model {

# process model

#random-effect for a - loop through years
for (i in 1:4)
{
        a[i] ~ dlnorm(amean,tau1)
}

# loop through sites
for (i in 1:NSites)
{
        #intercept for random-effect on initial population size
        intmean[i] <- sum(Y[i,1] * alpha)
        int[i] ~ dnorm(intmean[i],tau2)

        # sample density for first time step
        Lambda[i,1] <- exp(int[i])
        # D[i,j] is density
        # mean of dgamma(a, b) is a/b, so if Lambda[i] = a/b, we sample a and
        # calculate b deterministically using Lambda
        b[i,1] <- a[trunc((Year[i,1] - 1995)/5.1) + 1]/Lambda[i,1]
        D[i,1] ~ dgamma(a[trunc((Year[i,1] - 1995)/5.1) + 1],b[i,1])
        # simulate for model adequacy checks
        #D.sim[i,1] ~ dgamma(a[trunc((Year[i,1] - 1995)/5.1) + 1],b[i,1])
```

```
        #intercept for growth rate
        intr[i] <- sum(X[i,1,] * beta)

        # loop through remaining time steps
        for (j in 2:NSteps)
        {
                # sample density for remaining time step
                r[i,j - 1] <- exp(intr[i] + sum(Z[i,j - 1,] * epsilon))
                Lambda[i,j] <- D[i,j - 1] * r[i,j - 1]
                # D[i,j] is density
                # mean of dgamma(a, b) is a/b, so if Lambda[i] = a/b, we sample a and
                # calculate b deterministically using Lambda
                b[i,j] <- a[trunc((Year[i,j] - 1995)/5.1) + 1]/Lambda[i,j]
                D[i,j] ~ dgamma(a[trunc((Year[i,j] - 1995)/5.1) + 1],b[i,j])
                # simulate for model adequacy checks (uncomment to use)
                #D.sim[i,j] ~ dgamma(a[trunc((Year[i,j] - 1995)/5.1) + 1],b[i,j])
        }
}

# observation model - strip transects
# count data
for (i in 1:NStrips)
{
        #sample observed counts
        SNTrue[i] <- ifelse((round(D[SIndex[i,1],SIndex[i,2]] * Area[i]) - (D[SIndex[i,1],SIndex[i,2]] *
Area[i])) <= 0.5,round(D[SIndex[i,1],SIndex[i,2]] * Area[i]),trunc(D[SIndex[i,1],SIndex[i,2]] * Area[i]))
        NAll[i] ~ dbin(p,SNTrue[i])

        #goodness-of-fit & model adequacy (uncomment to use)
        #compute discrepancy statistics for observed data
        #expect[i] <- p * Lambda[SIndex[i,1],SIndex[i,2]] * Area[i]
        #res.obs[i] <- NAll[i] - expect[i]
        #R.obs[i] <- pow((NAll[i] - expect[i]),2) / expect[i]
        #compute discrepancy statistics for simulated data
        #SNT.sim[i] <- ifelse((round(D.sim[SIndex[i,1],SIndex[i,2]] * Area[i]) -
        (D.sim[SIndex[i,1],SIndex[i,2]] * Area[i])) <= 0.5,round(D.sim[SIndex[i,1],SIndex[i,2]] *
        #Area[i]),trunc(D.sim[SIndex[i,1],SIndex[i,2]] * Area[i]))
        #y.sim[i] ~ dbin(p,SNT.sim[i])
```

```
        #res.sim[i] <- y.sim[i] - expect[i]
        #R.sim[i] <- pow((y.sim[i] - expect[i]),2) / expect[i]
}

# observation model - line transects
# perpendicular distance data
# Distance Sampling (estimate f0) - this is separate from the density estimate
# because this should not be applied to any records with 0 observations, whereas
# the density estimate is applied to all line transects
for (i in 1:NDists)
{
        #likelihood function for half-normal
        zeros[i] ~ dpois(phi[i])
        phi[i] <- -(log(2 * DistLambda / 3.141593) / 2 - DistLambda * pow(PDist[i],2) / 2)
}
f0 <- sqrt(2 * DistLambda / 3.141593)
# count data
for (i in 1:NLines)
{
        #sample observed counts
        NAll[NStrips + i] ~ dpois((D[LIndex[i,1],LIndex[i,2]] * 2 * LL[i]) / (f0 * 10000))

        #goodness-of-fit & model adequacy (uncomment to use)
        #compute discrepancy statistics for observed data
        #expect[NStrips + i] <- (Lambda[LIndex[i,1],LIndex[i,2]] * 2 * LL[i]) / (f0 * 10000)
        #res.obs[NStrips + i] <- NAll[NStrips + i] - expect[NStrips + i]
        #R.obs[NStrips + i] <- pow((NAll[NStrips + i] - expect[NStrips + i]),2) / expect[NStrips + i]
        #compute discrepancy statistics for simulated data
        #y.sim[NStrips + i] ~ dpois((D.sim[LIndex[i,1],LIndex[i,2]] * 2 * LL[i]) / (f0 * 10000))
        #res.sim[NStrips + i] <- y.sim[NStrips + i] - expect[NStrips + i]
        #R.sim[NStrips + i] <- pow((y.sim[NStrips + i] - expect[NStrips + i]),2) / expect[NStrips + i]
}

#calculate goodness-of-fit statistics (uncomment to use)
#fit.obs <- sum(R.obs[])
#fit.sim <- sum(R.sim[])
#fit.test <- fit.obs - fit.sim
```

```
# priors
amean ~ dnorm(0,0.001)
tau1 <- sig1^-2
sig1 ~  dunif(0,10)
tau2 <- sig2^-2
sig2 ~  dunif(0,10)
for (i in 1:Ny)
{
        alpha[i] ~ dnorm(0,0.001)
}
for (i in 1:Nx)
{
        beta[i] ~ dnorm(0,0.001)
}
for (i in 1:Nz)
{
        epsilon[i] ~ dnorm(0,0.001)
}
p ~ dunif(0,1)
DistLambda ~ dgamma(0.001,0.001)

}
```

12.5 Appendix E. Quantile-quantile plots and spatial spline correlograms

<u>Spatial model</u>

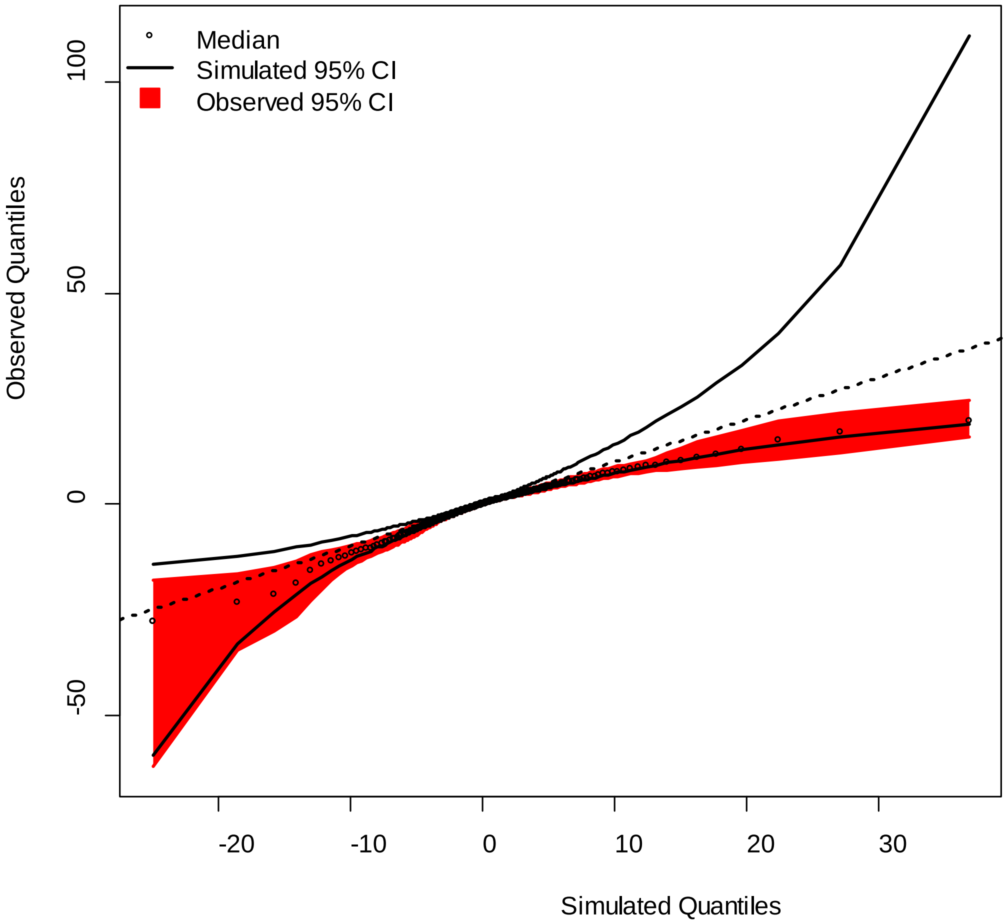

Figure E1. Quantile-quantile plot for the best spatial model (model 6). The median points and the observed credible interval (CI) lies below the 1:1 line for high quantile values indicating some under-dispersion in the observed data relative to the model. However, because the observed CI overlaps the simulated CI, this suggests that this is not statistically significant under-dispersion at the 5% significance level.

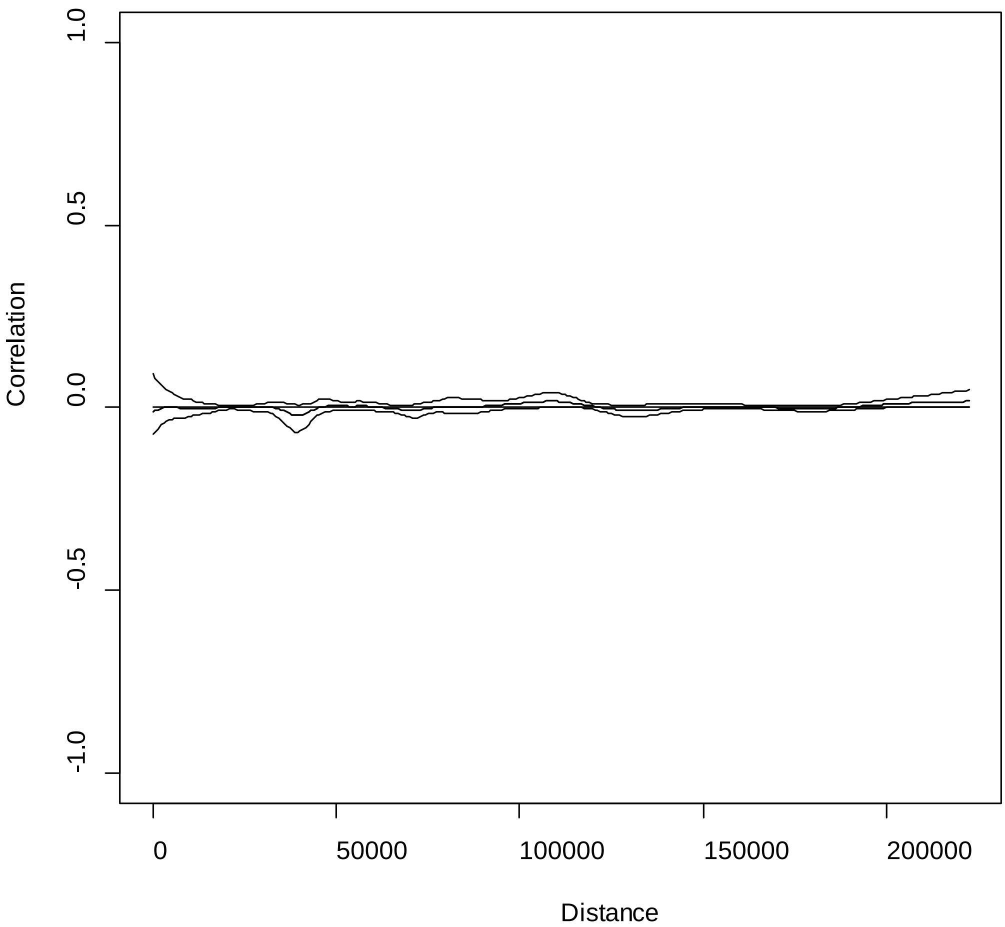

Figure E2. Spatial spline correlogram of the residuals from the best spatial model (model 6). Mean and 95% confidence intervals shown. Low correlations and 95% confidence intervals overlapping zero at all distances indicates no significant spatial autocorrelation in the residuals.

Trend model

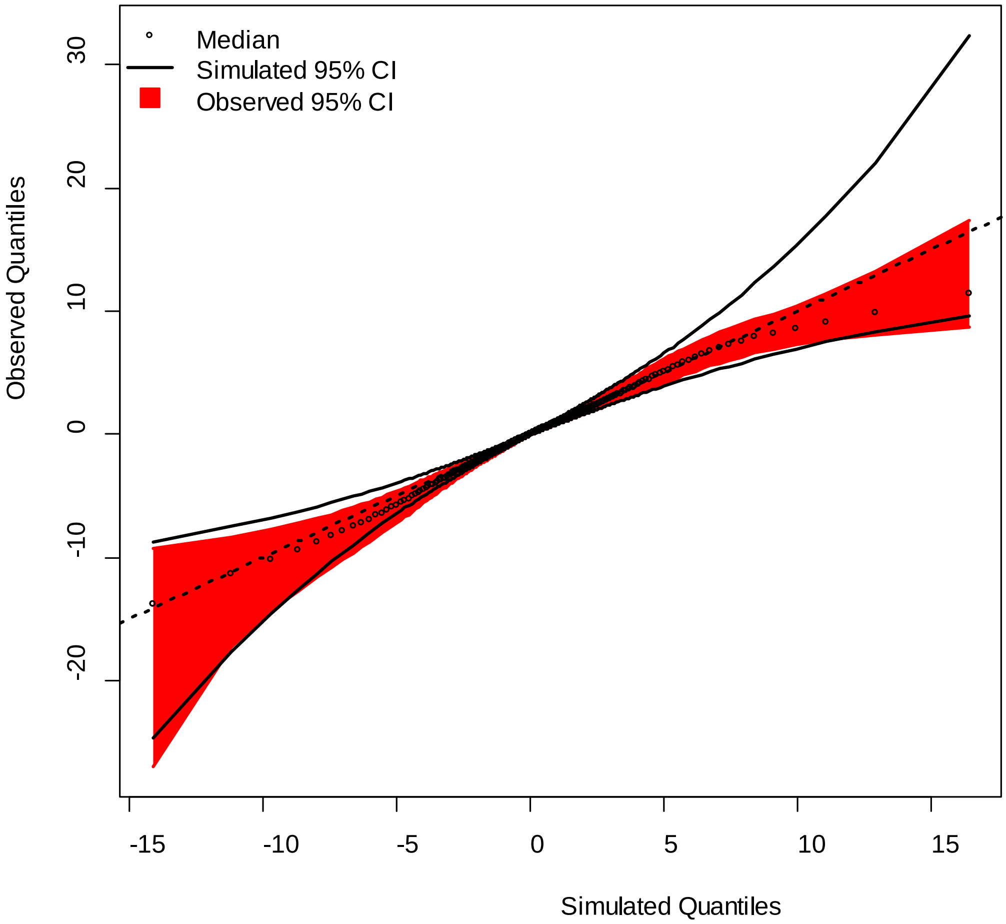

Figure E3. Quantile-quantile plot for the best trend model (model 1). The median points and the observed credible interval (CI) lies slightly below the 1:1 line for high quantile values indicating some minor under-dispersion in the observed data relative to the model. However, because the observed CI overlaps the simulated CI, this suggests that this is not statistically significant under-dispersion at the 5% significance level.

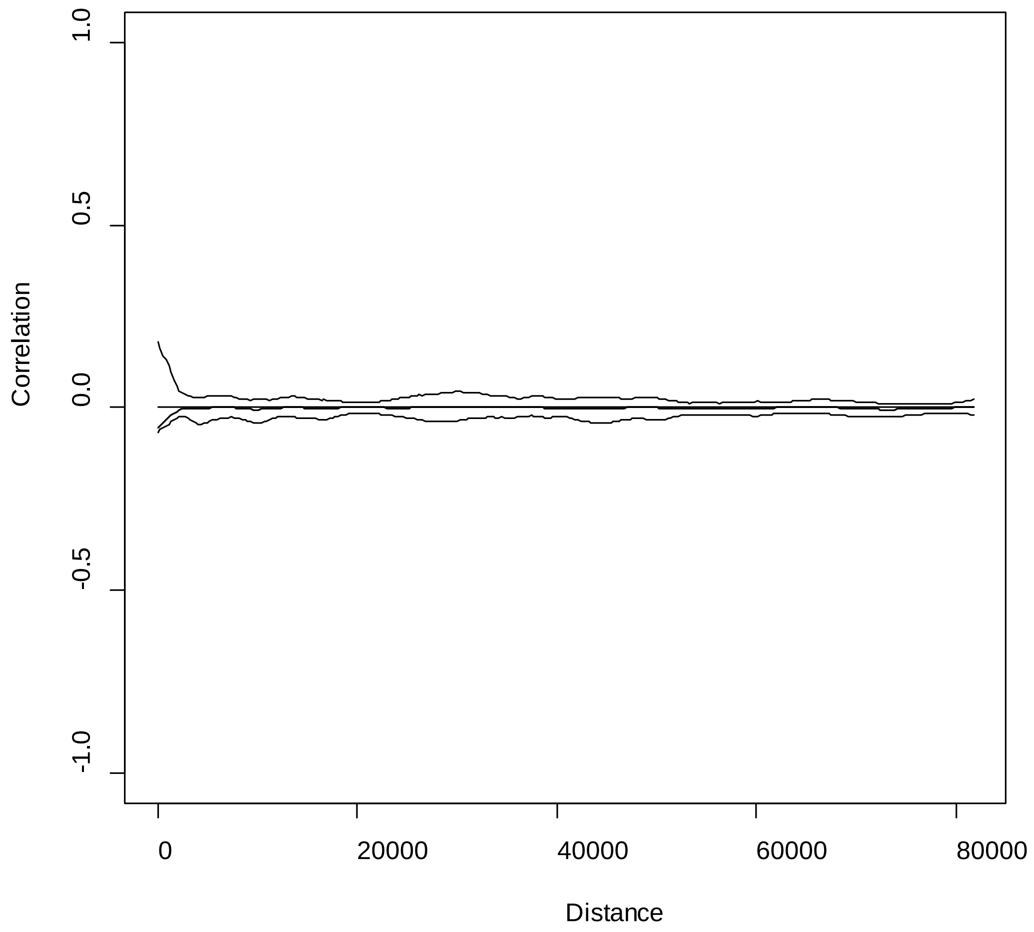

Figure E4. Spatial spline correlogram for the best trend model (model 1). Mean and 95% confidence intervals shown. Low correlations and 95% confidence intervals overlapping zero at all distances indicates no significant spatial autocorrelation in the residuals.

12.6 Appendix F. The 95% credible intervals for spatial predictions of koala density.

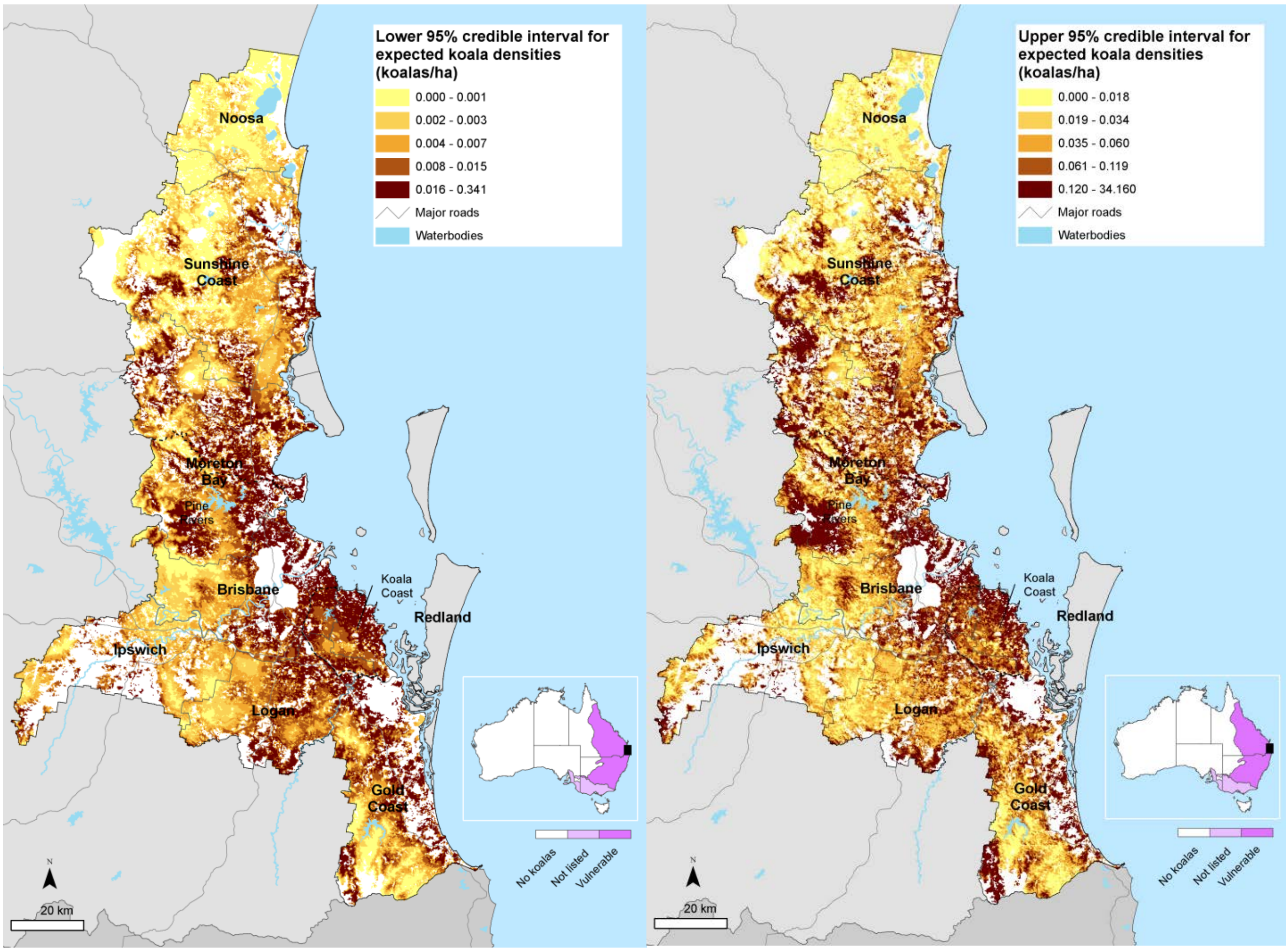

Figure F1. The upper and lower bounds for the expected koala densities based on the best spatial model (model 6). Maps were constructed at a resolution of 50ha, but excluding areas that were outside the range of covariate values at the surveyed sites for elevation, FPC, FPC buffer, and road density.

12.7 Appendix G. Spatial predictions for the second best spatial model.

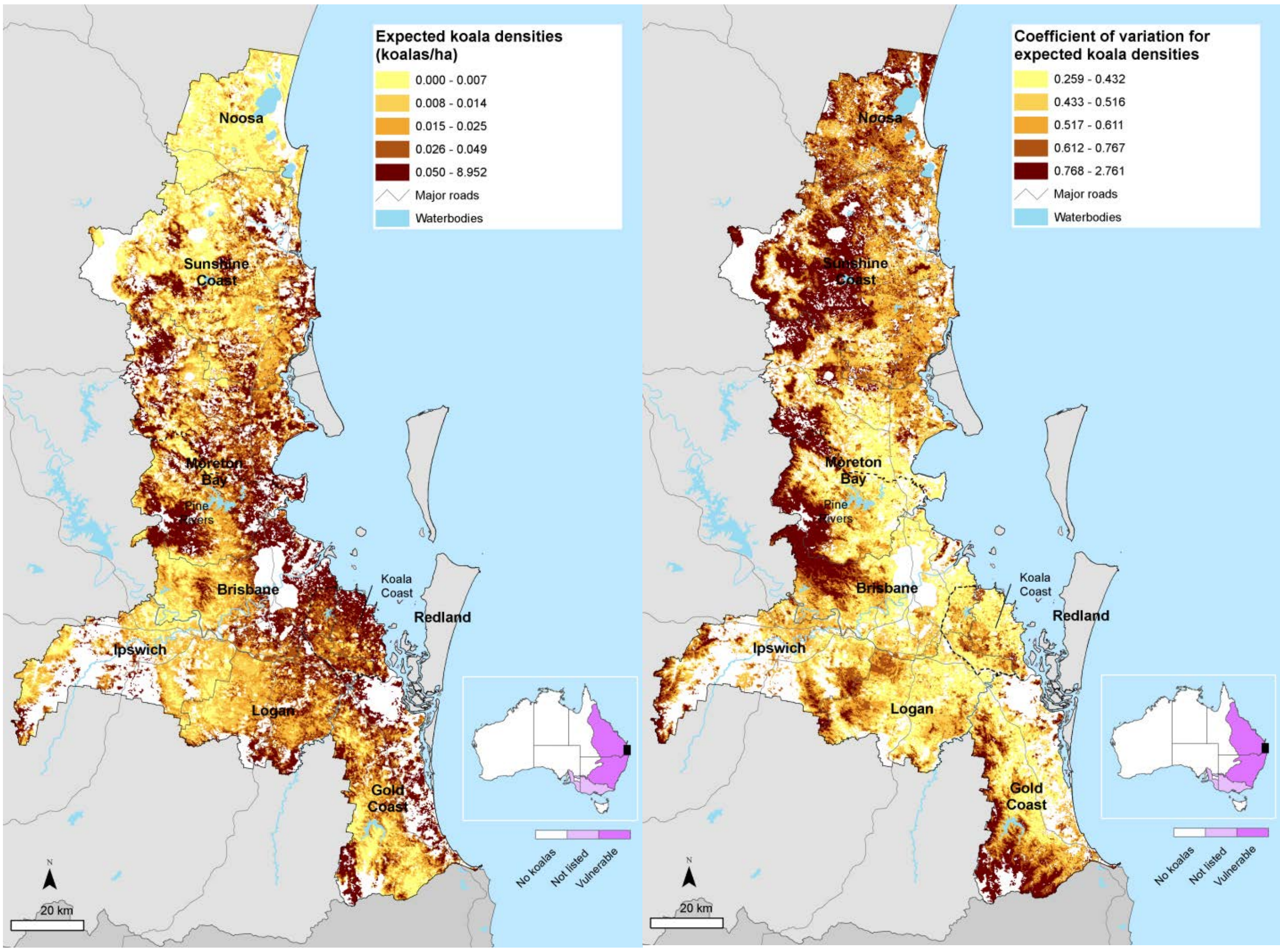

Figure G1. The spatial distribution of expected koala densities based on the second best spatial model (model 9) and the coefficient of variation for those densities. Maps were constructed at a resolution of 50ha, but excluding areas that were outside the range of covariate values at the surveyed sites for elevation, FPC, FPC buffer, and road density.

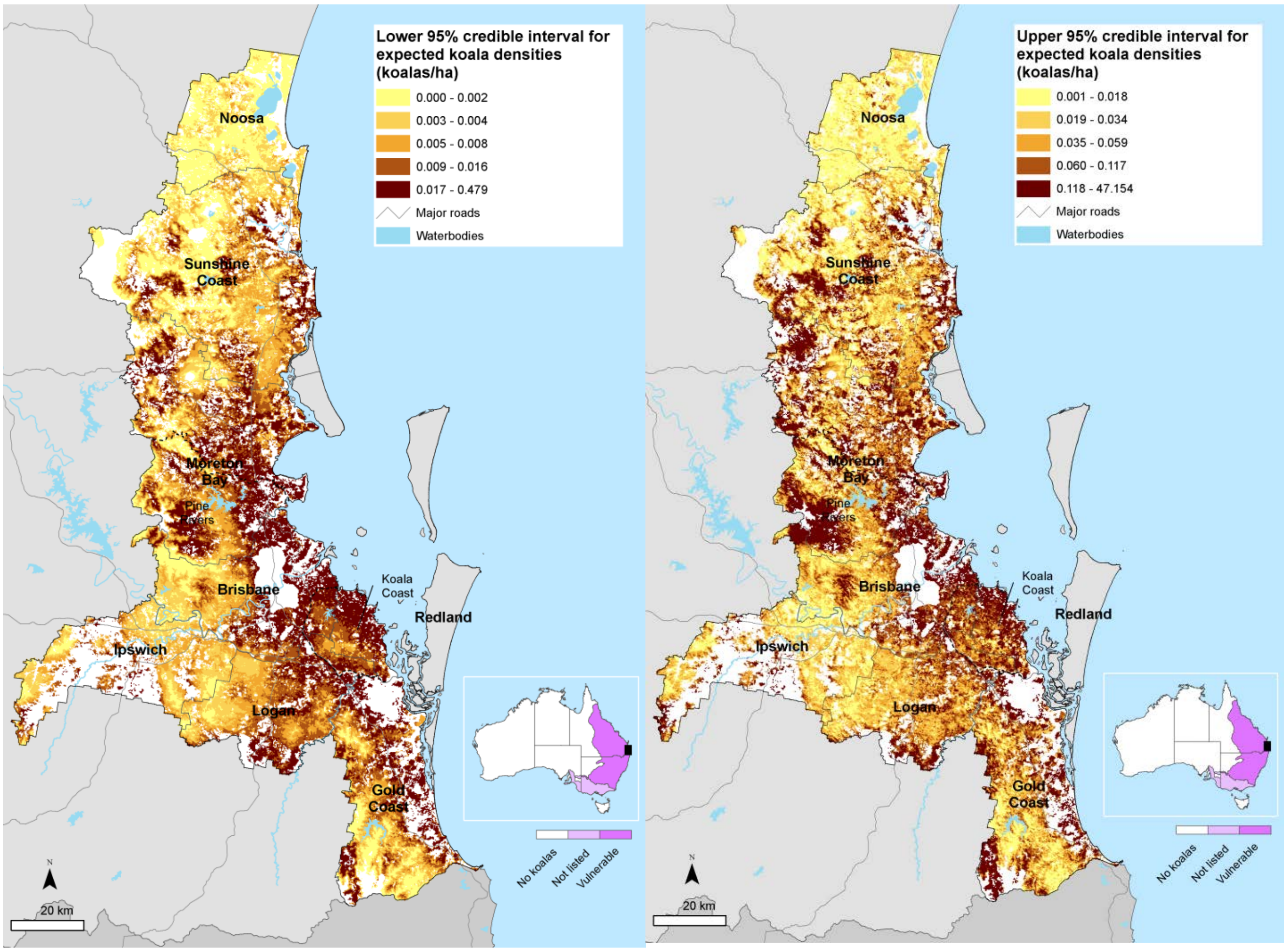

Figure G2. The upper and lower bounds for the expected koala densities based on the second best spatial model (model 9). Maps were constructed at a resolution of 50ha, but excluding areas that were outside the range of covariate values at the surveyed sites for elevation, FPC, FPC buffer, and road density.