



RESEARCH ARTICLE

Species distribution modelling of the endangered Mahogany Glider (*Petaurus gracilis*) reveals key areas for targeted survey and conservation

Yiyin Chang | Lorenzo V. Bertola | Conrad J. Hoskin

College of Science & Engineering, James Cook University, Townsville, Queensland, Australia

Correspondence

Yiyin Chang, College of Science & Engineering, James Cook University, Building 142, Townsville, Qld 4811, Australia.
Email: eryn.chang@my.jcu.edu.au

Funding information

Holsworth Wildlife Research Endowment; James Cook University; Terrain Natural Resource Management

Abstract

The Mahogany Glider (*Petaurus gracilis*) is one of the most endangered marsupials in Australia. Its known distribution is an approximately 120 km strip of fragmented coastal woodland in north-east Queensland, from north of Townsville to the Tully area. Records are clustered in a number of well-surveyed areas, with significant areas of lowland habitat unsurveyed. Around 30% of historic records fall in areas that were subsequently cleared for farmland, and ongoing clearing and fragmentation of lowland sclerophyll forest continues within the potential distribution. Resolving the distribution is an urgent requirement to guide conservation but Mahogany Gliders are difficult to detect in the field. Species distribution modelling offers a technique for estimating the fine-scale distribution and for targeting further field survey and conservation efforts. We used known occurrence records ($N = 481$) to predict the distribution of Mahogany Gliders across the Wet Tropics bioregion. We used climatic, topographic and other environmental predictors to generate distribution models using Maxent and Random Forest algorithms, each with two bias correction methods. The predictions revealed that many unknown populations may exist within the currently defined distribution and in important areas beyond this (e.g. Hinchinbrook Island). There was reasonable congruence between models, and we include syntheses of the models to present the most likely current distribution. The most important predictor variables across the models were precipitation seasonality (high seasonality), elevation (generally <100 m), soil type (hydrosols) and vegetation type (including *Eucalyptus* and *Melaleuca* woodlands). Our results identify core habitat and reveal key areas that require targeted field surveys. Importantly, the predicted suitable habitat is highly fragmented and ongoing conservation efforts need to improve habitat connectivity and limit further fragmentation.

KEYWORDS

Australian Wet Tropics, fragmentation, Mahogany Glider, Maxent, Random Forest, road bias

INTRODUCTION

Knowing the distribution of a species is fundamental to understanding its ecology, resolving threats and implementing conservation actions. Species distribution can rarely be described by knowing the whereabouts of

every population; instead, it must usually be estimated based on known occurrences and habitat requirements. Species distribution models (SDMs) can be developed to help estimate and define the likely distribution of a species (Cayuela et al., 2009; Drew et al., 2011; Gobeyn et al., 2019; Zhang & Li, 2017). Accurate SDMs can be a

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial](https://creativecommons.org/licenses/by-nc/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

© 2022 The Authors. *Austral Ecology* published by John Wiley & Sons Australia, Ltd on behalf of Ecological Society of Australia.

time- and cost-effective way to provide essential information for species conservation (Drew et al., 2011). Empirical studies have used SDMs to search for additional populations and suitable habitats for endangered species, such as the Gulbaru Leaf-tailed Gecko (*Phyllurus gulbaru*) in north-east Australia (Bertola et al., 2018) and Juliana's Golden Mole (*Neamblysomus julianae*) in South Africa (Jackson & Robertson, 2011). Distribution models are also powerful in assessing threats and distributional change through time; for instance, quantifying the range and population decline of Spotted-tailed Quolls (*Dasyurus maculatus gracilis*) in north-east Australia over the past century (Uzqueda et al., 2020), or evaluating the risk of climate change on the threatened Iberian Desman (*Galemys pyrenaicus*) in Europe (Morueta-Holme et al., 2010). The predictions from SDMs can also identify areas of high conservation value and improve conservation planning; for instance, systematically selecting reserves with high avian diversity (Moradi et al., 2019), or ranking threats and prioritizing management actions (Ricca et al., 2018).

A variety of algorithms have been developed for species distribution modelling. By overlaying environmental predictors (spatial data) with known sighting records of one or multiple species, the algorithms compute the probability (likelihood) of a species occurrence given a set of conditions. The distance-based BIOCLIM algorithm (Busby, 1991) was the first algorithm widely used to answer a variety of questions in ecology and conservation (Booth et al., 2014; Busby, 1991; Nix & Busby, 1986) but was largely replaced by machine-learning algorithms in the 2000s (Elith & Leathwick, 2009; Gobeyn et al., 2019; Pecchi et al., 2019). Machine-learning algorithms, especially Maxent (which is based on probability density, Berger et al., 1996; Rosenfeld, 1996) and Random Forest (which utilizes decision trees, Breiman, 2001), dominate current SDM methodology. They are known for being ecologically interpretable, stable and accurate, and being able to integrate categorical predictors and missing data (Pecchi et al., 2019; Zhang & Li, 2017). To account for uneven sampling/sightings, bias-correcting methods that manipulate the background selection (pseudo-absence) to reduce sampling bias were also established (Phillips et al., 2009; Vollerling, Halvorsen, & Mazzoni, 2019). Contemporary SDMs with corrected bias and testable accuracy have therefore become a powerful tool to model suitable habitat of a species currently, in the past, or in future scenarios (Zimmermann et al., 2010). Examples include managing natural resources (Booth, 2018) and predicting distributional change of invasive or endangered species under climate or other human-induced changes (Jaeschke et al., 2013; Rodríguez-Rey et al., 2019).

The Mahogany Glider (*Petaurus gracilis*) is an endangered arboreal marsupial endemic to the Australian Wet Tropics of north-eastern Queensland (Goldingay & Jackson, 2004; Figure 1c). The species was originally collected from a few specimens in the 1800s and then not seen for over a century (Van Dyck, 1992, 1993). Following rediscovery (Van Dyck, 1993), the species has been subject to survey and conservation efforts (Jackson, 1998; Jackson et al., 2019; Jackson & Diggins, 2020; Parson & Latch, 2006). Mahogany Gliders inhabit open canopy sclerophyll forests in the eastern lowlands of the Wet Tropics, with habitat determined by a complex interplay between rainfall, fire and possibly other factors (Jackson, 2000a; Jackson & Claridge, 1999; Jackson & Robertson, 2011; Van Dyck, 1993). The species does not occur in rainforests, which cover some of the lowlands and much of the mid and higher elevations of the region. Even within lowland woodland habitats, the glider has a patchy distribution, probably driven by a high diversity of flowering trees as a stable food source (Figure 1b; Jackson, 1998, 2000a, 2001; Van Dyck, 1993).

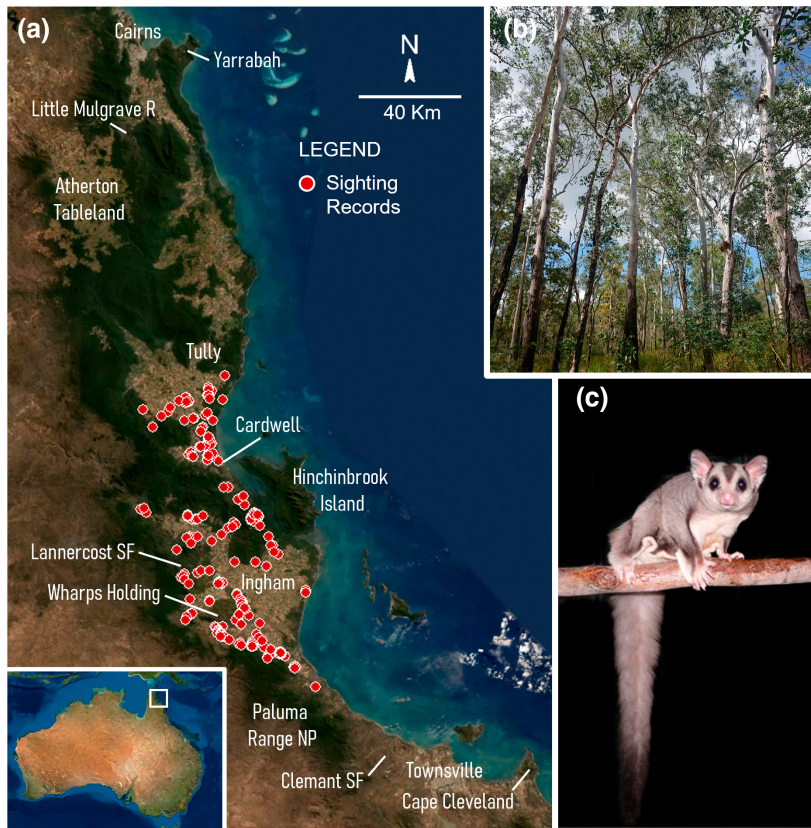


FIGURE 1 Sighting records and typical habitat of Mahogany Gliders (*Petaurus gracilis*). (a) Sighting records (red dots) demonstrate the known distribution of the gliders within the Wet Tropics, north-eastern Queensland, Australia. (b) Mahogany Gliders prefer sclerophyll forests of open structure and with a diversity of flowering plants at the tree and shrub level. (c) Photo of a Mahogany Glider, with characteristic long, tapering tail (Photo credit: Daryl Dickson).

All Mahogany Glider records are located in the southern and central Wet Tropics bioregion, along a coastal strip from Ollera Creek and Crystal Creek at the base of the Paluma Range, near Townsville, to 120 km north near Tully (Figure 1a). The lowland forests in this region have suffered extensive clearing in the last 150 years, due to clearing from forestry, cattle grazing and intensive large-scale sugar cane farming. It is estimated that about 50% of the glider's suitable habitat was lost between 1930 and 2007 (Jackson et al., 2011). Habitat loss and accompanying population fragmentation threaten Mahogany Gliders (Jackson et al., 2019; Jackson & Diggins, 2020; Jackson & Robertson, 2011; Parson & Latch, 2006), and it is therefore essential to understand their current distribution in detail.

The distribution of Mahogany Gliders has been modelled three times using BIOCLIM. The model from Van Dyck (1993) used 16 sighting records and 28 climatic variables, predicting a confined distribution around known points between Ingham and Tully. The second model (Jackson & Claridge, 1999) used 144 records and 35 climatic variables, and it extended predicted habitat south to the northern end of the Paluma Range lowlands. The most recent model (Jackson & Robertson, 2011) used 310 records, 10 climatic variables, manually incorporated vegetation types, and focussed more on identifying habitat remnants within the known range than assessing the full potential distribution. Two issues have limited the accuracy of modelling efforts to date: (i) bias caused by uneven survey effort has not been adequately accounted for, and (ii) BIOCLIM does not perform as well as subsequent modelling techniques

(Hijmans, 2012; Pecchi et al., 2019; Phillips et al., 2009). Therefore, the modelled distributions to date are likely to misrepresent the Mahogany Glider distribution, and hence populations both within and outside the known range may not be detected and protected. The more advanced modelling methods now available (Gobeyn et al., 2019; Hijmans & Elith, 2016), enable better correction for sampling bias, identification of important categorical variables (e.g. vegetation type) and quantification of habitat suitability with higher resolution and accuracy.

In this study, we modelled the potential distribution of Mahogany Gliders using two high-accuracy and ecologically interpretable SDM algorithms: Maxent and Random Forest (Elith et al., 2011; Zhang & Li, 2017). We used a comprehensive, vetted database of known sighting records and modelled all potential habitat in the Wet Tropics region. In the modelling process, we assessed the determinants of the glider's current distribution, including climatic and environmental factors, as well as human land use factors. We expected the new algorithms to provide finer-scale prediction of habitat suitability within the known range, and to better estimate the likelihood of occurrence beyond the known range. We aimed to use species distribution modelling to map all area of potential habitat, identify core and peripheral populations, and assess potential connectivity across the range. The ultimate objective of the modelling was to produce maps to guide on-ground actions such as surveys, replanting and habitat improvement, and inform broad-scale conservation actions such as genetic sampling to assess connectivity among populations.

METHODS

Our broad modelling approach was as follows, with all detail in the sections below. We collated all known sighting records and environmental predictor variables deemed relevant to Mahogany Gliders and modelled their distribution with both Maxent and Random Forest algorithms. We constructed all models in R (R Development Core Team, 2020), using three modelling packages (two Maxent packages and one Random Forest package) and two bias correction methods within each of these, resulting in six models in total (Table 1). We then tuned the hyperparameters of the models. For the final distribution maps, we summarized the predictions from Maxent and Random Forest models in two ways: by overlaying a threshold prediction from all six models, and by averaging the predicted probabilities weighted by their accuracy.

TABLE 1 Summary of species distribution models used in this study, including the bias correction approaches, the modelling algorithm, the R package (shown in *italic*) in which the model was implemented, and whether variable selection and model tuning were performed

Model	Bias correction	Algorithm	R package	Variable selection	Model tuning package
1	TGB+ <i>spThin</i>	Maxent	<i>MIAMaxent</i>	Yes	NA
2	TGB+ <i>spThin</i>	Maxent	<i>SDMtune</i>	Yes	<i>SDMtune</i>
3	TGB+ <i>spThin</i>	Random Forest	<i>randomForest</i>	Yes	<i>caret</i>
4	BT	Maxent	<i>MIAMaxent</i>	Yes	NA
5	BT	Maxent	<i>SDMtune</i>	Yes	<i>SDMtune</i>
6	BT	Random Forest	<i>randomForest</i>	Yes	<i>caret</i>

Abbreviations: BT, background thickening; TGB, target group background.

Sighting records

Sightings of Mahogany Gliders were obtained from Terrain Natural Resource Management (Terrain NRM) ($N = 394$) and the WildNet Database (Queensland Government) ($N = 292$). We combined the two datasets, removing duplicate records and records without GPS coordinates (i.e. with only a locality name). We also transformed all Cartesian coordinates (easting, northings) to a standardized datum WGS 84 (EPSG 4326) (R package *sf*, Pebesma, 2018). The final dataset consisted of 481 records, with 98.5% of these (i.e. 474 records) falling between 1990 and 2010 (Appendix S1).

Predictor dataset

We used 19 climatic variables from accuCLIM that were specifically adjusted for the Australian Wet Tropics bioregion, averaged from the time period between 1996 and 2015 (Storlie et al., 2013; Appendix S2). These climatic predictors have been widely applied to model Wet Tropics species (Bertola et al., 2018; Reside et al., 2019; Uzqueda et al., 2020). We included four topographic variables: elevation, aspect, slope and distance to major waterways (Queensland Government, 2017). These were all continuous numeric values. We also included five environmental variables: vegetation type, soil type, major land use, forest coverage and fire frequency (Appendix S2).

Vegetation type represented pre-clearing vegetation (to ensure the sighting records are not situated on farmland, due to subsequent clearing), and consisted of 41 vegetation types in the Wet Tropics (Department of the Environment, 2012). Land use type contained six categories: Conservation and Natural Environments, Relatively Natural Environment, Dryland Agricultural and Plantations, Irrigated Agricultural and Plantations, Intensive Uses, and Water (Department of Environment and Science, 2019). Soil type contained 14 major soil groups from the collation of Australian Soil Resource Information System (ACLEP, 2014). Land use data were obtained for 2 years: 1999 (to represent land use for records before the year 2000) and 2010 (to represent land use for records after the year 2000). Forest coverage contained Landsat satellite data that was classified using canopy cover: Non-woody (<5%), sparsely covered (5%–19%), and densely covered (>20%) (Department of Industry, Science, Energy, and Resources, 2020). Forest coverage was also obtained for two time periods by averaging yearly data from before (1908–1999) and after (2001–2010) the year 2000. Importantly, the two periods represent the time before and after the announcement of new tree-clearing laws (*Vegetation Management Act 1999*), which resulted in a peak in vegetation clearing in the region around the year 1999 (McGrath, 2007). Fire frequency was derived from AVHRR (the Advanced Very High Resolution Radiometer), representing the number of fires detected per pixel between 1997 and 2011 (Craig et al., 2002).

All 28 variables (19 climatic, 4 topographic and 5 environmental) were standardized to the same geographic extent and resolution (cell size = 0.0025 degree, about 250 m) as the climatic spatial layers and to the same coordination system matching the sighting records (WGS 84, EPSG 4326) (R package *sp*, Pebesma & Bivand, 2005; R package *raster*, Hijmans & van Etten, 2016). Correlated predictors were removed during model fitting as described below for each of the modelling approaches.

Model prediction

Current suitable habitat for the Mahogany Glider was identified based on the most recent available layers for vegetation type (current post-clearing vegetation, last updated for Queensland in 2006), land use (2019) and forest coverage (2018). All spatial layers used in model training and prediction are presented in Appendix S2.

Bias correction

Sighting records can result in bias in the modelling process due to geographically uneven survey effort or detection success, which can affect model performance (Hijmans, 2012; Veloz, 2009). We addressed sampling bias using two bias correction methods to identify and correct uneven sampling effort and localized clustering: (i) Target group background (TGB) (Phillips et al., 2009) in combination with species thinning (*spThin*) (Aiello-Lammens et al., 2015) (demonstrated in Appendix S3) and (ii) background thickening (BT) (Vollering, Halvorsen, & Mazzoni, 2019). Applying two bias correction methods allowed us to examine the effect of sampling bias in our datasets and the potential differences in model prediction based on the correction approach.

Species thinning in combination with target group background (TGB + *spThin*)

Target group background has been widely used to correct sampling bias in SDM with presence-only data (Phillips et al., 2009; Ranc et al., 2017). The methodology selects background points using sighting records of similarly surveyed species to assess survey effort across the environment and account for bias. We selected 27 Wet Tropics arboreal mammals that are surveyed in a similar way to Mahogany Gliders (i.e. spotlighting, cage trapping, camera trapping). These included other species of gliders, possums and tree-dwelling rats (Appendix S4). The sighting records of these animals were obtained from the WildNet Wildlife Records spatial dataset (Queensland Government, 2020) and were used to create a two-dimensional kernel density estimation, also known as TGB bias grid (R package *MASS*, Ripley et al., 2013; Appendix S5). We thinned the Mahogany Glider sighting records from 481 to 136 for the TGB dataset using a 1 km grid because over-clustered records further bias the prediction (R package *spThin*, Aiello-Lammens et al., 2015; Appendix S3).

Background thickening

Background thickening was proposed as an alternative correction for uneven sampling effort to species thinning because, unlike species thinning, background thickening does not remove sighting records. Instead, it increases the clustering of background points to match the bias in the sighting records (Vollering, Halvorsen, & Mazzoni, 2019). The method creates buffers around the sighting records, and then uses the buffers' intersection rate as an indicator of sampling effort. Following the methodology described in Vollering, Halvorsen, Auestad, et al. (2019), we created variograms to compute spatial continuity for the environmental variables selected by a pilot model (TGB model) (Gräler et al., 2016). Second, we created a geodesic buffer using the above continuity distance around the sighting records and

calculated the intersection rates of these buffers (Ştefan, 2019). The intersection rates served as sampling probability in the bias grid. We then selected the background points to match the sampling bias for sighting records (i.e. more background points being sampled in areas with clustered sighting records).

Model algorithms, variable selection, tuning and evaluation

We produced SDMs of Mahogany Gliders with two algorithms: Maximum Entropy (Maxent) and Random Forest. We applied these two broad approaches in R (R Development Core Team, 2020), using three modelling packages: *MIAMaxent* (Vollering, Halvorsen, & Mazzoni, 2019) and *SDMtune* (Vignali et al., 2020) for Maxent modelling, and *randomForest* (Breiman, 2018) for Random Forest modelling. We applied the two bias correction approaches (TGB+ *spThin*, BT) as described above in each modelling process, resulting in six SDMs in total (Table 1).

We examined and evaluated the models using standard evaluation metrics for SDMs: area under the receiver operating characteristic curve (AUC), variable response curves and Akaike information criterion (AIC). Being widely applied to SDM evaluations, AUC is a simple but important index that discriminates true positives and false positives (Fielding & Bell, 1997). However, using one index alone for model evaluation can be misleading (Jiménez-Valverde, 2012; Lobo et al., 2008; Ruete & Leynaud, 2015). Therefore, we also examined the variable response curves to make sure that the predictions were realistic. Lastly, we used AIC to represent model fitting and complexity (Sakamoto et al., 1986; Velasco & González-Salazar, 2019). In addition, we assessed similarity between predictions by calculating the percentage of overlapping pixels using Schoener's *D* test (Warren et al., 2010).

Maxent (MIAMaxent and SDMtune) models

The algorithm compares probability densities of the predictors between sighting records and bias-corrected background points, and estimates the habitat suitability for the target species (Elith et al., 2011; Phillips et al., 2004). We used two recently published R packages to construct Maxent models: *MIAMaxent* (Vollering, Halvorsen, Auestad, et al., 2019) and *SDMtune* (Vignali et al., 2020). Both packages adopt the Maxent algorithm and were created to increase ecological interpretability of SDMs. However, the two packages use different methods in variable selection and model selection (Vignali et al., 2020; Vollering, Halvorsen, Auestad, et al., 2019). Comparing the two procedures allows us to examine the consistency of the resulting predictions.

To select a useful subset of variables, *MIAMaxent* uses forward stepwise selection, which adds variables one by one until the penalty on complexity outweighs the goodness of fit. We withheld 20% of the dataset to test model accuracy (testing data). Instead of demonstrating the presence probability, the predictions of *MIAMaxent* used probability ratio output (PRO; Halvorsen, 2013) as a measure of 'relative suitability of one place versus another', where PRO = 1 represents a randomly chosen place with average suitability (Vollering, Halvorsen, Auestad, et al., 2019).

In *SDMtune*, variable selection was performed using a built-in function that pairs the correlated variables using Jackknife tests, retaining only the variable with the highest contribution for each pair. We divided the sighting

records into training, validation and testing datasets in a 3:1:1 proportion. The validation dataset was used to tune the hyper-parameters: feature class (variable transformation), regularization (penalty on model complexity) and iteration (repetitions) (Vignali et al., 2020).

Random Forest models

Random Forest is an algorithm widely applied for species distribution modelling (Evans et al., 2011; Mi et al., 2017; Zhang & Li, 2017). Using thousands of decision trees, Random Forest algorithms find the best determinants to correctly classify a location into presence or absence (Breiman, 2001). We constructed Random Forest models in the R package *randomForest* (Breiman, 2018). Variables were selected using the *varSelRF* package (Diaz-Uriarte, 2010, 2017) by removing the variables contributing the least but causing the highest classification error. We tuned the number of variables available for classification at each tree node with cross-validation in the *caret* R package (Kuhn, 2008). Classification accuracy (ratio of correctly classified samples to total samples) and confusion matrix (expression of true/false positives and negatives) were used to evaluate Random Forest models (Kuhn, 2008).

Summarizing habitat suitability across models

Choosing the 'best' SDM from different modelling approaches and algorithms is not trivial, due to the lack of standardized and universal measures, as well as pros and cons of different models for each species and study area (Allouche et al., 2006; Araújo & Guisan, 2006; Mouton et al., 2010). Thus, to summarize the findings from all six models, we produced two additional outputs: a summary map displaying the number of models in which an area was identified as suitable for the species; and a weighted average map.

For the summary map, we first classified each model output into suitable (1) and unsuitable (0), using a 0.5 probability threshold for *SDMtune* and *randomForest* outputs, and a threshold of 1 for *MIAMaxent* outputs. We overlaid these re-classified outputs, obtaining a map with values ranging from 0 (no model predicted the area as suitable) to 6 (all models predicted the area to be suitable).

The weighted average map was obtained by averaging the prediction probabilities of the *SDMtune* and *randomForest* SDMs, weighted by the model accuracy, using the formula:

$$\left(AUC^1 * P^1 + AUC^2 * P^2 + AUC^3 * P^3 + AUC^4 * P^4 \right) / 4.$$

AUCs 1–4 represent the AUC value from the four models included in the calculations (i.e. the *SDMtune* and *randomForest* models, each with TGB+ *spThin* and BT bias correction), and the *P* as predicted probability of occurrence of each pixel from each model. *MIAMaxent* models were not included in the weighted average map because *MIAMaxent* predicted the habitat suitability using the unit of Probability Ration Output (PRO, see [Model algorithms, variable selection, tuning and evaluation](#)) rather than probabilities.

We used the weighted averaged map to determine how many habitat patches, of various sizes, contain Mahogany Glider records. To do this we set habitat suitability at a threshold of 0.5, and identified all habitat patches

using the R package *terra* (Hijmans et al., 2022). We considered all eight neighbours surrounding a central cell as a patch (Queen's adjacency), and each patch is separated from the other with a minimum distance of 60 m (i.e. the maximum gliding distance of Mahogany Gliders; Jackson, 1998). We quantified all habitat patches with and without sighting records from the full database (i.e. sightings at any point in time). We assessed this at four patch sizes: <0.1, 0.1–1, 1–10 and >10 km². The minimum estimated home range of a Mahogany Glider is about 0.1 km² (11 ha) (Jackson, 2000b), so we consider patch sizes <0.1 km² unlikely to support a population.

Assessing road bias

The Wet Tropics, and particularly lowland areas of the Wet Tropics, are heavily bisected by roads. It is rare to be further than 5 km from a road, or even 2.5 km from a road in these areas. Mahogany Gliders are strictly arboreal and do not use roads but, like many species, observer accessibility likely results in sightings being clustered closer to roads (Kadmon et al., 2004). We assessed the Euclidean distance to roads of our SDMs to assess the degree to which the road bias was removed. We used a map of roads in Queensland (Queensland Government, 2017) and created a layer of Euclidean distance to roads in ArcGIS v.10.7, using the Spatial Analyst tool (ESRI, 2018). We compared and visualized the distance distributions of the whole Wet Tropics ($N = 499089$), chosen background points (BT, $N = 4000$; TGB, $N = 4000$), predicted suitable habitat from the weighted average map ($N = 61196$) and sighting records ($N = 481$), using an estimator of the empirical cumulative distribution function (ECDF). We then tested whether these five distributions are the same (Kolmogorov–Smirnov test, Lilliefors, 1967), to verify whether our bias correction approaches addressed road bias.

RESULTS

Species distribution models for the Endangered Mahogany Glider were produced using all known sighting records for this species, a set of biologically relevant environmental and climatic predictors, three modelling approaches, and two bias correction methods. In the sections below, we identify the most important predictor variables, present each of the six models produced (Table 1, Figure 2), present two summary models (Figure 3), and assess road bias and whether it was accounted for by the models (Figure 4).

Sighting records and predictor variables

After filtering, 137 and 187 Mahogany Glider sighting records were retained in the TGB and BT models respectively. Variable selection resulted in the subsets containing 5–13 predictors. The predictors that contributed most and were selected by more than three models were: elevation, precipitation seasonality, soil type and vegetation type (Table 2; Appendix S6). To facilitate comparisons between models, we divided the contribution of a single predictor by the total contribution of retained predictors for each model and present the relative contributions. Elevation was selected in all six models and ranked first in contribution in four models. Its relative importance ranged from 11% (*randomForest* with TGB) to 76% (*SDMtune* with TGB). All areas predicted as suitable were below 100 m above sea

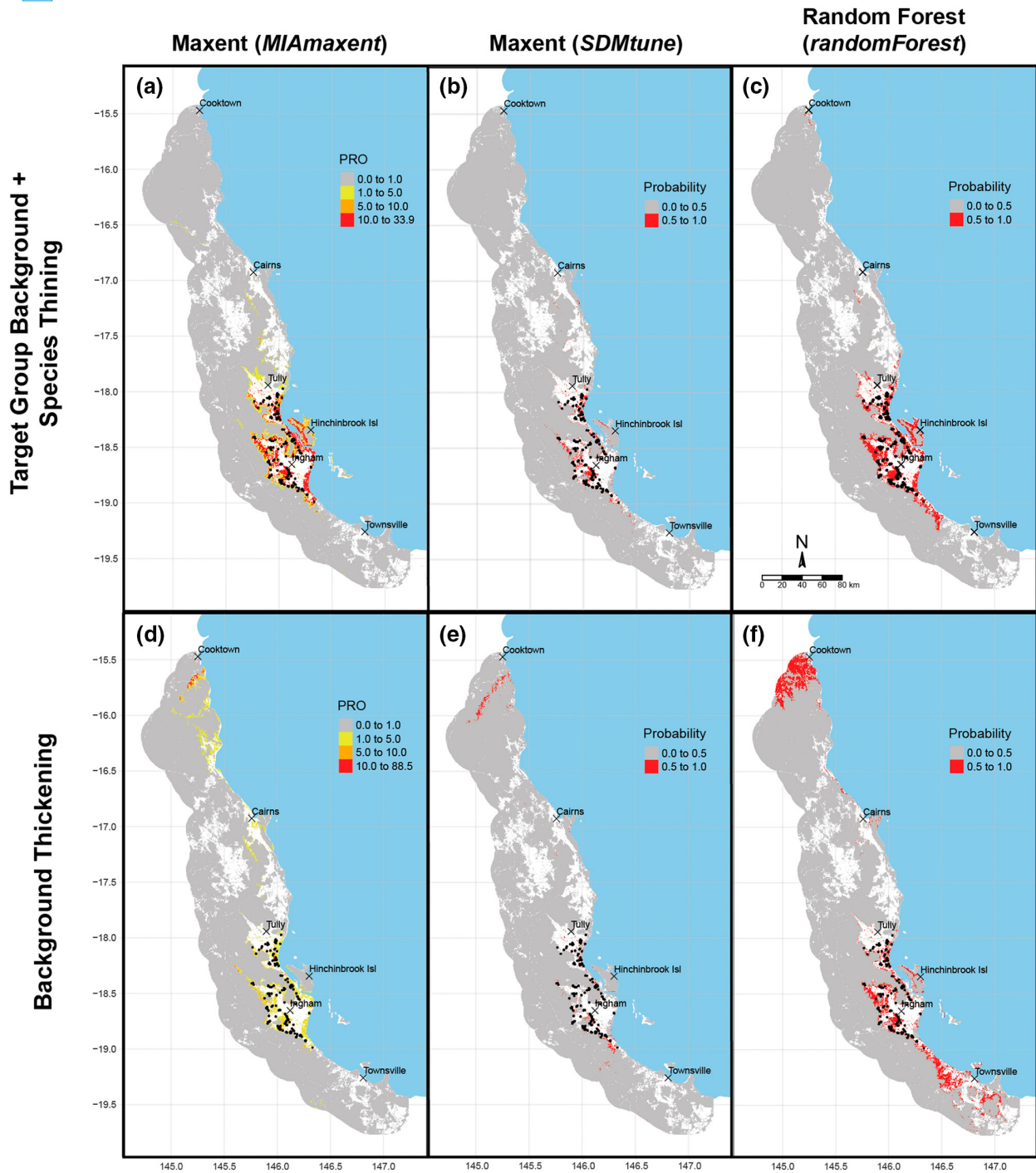


FIGURE 2 The six models from the combination of three different modelling packages and two bias correction methods within each. The *MIAMaxent* models predict suitability via the probability ratio output (PRO), a measure of ‘relative suitability of one place versus another’ (Vollering, Halvorsen, Auestad, et al., 2019). PRO = 1 represents a randomly chosen place with average suitability. In the *SDMtune* and *randomForest* models, the habitat suitability is shown as probability of occurrence with a threshold of 0.5 (locations above this threshold are depicted in red). Sighting records are shown as black dots. The white patches represent cleared, non-native vegetation (sugarcane and other crops, cattle grazing land, intensive pine plantation and urban areas), or areas outside of the modelled area (the Wet Tropics bioregion). Pale blue shading shows the sea.

level. Median elevation thresholds in five models fell below 90m. Only the *MIAMaxent* model with BT correction predicted higher median elevation (219m) (Table 2).

Precipitation seasonality was selected in all Maxent models but not in *randomForest* models, with a relative importance ranging between 2.8%

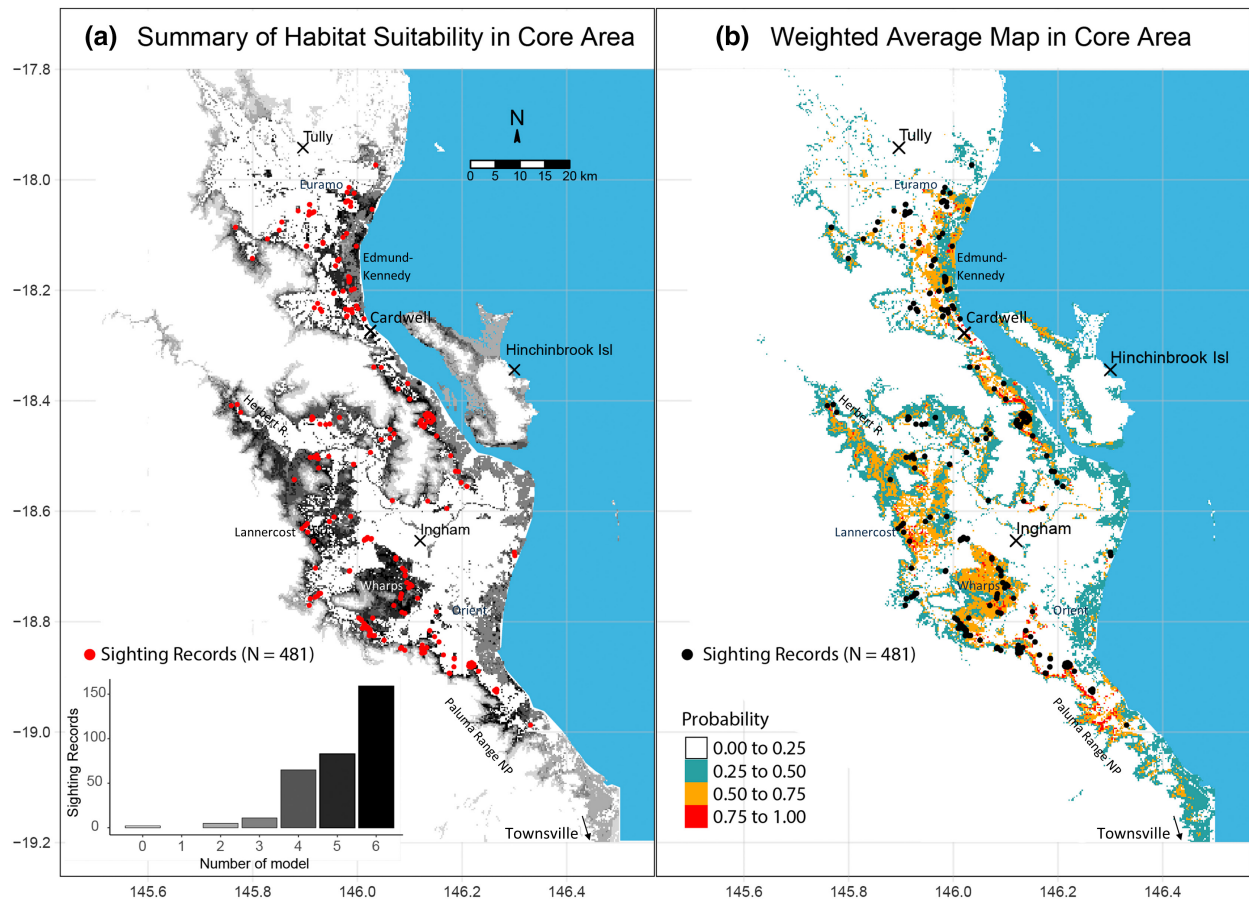


FIGURE 3 Summary and weighted average maps of predicted habitat suitability from the six models, focused within the known extent of Mahogany Gliders' distribution. (a) Model predictions were classified into suitable (1) or unsuitable (0) habitat using a 0.5 probability threshold for *SDMtune* and *randomForest*, and a probability ratio output of 1 for *MIAMaxent* models. The summary map shows the sum of these values. The grey scale from white (0) to black (6) thus represents the number of models predicting an area as suitable Mahogany Glider habitat. The red dots show all the sighting records, and the bar plot at the bottom left shows the number of sighting records that fall in each of the accumulated model categories. See Appendix S9 for a simplified summary map version that just shows areas predicted by more than three models. (b) For the weighted average map, probability predictions from *MIAMaxent* and *randomForest* models were weighted by AUC, summed and averaged. The weighted average map shows these synthesized probabilities. See Appendix S10 for a more detailed, regional set of weighted average maps for the core distribution of Mahogany Gliders.

(*SDMtune* with TGB) and 9.8% (*SDMtune* with BT). Median precipitation seasonality of predicted areas falls between 0.92 and 1 across the four models. The predicted high precipitation seasonality suggests the suitable habitat for Mahogany Glider has a marked seasonal rainfall, with a long dry season (seasonality Index 0.80–0.99, O'Donnell & Ignizio, 2012; Walsh & Lawler, 1981).

Soil type was selected in five models, with a relative importance between 2.8% (*SDMtune* with TGB) and 26% (*MIAMaxent* with TGB). Among 14 soil types, Hydrosols were consistently predicted with higher suitability (Table 2; Appendix S7).

Vegetation type was selected in four models. Relative importance of vegetation type ranged between 2% (*SDMtune* with BT) and 17% (*randomForest* with BT). *Eucalyptus* woodlands with a tussock grass understorey and *Melaleuca* open forests and woodlands were identified as the most important vegetation types for Mahogany Gliders in the models (Table 2). Details of other less frequently selected vegetation types can be found in Appendix S7.

Model evaluation

Area under the curve (AUC; Maxent models) and accuracy (*randomForest* models) were high across all six SDMs (Table 3). Models corrected with target group background and species thinning (TGB + *spThin*) generally had higher AUC than the models corrected by BT (Table 3). In Maxent models, the AUC scores differed only slightly (0.92–0.96), while in Random Forest models the accuracy differed by nearly 20% between the two bias correction methods. The *randomForest* model with BT corrections recorded

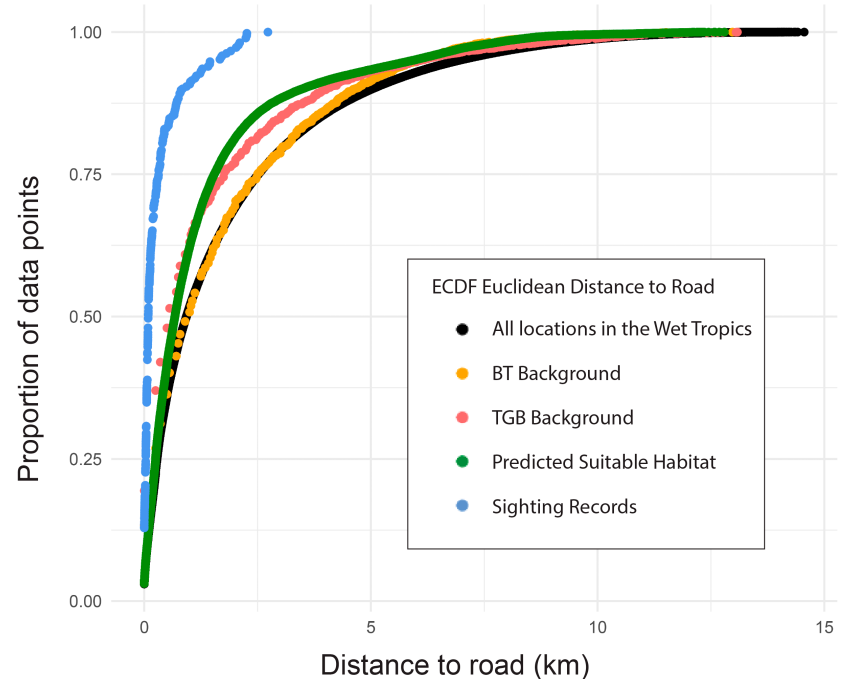


FIGURE 4 Estimator of empirical cumulative distribution function (ECDF) of the Euclidean distances to roads in five different datasets. Cumulative distribution of distance in BT backgrounds (yellow dots) has the least deviation ($D = 0.10$) from the control (all locations in the Wet Tropics, black dots). The cumulative distribution of TGB backgrounds (pink dots) and predicted suitable habitats (green dots) are the second ($D = 0.13$) and third ($D = 0.16$) most similar to the control, respectively. The cumulative distribution of sighting records (blue dots), in comparison, appears heavily road biased ($D = 0.49$).

TABLE 2 Details of the four most selected predictors (selected in more than half of the models)

R package	MIAMaxent		SDMtune		randomForest	
	TGB	BT	TGB	BT	TGB	BT
Elevation (m)	84 (61–112)	219 (148–290)	40 (24–56)	51 (34–67)	30 (13–62)	33 (15–58)
Precipitation seasonality	0.96 (0.92–1)	0.96 (0.91–0.99)	0.92 (0.88–0.97)	1 (0.98–1.01)	—	—
Soil	Chromosols Hydrosols Kandosols	Hydrosols	Hydrosols	Hydrosols	Hydrosols	—
Vegetation	—	9, 15	9, 14, 15, 44	5, 9, 15, 26, 44, 63	—	5, 9, 15

Note: Variables selected by more than half of the models are marked in bold. Numbers show the median, with first and third quantile shown in the brackets. The two vegetation types consistently selected were: (9) *eucalyptus* woodlands with a tussock grass understory; and (15) *melaleuca* open forests and woodlands.

Abbreviations: BT, background thickening; TGB, target group background.

the lowest AUC among all models, while the *randomForest* model with TGB correction reached the highest AUC of 0.99 (confusion matrix sensitivity = 1, specificity = 0.98).

Species distribution models for the Mahogany Glider

Schoner's *D* similarity tests showed a very wide range of similarity (7%–73%) (Appendix S8). We attribute this to some models predicting heavily around known localities (Figure 2a), while others predicted much more broadly (Figure 2b,f). However, three of six models (Figure 2a,c,d) had moderate to high similarity (range 54%–73%). Nevertheless, all models consistently identified suitable habitat around known records between Ingham and Tully (Figure 2), including areas with many sightings and areas with few known sightings (notably, Lannercost State Forest and forest along the Herbert River near Abergowrie in the Ingham area, and the base of the range around Tully). Additionally, all models identified suitable habitat in multiple areas beyond the known distribution (Figure 2), including: lowland areas on the west and north of Hinchinbrook Island (all six models); north of the known distribution in the vicinity of Little Mulgrave River/Gillies Range (all six models); the eastern lowlands of Paluma Range National Park south to Clemant State Forest (three models, Figure 2b,c,f); the Yarrabah region near Cairns (five models, Figure 2b–f); and even further north around Cooktown (four models, Figure 2c–f).

Comparing predictions between bias correction methods, TGB models predicted more conservatively and identified suitable habitat mostly around known sightings (Figure 2a–c), while BT models identified suitable habitat up to ~300km north and ~100km south of known sightings. For instance, three different BT models identified large patches of suitable habitat near Cooktown (Figure 2d–f). Comparing predicted areas between packages, *SDMtune* models produced the most conservative predictions (Figure 2b,e), with most suitable habitat being in close proximity to known records. Random Forest models on the other hand were the least conservative, predicting further from known records, and more often outside the known extent of the species (Figure 2c,f).

Summarizing habitat suitability across models

We summarized the findings from the six models to identify areas consistently modelled as suitable regardless of the modelling approach. To achieve this, we produced both a summary map (Figure 3a) and a weighted average map (Figure 3b). Both maps identified similar areas within the core range as suitable habitat for Mahogany Gliders (Figure 3). Additionally, detailed regional summary maps are presented, showing: the suitable habitat supported by four or more of the six models (Appendix S9), and the weighted average map at a fine scale (Appendix S10). These detailed maps may be valuable for local stakeholders and conservation managers. The summary map considered all models equally and ignored model accuracy; whereas the weighted average map depicts habitat suitability as a probability, and thus may be particularly useful at a fine scale (Appendix 10).

Assessing road bias

We examined the effect of road bias on model prediction because the sighting records are clearly biased by observer accessibility (Figure 4). In our

TABLE 3 Evaluation metrics and tuning parameters for the six tuned models

R package	MIAMaxent		SDMtune		randomForest	
	TGB	BT	TGB	BT	TGB	BT
Algorithm	Maxent	Maxent	Maxent	Maxent	Random Forest	Random Forest
Tuning package	NA	NA	SDMtune	SDMtune	caret	caret
Test data evaluation	AUC = 0.96 AIC = 1380	AUC = 0.92 AIC = 2738	AUC = 0.96 AIC = 2886	AUC = 0.95 AIC = 9534	AUC = 0.99 Accuracy: 0.98 (95% CI = 0.94, 1.00)	AUC = 0.89 Accuracy: 0.79 (95% CI = 0.72, 0.86)
Tuning parameters	NA	NA	fc = lh reg = 1.2 iter = 500	fc = lqp reg = 2.1 iter = 500	mtry = 2	mtry = 2

Abbreviations: AIC, Akaike information criterion; AUC, area under the curve; fc, feature classes; iter, iteration; mtry, number of variables available for splitting at each tree node; reg, regularization.

exploratory models, Euclidean distance to road was consistently selected as an important variable when included as a predictor. However, when projected, the model prediction with Euclidean distance to road shows very strong, unrealistic, habitat suitability tied to roads (Appendix S11). Because the road effect is not biologically relevant to the gliders' habitat (i.e. they do not use roads), we removed distance to roads from the set of predictor variables. As shown in the six models we present here (Figures 2 and 3), and explained in detail below, our two bias correction methods accounted for road bias in observations.

To examine the magnitude of road bias in the sighting records and in our modelling results, we compared the cumulative distributions of distance to roads from sighting records, bias-corrected background points, predicted suitable habitat, and all locations in the Wet Tropics. Figure 4 compares the distributions of Euclidean distance to roads in different datasets, as ECDF. The ECDF shows that sighting records are extremely close to roads compared to the other curves. All except two sighting records are within 2.5 km of a road and their median distance (0 km, quartiles: 0–0.25 km, blue dots) is much smaller than the median distance of all locations in the Wet Tropics to roads (0.94 km, quartiles: 0.31–2.64 km, black dots). The ECDF of the bias-corrected background points we selected to build the SDM models, however, shows less deviation from all locations in the Wet Tropics (Figure 4).

We tested the deviation of sighting records and selected backgrounds to the cumulative distribution of all locations in the Wet Tropics. All deviations are significant ($p < 0.001$), but the magnitude of deviation for the sighting records ($D = 0.49$) is much greater than that of the background points (BT-corrected background points: $D = 0.10$; TGB-corrected background points: $D = 0.16$). The predicted suitable habitats from the models (from the weighted averaged map, with probability > 0.5) also shows significant deviation ($D = 0.13$, $p < 0.001$) (Figure 4), of a magnitude similar to the background points. However, suitable habitat was predicted as far as 12 km from the road and was not constrained to being near roads. These results suggest our bias correction methods sufficiently removed road bias in our modelling.

DISCUSSION

Using all known sighting records and biologically relevant environmental and climatic predictors, we produced SDMs for the endangered Mahogany Glider (*P. gracilis*). Elevation, precipitation seasonality, soil and vegetation

type were identified as key predictors of Mahogany Gliders' distribution (Table 2). All models identified suitable habitat in the coastal lowlands in the known extent of Mahogany Gliders, between Paluma and Tully, including many areas of moderate to high suitability habitat with no known sighting records. The models showed that suitable habitat within the known distribution is highly fragmented, and some areas with historical records have since been cleared of native vegetation (Figure 3). Beyond the known distribution, the models also predicted potentially suitable habitat to the south (coastal woodland north of Townsville), east (lowlands of Hinchinbrook Island) and north (particularly several lowland areas in the vicinity of Cairns).

Ecological insights of the selected predictors

The four predictor variables consistently identified as important in the six final models (elevation, precipitation seasonality, soil and vegetation type) summarize the most suitable habitat for Mahogany Gliders—*Eucalyptus* and *Melaleuca* open woodlands with grassy understory, growing on Hydrosols, in areas below 100 m elevation, and with highly seasonal precipitation. The modelling methodology accounts for correlation between continuous variables (indeed, most of the temperature and precipitation predictors are inter-correlated; Appendix S11) but is limited in accounting for correlations involving categorical factors. Therefore, the key predictors may not be independent and the biological links between them, and their direct or indirect influence on the species, are worth investigating.

Elevation

The restriction of Mahogany Gliders to low elevations has been discussed in detail previously; for example, Van Dyck (1993) noted that all records were found below 90 m in elevation, with most records falling below 20 m. Median elevation thresholds in five of our six models fell below 90 m. Only the *MIAmaxent* model with BT correction predicted higher median elevation (219 m) (Table 2), but it is not clear why this was the case for this one model/correction method combination. It is unlikely that elevation has a direct effect on gliders (e.g. that gliders are physiologically restricted to the hotter lowlands) and the importance of elevation more likely reflects correlations with the other three key predictor variables (distribution of *Eucalyptus* and *Melaleuca* open woodlands with grassy understory; distribution of Hydrosols; highly seasonal precipitation). Diversity in the Wet Tropics bioregion is generally greatest in mid elevation and upland rainforest areas, particularly when considering the endemic species (Leahy et al., 2020; Staunton et al., 2014; Uzqueda et al., 2020; Williams et al., 1995), and the Mahogany Glider is an interesting exception.

Precipitation seasonality, soil type and vegetation type

Precipitation seasonality has been previously identified as an important predictor in BIOCLIM models for Mahogany Gliders (Jackson & Claridge, 1999; Van Dyck, 1993), with suitable habitat having marked seasonal rainfall and a long dry season (O'Donnell & Ignizio, 2012; Walsh & Lawler, 1981). Such seasonal variation may limit the growth of unsuitable rainforest habitats, which generally prefer lower precipitation seasonality

(Neldner et al., 2019). It may also facilitate the formation of Hydrosol soils, which are defined as a group of soils that are seasonally saturated with water for 2–3 months per year (Isbell, 2016). Hydrosols per se will not be directly impacting arboreal Mahogany Gliders but they promote the development of certain vegetation types, including forests dominated by *Eucalyptus*, *Corymbia* and *Melaleuca* species in the Wet Tropics (Neldner et al., 2019). *Eucalyptus* and *Melaleuca* open woodlands were identified as a key predictor in all models, and have been broadly recognized as key habitat for Mahogany Gliders (Jackson, 2000a; Jackson et al., 2011). These vegetation communities provide year-round food sources and den trees (Jackson, 2000b; Van Dyck, 1993). Vegetation type is intuitively thought to be important for habitat suitability of particular arboreal mammals, but has not been included as a predictor variable in previous SDMs on gliders or possums (Jackson & Claridge, 1999; Lindenmayer et al., 1991; Rees et al., 2007). Our study shows that it is an important predictor and may reflect the underlying contributions of other less intuitive variables (e.g. precipitation seasonality, soil type).

Fire management

Fire management has been widely recognized as an important factor in maintaining Mahogany Glider habitat, by limiting vegetation thickening (Jackson, 2000a; Jackson et al., 2011; Van Dyck, 1993). However, fire frequency (as measured by TERN AusCover, 2013) was not selected as an important predictor in our models, possibly because it does not reflect the fine-scale fire patterns of relevance to the gliders. Fire management in Mahogany Glider habitat usually consists of planned burns in the understory, and this fine-scale, below-canopy burning may not be detected by satellite remote sensing that aims to detect wildfire of larger scale and higher intensity. The impact of fire on mammal species has been found to be complicated and dependent on site, context and other factors (Driessen et al., 2021). Our modelling did not adequately incorporate the role of fire in habitat suitability, and it requires further investigation.

Removing road bias from models

The sighting records of Mahogany Gliders were strongly biased by observer accessibility—most fall within 100 m of a road and none come from more than 2.5 km from roads (Figure 4). The ECDF curves and the distribution tests showed that road bias was largely accounted for in both the TGB and BT bias correction methods (Figure 4). Predicted suitable habitat occurs up to 12.8 km away from roads, which is as far as any point in Wet Tropics lowland sclerophyll forest is from roads. Although some species, especially some invasive species, use roads to forage and move through the landscape (Brown et al., 2006; Rauschert et al., 2017; Wysong et al., 2020), this is not the case for arboreal Mahogany Gliders, and road bias is driven by observer accessibility. Our results show the importance of testing for road bias in SDM and assessing whether the road is a sensible predictor for the species.

Predicting current suitable habitats for Mahogany Gliders

Our models are an improvement on previous modelling for Mahogany Gliders (Jackson et al., 2011; Jackson & Claridge, 1999; Van Dyck, 1993)

because they incorporate more variables, including categorical variables, and have higher spatial resolution (~250m) and accuracy (AUC of 0.89–0.99). The six models generally predicted similar areas as suitable habitat for Mahogany Gliders within the known distribution area, but the predictions outside the core area varied. Models using the TGB+ *spThin* bias correction method were more reflective of the known distribution (but identified many suitable patches that do not contain Mahogany Glider records; see below) and had high prediction accuracy (Figure 2a–c). They would therefore be useful to focus on the fine-scale distribution within the known range limits. In contrast, models using BT bias correction were more likely to identify similar habitats distant from the known distribution; for example, woodlands near Cooktown (Figure 2d–f). The spatially broader predictions from models with BT bias correction may result from the large geodesic buffer (75.6 km) used in the process (Ştefan, 2019; Vollerling, Halvorsen, & Mazzoni, 2019), potentially resulting in the inclusion of a broader range of backgrounds around the sighting records and thus less conservative models. The positive is that models using BT bias correction could lead to the discovery of unknown populations well outside the currently known range.

The summary map and the weighted average map provide syntheses of our modelling results. There is notable consistency in areas identified as high suitability habitat. These maps, particularly the fine-scale depictions in Appendices S9 and S10, will be useful for identifying the size and connectivity of remnant habitat patches (Jackson et al., 2019; Jackson & Diggins, 2020), and targeting survey effort to patches with no, or few, records. We found that a large number of predicted suitable habitat patches have no sighting records (Figure 5). Importantly, 266 of these patches (i.e. 55% of all habitat patches without sightings records) are of sufficient size to potentially support a population of Mahogany Gliders (i.e. 0.1–10 km²; Figure 5). These patches are a priority for future survey efforts, working from largest to smallest patch size. Our results also showed that 156 out of the total 481 sightings of Mahogany Gliders (i.e. ~30% of all sightings) are now situated in deforested areas; in most cases cleared for sugarcane or cattle grazing. This highlights the need to quantify and monitor habitat loss and ensure high suitability habitat on private land is adequately mapped and protected.

The synthesized maps allow broad assessment of the distribution and connectivity of the modelled habitat. Most of the larger areas of suitable habitat are in the Ingham region and north to Cardwell (Figure 3; Appendix S10). This includes the large patch at Warps Holding (Appendix S10C) and the fairly continuous large area of habitat from Lannercost State Forest to the Herbert River valley (Appendix S10B,C). Additionally, an extensive ribbon of predicted high suitability habitat runs along the base of the ranges through much of the species' distribution, with the continuous strip of high suitability habitat along the base of the Paluma Range of particular note (Appendix S10D). This ribbon of habitat connects with many of the core habitat patches on the coastal flats, particularly in the southern two-thirds of the range. However, many patches, particularly in the north of the range (Kennedy to Tully valley; Appendix S10A) and in the Ingham region (Appendix S10C) are disjunct and isolated.

Management recommendations

1. Survey areas of high suitability habitat within the known range, particularly those without sightings records (Figure 5), to identify all remnant populations within the core distribution of the species. Priorities include: large areas west of Ingham (Warps Holding, and Lannercost

- State Forest; and north along the base of the range up the Herbert River valley); coastal forests east of the Bruce Highway between Big Crystal Creek and Ingham, and between Edmund Kennedy and Tully; and the Big Crystal Creek area in the south (Appendix S10).
- Survey areas predicted as moderate to high habitat suitability habitat outside of the known range to resolve the true distribution of the Mahogany Glider. Priorities are: Hinchinbrook Island; lowland woodlands in the Cairns–Yarrabah–Gordonvale areas, and south of Cooktown; and the Clemant State Forest area at the southern end of Paluma Range (Figures 3 and 4; Appendices S9 and S10).
 - Identify key populations across the range to establish long-term camera trap monitoring, including in the north (e.g. Edmund Kennedy–Euramo area), centre (e.g. Cardwell Range area) and south (e.g. Paluma Range area) of the range.

Future directions

Attempts have been made to identify key populations of Mahogany Gliders and map corridors between them (Jackson et al., 2019). The results gained herein could be used to refine landscape assessments (Tarabon et al., 2019) and perform connectivity analyses (Esselman & Allan, 2011; Torabian et al., 2021) based on the modelled moderate and high suitability patches and corridors (e.g. using the weighted average mapping). Genetic analyses could also be used to test connectivity, focussing on areas with patches of varied size and connectivity.

An updated SDM for Mahogany Gliders is recommended once more recent sighting records accumulate and more advanced spatial data are available. Spatial data that could better refine the models include additional fine-scale fire layers (Driessen et al., 2021), mapping of forest age or structure, to capture important factors such as abundance of tree hollows (Linnell

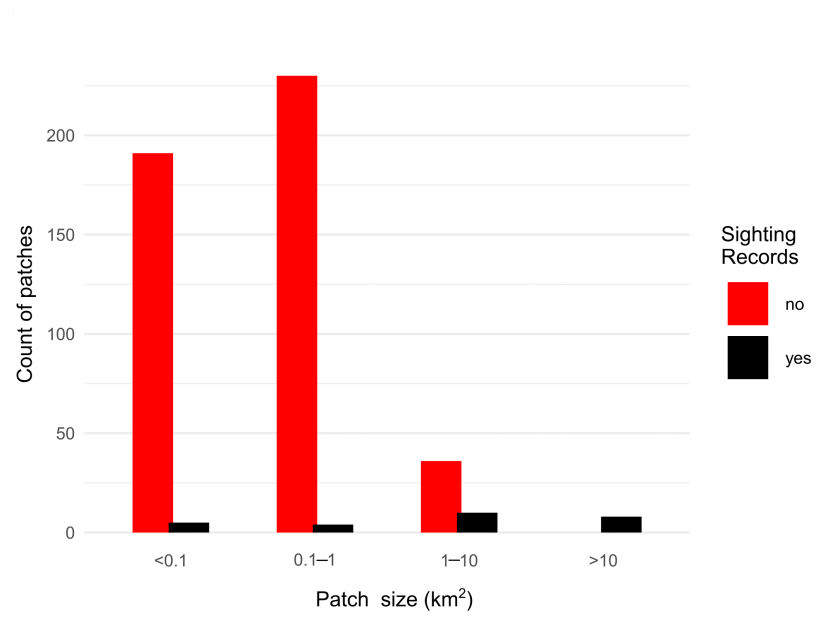


FIGURE 5 Histogram showing the number of patches within patch size bins, split by patches with Mahogany Glider sighting records (black) and without a record (red). The minimum estimated home range of a male Mahogany Glider is about 0.1 km² (11 ha) (Jackson, 2000a, 2000b), so we consider patch sizes <0.1 km² unlikely to support a population.

et al., 2017), mapping of the impact of recent extreme weather events, in this case cyclones (Bateman et al., 2012) and mapping of thin lines of roadside vegetation that may act as species dispersal or movement corridors (Vasudev et al., 2015). Additionally, the SDM could be used to model the potential effect of climate change on Mahogany Gliders, as done for other possums and gliders (Handayani et al., 2019; Molloy et al., 2013), but noting that post-model refining from expert knowledge (e.g. micro-refugia, barriers; Reside et al., 2019) would be required for this species.

AUTHOR CONTRIBUTIONS

Yiyin Chang: Conceptualization (lead); data curation (lead); formal analysis (lead); funding acquisition (lead); investigation (lead); methodology (lead); project administration (lead); validation (lead); visualization (lead); writing – original draft (lead); writing – review and editing (lead). **Lorenzo V. Bertola:** Conceptualization (supporting); data curation (supporting); investigation (supporting); methodology (supporting); supervision (supporting); validation (supporting); visualization (supporting); writing – review and editing (supporting). **Conrad J. Hoskin:** Conceptualization (lead); data curation (supporting); funding acquisition (lead); investigation (supporting); project administration (supporting); resources (supporting); supervision (lead); validation (supporting); visualization (supporting); writing – review and editing (lead).

ACKNOWLEDGEMENTS

The project was funded by Terrain National Resource Management, the Holsworth Wildlife Research Endowment (Equity Trustees Charitable Foundation & the Ecological Society of Australia) and James Cook University. We thank Steve Jackson for discussions on the habitat and ecology of the species, Jacqui Diggins from Terrain NRM, Girringun Aboriginal Corporation, Mark Parson from Queensland Parks and Wildlife Service, Daryl Dickson and the Mahogany Glider Recovery Team for access to occurrence records and other data.

DATA AVAILABILITY STATEMENT

The datasets generated during and analysed in the study are available from the corresponding author on reasonable request.

ORCID

Yiyin Chang  <https://orcid.org/0000-0002-3575-1619>

Lorenzo V. Bertola  <https://orcid.org/0000-0002-1927-308X>

Conrad J. Hoskin  <https://orcid.org/0000-0001-8116-6085>

REFERENCES

- ACLEP. (2014) Soil classification and attributes geographic extent: Australia year range: 2012 resolution: 9 arcsec (~250 m) data layers: soil classification, bulk density, clay content, plant available water capacity, pH. *National soil data provided by the Australian Collaborative Land Evaluation Program, endorsed through the National Committee on Soil and Terrain NCST*. Available from: www.clw.csiro.au/aclep [Accessed 6th April 2020].
- Aiello-Lammens, M.E., Boria, R.A., Radosavljevic, A., Vilela, B. & Anderson, R.P. (2015) spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. *Ecography*, 38, 541–545. Available from: <https://doi.org/10.1111/ecog.01132>
- Allouche, O., Tsoar, A. & Kadmon, R. (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology*, 43, 1223–1232. Available from: <https://doi.org/10.1111/j.1365-2664.2006.01214.x>
- Araújo, M.B. & Guisan, A. (2006) Five (or so) challenges for species distribution modelling. *Journal of Biogeography*, 33, 1677–1688. Available from: <https://doi.org/10.1111/j.1365-2699.2006.01584.x>
- Bateman, B.L., Vanderwal, J. & Johnson, C.N. (2012) Nice weather for bettongs: using weather events, not climate means, in species distribution models. *Ecography*, 35, 306–314. Available from: <https://doi.org/10.1111/j.1600-0587.2011.06871.x>

- Berger, A.L., Della Pietra, V.J. & Della Pietra, S.A. (1996) A maximum entropy approach to natural language processing. *Computational Linguistics*, 22, 39–68.
- Bertola, L.V., Higgie, M. & Hoskin, C.J. (2018) Resolving distribution and population fragmentation in two leaf-tailed gecko species of north-east Australia: key steps in the conservation of microendemic species. *Australian Journal of Zoology*, 66, 152–166. Available from: <https://doi.org/10.1071/ZO18036>
- Booth, T.H. (2018) Species distribution modelling tools and databases to assist managing forests under climate change. *Forest Ecology and Management*, 430, 196–203. Available from: <https://doi.org/10.1016/j.foreco.2018.08.019>
- Booth, T.H., Nix, H.A., Busby, J.R. & Hutchinson, M.F. (2014) Bioclim: the first species distribution modelling package, its early applications and relevance to most current MaxEnt studies. *Diversity and Distributions*, 20, 1–9. Available from: <https://doi.org/10.1111/ddi.12144>
- Breiman, L. (2001) Random forests. *Machine Learning*, 45, 5–32. Available from: <https://doi.org/10.1023/A:1010933404324>
- Breiman, L. (2018) *randomForest: Breiman and Cutler's random forests for classification and regression*. R package version 4.6. Available from: <https://cran.r-project.org/web/packages/randomForest/index.html> [Accessed 27th August 2022].
- Brown, G.P., Phillips, B.L., Webb, J.K. & Shine, R. (2006) Toad on the road: use of roads as dispersal corridors by cane toads (*Bufo marinus*) at an invasion front in tropical Australia. *Biological Conservation*, 133, 88–94. Available from: <https://doi.org/10.1016/j.biocon.2006.05.020>
- Busby, J. (1991) BIOCLIM – a bioclimate analysis and prediction system. *Plant Protection Quarterly*, 6, 8–9.
- Cayuela, L., Golicher, D.J., Newton, A.C., Kolb, M., de Albuquerque, F.S., Arets, E.J.M.M. et al. (2009) Species distribution modeling in the tropics: problems, potentialities, and the role of biological data for effective species conservation. *Tropical Conservation Science*, 2, 319–352. Available from: <https://doi.org/10.1177/194008290900200304>
- Craig, R., Heath, B., Raisbeck-Brown, N., Steber, M., Marsden, J. & Smith, R. (2002) The distribution, extent and seasonality of large fires in Australia, April 1998–March 2000, as mapped from NOAA-AVHRR imagery. *Australian fire regimes: contemporary patterns (April 1998–March 2000) and changes since European settlement*, pp. 1–77.
- Department of Environment and Science. (2019) *Land use mapping – 1999 to current – Queensland*. Available from: <http://www.qld.gov.au/environment/land/vegetation/mapping/qlump> [Accessed 14th June 2018].
- Department of Industry, Science, Energy, and Resources. (2020) *National Forest and Sparse Woody Vegetation Data version 4.0 (2019 release)*. Available from: <http://www.environment.gov.au/system/files/resources/29eca947-af49-4ed1-8369-%0Ae68d74730cf9/files/national-inventory-report-2017-volume-2.pdf> [Accessed 14th June 2018].
- Department of Industry, Science, Energy, and Resources. (2020) *National Forest and Sparse Woody Vegetation Data version 4.0 (2019 release)*. Available from: <http://www.environment.gov.au/system/files/resources/29eca947-af49-4ed1-8369-%0Ae68d74730cf9/files/national-inventory-report-2017-volume-2.pdf> [Accessed 14th June 2018].
- Diaz-Uriarte, R. (2010) *varSelRF: variable selection using random forests*. R package version 0.7-3. Vienna: TU Wien.
- Diaz-Uriarte, R. (2017) *varSelRF: variable selection using random forests*. R package version 0.7-8. Available from: <https://cran.r-project.org/web/packages/varSelRF/index.html> [Accessed 27th August 2022].
- Drew, C.A., Wiersma, Y.F. & Huettmann, F. (2011) *Predictive species and habitat modeling in landscape ecology: concepts and applications*. New York, NY: Springer.
- Driessen, M.M., Jarman, P.J., Visoiu, M. & Dewar, E. (2021) Mammal responses to moderate-intensity planned burning in a small, isolated woodland reserve. *Wildlife Research*, 48, 561–576. Available from: <https://doi.org/10.1071/WR20165>
- Elith, J. & Leathwick, J.R. (2009) Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, 40, 677–697. Available from: <https://doi.org/10.1146/annurev.ecolsys.110308.120159>
- Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E. & Yates, C.J. (2011) A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*, 17, 43–57. Available from: <https://doi.org/10.1111/j.1472-4642.2010.00725.x>
- Environmental Systems Research Institute (ESRI). (2019) *ArcGIS desktop help 10.8 geo-statistical analyst*.
- Esselman, P.C. & Allan, J.D. (2011) Application of species distribution models and conservation planning software to the design of a reserve network for the riverine fishes of northeastern Mesoamerica. *Freshwater Biology*, 56, 71–88. Available from: <https://doi.org/10.1111/j.1365-2427.2010.02417.x>
- Evans, J.S., Murphy, M.A., Holden, Z.A. & Cushman, S.A. (2011) Modeling species distribution and change using random forest. In: Drew, C.A., Wiersma, Y.F. & Huettmann, F. (Eds.) *Predictive species and habitat modeling in landscape ecology: concepts*

- and applications. New York, NY: Springer, pp. 139–159. Available from: https://doi.org/10.1007/978-1-4419-7390-0_8
- Fielding, A.H. & Bell, J.F. (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, 24, 38–49. Available from: <https://doi.org/10.1017/S0376892997000088>
- Gobeyn, S., Mouton, A.M., Cord, A.F., Kaim, A., Volk, M. & Goethals, P.L.M. (2019) Evolutionary algorithms for species distribution modelling: a review in the context of machine learning. *Ecological Modelling*, 392, 179–195. Available from: <https://doi.org/10.1016/j.ecolmodel.2018.11.013>
- Goldingay, R.L. & Jackson, S.M. (2004) *The biology of Australian possums and gliders*. Chipping Norton, NSW: Surey Beatty and Sons.
- Gräler, B., Pebesma, E.J. & Heuvelink, G.B.M. (2016) Spatio-temporal interpolation using gstat. *The R Journal*, 8, 204.
- Halvorsen, R. (2013) A strict maximum likelihood explanation of MaxEnt, and some implications for distribution modelling. *Sommerfeltia*, 36, 1–132. Available from: <https://doi.org/10.2478/v10208-011-0016-2>
- Handayani, F., Goldingay, R.L., McHugh, D. & Leslie, N. (2019) Extensive range contraction predicted under climate warming for a gliding mammal in north-eastern Australia. *Australian Mammalogy*, 41, 99–111. Available from: <https://doi.org/10.1071/AM16062>
- Hijmans, R.J. (2012) Cross-validation of species distribution models: removing spatial sorting bias and calibration with a null model. *Ecology*, 93, 679–688. Available from: <https://doi.org/10.1890/11-0826.1>
- Hijmans, R.J., Bivand, R., Forner, K., Ooms, J., Pebesma, E. & Sumner, M.D. (2022) *terra: spatial data analysis*. R package version 1.6-7. Available from: <https://cran.r-project.org/web/packages/terra/index.html> [Accessed 27th August 2022].
- Hijmans, R.J. & Elith, J. (2016) *Species distribution modeling with R*. Available from: <http://www.idg.pl/mirrors/CRAN/web/packages/dismo/vignettes/sdm.pdf> [Accessed 27th August 2022]. [https://doi.org/10.1016/S0550-3213\(02\)00216-X](https://doi.org/10.1016/S0550-3213(02)00216-X)
- Hijmans, R.J. & van Etten, J. (2016) *raster: geographic data analysis and modeling*. R package version 3.5. Available from: <https://cran.r-project.org/web/packages/raster/index.html> [Accessed 27th August 2022].
- Isbell, R. (2016) *The Australian soil classification*. Clayton, Vic.: CSIRO Publishing.
- Jackson, C.R. & Robertson, M.P. (2011) Predicting the potential distribution of an endangered cryptic subterranean mammal from few occurrence records. *Journal for Nature Conservation*, 19, 87–94. Available from: <https://doi.org/10.1016/j.jnc.2010.06.006>
- Jackson, S.M. (1998) *Foraging ecology, behaviour and management of the mahogany glider Petaurus gracilis*. PhD thesis, James Cook University, Douglas, Qld.
- Jackson, S.M. (2000a) Habitat relationships of the mahogany glider, *Petaurus gracilis*, and the sugar glider, *Petaurus breviceps*. *Wildlife Research*, 27, 39–48. Available from: <https://doi.org/10.1071/WR98045>
- Jackson, S.M. (2000b) Home-range and den use of the mahogany glider, *Petaurus gracilis*. *Wildlife Research*, 27, 49–60. Available from: <https://doi.org/10.1071/WR98046>
- Jackson, S.M. & Claridge, A. (1999) Climatic modelling of the distribution of the mahogany glider (*Petaurus gracilis*), and the squirrel glider (*P. norfolcensis*). *Australian Journal of Zoology*, 47, 47–57. Available from: <https://doi.org/10.1071/ZO98044>
- Jackson, S.M. & Diggins, J. (2020) *National recovery plan for the mahogany glider (Petaurus gracilis)*. Available from: <https://www.dcceew.gov.au/environment/biodiversity/threatened/recovery-plans/comment/draft-recovery-plan-mahogany-glider> [Accessed 26th November 2022].
- Jackson, S.M., Morgan, G., Kemp, J.E., Maughan, M. & Stafford, C.M. (2011) An accurate assessment of habitat loss and current threats to the mahogany glider (*Petaurus gracilis*). *Australian Mammalogy*, 33, 82–92. Available from: <https://doi.org/10.1071/AM10021>
- Jackson, S.M., Parsons, M., Baseler, M. & Stanton, D. (2019) Landscape management of the mahogany glider (*Petaurus gracilis*) across its distribution: subpopulations and corridor priorities. *Australian Mammalogy*, 42, 152–159. Available from: <https://doi.org/10.1071/AM19010>
- Jackson, S.M. (2001) Foraging behaviour and food availability of the mahogany glider *Petaurus gracilis* (Petauridae: Marsupialia). *Journal of Zoology*, 253(1), 1–13. Available from: <https://doi.org/10.1017/s0952836901000012>
- Jaeschke, A., Bittner, T., Reineking, B. & Beierkuhnlein, C. (2013) Can they keep up with climate change? – integrating specific dispersal abilities of protected Odonata in species distribution modelling. *Insect Conservation and Diversity*, 6, 93–103. Available from: <https://doi.org/10.1111/j.1752-4598.2012.00194.x>
- Jiménez-Valverde, A. (2012) Insights into the area under the receiver operating characteristic curve (AUC) as a discrimination measure in species distribution modelling. *Global Ecology and Biogeography*, 21, 498–507. Available from: <https://doi.org/10.1111/j.1466-8238.2011.00683.x>

- Kadmon, R., Farber, O. & Danin, A. (2004) Effect of roadside bias on the accuracy of predictive maps produced by bioclimatic models. *Ecological Applications*, 14, 401–413. Available from: <https://doi.org/10.1890/02-5364>
- Kuhn, M. (2008) Building predictive models in R using the caret package. *Journal of Statistical Software*, 28, 1–26. Available from: <https://doi.org/10.18637/jss.v028.i05>
- Leahy, L., Scheffers, B.R., Williams, S.E. & Andersen, A.N. (2020) Diversity and distribution of the dominant ant genus *Anonychomyrma* (Hymenoptera: Formicidae) in the Australian wet tropics. *Diversity*, 12, 1–28. Available from: <https://doi.org/10.3390/d12120474>
- Lilliefors, H.W. (1967) On the Kolmogorov-Smirnov test for normality with mean and variance unknown. *Journal of the American Statistical Association*, 62, 399–402. Available from: <https://doi.org/10.1080/01621459.1967.10482916>
- Lindenmayer, D.B., Nix, H.A., McMahon, J.P., Hutchinson, M.F. & Tanton, M.T. (1991) The conservation of Leadbeater's possum, *Gymnobelideus leadbeateri* (McCoy): a case study of the use of bioclimatic modelling. *Journal of Biogeography*, 18, 371. Available from: <https://doi.org/10.2307/2845479>
- Linnell, M.A., Davis, R.J., Lesmeister, D.B. & Swingle, J.K. (2017) Conservation and relative habitat suitability for an arboreal mammal associated with old forest. *Forest Ecology and Management*, 402, 1–11. Available from: <https://doi.org/10.1016/j.foreco.2017.07.004>
- Lobo, J.M., Jiménez-Valverde, A. & Real, R. (2008) AUC: a misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography*, 17, 145–151. Available from: <https://doi.org/10.1111/j.1466-8238.2007.00358.x>
- McGrath, C. (2007) End of broadscale clearing in Queensland. *Environmental and Planning Law Journal*, 24, 5–13.
- Mi, C., Huettmann, F., Guo, Y., Han, X. & Wen, L. (2017) Why to choose Random Forest to predict rare species distribution with few samples in large undersampled areas? Three Asian crane species models provide supporting evidence. *PeerJ*, 5, e2849. Available from: <https://doi.org/10.7717/peerj.2849>
- Molloy, S.W., Davis, R.A. & Van Etten, E.J.B. (2013) Species distribution modelling using bioclimatic variables to determine the impacts of a changing climate on the western ringtail possum (*Pseudocheirus occidentalis*; Pseudocheiridae). *Environmental Conservation*, 41(2), 176–186. Available from: <https://doi.org/10.1017/s0376892913000337>
- Moradi, S., Sheykhi Ilanloo, S., Kafash, A. & Yousefi, M. (2019) Identifying high-priority conservation areas for avian biodiversity using species distribution modeling. *Ecological Indicators*, 97, 159–164. Available from: <https://doi.org/10.1016/j.ecolind.2018.10.003>
- Morueta-Holme, N., Fløjgaard, C. & Svenning, J.C. (2010) Climate change risks and conservation implications for a threatened small-range mammal species. *PLoS One*, 5, e10360. Available from: <https://doi.org/10.1371/journal.pone.0010360>
- Mouton, A.M., De Baets, B. & Goethals, P.L.M. (2010) Ecological relevance of performance criteria for species distribution models. *Ecological Modelling*, 221, 1995–2002. Available from: <https://doi.org/10.1016/j.ecolmodel.2010.04.017>
- Neldner, V.J., Niehus, R.E., Wilson, B.A., McDonald, W.J.F., Ford, A.J. & Accad, A. (2019) *The vegetation of Queensland. Descriptions of broad vegetation groups. Version 4.0*. Queensland Herbarium. Department of Science, Information, Technology, and Innovation. Available from: https://www.des.qld.gov.au/__data/assets/pdf_file/0029/81929/descriptions-of-broad-vegetation-groups.pdf [Accessed 26th November 2022].
- Nix, H.A. & Busby, J. (1986) *BIOCLIM, a bioclimatic analysis and prediction system*. Canberra, ACT: Division of Water and Land Resources.
- O'Donnell, M.S. & Ignizio, D.A. (2012) Bioclimatic predictors for supporting ecological applications in the conterminous United States. *US Geological Survey Data Series*, 691, 4–9.
- Parson, M. & Latch, P. (2006) *Recovery plan for the mahogany glider Petaurus gracilis*. Brisbane, Qld: Environmental Protection Agency.
- Pebesma, E. & Bivand, R.S. (2005) S classes and methods for spatial data: the sp package. *R News*, 5, 9–13.
- Pebesma, E.J. (2018) Simple features for R: standardized support for spatial vector data. *The R Journal*, 10, 439.
- Pecchi, M., Marchi, M., Burton, V., Giannetti, F., Moriando, M., Bernetti, I. et al. (2019) Species distribution modelling to support forest management. A literature review. *Ecological Modelling*, 411, 108817. Available from: <https://doi.org/10.1016/j.ecolmodel.2019.108817>
- Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J. et al. (2009) Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecological Applications*, 19, 181–197. ACM digital library, Available from: <https://doi.org/10.1890/07-2153.1>
- Phillips, S.J., Dudík, M. & Schapire, R.E. (2004) A maximum entropy approach to species distribution modeling. In: *Proceedings of the twenty-first international conference on*

- machine learning*, p. 83. New York, NY: ACM digital library. Available from: <https://doi.org/10.1145/1015330.1015412>
- Queensland Government. (2017) *Queensland spatial catalogue*. Available from: <http://qldspatial.information.qld.gov.au/catalogue/> [Accessed 6th April 2020].
- Queensland Government. (2020) WildNet database. *The State of Queensland 1995–2020*. Available from: <https://www.qld.gov.au/environment/plants-animals/species-information/wildnet> [Accessed 6th April 2020].
- R Development Core Team. (2020) *R: a language and environment for statistical computing*, v4.1.2. Vienna: R Foundation for Statistical Computing.
- Ranc, N., Santini, L., Rondinini, C., Boitani, L., Poitevin, F., Angerbjörn, A. et al. (2017) Performance tradeoffs in target-group bias correction for species distribution models. *Ecography*, 40, 1076–1087. Available from: <https://doi.org/10.1111/ecog.02414>
- Rauschert, E.S.J., Mortensen, D.A. & Bloser, S.M. (2017) Human-mediated dispersal via rural road maintenance can move invasive propagules. *Biological Invasions*, 19, 2047–2058. Available from: <https://doi.org/10.1007/s10530-017-1416-2>
- Rees, M., Paull, D.J. & Carthew, S.M. (2007) Factors influencing the distribution of the yellow-bellied glider (*Petaurus australis australis*) in Victoria, Australia. *Wildlife Research*, 34, 228–233. Available from: <https://doi.org/10.1071/WR06027>
- Reside, A.E., Critchell, K., Crayn, D.M., Goosem, M., Goosem, S., Hoskin, C.J. et al. (2019) Beyond the model: expert knowledge improves predictions of species' fates under climate change. *Ecological Applications*, 29, e01824. Available from: <https://doi.org/10.1002/eap.1824>
- Ricca, M.A., Coates, P.S., Gustafson, K.B., Brussee, B.E., Chambers, J.C., Espinosa, S.P. et al. (2018) A conservation planning tool for greater sage-grouse using indices of species distribution, resilience, and resistance. *Ecological Applications*, 28, 878–896. Available from: <https://doi.org/10.1002/eap.1690>
- Ripley, B., Venables, B., Bates, D.M., Hornik, K., Gebhardt, A. & Firth, D. (2013) Package 'mass'. R package version 7.3-58.1. Available from: <https://cran.r-project.org/web/packages/MASS/index.html> [Accessed 27th August 2022].
- Rodríguez-Rey, M., Consuegra, S., Börger, L. & de Leaniz, C.G. (2019) Improving species distribution modelling of freshwater invasive species for management applications. *PLoS One*, 14, e0217896. Available from: <https://doi.org/10.1371/journal.pone.0217896>
- Rosenfeld, R. (1996) A maximum entropy approach to adaptive statistical language modelling. *Computer Speech and Language*, 10, 187–228. Available from: <https://doi.org/10.1006/csla.1996.0011>
- Ruete, A. & Leynaud, G.C. (2015) Goal-oriented evaluation of species distribution models' accuracy and precision: true skill statistic profile and uncertainty maps. *PeerJ PrePrints*, 3, e1208v1. Available from: <https://doi.org/10.7287/peerj.preprints.1208v1>
- Sakamoto, Y., Ishiguro, M. & Kitagawa, G. (1986) *Akaike information criterion statistics*, Vol. 81. Dordrecht: D. Reidel, p. 26853.
- Staunton, K.M., Robson, S.K.A., Burwell, C.J., Reside, A.E. & Williams, S.E. (2014) Projected distributions and diversity of flightless ground beetles within the Australian wet tropics and their environmental correlates. *PLoS One*, 9, e88635. Available from: <https://doi.org/10.1371/journal.pone.0088635>
- Ştefan, V. (2019) *geobuffer: R package for constructing geodesic buffers using metric radius*. R package version. Available from: <https://rdr.io/cran/spatialEco/man/geo.buffer.html> [Accessed 27th August 2022].
- Storlie, C.J., Phillips, B.L., Vanderwal, J.J. & Williams, S.E. (2013) Improved spatial estimates of climate predict patchier species distributions. *Diversity and Distributions*, 19, 1106–1113. Available from: <https://doi.org/10.1111/ddi.12068>
- Tarabon, S., Bergès, L., Dutoit, T. & Isselin-Nondedeu, F. (2019) Environmental impact assessment of development projects improved by merging species distribution and habitat connectivity modelling. *Journal of Environmental Management*, 241, 439–449. Available from: <https://doi.org/10.1016/j.jenvman.2019.02.031>
- TERN AusCover. (2013) *Fire frequency – AVHRR, Australian algorithm, Australia coverage (Product pages.FireFreq AVHRR) – XWiki*. Made available by the AusCover facility (<http://www.auscover.org.au>) of the Terrestrial Ecosystem Research Network (TERN, <http://www.tern.org.au>). Available from: <http://www.auscover.org.au/purl/avhrr-fire-frequency> [Accessed 13th May 2020].
- Torabian, S., Ranaie, M., Feizabadi, H.A. & Chisholm, L. (2021) Integrating gap analysis and corridor design with less used species distribution models to improve conservation network for two rare mammal species (*Gazella bennettii* and *Vulpes cana*) in Central Iran. *Contemporary Problems of Ecology*, 14, 550–563. Available from: <https://doi.org/10.1134/S1995425521050103>
- Uzqueda, A., Burnett, S., Bertola, L.V. & Hoskin, C.J. (2020) Quantifying range decline and remaining populations of the large marsupial carnivore of Australia's tropical rainforest.

- Journal of Mammalogy*, 101, 1021–1034. Available from: <https://doi.org/10.1093/jmammal/gyaa077>
- Van Dyck, S. (1992) Raising an old glider's ghost – a devil of an exorcise. *Wildlife Australia*, 28, 10–13.
- Van Dyck, S. (1993) The taxonomy and distribution of *Petaurus gracilis* (Marsupialia: Petauridae), with notes on its ecology and conservation status. *Memoirs of the Queensland Museum*, 33, 122.
- Vasudev, D., Fletcher, R.J., Goswami, V.R. & Krishnadas, M. (2015) From dispersal constraints to landscape connectivity: lessons from species distribution modeling. *Ecography*, 38, 967–978. Available from: <https://doi.org/10.1111/ecog.01306>
- Velasco, J.A. & González-Salazar, C. (2019) Akaike information criterion should not be a “test” of geographical prediction accuracy in ecological niche modelling. *Ecological Informatics*, 51, 25–32. Available from: <https://doi.org/10.1016/j.ecoinf.2019.02.005>
- Veloz, S.D. (2009) Spatially autocorrelated sampling falsely inflates measures of accuracy for presence-only niche models. *Journal of Biogeography*, 36, 2290–2299. Available from: <https://doi.org/10.1111/j.1365-2699.2009.02174.x>
- Vignali, S., Barras, A.G., Arlettaz, R. & Braunisch, V. (2020) SDMtune: an R package to tune and evaluate species distribution models. *Ecology and Evolution*, 10, 11488–11506. Available from: <https://doi.org/10.1002/ece3.6786>
- Vollering, J., Halvorsen, R., Auestad, I. & Rydgren, K. (2019) Bunching up the background betters bias in species distribution models. *Ecography*, 42, 1717–1727. Available from: <https://doi.org/10.1111/ecog.04503>
- Vollering, J., Halvorsen, R. & Mazzoni, S. (2019) The MIAMaxent R package: variable transformation and model selection for species distribution models. *Ecology and Evolution*, 9, 12051–12068. Available from: <https://doi.org/10.1002/ece3.5654>
- Walsh, R.P.D. & Lawler, D.M. (1981) Rainfall seasonality: description, spatial patterns and change through time. *Weather*, 36, 201–208. Available from: <https://doi.org/10.1002/j.1477-8696.1981.tb05400.x>
- Warren, D.L., Glor, R.E. & Turelli, M. (2010) ENMTools: a toolbox for comparative studies of environmental niche models. *Ecography*, 33, 607–611. Available from: <https://doi.org/10.1111/j.1600-0587.2009.06142.x>
- Williams, S.E., Pearson, R.G. & Walsh, P.J. (1995) Distributions and biodiversity of the terrestrial vertebrates of Australia's wet tropics: a review of current knowledge. *Pacific Conservation Biology*, 2, 327–362. Available from: <https://doi.org/10.1071/PC960327>
- Wysong, M.L., Iacona, G.D., Valentine, L.E., Morris, K. & Ritchie, E.G. (2020) On the right track: placement of camera traps on roads improves detection of predators and shows non-target impacts of feral cat baiting. *Wildlife Research*, 47, 557–569. Available from: <https://doi.org/10.1071/WR19175>
- Zhang, J. & Li, S. (2017) A review of machine learning based Species' distribution modelling. In: *2017 International conference on Industrial Informatics-Computing Technology, Intelligent Technology, Industrial Information Integration (ICIICII)*. Wuhan, China: IEEE, pp. 199–206. Available from: <https://doi.org/10.1109/ICIICII.2017.76>
- Zimmermann, N.E., Edwards, T.C., Graham, C.H., Pearman, P.B. & Svenning, J.C. (2010) New trends in species distribution modelling. *Ecography*, 33, 985–989. Available from: <https://doi.org/10.1111/j.1600-0587.2010.06953.x>

How to cite this article:

Chang, Y., Bertola, L.V. & Hoskin, C.J. (2023) Species distribution modelling of the endangered Mahogany Glider (*Petaurus gracilis*) reveals key areas for targeted survey and conservation. *Austral Ecology*, 48, 289–312. Available from: <https://doi.org/10.1111/aec.13266>

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.