Modelling Koala abundance across Victoria

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Front cover photo: Koala with young, Cape Otway. Photo courtesy of Geoff Brown, ARI.

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Contents

Summary

Context:

This project informs a review of the Victorian Koala Management Strategy by the Victorian Department of Environment, Land, Water and Planning (DELWP). It represents the first attempt to collate Koala count data from across Victoria for the purposes of developing a statistical model of Koala abundance, as well as producing State-wide and regional estimates of Koala abundance.

Aims:

1. Review and collate existing data on the distribution and abundance of Koalas across Victoria.
2. Assess the suitability of these data for developing model-based estimates of Koala abundance.
3. Review environmental variables likely to be important determinants of Koala density, and identify and collate raster-based vegetation and biophysical variables that may be used as proxies for these.
4. Develop a model of Koala abundance using existing data and use the model to derive estimates of Koala abundance (and their associated uncertainty) across the State.

In response to the significant wildfires across Victoria during the preparation of this report, a further objective of providing a preliminary assessment of the impact of these fires on the species was also pursued.

Methods:

This study collated Koala counts conducted over the last 15 years across Victoria. The data included 1,494 diurnal double-count surveys, 115 nocturnal double-count surveys and 414 single-count surveys. Double-counts are those with replicate, independent counts completed by two observers, with single-counts being counts completed by one or more observers in a single sweep. Following amalgamation of these counts to 1×1 km grid cells, a statistical model was fitted to counts from 908 grid cells across Victoria. Predictions of Koala abundance were subsequently generated across the State from the fitted relationships with climate, topography and the abundance of eucalypts (both in remnant forest and woodland, and eucalypt plantations).

Estimates of the area of suitable habitat for Koalas in Victoria and density across the State were overlaid with mapped fire extent (as of 11 February 2020) to estimate both the proportion of the species' habitat affected, plus the proportion of the Victorian population affected.

Results:

Koala population – native vegetation

Estimates of the state-wide Koala population suggest that it may be larger than previously thought, with a prediction of around 413,000 individuals in native forest and woodland. Three DELWP regions – Barwon South West, Gippsland and Hume – were predicted to support 80% of Victoria's Koala population in native forest and woodland.

Observed Koala densities from diurnal double-count surveys (the most reliable data available to us) averaged 0.75 ha^{-1} in native vegetation, with a range of 0–7 ha^{-1}. Overall, density was generally higher at lower elevations, in areas with relatively high annual rainfall, low summer temperatures and high abundance of key eucalypts, particularly Manna Gum, Swamp Gum, Blue Gum and River Red Gum. Nevertheless, complex interactive relationships between these variables and Koala density were apparent.

Koala population – eucalypt plantations

The Koala population in eucalypt plantations across the State was estimated to be around 47,000 individuals. Three DELWP regions – Barwon South West, Gippsland and Grampians – were predicted to support 99% of Victoria's Koala population in eucalypt plantations.

Count data from eucalypt plantations available to this project were available from the Strzelecki Ranges in Gippsland (1,104), with a further 173 counts available from Blue Gum plantations in the south-west of the State. All were in the form of diurnal double-count surveys. In the Strzelecki Ranges, observed Koala density in plantations averaged just 0.03 ha^{-1}, with a range of 0–5 ha^{-1}. In the south-west, observed Koala densities in plantations averaged 0.89 ha^{-1}, with a range of 0–6ha^{-1}. Modelling revealed both positive and negative effects of surrounding plantation extent on Koala densities through interactions with other environmental

variables, suggesting that the suitability of eucalypt plantations for the species is context dependent, but primarily driven by koala densities in neighbouring native forest and woodland.

Impact of Victorian wildfires

As of 11 February 2020, it was estimated that 3% of Koala habitat in native forest and woodland in Victoria was affected by wildfires, with 0.59% affected in eucalypt plantations. In total, around 15,000 Koalas were predicted to have been impacted by wildfires in the 2019-2020 summer season, or roughly 4% of the State population.

Conclusions and recommendations:

This project provides new insights into the abundance of Koalas in Victoria, including broad-scale environmental correlates of density and the first estimates of Koala abundance across the State. Refinement of the work present here should seek to:

Improve the underlying dataset: State-wide or regional Koala surveys conducted using standard double-count approaches would improve our ability to estimate trends in Koala populations. This study relied on counts with various spatial biases and considerable methodological variation. We advocate standardised surveys across the native forest and woodland estate, as well as eucalypt plantations. This work should be guided by the spatial projections of model uncertainty, as per Figure 7. These surveys would be particularly useful in the wake of the significant wildfires of the 2019-2020 summer season, which have had an unknown impact on Koala population sizes.

Improve the model: The current model could be improved and/or extended by the incorporation of additional environmental predictors, such as measures that quantify soil properties, past disturbance regimes (particularly forest fires), forest fragmentation and road density.

1 Introduction

The Koala (*Phascolarctos cinereus*) is an iconic marsupial that is distributed widely across eastern Australia. The species is a unique component of the continent's fauna, being the only extant member of the *Phascolarctidae*, and displaying a peculiar set of morphological, physiological and ecological traits adapted to a specific dietary niche of *Eucalyptus* foliage (Menkhorst and Knight 2010). For these reasons, and their broader aesthetic appeal, Koalas have assumed considerable cultural, environmental and economic importance, with the latter being based on the extensive tourism revenue the species' aids in generating (Hundloe and Hamilton 1997). In turn, there is considerable concern about the conservation status of Koalas, both in Australia and internationally (McAlpine *et al.* 2015).

Koalas face numerous threatening processes across their range, with habitat loss and fragmentation, attacks from domestic and wild dogs, road mortality and chlamydial disease caused by the pathogen *Chlamydia pecorum* being particularly important (Melzer *et al.* 2000, McAlpine *et al.* 2015). The combination of increasingly intense heat waves, drought and fires is thought to represent a significant threat to the species over the medium- to long-term under climate change, and may have already contributed to declines in the northern parts of the species' range (Santika *et al.* 2014, McAlpine *et al.* 2015). Koalas were listed as *Vulnerable to Extinction* in Queensland, New South Wales and the Australian Capital Territory in 2012 as a result of these threatening processes (DOE 2014). However, the species is not listed as threatened across the remainder of its range in Victoria and South Australia.

In Victoria, the management of Koalas is complicated by regional differences in population status and the presence of the species in eucalypt plantations that are regularly harvested. The species was subject to intense hunting for the fur trade during the 19th and early 20th century, driving significant population declines and local extinctions. Resulting conservation efforts are the longest dedicated wildlife management program undertaken in Australia, including the establishment of island 'refuge' populations and subsequent reintroductions and translocations over much of the species' former range (Menkhorst 2008). Today, Koalas occur in naturally low densities throughout much of Victoria's lowland and foothill forests and woodland (DSE 2004). In these environments, management objectives focus on ensuring habitat protection and stewardship is adequate to support viable populations of the species. However, Koala populations can reach unsustainable densities in areas of the State's south – including islands used to establish refuge populations – leading to over-browsing and ultimately both significant mortality of highly preferred eucalypts and starvation of resident Koalas (DSE 2004, Menkhorst 2008). The Victorian Government has been actively managing these over-abundant Koala populations through translocation and fertility control to reduce population growth rates (DSE 2004). Similarly, active management of Koalas within eucalypt plantations seeks to balance minimisation of impacts on resident Koala populations with the necessity to continue harvesting the timber resource.

This project seeks to inform revision of Victoria's Koala Management Strategy (DSE 2004). Despite numerous surveys for Koalas across Victoria, including detailed monitoring of specific populations of management concern, no systematic estimates of the abundance of Koalas across the State have been attempted. This project sought to compile counts of Koalas completed across Victoria over the last 15 years, and to use these data to develop a model of Koala abundance for the purposes of predicting State-wide and regional Koala abundance.

Specific aims were as follows:

1. Review and collate existing data on the distribution and abundance of Koalas across Victoria.
2. Assess the suitability of these data for developing model-based estimates of Koala abundance.
3. Review environmental variables likely to be important determinants of Koala density, and identify and collate raster-based vegetation and biophysical variables that may be used as proxies for these.
4. Develop a model of Koala abundance using existing data and use the model to derive estimates of Koala abundance (and their associated uncertainty) across the State.

In response to the significant wildfires across Victoria during the preparation of this report, a further objective of providing a preliminary assessment of the impact of these fires on Koala populations was added. Specifically, we sought to estimate the proportion of the species' habitat in Victoria that has been affected by these fires (as of 11 February 2020), plus the proportion of the Victorian population affected.

2 Methods

2.1 Data collation

2.1.1 Atlas data

We began by collating all records of Koalas available within the Victorian Biodiversity Atlas (VBA), totalling 10,724 records as of March 2019. Records where screened for spatial accuracy, removing all those with error margins >1 km (*n* = 1,709) leaving 7,592 records used in subsequent analyses (Figure 1).

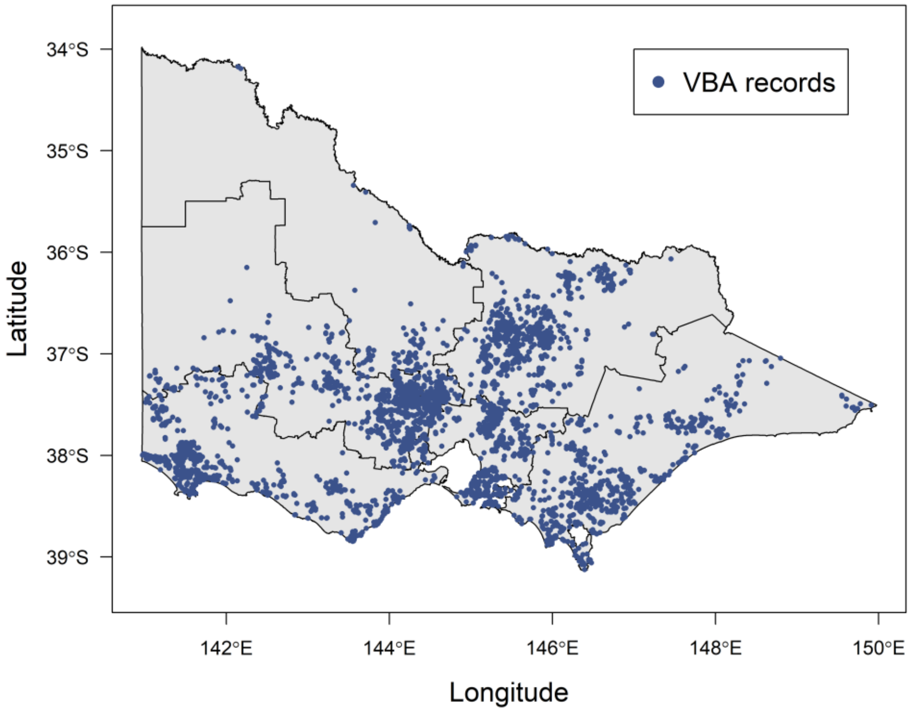

Figure 1. Records of Koalas from the Victorian Biodiversity Atlas, with a spatial accuracy of ≤ 1 km. Internal polygons show the DELWP regions.

2.1.2 Count data

For the purposes of building a statistical model of Koala abundance, we sought count data from across the species' Victorian range for which both the area searched and survey effort (number of observers) were known. Data were acquired by requests to wildlife ecologists in the government, academic and private sectors, drawing on knowledge of past research on Koalas across the State. Counts obtained are depicted in Figure 2. They were of three broad types, as outlined below.

1) Double-count surveys (diurnal)

Double-count surveys conducted during daylight hours are the preferred technique for estimating Koala abundance in Victoria, and have been used extensively for monitoring over-abundant populations in the State's south (Ramsey *et al.* 2010, 2016, Wood 2016, Tolsma *et al.* 2017a,b). Double-counts are conducted on transects of varying length through suitable habitat, with two observers independently counting all Koalas within a set distance of the transect line (generally 25 m). Both observers record the location of each individual sighted, allowing cross-validation of observations and construction of Koala detection histories as: 1) individuals seen by only the first observer; 2) individuals seen by only the second observer, and; 3) individuals seen by both observers. It is imperative that the second count is made immediately following the first (to ensure movement of animals does not confound observer counts), but that neither observer is aware of the others progress along the transect line (to ensure each count is derived independently). A total of 1,494 counts following this protocol were collated for this project.

Some 105 counts were available from habitat condition assessments conducted across the State's south-west between 2015 and 2017, including Cape Otway and public land west to the South Australian border (see Ramsey *et al.* 2016, Tolsma *et al.* 2017b). Long-term population monitoring data from 40 transects at Budj Bim (formerly Mt Eccles) National Park were also collated, spanning the years 2004 - 2016 (Ramsey *et al.* 2015, Wood 2016). In that same region, counts from 72 sites were available from recent work conducted by Deakin University (Ashman *et al.* 2020).

Island populations were represented by counts along 20 transects at French Island in 2017, conducted for the purposes of monitoring habitat condition and informing ongoing management programs (Tolsma *et al.* 2017a). Note that while long-term monitoring data was also available for Raymond Island, these data were not in the form of consistent area-constrained searches nor was the number of observers available, and so these were excluded from our analyses.

Counts completed for the purposes of assessing potential translocation sites for excess animals from French Island (Menkhorst *et al.* 2017) were also collated, totalling 19 sites across central Victoria (Murrundindi, Tallarook, Blackwood and Daylesford).

Hancock Victorian Plantations Holdings (HVP) generously provided access to 1,104 counts from their estate within the Strzelecki Ranges, covering eucalypt plantations (*E. globulus*, *E. nitens* and *E. regnans*) and remnant native forest and woodland. In addition, double-count data from 54 sites in Blue Gum (*E. globulus*) plantations in the State's south-west were obtained from Ecoplan Australia (Emily Hynes unpublished data), with 24 of the sites of Ashman *et al.* (2020) also undertaken in Blue Gum plantations.

2) Double-count surveys (nocturnal)

Given a paucity of data from the Central Highlands and Strathbogie Ranges of central Victoria, we integrated 115 nocturnal double-count surveys recently conducted across timbered portions of this region (Nelson *et al.* 2018, J. Cripps, L. Durkin and J. Nelson, ARI, unpublished data). These surveys were completed primarily to estimate the abundance of Greater Gliders (*Petauroides volans*); however, detections of all arboreal marsupials were recorded. Nocturnal double-counts were conducted using the same protocol as diurnal double-counts, with the exception that they were conducted after dark using spotlights and there was no limit on transect width (instead, distance from the transect line to each individual was estimated for the purposes of a distance sampling design). To ensure consistency with diurnal double-counts, we limited detections from nocturnal double-counts to those within 25 m of the transect line. Differences in the detection rate of Koalas between diurnal and nocturnal double-count surveys were accounted for in the analysis (see below).

3) Single-count surveys

A total of 414 single-count surveys for Koala were compiled to supplement the double-count dataset, where 'single-counts' are those in which an area-constrained search was conducted by a known number of observers, but for which independent, replicate counts were not available. Two datasets of this type were available.

The 'Great Victorian Koala Count' (GVKC) was completed between 7 and 15 November 2015 as a citizen science initiative of the Department of Environment, Land, Water and Planning. A total of 651 volunteers completed counts of Koalas across the State, with instructions to report transect coordinates, transect length and the number of observers involved. Transect length was reported in broad categories (< 500 m, 500–1000 m, 1001–2500 m, 2501–5000 m, > 5000 m). We excluded all counts conducted over transects > 2500 m in length, given the high uncertainty in density estimates that would result from the broad distance categories applied above this threshold. For all remaining counts, we used the mid-point of the relevant distance class as a point estimate of transect length and assumed a transect width of 25 m each side of the line (as is standard for transect surveys for Koala) in the absence of information on this parameter. A total of 255 counts from the GVKC were included after also removing those for which search area or effort were not reported.

The second single-count dataset available for this study was collected across the Strzelecki Ranges between 2013 and 2014 by the NSW Office of Environment and Heritage, as part of that State's 'Corridors and Core Habitat for Koalas Project' (with Victorian surveys being motivated by a desire to identify source populations for possible translocations into NSW). Spot counts within a 25 m fixed radius area (0.196 ha) were completed by small teams of observers (range = 1–8; mean = 3) as an addition to spot assessments of Koala scats (the primary sampling technique applied). A total of 159 single-counts were available from this study.

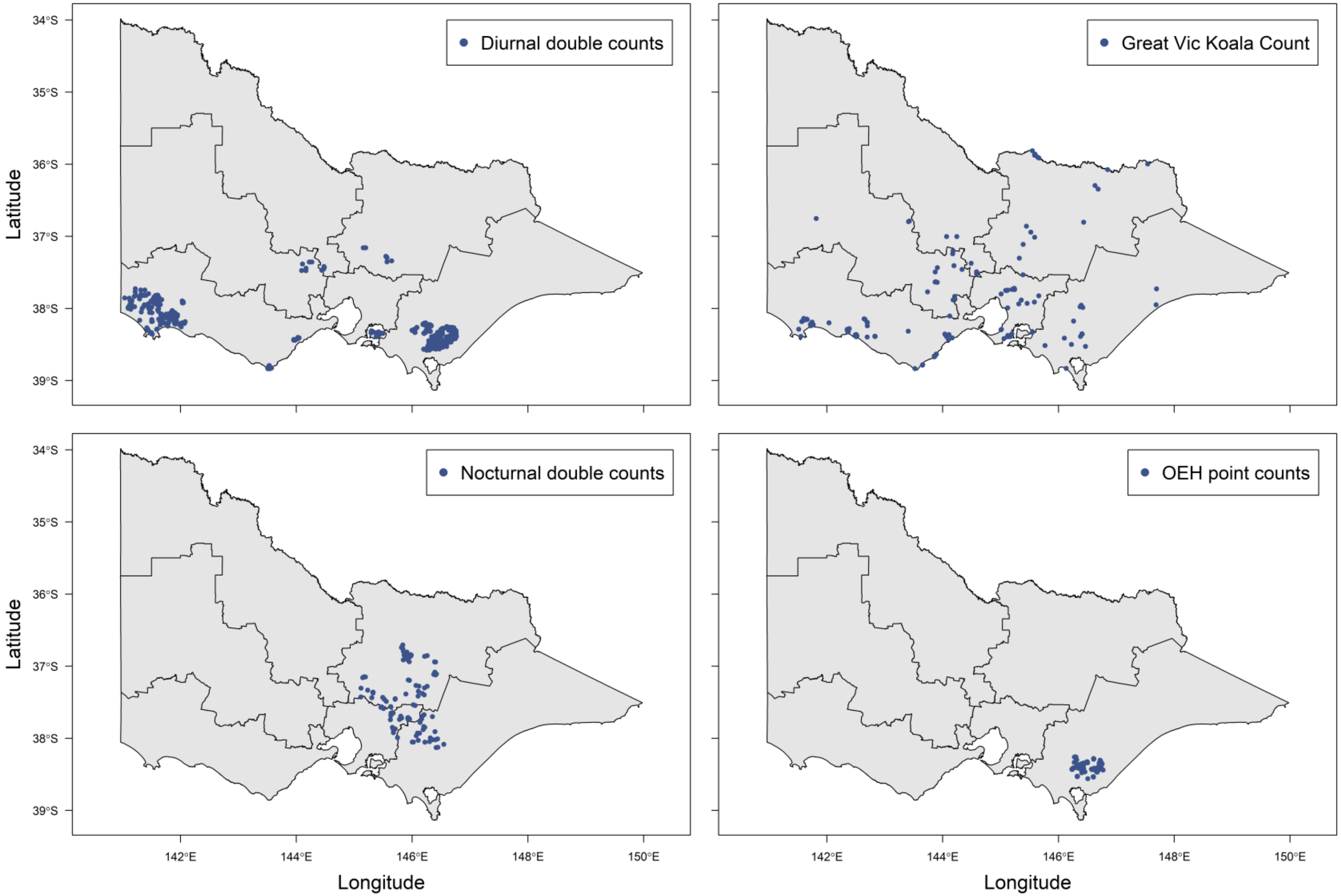

Figure 2. The distribution of Koala counts collated for this project, including two types of 'double counts' (left column) following formal double-observer protocols, and two types of 'single counts' (right column) in which one-off counts were completed, either along transects or as point counts. 'OEH' stands for the NSW Office of Environment and Heritage. Internal polygons show the DELWP regions.

2.1.3 Environmental predictors

Identification of potential environmental predictors of Koala distribution and density across Victoria was guided by previous distribution modelling exercises for the species in the State, and a review of the broader literature on the habitat affiliations of this species across its range.

Previous modelling projects for Koalas in Victoria (e.g., Menkhorst *et al.* 2017) used raster layers of the prevalence of preferred eucalypts as primary predictors. These layers are model predictions of the occurrence of preferred eucalypts, produced by the Ecological Analysis and Synthesis Group of the Arthur Rylah Institute for Environmental Research (ARI) using presence and absence data from around 50,200 vegetation plots across Victoria, New South Wales and South Australia (see Liu *et al*. 2011). On the basis of previous modelling exercises for Koala distribution in Victoria (M. White, ARI, unpublished), we used state-wide raster layers of the predicted prevalence of River Red Gum (*E. camaldulensis*), Mountain Swamp Gum (*E. camphora*), Mountain Grey Gum (*E. cypellocarpa*), Blue Gum (*E. globulus*), Swamp Gum (*E. ovata*), Candlebark (*E. rubida*) and Manna Gum (*E. viminalis*) at a 75×75 m grid cell resolution, plus a prediction of the combined prevalence of these eucalypts across the State at this resolution (produced by simply taking the maximum predicted prevalence of any of these species as the value for a given grid cell). A layer of the occurrence of eucalypt plantations across Victoria (circa 2015) was also obtained at a 75×75 m grid cell resolution given the occurrence of Koalas within this habitat type.

Ten climatic and topographic variables were identified as potential predictors of Koala density across Victoria on the basis of their relationship with Koala occurrence across the species' range (Adams-Hosking *et al.* 2012; Santika *et al.* 2014; Sequeira *et al.* 2014; Briscoe *et al.* 2016; Law *et al.* 2017). They were: (i) elevation (m asl); (ii) slope (degrees); (iii) topographic roughness; (iv) annual rainfall (mm); (v) rainfall seasonality; (vi) annual temperature range (°C); (vii) diurnal temperature range (°C), (viii) mean summer temperature (°C); (ix) mean temperature of the warmest month (°C), and; (x) temperature seasonality. Raster layers for each variable except slope and topographic roughness were downloaded from WorldClim version 2 (Fick and Hijmans 2017) at a 746×925 m grid cell resolution. Slope and topographic roughness were subsequently calculated from the elevation layer with the aid of the `raster` package (Hijmans and van Etten 2019) for `R` version 3.5.3 (R Core Team 2019).

Rasters of environmental predictors were aligned for subsequent analyses by resampling each to a 1×1 km grid cell resolution.

2.2 Modelling approach

2.2.1 Koala habitat distribution model

Estimating the abundance of species across a broad geographic area fundamentally hinges on the capacity to delineate the species' range across that area. For this reason, we began by constructing a Habitat Distribution Model (HDM) for Koalas across Victoria using occurrence records in the VBA. The Maxent algorithm (Phillips *et al.* 2004) was selected for this purpose, being readily applied to presence-only distribution data and displaying strong predictive performance relative to alternative methods (Elith *et al.* 2006).

Model fitting began by first identifying highly correlated variables among the 10 climatic and topographic variables and selecting a single variable from pairs displaying correlation coefficients ≥ 0.8. Temperature layers were highly correlated in most pairwise comparisons; of the five originally selected, we retained mean summer temperature (MST, which is a useful surrogate for heat stress; Santika *et al.* 2014; Briscoe *et al.* 2016) and temperature seasonality (which was not highly correlated with MST). Slope was strongly correlated with topographic roughness; we retained the former as it is a more easily interpreted measure of topographic complexity.

A small set of candidate models was defined using the remaining variables and sequentially fitted to the data. Model comparison proceeded using Area Under the Curve (AUC; a measure of a model's predictive accuracy) and Akaike's Information Criterion (AIC; a measure of a model's predictive capacity relative to other candidate models examined). All candidate models included the climatic and topographic variables described above, but differed in the inclusion of eucalypt layers. On the basis of documented eucalypt preferences of Koalas (reviewed by Moore and Foley 2000), and/or associations between particular eucalypt species and high Koala densities in Victoria (Ramsey *et al.* 2010, Tolsma *et al.* 2017a,b, Ashman *et al.* 2020), we classified *E. viminalis* as high preference, *E. camaldulensis, E. globulus* and *E. ovata* as medium preference and *E. camphora*, *E. cypellocarpa* and *E. rubida* as low preference. Spatial layers of each preference grouping were derived by taking the maximum predicted prevalence for each grid cell among the constituent species. The candidate model set included either: 1) each eucalypt preference layer, at a 1 km^2

resolution; 2) the collective eucalypt layer [all species combined], at a 1 km^2 resolution, or; 3) eucalypt layers resampled to reflect the average prevalence in a focal grid cell and surrounding eight grid cells (giving a measure of the prevalence of preferred eucalypts at a neighbourhood scale). Equivalent layers were produced for eucalypt plantations, by calculating the prevalence of plantations at a 1 km grid cell resolution, and calculating neighbourhood prevalence for each cell as above.

Models were fitted using the '`maxent`' function in the `dismo` package (Hijmans *et al.* 2017) in `R`, selecting hinge features only as they produce more biologically-realistic response curves, reduce the likelihood of over-fitting and produce more robust predictions beyond the environmental space of the data (Elith *et al.* 2010). Background samples (*n* = 7,592, matching the number of presence records) were drawn from the entire State.

The best fitting model was subsequently used to generate predictions of Koala habitat suitability across Victoria, using fitted relationships with the relevant climatic, topographic and eucalypt layers. In turn, these predictions were used to delineate the range of Koala habitat across Victoria (that is, the presence or absence of suitable habitat), using the 'maxSSS' thresholding approach which seeks to maximise the sum of model specificity and sensitivity (following the recommendations of Lui *et al.* 2013). Thresholding was implemented using the `dismo` package.

2.2.2 Koala abundance model

The peculiarities of the count data available for this project necessitated a custom approach to developing a statistical model of Koala abundance. These peculiarities included an amalgamated count dataset from largely separate studies in different parts of the species' Victorian range, count data collected using different protocols (two double-count protocols and two single-count protocols), counts conducted over differing areas and with differing observer effort, counts from populations in which abundance was being actively managed, diurnal double-counts (which are more reliable) biased to over-abundant populations, and counts from two broad habitat types (native forest and woodland vs. eucalypt plantations).

We began by screening counts from native forest and woodland to exclude: 1) surveys over very large areas (>10 ha), in which abundance estimates were likely to be unreliable, and; 2) surveys in which Koala density was > 7 ha^{-1}, which was the case only at severely over-abundant populations (Cape Otway and French Island). Similarly, we sought to minimise the influence of active management on the modelled abundance estimates. As such, surveys from Budj Bim National Park were restricted to those from 2004 (pre translocations and fertility control), with surveys from French Island restricted to those conducted in 2017 (six years after past translocations; Tolsma *et al.* 2017a).

Counts were allocated to 1 km^2 grid cells across Victoria for the purposes of model building, and values for each of the above environmental layers extracted. Surveys that occurred in the same grid cell were combined by simply summing the Koala count, search area and number of observers.

We undertook an initial screening of covariates to identify plausible relationships between Koala density and environmental variables that would be suitable to include in the model. In addition to the variables described above, we added a binary 'habitat' indicator variable to the candidate set to discriminate between counts derived from native forest and woodland (scored as 1) or eucalypt plantations (scored as 0). For the purposes of this initial screening, we ignored detection error and amalgamated all counts into a single dataset. Relationships between counts and the environmental predictors were explored using a generalised linear model in which the count within cell i (y_i) was assumed to be random variable from a Poisson distribution, with y_i a function of the mean expected density in cell i (λ_i) and the area searched (in ha) in cell i (A_i):

$$y_i \sim Poisson(\lambda_i A_i). \qquad \text{Eq. 1}$$

Effects of each environmental variable (E) on the expected density in cell i were incorporated using a log-linear model, such that:

$$\lambda_i = exp\left(\alpha + \sum_{k=1}^{n} \beta_k E_{i,k}\right), \qquad \text{Eq. 2}$$

where α is the intercept and β_k are regression coefficients for the n respective environmental variables E_k ($k = 1 \cdots n$). Prior to model fitting, each continuous environmental variable was standardised by subtracting the mean and dividing by two standard deviations.

To enable rapid filtering of potential covariate structures, a global model was constructed that included all main effects plus a maximum of two-way interactions between the eucalypt layers and each climatic and topographic variable. Forwards and backwards stepwise procedures starting from this global model were used to identify the most parsimonious combination of variables to include, with model selection based on AIC using the ‘stepAIC’ function in the MASS package (Venables and Ripley 2002) in R.

Although the above procedure was suitable for identifying a plausible model of Koala abundance, it ignored detection error during surveys (failure to detect individuals that were present but unseen). Hence, we developed a novel statistical model that explicitly accounted for imperfect detection and was also capable of incorporating survey data from various sources, notably the combination of double-count and single-count survey data in the one framework. We detail how we incorporated counts from these two sources below.

Surveys undertaken using the double-count protocol can be used to estimate the detection probability of each observer, and hence correct the observed counts for imperfect detection. The number of Koalas seen independently by observer 1 (y_1) and 2 (y_2) and the number of Koalas observed by both observers (y_3) at site i [$y_i = (y_{i1}, y_{i2}, y_{i3})$] were assumed to follow a multinomial distribution, such that:

$$y_i | N_i, p_1, p_2 \sim Multinomial(N_i, \pi_1, \pi_2, \pi_3) g(N_i | \lambda_i, A_i)$$

$$\pi_1 = p_1(1 - p_2); \pi_2 = (1 - p_1)p_2;\ \pi_3 = p_1\, p_2, \qquad \text{Eq. 3}$$

where p_1, p_2 are the detection probabilities of observers 1 and 2, N_i is the Koala abundance at site i (which was conditional on the mean expected density λ_i as per Equation 2) and π are the multinomial cell probabilities. Estimation proceeds using the marginal distribution of Equation 3, by assuming a model for $g(\cdot)$ (e.g. Poisson, Negative Binomial) and integrating over the latent abundance N_i. Alternatively, if a Poisson distribution is adopted for N_i, the marginal distribution can be specified analytically as a Multinomial-Poisson mixture over the j observation categories:

$$y_{i,j} | \lambda_i, p_1, p_2 \sim \prod_{j=1}^{3} Poisson(\lambda_i \pi_j A_i), \qquad \text{Eq. 4}$$

Surveys using single-counts were incorporated into the model by assuming that they were conditional on the same abundance model as the double-count surveys and using a similar marginal formulation as for the double-count survey data. Hence:

$$y_{i,s} \sim Poisson(\lambda_i \theta_{i,s} A_i), \qquad \text{Eq. 5}$$

where $y_{i,s}$ is Koala count during single count survey s and site i, and the probability of detecting Koalas ($\theta_{i,s}$) was estimated assuming that it would be proportional to the number of observers present during survey s,

$$\theta_{i,s} = 1 - (1 - p_a)^{obs_{i,s}},$$

where p_a is the mean detection probability of a single observer estimated from the (diurnal) double-count surveys and $obs_{i,s}$ is the number of observers present during survey s and site i.

This model (Equations 3 – 5) was fitted to the data in a Bayesian framework using Markov Chain Monte Carlo (MCMC) sampling in Stan (Stan Development Team 2018a) using package rstan (Stan Development Team 2018b) in R. Main and interactive effects of the environmental predictors on density (λ_i) mirrored those of the most parsimonious model identified during initial variable screening (Equation 2). However, heterogeneity in the count data that could not be explained by the Poisson model was accounted for by adding a separate random effect term (with mean of zero and standard deviation to be estimated) for each of the count types. Joint posterior distributions of the parameters were derived from 1000 iterations of the MCMC algorithm from five chains after a burn-in of 1000 iterations, with convergence of the algorithm judged using the Brook-Rubin-Gelman statistic (Brooks and Gelman 1997). Posterior predictive checks (Gelman *et al.* 1996) were used to assess model fit with the aid of the DHARMa and bayesplot packages for R.

2.2.3 State and regional abundance predictions

State-wide and regional estimates of Koala abundance were derived separately for the native vegetation and plantation estates, using the fitted relationships between Koala density and the climatic, topographic, habitat and eucalypt preference layers described above, as well as their interactions.

To enable predictions of Koala abundance in native forest and woodland it was first imperative to define those large tracts of the State that are unlikely to be occupied by the species. We did this in two steps:

1. First, the thresholded Koala HDM generated using Maxent (as described section 2.2.1) was used to exclude all 1 km^2 grid cells predicted to contain unsuitable habitat for the species.

2. Within the remaining set of cells, we then excluded all those in which the mapped extent of native tree cover was <5%, under the assumption cells with less than 5 ha of native tree cover would be incapable of supporting Koala populations (although home-ranges of 1-3 ha have been reported for the species in Victoria, the majority of telemetry studies of Koalas report home-ranges >5 ha, and often substantially so [Melzer and Houston 1997, Matthews *et al.* 2016]). Native tree cover at the 1 km^2 resolution was determined by aggregating a spatial layer at 75 m^2.

For each of the remaining set of 33,019 grid cells, the fitted relationships between Koala density and the suite of climatic, topographic, habitat and eucalypt layers were used to predict Koala abundance. Specifically, the abundance of Koalas in each grid cell i (N_i) was estimated as:

$$N_i \sim Poisson(\lambda_i V_i), \quad \text{Eq. 6}$$

where λ_i is the expected density (per ha) in grid cell i estimated as per Equation 2 using the posterior distribution of parameter estimates and the measures of the relevant environmental variables for cell i, and V_i is the area of native tree cover (in hectares) for cell i. Random effects were set to their mean (zero) for these predictions (i.e. population-level). Cell-by-cell predictions were summed to give a state-wide prediction of Koala abundance in native vegetation.

The above approach was repeated for each of the six DELWP regions of Victoria (Barwon South West, Gippsland, Grampians, Hume, Loddon-Mallee and Port Phillip), providing estimates of Koala abundance in native vegetation across the primary management jurisdictions.

Abundance predictions for the plantation estate were made using the spatial layer of the distribution of eucalypt plantations described in section 1.1.3. To match the approach used for native vegetation, we calculated the area of eucalypt plantations for each 1 km^2 grid cell across the State, and subsequently excluded cells that either:

1. Were beyond the distribution of Koala in the State (in practice, a small number of plantations across the northern plains), or;
2. Contained less than 5 ha of eucalypt plantations and were isolated from native forest and woodland (under the assumption that cells with less than 5 ha of habitat could not support Koala populations).

For each of the 6,885 grid cells remaining after applying these criteria, we collated the environmental predictors included in the final model and derived both state-wide and regional predictions of Koala abundance using the same approach as that for native vegetation, with V_i in Equation 6 representing the area of eucalypt plantation within cell i.

All predictions were formulated as derived parameters to be monitored during model fitting in `Stan`, allowing the full posterior distribution of these predictions to be generated and extracted. We report mean estimates and 95% credible intervals of each predicted quantity.

2.2.4 Predicting the impact of Victorian wildfires

To provide a preliminary assessment of the impact of Victoria's extensive recent wildfires on Koala populations, we estimated both the proportion of the species' habitat that has been affected by these fires, and the proportion of the population affected, both State-wide and for each of the DELWP regions. To do so, mapped fire extent (as of 11 February 2020) was used to calculate the area of Koala habitat that had been affected (based on the HDM described above), with predictions of abundance within this area produced using the abundance model and approach described in the section 2.2.3. The proportion of the population affected by wildfires – State-wide and for each DELWP region – could then be estimated from these predictions.

2.3 Assumptions and limitations

As described above, this project collated existing count data from across Victoria for the purposes of building a statistical model of Koala abundance. Although a large number of counts were obtained, with a reasonable spatial spread across the species' Victorian range (Figure 2), the dataset was nevertheless constructed from surveys that were conducted for purposes other than modelling abundance at large spatial scales. As such, the count data were biased to parts of the range in which Koalas are of specific management concern, such as over-abundant populations in the south of the State, and populations throughout the Strzelecki Ranges. Of particular note in this regard is the bias in the diurnal double-count data (the most reliable count information available to this study) to the southern portion of the species' range in Victoria, such as populations in Barwon South West region and French Island, where density is known to be relatively high.

Large areas of the Loddon-Mallee, Grampians, Port Phillip, Hume and Gippsland regions were either represented by a few scattered counts, or no counts at all.

Likewise, while we endeavoured to implement a rigorous approach to defining occupied habitat across Victoria for the purposes of abundance predictions, such delineations will always be imperfect. Some occupied areas will have been excluded, while other unoccupied areas have been retained.

3 Results

3.1 Koala habitat distribution model

Model selection statistics for the four Maxent models fitted to the Koala VBA data are presented in Table 1. Models varied little in their predictive performance, with each displaying moderate AUC values of ~0.78. Model 4 displayed the lowest AIC and was ranked substantially higher than the next best model. It differed from all other models in including eucalypt preference layers measured at the neighbourhood scale (mean prevalence over the surrounding eight grid cells). Predicted habitat suitability for the Koala across Victoria derived using the top-ranked model is displayed in Figure 3, along with the resulting thresholded prediction of the presence or absence of suitable habitat for the species.

The total area of suitable forest and woodland for Koala in Victoria was predicted to be 2,021,967 ha. The equivalent figure for eucalypt plantations was 167,098 ha.

Table 1. Model selection statistics for the four Maxent models fit to the Koala distribution data. Models differed in the treatment of eucalypt layers; either an amalgamated layer of the prevalence of all eucalypts (models 1 and 2) or layers of the prevalence of eucalypts classified into three preference categories (models 3 and 4). See section 2.1.3 for further information. AIC, Akaike's Information Criterion; ∆AIC, distance from the top model; AUC, Area under the Curve.

Model	Effective number of parameters	Log-likelihood	AIC	∆AIC	AUC
Model 4: Eucalypt preference layers, neighbourhood scale	130	-37587.03	75434.05	0.000	0.787
Model 2: Combined eucalypt layer, neighbourhood scale	137	-37632.53	75539.07	105.01	0.784
Model 3: Eucalypt preference layers, cell scale	144	-37683.45	75654.91	220.86	0.783
Model 1: Combined eucalypt layer, cell scale	140	-37711.24	75702.48	268.43	0.781

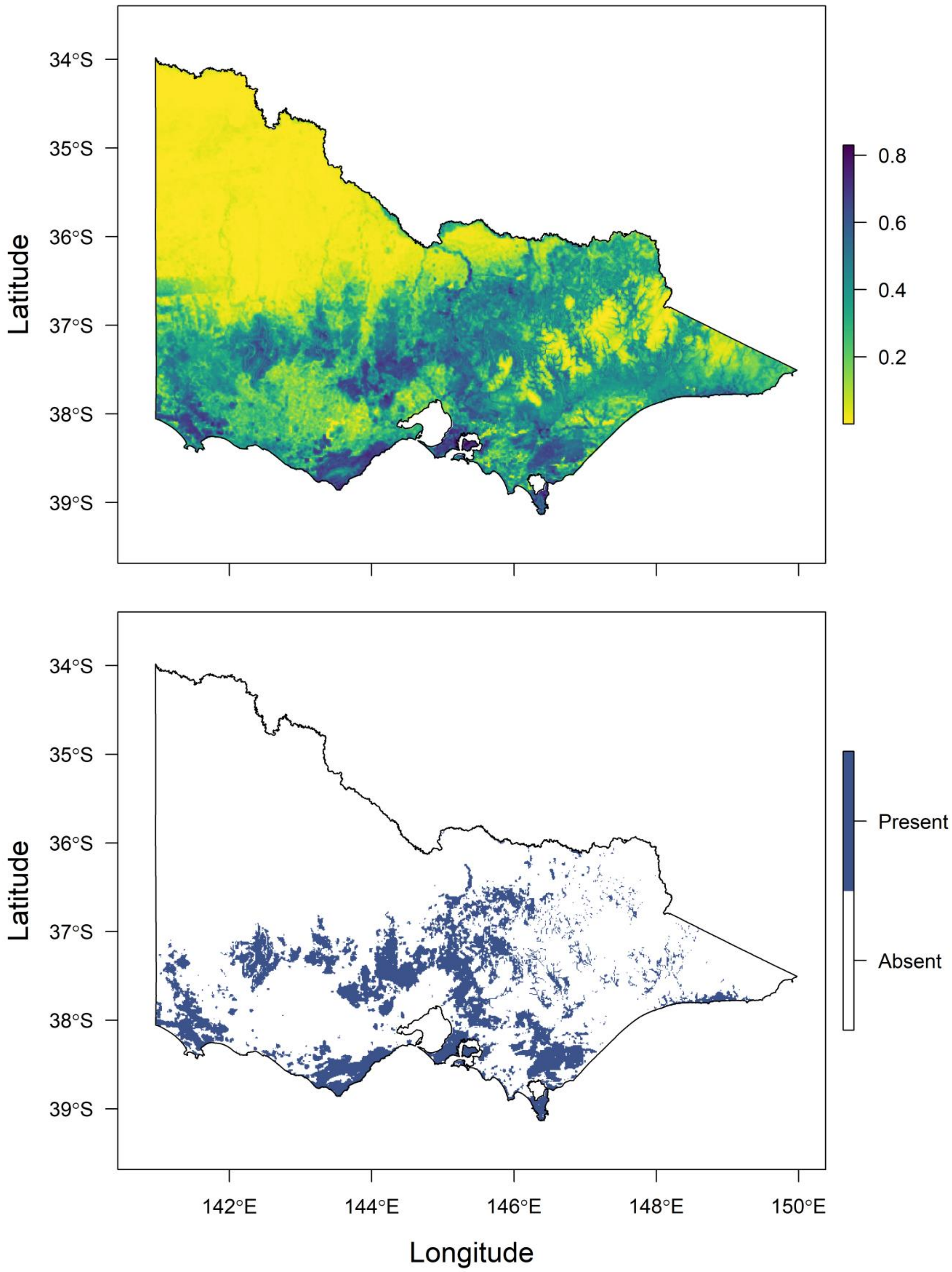

Figure 3. Predicted habitat suitability for Koala across Victoria (top panel, Maxent logistic output) and thresholded prediction of presence and absence of suitable habitat for the species across the State (bottom panel).

3.2 Koala abundance model

Model selection statistics from the initial screening of environmental variables for inclusion in the abundance model are shown in Table 2. Parameter estimates derived from re-fitting the top model while accounting for imperfect detection are provided in the Appendix (Table A1).

The top-ranked model included the following primary effects, as shown by 95% credible intervals that did not overlap zero or only did so slightly:

1. Positive interactive effect of annual rainfall and the neighbourhood prevalence of medium preference eucalypts (higher density with high rainfall and high prevalence of medium preference eucalypts);
2. Negative interactive effect of annual rainfall and the neighbourhood prevalence of eucalypt plantations (higher density with high rainfall and low prevalence of eucalypt plantations).
3. Negative interactive effect of elevation and the neighbourhood prevalence of high preference eucalypts (higher density at low elevation and high prevalence of high preference eucalypts);
4. Negative interactive effect of elevation and the neighbourhood prevalence of eucalypt plantations (higher density at low elevation and low prevalence of eucalypt plantations);
5. Negative interactive effect of mean summer temperature and the neighbourhood prevalence of high prevalence eucalypts (higher density with low summer temperatures and high prevalence of high preference eucalypts);
6. Positive interactive effect of mean summer temperature and the neighbourhood prevalence of medium prevalence eucalypts (higher density with higher summer temperatures and high prevalence of medium preference eucalypts);
7. Negative interactive effect of mean summer temperature and the neighbourhood prevalence of eucalypt plantations (higher density with low summer temperatures and high prevalence of eucalypt plantations);

Detection probabilities for double-count surveys in native forest and woodland were high, averaging 0.76 per observer and slightly lower in plantations (average of 0.67). Detection probabilities were substantially lower for nocturnal double-count surveys, averaging just 0.25 per observer.

Predictive capacity of the final fitted model to the original data was excellent, with a model R^2 of 0.97 and root mean squared error between predicted and observed counts of 0.49 (meaning, on average, the predicted counts are in error by <1 individual). The relationship between the observed and predicted counts for each of the datasets is depicted in Figure 4, and a quantile-quantile plot of the observed versus expected distribution of the count data displayed in Figure 5 (where 'expected distribution' is that derived from predicting the number of Koalas observed during each count used for model fitting).

Figures 4 and 5, as well as additional diagnostic plots derived from posterior predictive checks (Figures A1-A3 in the Appendix), may be used to further interrogate the fit and predictive capacity of the model. It is clear from these various diagnostics that the fit of the model is weakest at the extremes of the observed data. While the mean of observed counts and the proportion of zero counts were both well predicted (Figure A2), the model did relatively poorly at predicting the maximum count (Figure A2) and the poorest alignment between the observed and expected distribution of counts occurred at the higher quantiles (Figure 5). Figure A1 also shows that the predictive error of the model was, on average, greatest for high counts (Figure A1).

Encouragingly, posterior predictive distributions from the fitted model generally encompassed the observed data, including the proportion of zero counts, standard deviation of counts and the mean count (Figures A2 and A3). Likewise, the distribution of predicted and observed counts aligned well (Figure A2).

Table 2. Model selection statistics for the top models of Koala abundance. Models are those that ranked highest under four broad model structures, differing in the treatment of eucalypt layers; either an amalgamated layer of the prevalence of all eucalypts (models 1 and 2) or layers of the prevalence of eucalypts classified into three preference categories (models 3 and 4). See section 2.1.3 for further information. The top model in each case was identified using a stepwise fitting approach. AIC, Akaike's Information Criterion; ∆AIC, distance from the top model.

Model	Number of parameters	Deviance	AIC	∆AIC
Model 4: Eucalypt preference layers, neighbourhood scale	22	1227.61	1970.81	0.00
Model 3: Eucalypt preference layers, cell scale	25	1227.98	1977.18	6.37
Model 2: Combined eucalypt layer, neighbourhood scale	14	1371.25	2098.44	127.63
Model 1: Combined eucalypt layer, cell scale	14	1438.35	2165.55	194.74

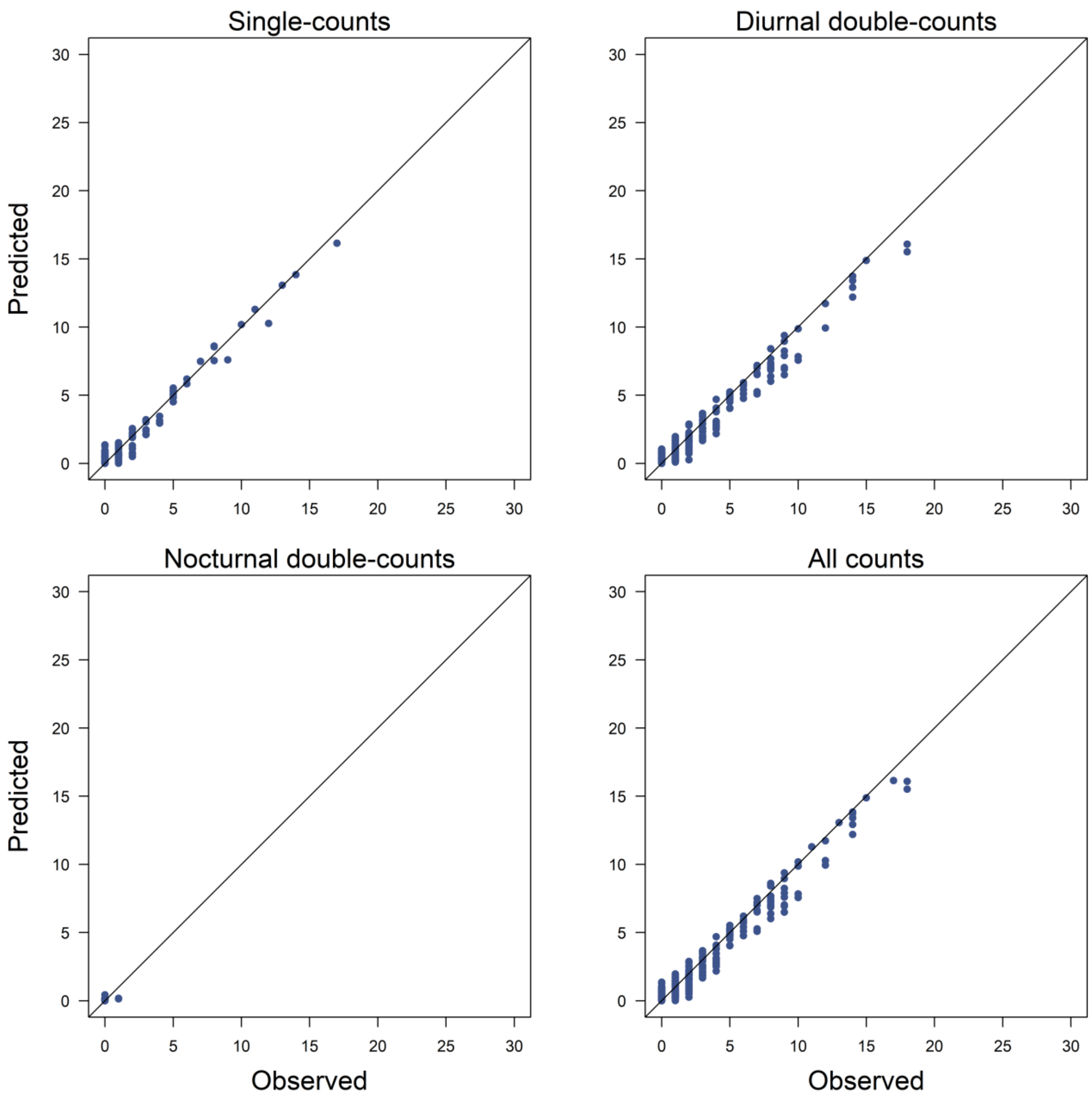

Figure 4. Relationship between the observed and predicted counts for surveys used to parameterise the Koala abundance model.

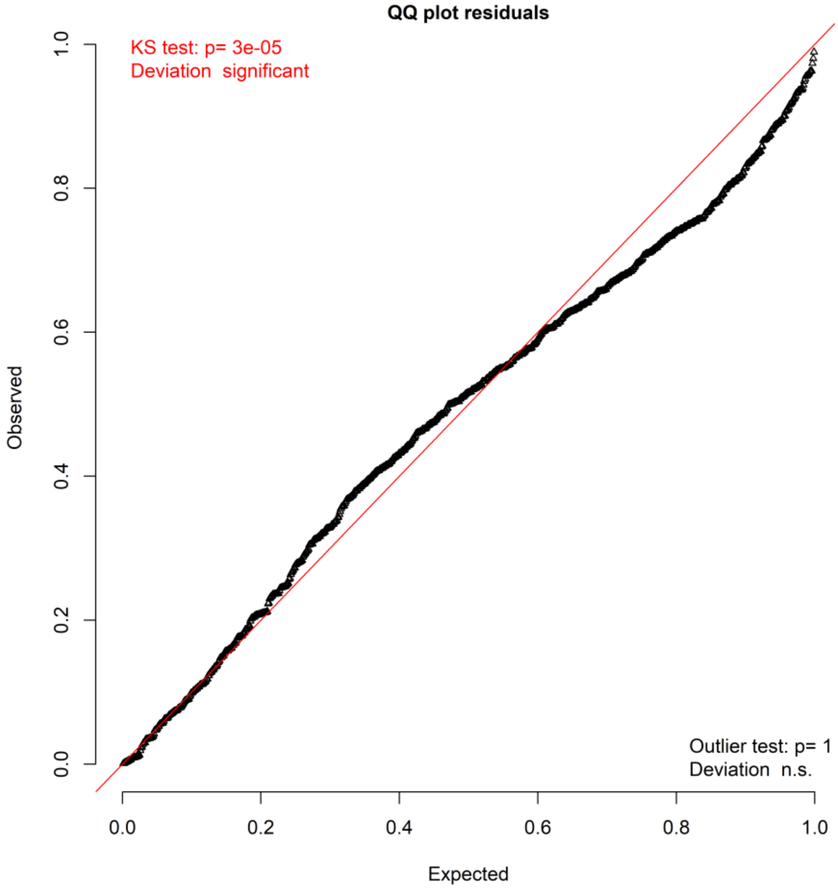

Figure 5. Quantile-quantile plot for the observed and expected distribution of the data, where the 'expected' data is that simulated from the fitted model. 'KS test' stands for Kolmogorov-Smirnov test of the equality of the two distributions. The significant result is reflective of the fact that the model underpredicts high counts (see Figures A1-A3).

3.3 State and regional abundance predictions

State and regional predictions of Koala abundance in native forest and woodland derived from the top model are provided in Table 3, with state-wide predictions of density and uncertainty in these predictions depicted in Figures 6 and 7. Figure 8 provides histograms of predicted densities across Victoria, and within the four DELWP regions with the most extensive Koala habitat.

The total abundance of Koalas in native forest and woodland in Victoria was predicted to be 412,948, with 95% credible interval of 324,772–519,578. Largest populations were predicted to occur in the Barwon South West, Gippsland and Hume regions (in that order), followed by Port Phillip, Grampians and Loddon-Mallee. Barwon South West was predicted to contain around half of Victoria's Koala population, with the combined abundance in the Barwon South West, Gippsland and Hume regions being roughly 82% of the total predicted Victorian population.

Predicted densities within the native forest estate ranged up to 13 ha^{-1}, with a mean of 0.22 ha^{-1} (Figure 8). This equates to maximum abundances up to 1,300 Koalas per square kilometre of suitable habitat, with an average of 22 per square kilometre. Density was predicted to be high through the wetter forest and woodland of south-west Victoria (bounded roughly by Edenhope in the north, the South Australian border in the west and Port Fairy in the east), as well as Cape Otway, parts of Mornington Peninsula, French Island, the northern and eastern shores of Western Port Bay, and the Strathbogie Ranges and lower Ovens River floodplain in north-eastern Victoria (Figure 6, top panel). Uncertainty in these predictions, as quantified by the coefficient of variation (ratio of the standard error to the mean estimate), is greatest in the northern areas of habitat in the State's south-west, as well valleys and lower slope of the Grampians, areas of the Pyrenees Ranges, the Wombat State Forest and surrounding public land, and foothills of the Great Dividing Range in the Hume and Gippsland regions (Figure 7, top panel).

Predicted abundance in eucalypt plantations across Victoria and in each of the DELWP regions is provided in Table 4, with predicted densities shown in Figures 6 and 8. The total abundance estimate for Koalas in eucalypt plantations in Victoria was 46,917 (95% CI, 35,998–60,054), of which 91% were predicted to occur in the *E. globulus* plantations of the Barwon South West region. Almost all remaining individuals are predicted to occur in the Gippsland and Grampians regions (3% and 5%, respectively), with very small numbers predicted for the Hume, Loddon Mallee or Port Phillip regions (< 350 individuals total across these regions). Predicted densities in eucalypt plantations follow the same general spatial pattern as that for native vegetation, being highest in Barwon South West. Predicted densities were generally similar to those in native forest and woodland in the same regions (Figure 6, bottom panel; Figure 8). Densities within plantations were predicted to average 0.24 ha^{-1} across the entire state, ranging up to 1.8 ha^{-1}. Corresponding abundance figures are therefore an average of 24 Koalas per square kilometre of eucalypt plantation, ranging up to 180 per square kilometre (Figure 8). Uncertainty in predicted densities within eucalypt plantations were highest across northern sections of the south-west, and the northern and western fall of the Great Dividing Range, with some areas of high uncertainty on the edges of the Strzelecki Ranges (Figure 7, bottom panel).

Table 3. Predicted Koala abundance in native forest and woodland across Victoria. The total state-wide prediction is provided, along with predictions for each of the six DELWP regions. LCI, lower credible interval; UCI, upper credible interval.

State / DELWP Region	Predicted abundance	Standard deviation	Coefficient of variation	LCI	UCI
Victoria	412,948	49,755	0.12	324,772	519,578
Barwon South West	210,277	26,323	0.13	163,188	267,867
Gippsland	75,134	10,800	0.14	56,313	98,687
Grampians	32,552	10,449	0.32	17,051	57,490
Hume	55,180	24,361	0.44	25,639	111,333
Loddon-Mallee	8,728	3,563	0.41	3,880	17,763
Port Phillip	31,076	6,326	0.20	20,718	45,207

Table 4. Predicted Koala abundance in the eucalypt plantation estate across Victoria. The total state-wide prediction is provided, along with predictions for each of the six DELWP regions. LCI, lower credible interval; UCI, upper credible interval.

State / DELWP Region	Predicted abundance	Standard error	Coefficient of variation	LCI	UCI
Victoria	46,917	6,176	0.13	35,998	60,054
Barwon South West	42,581	5,731	0.13	32,265	54,880
Gippsland	1,462	256	0.17	1,040	2,002
Grampians	2,534	889	0.35	1,237	4,698
Hume	256	124	0.48	104	556
Loddon-Mallee	44	23	0.51	15	101
Port Phillip	40	12	0.29	21	66

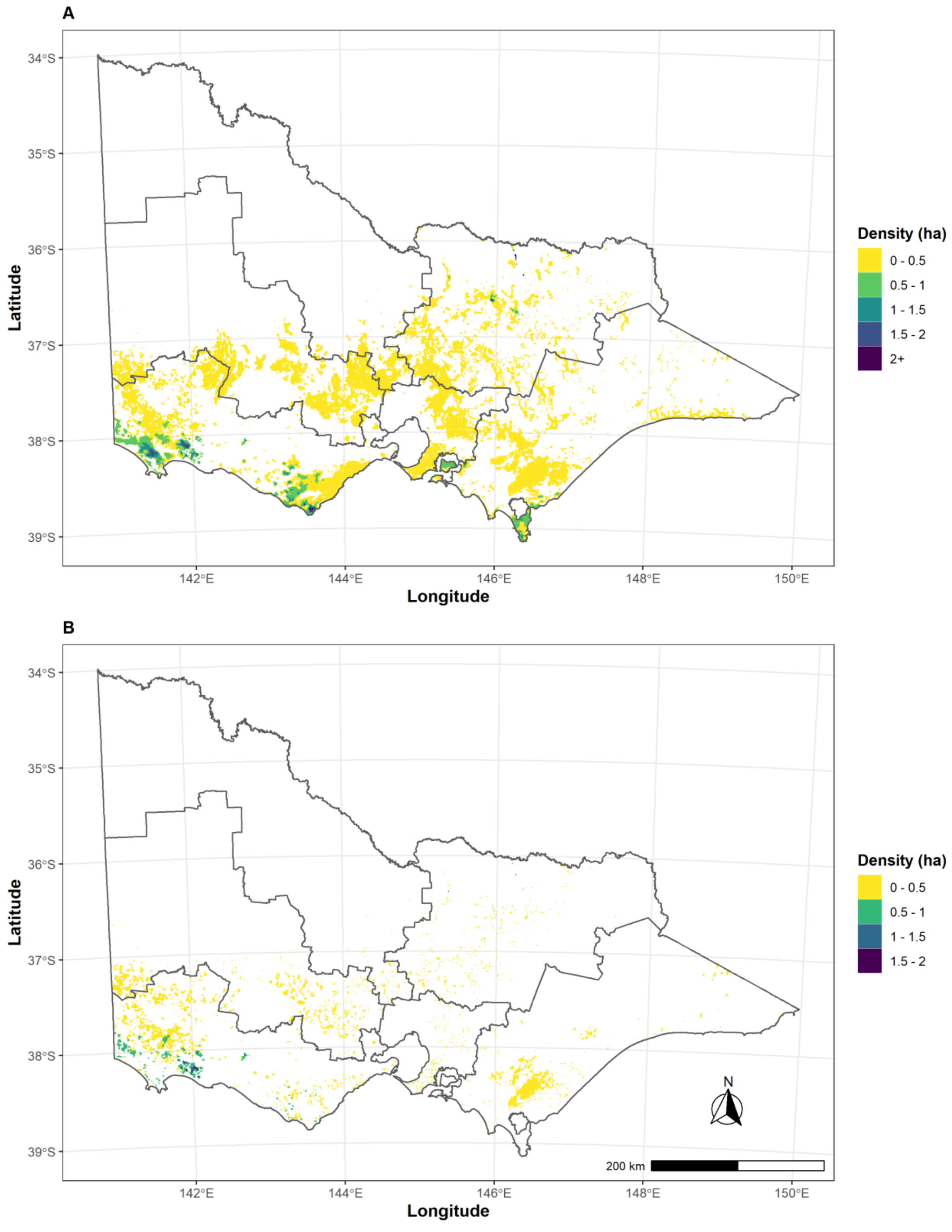

Figure 6. Predicted density of Koalas across Victoria in native forest and woodland (A) and eucalypt plantation (B).

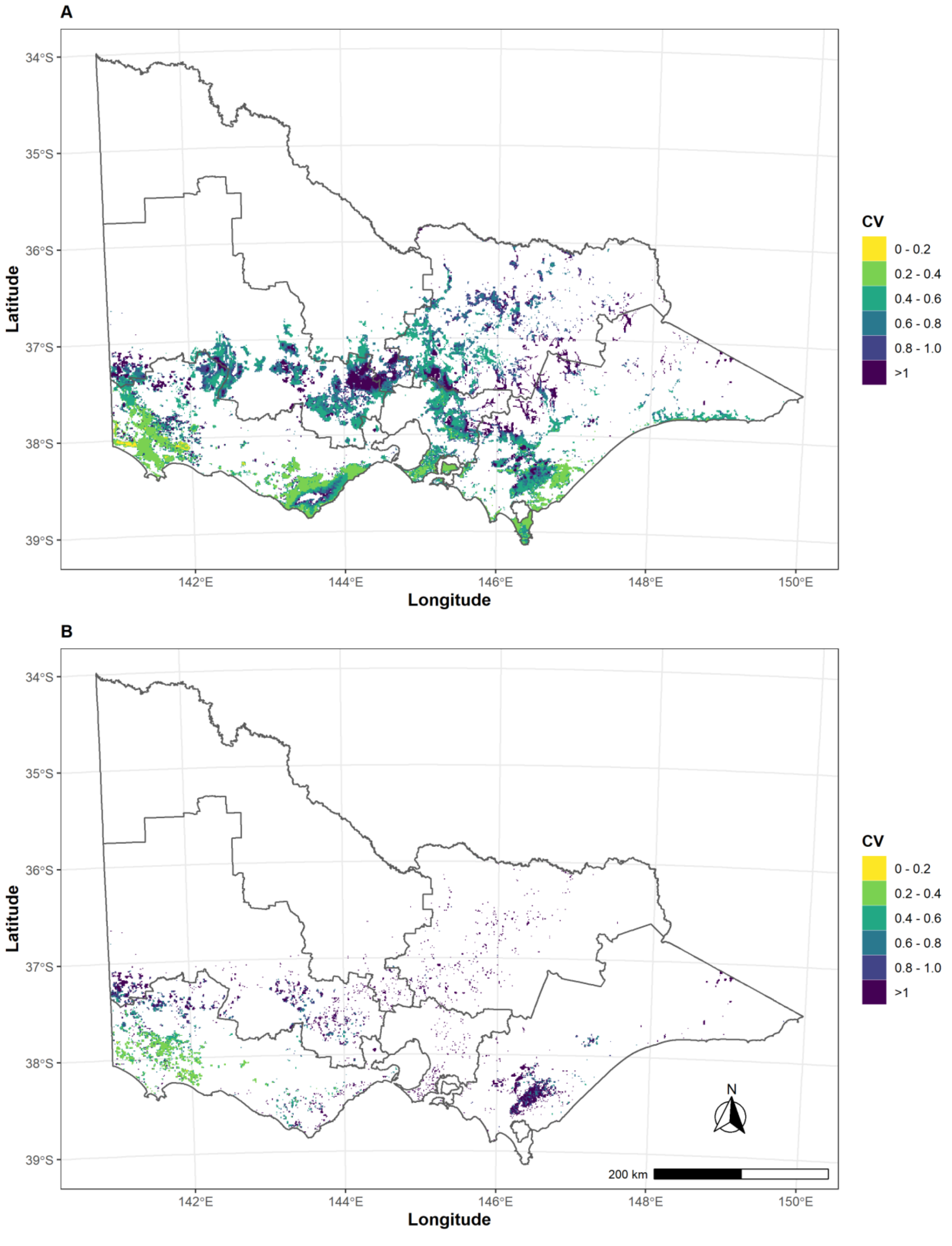

Figure 7. Coefficient of variation for the predicted density of Koalas across Victoria in both native forest and woodland (A) and eucalypt plantation (B). The coefficient of variation is the standard deviation of the estimate divided by the estimate and hence is a measure of relative precision.

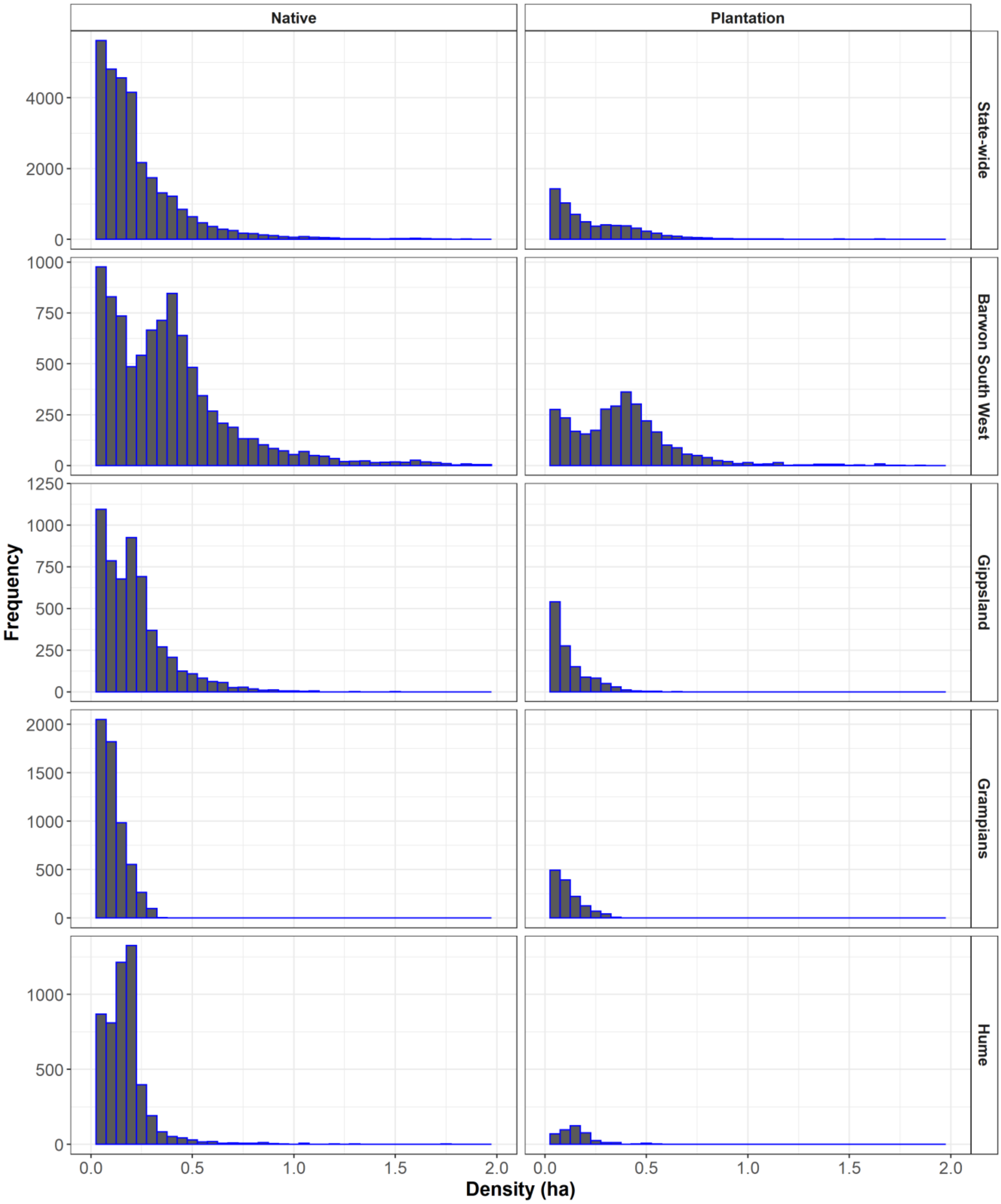

Figure 8. Histograms of predicted Koala density in native forest and woodland (left column) and eucalypt plantation (right column) in Victoria. Densities are shown across the entire State and across the four DELWP regions with extensive Koala habitat.

3.4 Impact of Victorian wildfires

Figure 9 overlays the mapped extent of wildfires during the 2019-2020 season (as of 11 February 2020) on the Koala density predictions across the State (as per Figure 6).

In total, 2.85% of suitable forest and woodland for Koalas in Victoria was predicted to have been impacted by these fires (57,722 ha of 2,021,967 ha), with 0.59% of habitat in eucalypt plantations affected (979 ha of 167,098 ha). The total number of Koalas predicted within these fire affected areas was 15,085 (95% CI: 11,592 – 19,442), of which 14,927 (95% CI: 11,452 – 19,298) derive from native forest and woodland (Table 5) and 158 (95% CI: 107 – 226) derive from eucalypt plantations (Table 6). These figures equate to 3.61% of the total population predicted across native forest and woodland and 0.34% of the population predicted in eucalypt plantations.

By number of individuals affected, largest impacts in native forest and woodland were predicted for Barwon South West (9,531 individuals) and Gippsland (4,588 individuals). Impacts in Barwon South West stem largely from Budj Bim National Park, in which a significant fire occurred early in January 2020 (see Figure 9, top). In eucalypt plantations, predicted impacts were highest for Barwon South West (141 individuals) and Gippsland (14 individuals); however, only a very small percentage of the total population in these regions was predicted to have been affected (<1% in both cases).

Table 5. Predicted impact of recent wildfires on Koalas in native forest and woodland in Victoria. The 'pre-fire' population estimate is provided, along with the population predicted to be affected by fire and the percentage of the population predicted to be affected.

State / DELWP Region	Population estimate	Population affected	Percentage affected
Victoria	412,948	14,927	3.61%
Barwon South West	210,277	9,531	4.53%
Gippsland	75,134	4,588	6.11%
Grampians	32,552	81	0.25%
Hume	55,180	649	1.18%
Loddon-Mallee	8,728	78	0.89%
Port Phillip	31,076	0	0

Table 6. Predicted impact of recent wildfires on Koalas in eucalypt plantations in Victoria. The 'pre-fire' population estimate is provided, along with the population predicted to be affected by fire and the percentage of the population predicted to be affected.

State / DELWP Region	Population estimate	Population affected	Proportion affected
Victoria	46917	158	0.34%
Barwon South West	42581	141	0.33%
Gippsland	1462	14	0.93%
Grampians	2534	2	0.07%
Hume	256	2	0.76%
Loddon-Mallee	44	0	0
Port Phillip	40	0	0

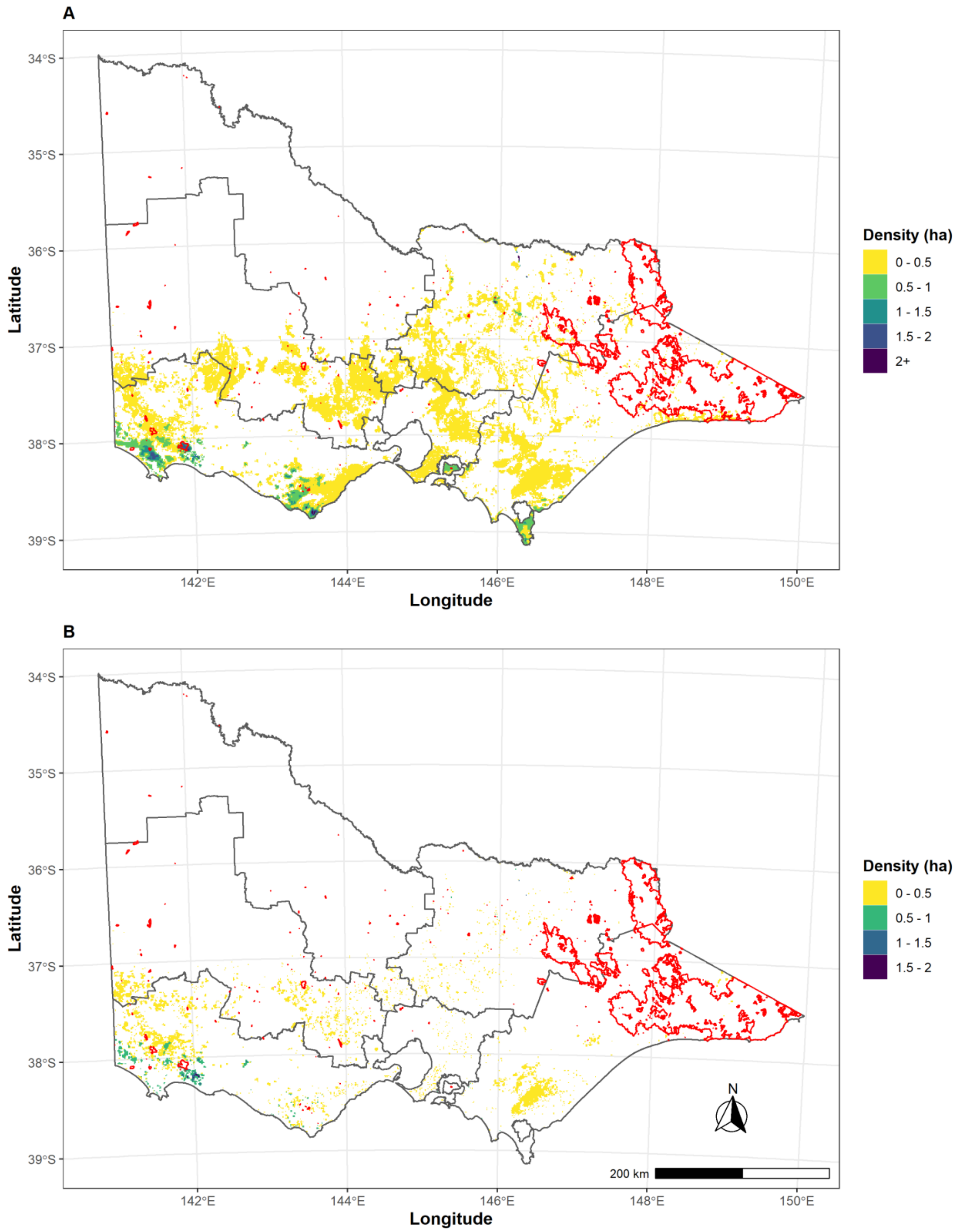

Figure 9. Comparison of the mapped extent of wildfires during the 2019-2020 fire season and predicted Koala density across Victoria, for both native forest and woodland (A) and eucalypt plantations (B). Red polygons show areas affected by wildfire as of 11 February 2020.

4 Discussion

This study represents the first systematic attempt to develop a model of Koala abundance in Victoria, and produce abundance estimates for the species at either state-wide or regional levels. Below we discuss the ecological drivers of abundance identified during the modelling process and the strengths and weaknesses of the resulting model, before discussing the abundance estimates and resulting predictions of the number of Koalas impacted by recent wildfires in Victoria. We close with recommendations about how future research, particularly a dedicated field program of counts across the Victorian range of Koala, could refine our understanding of abundance and trends for the species.

4.1 Abundance model

Our model of Koala abundance, derived with the aid of counts completed across the species' range in Victoria over the last 15 years, includes several key predictors of Koala density. A positive interactive effect of annual rainfall and the prevalence of medium preference eucalypts (defined as *E. camaldulensis*, *E. globulus* and *E. ovata*) was identified, as was a positive interactive effect of mean summer temperature and the prevalence of medium preference eucalypts. There were also negative interactive effects of (i) annual rainfall and the prevalence of eucalypt plantations (higher density in areas of higher rainfall and lower plantation prevalence); (ii) elevation and the prevalence of high preference eucalypts (higher density in areas of low elevation and high *E. viminalis* prevalence); (iii) elevation and the prevalence of eucalypt plantations (higher density at low elevation and low plantation prevalence); (iv) mean summer temperature and the prevalence of high preference eucalypts (higher density with low summer temperatures and high *E. viminalis* prevalence), and (v) mean summer temperature and prevalence of eucalypt plantations (higher density with low summer temperatures and high plantation prevalence). The analysis also revealed that Koala densities are higher in native forest and woodland than eucalypt plantations, on average.

Although there are essentially no other studies of relationships between Koala density and environmental variables over an equivalent spatial scale, the relationships detailed above have precedence as determinants of the distribution of species, at either regional or range-wide scales. A negative effect of elevation is reported by Rhodes *et al.* (2015), and either negative or quadratic effects of temperature regimes are reported by Adams-Hosking *et al.* (2011), Santika *et al.* (2014), Sequeira *et al.* (2014), Rhodes *et al.* (2015) and Briscoe *et al.* (2016). The negative effects of elevation on Koala abundance likely relates to poorer soils and lower foliage nutrients on higher, steeper slopes (see Moore and Foley 2000), while effects of temperature relate to sensitivity to heat stress (Santika *et al.* 2014, Briscoe *et al.* 2016). Positive effects of annual rainfall (or other environmental moistures indices) are reported by Adams-Hosking *et al.* (2012), Santika *et al.* (2014), Sequeira *et al.* (2014), Briscoe *et al.* (2016) and Law *et al.* (2017), and likely relate to the sensitivity of Koala to water stress, with the vast majority of hydration in this species being via foliage. A strong preference for foliage with a higher water content has been observed in several studies (Moore and Foley 2000). Estimated effects of eucalypt preference categories generally match with those expected *a priori*, although the interactive effects identified here provide some greater insights into how Koala density is influenced by the coincidence of eucalypts and either climate or topography. The propensity for higher density with lower elevation, higher rainfall and lower mean summer temperature in areas with a higher prevalence of *E. viminalis* (classed as high preference) or *E. camaldulensis*, *E. globulus* and *E. ovata* (classed as medium preference) is a hypothesised driver of high densities in Victoria's south-west, particularly with regard to *E. viminalis* (Ramsey *et al.* 2010). However, the positive interactive effect of the prevalence of medium preference eucalypts and mean summer temperature demonstrates the capacity of woodland in foothill and floodplain environments across northern Victoria to support Koala populations, sometimes with high densities.

The data collated for this study also suggest that Koala densities in eucalypt plantations are similar to those in adjacent native forest and woodlands. The negative interactive effect of mean summer temperature and the prevalence of eucalypt plantations (translating to higher density with low summer temperatures and high prevalence of eucalypt plantations) suggests that neighbouring eucalypt plantations can increase densities across the cooler regions of the species' Victorian range, such as in the south-west. Ashman *et al.* (2020) studied drivers of Koala density in Victoria's far south-west, and report higher densities in eucalypt plantations than in native woodland within their study area. Likewise, they documented a strong positive effect of plantation cover on Koala density. Assuming our finding of higher density in areas of cooler summer temperatures and higher plantation prevalence is driven by patterns across the south-west, our results accord with those of Ashman *et al.* (2020), and suggest *E. globulus* plantations in this part of the state can act as important source or refuge habitat for Koalas, supporting populations in both adjoining plantations and native woodland.

As highlighted above, the model developed here proved to have strong predictive performance for the counts collated across Victoria. Nevertheless, further model refinement could be pursued, as model performance in the absence of random effects (that is, based purely on the environmental correlates) was moderate (R^2 = 0.47). Additional factors beyond the environmental layers available to us could therefore be pursued to improve model performance. Soil properties may be important in this regard, being determinants of the chemical and water content of eucalypt leaves, and in turn, forage quality (Moore and Foley 2000). Likewise, the degree of past disturbance, forest fragmentation and road density may be influential, either by reducing local population sizes through increased mortality, or increasing density through spatial constriction of local populations. Soil properties, past disturbance, forest fragmentation and road density have all been identified as important determinants of Koala distribution at regional levels (Rhodes *et al.* 2006, McAlpine *et al.* 2008, Sanitka *et al.* 2014, Ashman *et al.* 2020). In response to the positive relationship between soil carbon and Koala density in Barwon South West reported by Ashman *et al.* (2020) during the preparation of this report, we trialled this variable as a predictor of Koala density across the State, but did not identify any clear relationship at our larger spatial scale. We also attempted to account for fragmentation through neighbourhood estimates of eucalypt prevalence; however, this may not capture the fine-scale fragmentation to which Koalas may respond.

Incorporation of spatial interdependencies in density through a spatial autocorrelation term could also improve model performance, especially for the plantation estate. Spatial dependencies in occurrence have been documented in populations of Koala from South-East Queensland (Rhodes *et al.* 2006), and could enable inclusion of localised variation in density from sources such as chlamydial disease, which can be an important determinant of Koala abundance in Victoria (DSE 2004).

Finally, acquisition of a larger and spatially more representative dataset could greatly improve the predictive capacity of the model produced here. This study relied on counts with various spatial biases and considerable methodological variation. Standardised surveys in eucalypt plantations across Barwon South West, and in native forest and woodland across Gippsland and central and northern Victoria, would be particularly useful.

4.2 Abundance estimates

Few rigorous estimates of the contemporary abundance of Koalas are available across the species' range, and abundance estimates vary widely as a result. While the Australian Koala Foundation estimates a national population size of less than 100,000 (AKF 2010), this estimate is wildly inconsistent with many regional estimates. For example, in South Australia, Masters *et al.* (2004) estimated 27,000 individuals occupy Kangaroo Island, while Sequeira *et al.* (2014) estimated 114,000 occupy the Adelaide Hills and Mt Lofty Ranges.

In Victoria, abundance estimates have been made for several discrete populations. Prior to translocation and sterilisation programs at Raymond Island in 2004, the population size was estimated at 515 (Waldergrave-Knight 2004). The equivalent figure for Budj Bim National Park in that year (also prior to population management) was around 11,000 (Ramsey *et al.* 2010). Recent estimates are also available from French Island and parts of the Strzelecki Ranges. In 2017, Tolsma *et al.* (2017a) estimated the French Island population to number around 3,800 (with a 95% CI of ~ 2000 - 5500), while Allen (2015) estimated a 3,525 ha study area in the Strzelecki Ranges to support around 800 Koalas based on 141 point counts (the same point counts integrated into this project). Populations in Victoria's eucalypt plantation estate have been a point of conjecture, with estimates as high as 150,000 within *E. globulus* plantations alone (McAlpine *et al*. 2015).

Our study suggests that the abundance of Koala in Victoria may be larger than previously thought, with a mean estimate of around 413,000 individuals in native forest and woodland (95% CI, ~325,000 - 520,000) and around 47,000 (95% CI, ~36,000 - 60,000) in eucalypt plantations. Nevertheless, we reiterate that these estimates should be treated with some caution. As per section 1.4, this study made use of a count dataset that was collated mostly from individual projects on specific Koala populations, particularly those with relatively high abundance in Victoria's south.

4.3 Impact of Victorian wildfires

Wildfires during the 2019-2020 summer season are predicted to have affected a relatively small proportion of the Victorian Koala population. Around 2.85% of suitable forest and woodland was predicted to have been impacted by these fires, with 0.59% of habitat in eucalypt plantations affected. Resulting predictions suggest around 4% of the Victorian Koala population has been impacted by wildfires as of 11 February 2020.

Impacts are concentrated in the Barwon South West and Gippsland regions. While Koala density across Gippsland is predicted to be relatively low, very extensive areas of East Gippsland were impacted by wildfires (Figure 9). On the contrary, only small areas of Barwon South West were affected, but relatively high Koala densities in this region ensured it had the highest number of individuals predicted to have been impacted (~9000). The large fire in Budj Bim National Park in early January 2020 contributed most individuals to this total. Impacts in eucalypt plantations appear minimal, representing less than 1% of the predicted Koala population in all DELWP regions.

These estimates provide a first step in estimating the impact of recent wildfires on Victoria's Koala population. However, it is not possible at this stage to estimate impacts on population sizes, with mortality during these fires being unknown and likely to have varied considerably dependent on fire severity and terrain.

4.4 Conclusions and recommendations

This study provides a basis for further refinement of our understanding of the Victorian Koala population, producing the first statistical model of variation in Koala abundance across the State, as well as predictions of Koala abundance at both state-wide and regional levels. The work suggests:

1. Koala density in Victoria is a function of annual rainfall, temperature regimes, elevation, the prevalence and composition of preferred eucalypts and the extent of eucalypt plantations.
2. The state-wide Koala population in Victoria may be larger than previously thought, with a prediction of around 413,000 individuals in native forest and woodland and 47,000 in the eucalypt plantation estate.
3. Three DELWP regions – Barwon South West, Gippsland and Hume – support ~80% of Victoria's Koala population in native vegetation, with the Barwon South West, Gippsland and Grampians regions supporting 99% of the population inhabiting eucalypt plantations.
4. Around 3% of suitable forest and woodland for Koalas in Victoria is predicted to have been affected by wildfires thus far during the 2019-2020 fire season, with 0.59% of habitat in eucalypt plantations affected. In total, around 15,000 Koalas are predicted to have been impacted, or around 4% of the State population.

Our project provides proof of concept for a statistical model of Koala abundance in Victoria. Further work in the following areas would allow the model to be refined, with resulting increases in predictive reliability.

Improve the underlying dataset: State-wide or regional Koala surveys conducted using standard double-count approaches would improve our ability to estimate trends in Koala populations. This study relied on counts with various spatial biases and considerable methodological variation. We advocate standardised surveys across the native forest and woodland estate and eucalypt plantations. This work should be guided by the spatial projections of model uncertainty, as per Figure 7. These surveys would be particularly useful in the wake of the significant wildfires of the 2019-2020 summer season, which have had an unknown impact on Koala population sizes.

Improve the model: The current model could be improved and/or extended by the incorporation of additional environmental predictors, such as measures that quantify soil properties, past disturbance regimes (particularly forest fires), forest fragmentation and road density.

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Appendix

Table A1. Parameter estimates for the top Koala abundance model, incorporating imperfect detection. Only estimates of the fixed effects are shown. Variables were standardised prior to model fitting, meaning parameter estimates are directly comparable. Feed tree preference layers are the average neighbourhood prevalence in all cases. LCI, lower credible interval; UCI, upper credible interval.

Parameter	Mean	LCI	UCI
Intercept	-2.35	-3.97	-2.09
Habitat type (native = 1, plantation = 0)	-0.05	0.25	1.12
Annual rainfall	0.26	-0.57	1.71
Elevation	-1.18	-2.25	0.24
Mean summer temperature (MST)	-1.63	-2.93	0.20
Slope	-0.34	-0.89	0.41
High preference eucalypt prevalence	-1.17	-2.47	0.08
Medium preference eucalypt prevalence	0.31	-0.57	0.95
Low preference eucalypt prevalence	-1.01	-2.79	0.86
Eucalypt plantation prevalence	-1.45	-2.03	-0.50
Rainfall × High preference eucalypt prevalence	0.68	-0.86	2.23
Rainfall × Medium preference eucalypt prevalence	2.39	0.73	4.07
Rainfall × Low preference eucalypt prevalence	-0.65	-3.11	0.71
Rainfall × Plantation prevalence	-1.08	-1.52	-0.09
Elevation × High preference eucalypt prevalence	-2.05	-3.75	-0.54
Elevation × Medium preference eucalypt prevalence	0.81	-0.90	2.82
Elevation × Low preference eucalypt prevalence	-1.21	-3.43	0.65
Elevation × Plantation prevalence	-0.97	-2.01	-0.36
MST × High preference eucalypt prevalence	-2.05	-4.57	0.09
MST × Medium preference eucalypt prevalence	1.82	0.53	3.44
MST × Low preference eucalypt prevalence	0.43	-3.47	2.38
MST × Plantation prevalence	-3.13	-4.25	-1.34

Posterior Predictive Checks of Model Fit

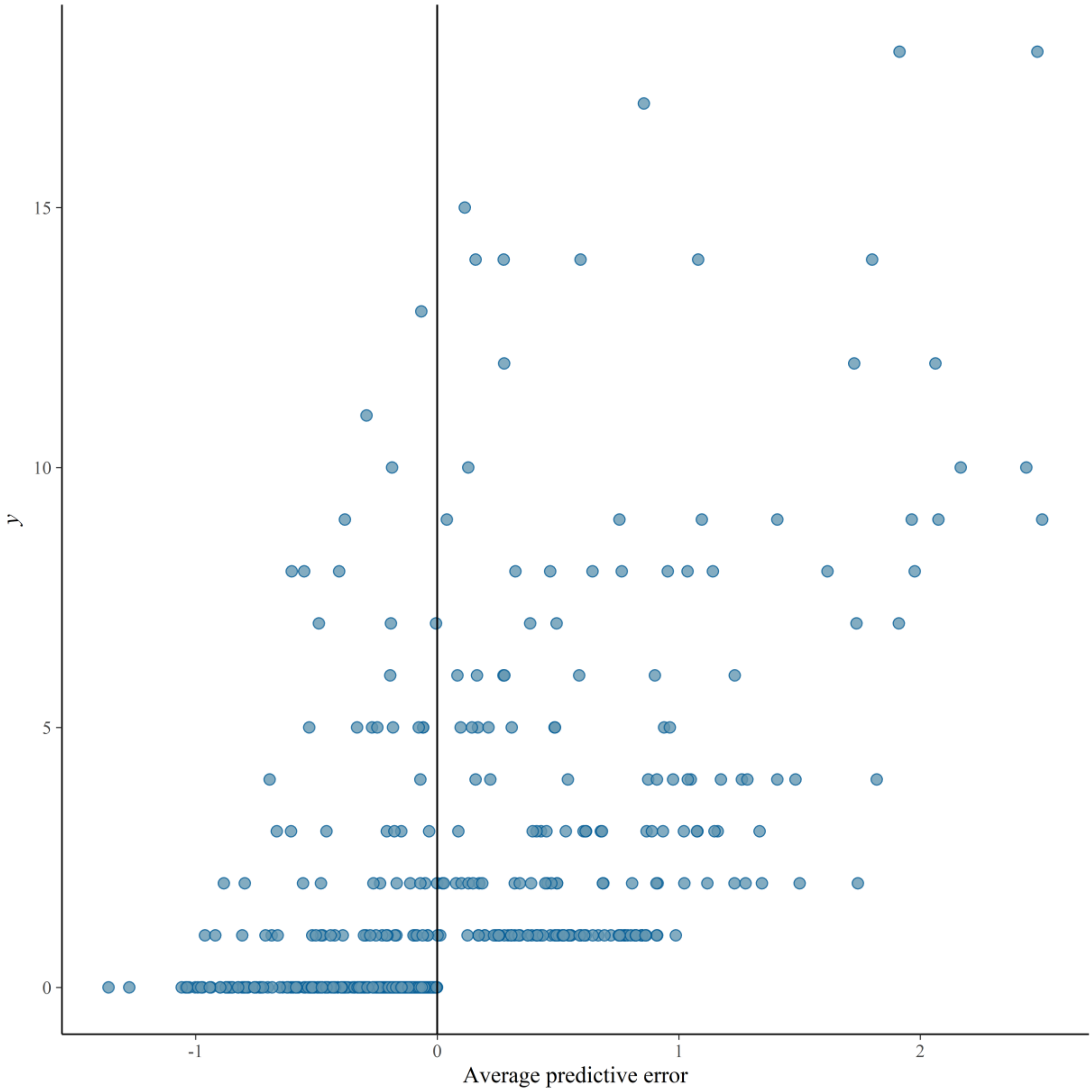

Figure A1. Scatterplot of predictive error, where the y-axis shows the observed counts and the x-axis shows the predictive error (observed count (*y*) minus the predicted count). The plot shows that predictive error is high, on average, at the extremities of the distribution of observed counts, particularly the highest counts.

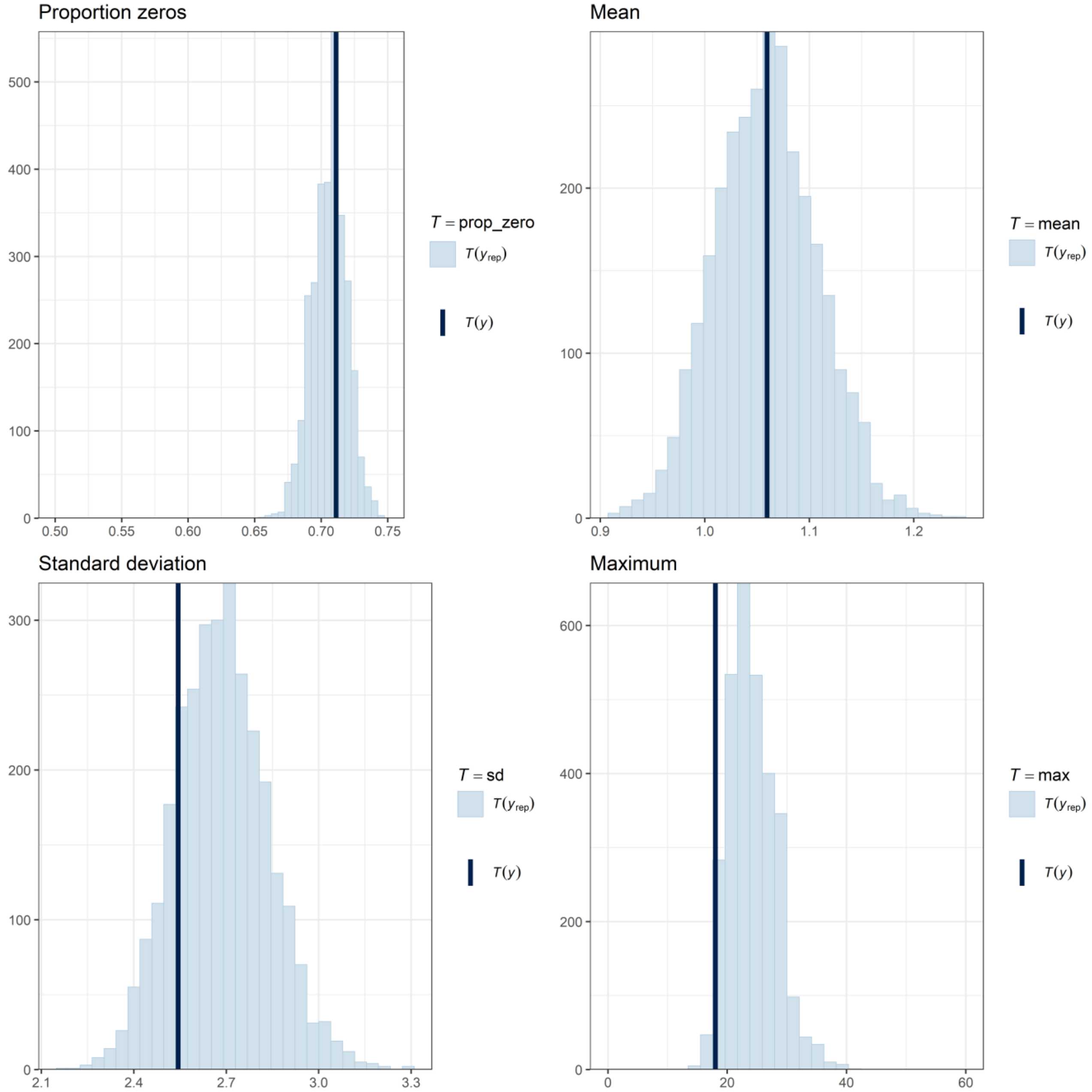

Figure A2. Histograms for posterior predictive checks of model fit. The y-axis in each case is the frequency of values for each statistic (proportion zeros, mean etc) derived from simulating from the fitted model (‘$T(y_{rep})$’), with the solid blue line being the actual value from the data (‘$T(y)$’). Hence, histograms show the relationships between posterior predictions from the model and the observed data for each test statistic.

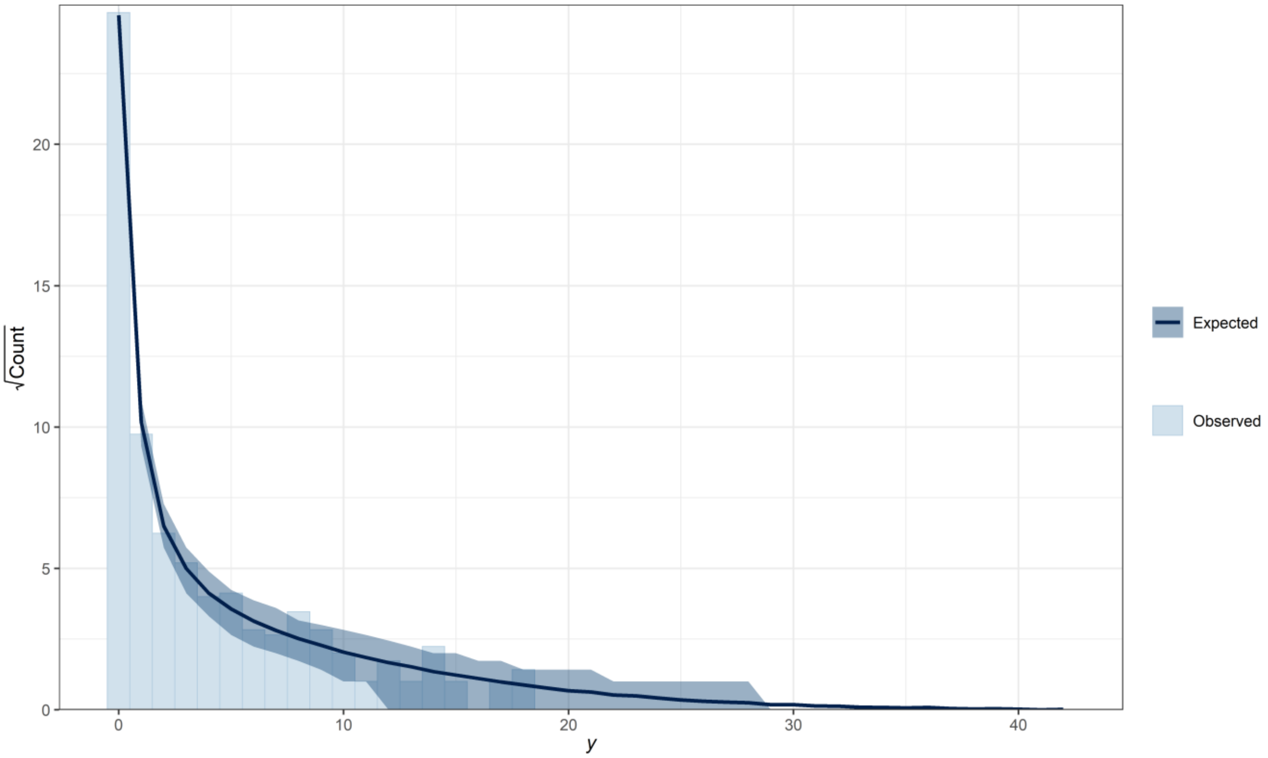

Figure A3. Histogram of the observed counts (*y*) and the expected distribution of counts from the fitted model.

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