Global Ecology and Conservation 24 (2020) e01341

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: http://www.elsevier.com/locate/gecco

Modelling the habitat of the endangered Carpentarian Grasswren (*Amytornis dorotheae*): The importance of spatio-temporal habitat availability in a fire prone landscape

Henry J. Stoetzel [a, *], Nicholas P. Leseberg [a], Stephen A. Murphy [a], Margaret E. Andrew [b], Kayler J. Plant [c], Graham N. Harrington [d], James E.M. Watson [a, e]

[a] *School of Earth and Environmental Sciences, University of Queensland, St Lucia, QLD, 4072, Australia*
[b] *Environmental and Conservation Sciences, Murdoch University, Murdoch, WA, 6150, Australia*
[c] *Southern Gulf NRM, 43 Barkly Hwy, Mount Isa, QLD, 4825, Australia*
[d] *Birdlife Northern Queensland, PO Box 680, Malanda, QLD, 4885, Australia*
[e] *Wildlife Conservation Society, Global Conservation Program, 2300 Southern Boulevard Bronx, New York, 10460, NY, USA*

ARTICLE INFO

Article history:
Received 22 October 2020
Accepted 23 October 2020

Keywords:
Habitat dynamics
Species distribution modelling
Threatened species
Extinction risk
Fire frequency
Time since fire

ABSTRACT

Species distribution modelling (SDM), a tool increasingly adopted to quantify geographic range size, often predicts species' distributions as static. However, habitat availability may exhibit spatial and temporal variation when dynamic processes, such as fire, determine suitability. Static SDM approaches may not satisfactorily represent this dynamic process. We investigated the potential use of SDM to quantify dynamic habitat availability by applying the MaxEnt SDM technique to model the habitat of the Carpentarian Grasswren (*Amytornis dorotheae*), an endangered Australian passerine dependent on long unburnt vegetation in a fire prone system. By adjusting a typical SDM approach to incorporate the dynamic nature of fire, we modelled the spatio-temporal variation of suitable habitat over 12 years and compared it to a static modelling approach. Incorporating fire as a dynamic process increased the importance of the fire variable to models (from <18% to >35% permutation importance) and improved model performance, as evaluated by the AUC using cross-validation. Our dynamic model revealed sizeable temporal variation in the area and spatial arrangement of suitable habitat that was not apparent in the static model. This result may partly solve the mystery of why the species occurs as widely separated populations despite the presence of seemingly suitable intervening habitat. In areas where the species is no longer found, habitat availability was less consistent due to frequent fire, and fire refugia was more limited and isolated, when compared to sites with recent records. These results demonstrate that, when compared to a static approach, a dynamic SDM approach can lead to improved understanding of dynamic ecological processes, and their impact on a species.
© 2020 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/).

* Corresponding author. Level 2, Steele Building (3), Room 210, University of Queensland, St Lucia, QLD, 4072, Australia.
E-mail address: h.stoetzel@uq.net.au (H.J. Stoetzel).

https://doi.org/10.1016/j.gecco.2020.e01341
2351-9894/© 2020 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/).

1. Introduction

Understanding the distribution of a species, and the environmental variables that constrain it, is essential when evaluating that species' threat status and conservation requirements (Kukkala and Moilanen 2013; Kujala et al., 2018). Species distribution modelling (SDM) is an established approach that uses environmental characteristics and known occurrence locations to predict the spatial extent of suitable habitat, and therefore a species' potential distribution (Pearson 2007). The outputs from SDMs can provide information useful for conservation management (Pearson 2007; Villero et al., 2017), identifying previously unknown sites of occurrence and mechanisms of population separation (Lu et al., 2012; Fois et al., 2018; Bertola et al., 2019). SDMs typically combine static environmental predictors, or predictors that average environmental variability over time, with a set of species occurrence records (Thuiller and Münkemüller 2010). However, it has been established that these static models are unlikely to capture complex patterns of species occurrence when dynamic ecological processes are present (Franklin 2010; Runge et al., 2015; Zurell et al., 2016; Williams et al., 2017a; Andrew and Fox 2020). Therefore, a static SDM approach may not accurately estimate a species' status if population size responds to significant changes in suitable habitat through time (Purvis et al., 2000; Runge et al., 2015; Webb et al., 2017).

One approach to understanding dynamic distributions is to project an SDM model onto temporally explicit environmental conditions. Numerous studies have used this approach to predict potential distribution shifts for species under future climate scenarios (Kearney et al., 2010; Thuiller and Münkemüller 2010; Austin and Van Niel 2011; Reside et al., 2012b). More recently, distribution modellers have revealed temporal variation in suitable habitat at shorter time scales in response to dynamic resource availability (Osborne and Suárez-Seoane 2007; Runge et al., 2015; Webb et al., 2017; Andrew and Fox 2020). For example, Runge et al. (2015) created a series of time sliced layers depicting temporally explicit weather conditions that drive resource availability for many of Australia's nomadic, arid zone avifauna. Dynamic habitat availability is relevant to many species worldwide, and we propose dynamic modelling, using time-sliced predictions, is potentially applicable to understanding species responses to ecological disturbance.

The tropical savannas of Australia's north are an environment that experiences conditions that are highly variable at the local scale but broadly predictable at the landscape scale (Williams et al., 2017b). In the open grassy woodlands that dominate the region, wet-season rainfall is followed by a hot dry-season, allowing for a cycle of prolific growth and curing and creating ideal conditions for fire (Russell-Smith and Edwards 2006). Large proportions of this biome burn each year (Russell-Smith et al., 2003). While some species use recently burnt habitat, others are dependent on vegetation structure only provided by late-successional habitat (Clarke 2008; Connell et al., 2017). For both cases, the occurrence of fire will result in spatio-temporal shifts in habitat suitability. For some systems, such as those dominated by the genus of highly flammable grass *Triodia*, the return to their pre-fire state may take several years. Species that depend on late successional habitat within these systems are therefore vulnerable to the impacts of frequent fire (Horton 2011). Changes in the nature and frequency of fire across northern Australia is a known threatening process that has been implicated in changes to species assemblages (Woinarski and Legge 2013) and declines of many species (Garnett et al., 2011).

One such species is the Carpentarian Grasswren (*Amytornis dorotheae*), a small passerine (16–17.5 cm; 21–25 g), endemic to northern Australia (Higgins 2001). It occurs in four recognised sub-populations that each occupy distinct localities stretching from the McArthur River in the Northern Territory, southeast to Mount Isa in north-western Queensland (Harrington and Murphy 2016). Long unburnt and therefore structurally complex *Triodia* hummocks provide the Carpentarian Grasswren with foraging substrates, nest sites and refuge from predators and bad weather (Higgins 2001; Perry et al., 2011; Harrington and Murphy 2016). Altered fire regimes that reduce the availability of long unburnt habitat are assumed to be the species' main threat, and as a result, it has been listed federally as endangered (Australian Government 2019). However, the link between fire and population decline is largely circumstantial (Harrington and Murphy 2016) and a more thorough exploration of this relationship is needed to better define the species' population trajectory and true conservation status.

Fire is known to influence the distributions of many species, and the most appropriate measures of fire to consider when modelling a species' distribution will depend on the species of interest (Reside et al., 2012a; Tucker et al., 2012; Watson et al., 2012; Connell et al., 2017; Kelly et al., 2017). Temporal summaries like fire frequency and inter-fire interval have been used to account for fire regimes in SDM (Kelly et al., 2017). Single predictions derived from these measures of fire may only identify areas that have fire regimes broadly suitable for a species persistence, but may fail to identify suitable habitat at any given point in time. Alternatively, a time since fire layer can account for a species preference for particular post-fire successional habitat in SDM (Connell et al., 2017; Lee et al., 2018). However, a single SDM prediction using time since fire depicts habitat at an exact point in time and does not reflect the variation of this habitat through time.

To our knowledge, using SDM to investigate the dynamic nature of suitable habitat over successive years in response to annual fire occurrence has not been explored. This research aims to address uncertainty surrounding the species' distribution, and investigate the role habitat dynamics plays in shaping that distribution, by modelling Carpentarian Grasswren habitat using both static and dynamic approaches. Using the Carpentarian Grasswren as a case study, we develop an approach to evaluate habitat dynamics in response to fire occurrence using Maximum Entropy species distribution modelling (MaxEnt) (Phillips et al., 2006). For the purpose of this research, we define a dynamic modelling approach as one that is developed and applied over space and time. Carpentarian Grasswrens are thought to have limited dispersal capabilities, due to their morphology and/or strong sex-biased philopatry as is observed in other malurids (Cockburn et al., 2003). This is likely to limit the species' occurrence to regions where suitable habitat is consistently available and challenge the species' colonisation of large areas that become unsuitable regularly (Murphy et al., 2011; Perry et al., 2011; Harrington and Murphy 2016). For that

reason, an SDM approach that investigates the dynamic nature of suitable habitat may reveal the impact of these processes better than a static modelling approach. Fire frequency is a measure of fire represented as a static predictor in the only other Carpentarian Grasswren habitat model (Perry et al., 2011), and it is often the chosen measure of fire in SDM studies (Bradie and Leung 2017). To explore potential advancements made by our dynamic approach, we compare it to a static approach that uses fire frequency as a predictor. If an SDM can reasonably model the dynamic availability of Carpentarian Grasswren habitat with the limited available data, it may help conservation managers better understand the processes that are threatening the species. As such, this research is relevant to other threatened species that occur in disturbance prone environments.

2. Materials and methods

2.1. Study area and species occurrence data

The study area encompassed the entire historical range of the Carpentarian Grasswren, within which there are four recognised sub-populations: 'Buckley River', 'Boodjamulla', 'Wollogorang' and 'Borroloola' (Harrington and Murphy 2016)

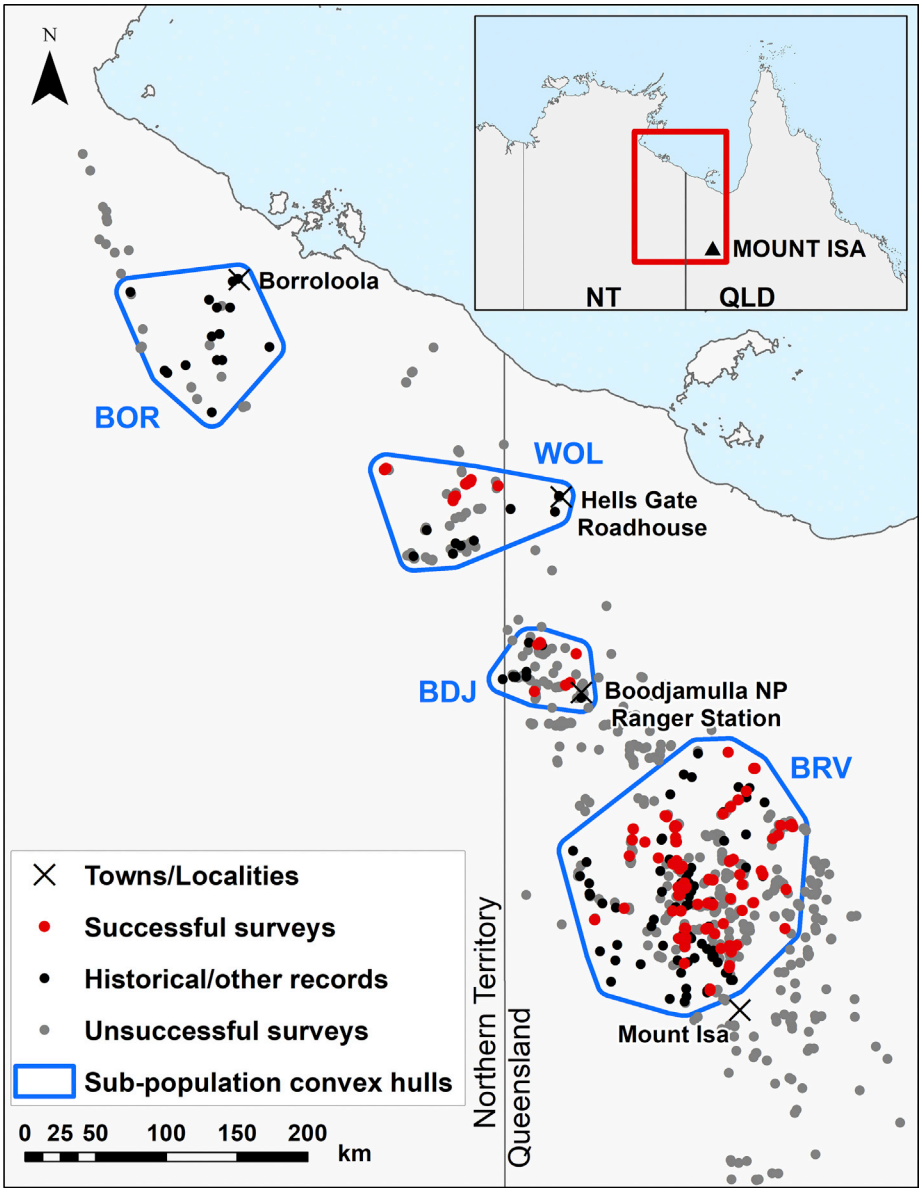

Fig. 1. The four recognised sub populations; Borroloola (BOR), Wollogorang (WOL), Boodjamulla (BDJ) and Buckley River (BRV), are represented with convex hulls encompassing all known Carpentarian Grasswren records and shown alongside successful and unsuccessful grasswren surveys.

(Fig. 1). We obtained 143 georeferenced records of Carpentarian Grasswren from the study from a database compiled by a local conservation organisation that has been conducting regular surveys for Carpentarian Grasswrens throughout their range during since 2008 (Birdlife Northern Queensland, unpublished data); taking place in July 2008–09 and May 2011, 2013, 2016–2019. Survey effort involved call-playback coupled with observation, as described in Harrington and Murphy (2016), and successful surveys represent localities where the species responded to call playback or was observed incidentally when moving within or between sites (Fig. 1). Unsuccessful surveys represent sites at which call-playback failed to confirm the species presence (n = 1172) (Fig. 2). Only successful survey locations, with duplicates removed (n = 115), were used to calibrate models as other historical or incidental records were either outside the temporal range of fire data, or they exhibited high spatial autocorrelation with survey data (Dormann 2007; Crase et al., 2012).

Carpentarian Grasswren exhibit cryptic behaviour and often respond to call playback weakly or not at all. We decided unsuccessful surveys should not be considered as absences in the context of a Carpentarian Grasswren distribution model because they are likely to include false negatives. Alternatively, we chose to use MaxEnt because it is a presence-background approach that does not require absence data, and has performed well in comparison with presence-absence approaches when absence data has high uncertainty (Gibson et al., 2007; Ray et al., 2018).

2.2. Environmental data

Models included up to six spatial predictor variables that previous research has suggested could potentially drive changes in habitat suitability for the species. Predictor variables represented topography, lithology, and either static or temporally explicit fire data. Initially, climatic variables were included as predictors. However, at the regional scale of the study, we expect habitat variables determine habitat suitability. Preliminary models including climatic predictors were noticeably more overfit to the training data, and the climatic variables generally had low importance in the models with abnormal response curves. Thus, these variables were excluded from further analyses.

Two topographic variables, Roughness and Distance to Topographic Feature, were chosen to represent the Carpentarian Grasswren's preference for topographically complex terrain and proximity to hills (Perry et al., 2011). The topographic roughness layer was sourced from a GMTED2010 derived topographic dataset designed for ecological modelling, at a resolution of 1 km (Amatulli et al., 2018). To generate the distance to topographic feature layer, ArcMap v10.5 (Environmental System Research Institute Inc., Redlands, CA, USA) was used to assign cells a value representing the Euclidean distance to the nearest 'peak', 'ridge', 'shoulder' or 'spur' as defined by a 90 m geomorphological landform class layer (Amatulli et al., 2019). The Euclidean distance layer was then resampled to 1 km pixels and the maximum distance was capped at 5 km to ensure the distance range was ecologically relevant to the Carpentarian Grasswren's limited dispersal capability.

To represent lithology and its association with Carpentarian Grasswren occurrence (Murphy et al., 2011; Perry et al., 2011) we used a rasterised version (with 1 km cell size) of the Surface Geology of Australia (1:1,000,000 scale) polygon shapefile (Raymond et al., 2012). Raster cell values in the lithology layer were integer values referencing the 15 broad lithology groups found in the study area. We created an additional variable depicting the Euclidean distance to siliciclastic or metasedimentary siliciclastic lithologies because Carpentarian Grasswren are known to prefer sandstone and metamorphosed sandstone substrates (Murphy et al., 2011). This distance raster was first generated from a fine scale lithology raster before being resampled to 1 km and distances capped to 5 km, as above.

We used Northern Australia Fire Information for fire data (NAFI, https://www.firenorth.org.au/nafi3/, accessed 01/03/2019). Fire scars in NAFI data are mapped monthly and were available from 2000 to 2019. To represent fire as a static environmental layer we built a layer of the minimum fire frequency within each analysis pixel, using a sub-pixel approach. Initially, annual fire scars were amalgamated to produce polygons attributed a 19-year fire frequency (2000–2019) before being rasterised to a fine resolution to preserve polygon boundaries. This raster was then aggregated to 1 km, keeping the minimum fire frequency (i.e. the number of fires that occurred over the full 19-year period) found within each 1 km pixel. We included fire scars from 2000 onwards to account for lag effects of fire patterns prior to occurrence data (which began in 2008) and to give a better representation of the long-term fire frequency patterns expected to be important for Carpentarian Grasswren population persistence. We also trialled variables that depicted the majority fire frequency and the maximum fire frequency of a pixel, but found that the minimum fire frequency was better at explaining the species presence, likely because it is more sensitive to the unburned habitat selected by the species.

For our dynamic approach, we aimed to produce independent, time-sliced, spatial predictions of suitable habitat for each consecutive year from 2008 to 2019. While long term fire frequencies partially determine whether an area is suitable for Carpentarian Grasswren persistence (Perry et al., 2011; Harrington and Murphy 2016), we hypothesise that time since fire is a more appropriate measure of fire for making time-sliced predictions because fire frequency does not directly reflect the post-fire age and thus the structural suitability of spinifex for Carpentarian Grasswrens. Previous research has established that Carpentarian Grasswrens will not occupy spinifex for at least three years post-fire (Perry et al., 2011; Harrington and Murphy 2016). Therefore, for the inclusion of fire as a dynamic variable, we built a time-sliced fire history layer for each year depicting the proportion of each pixel that had experienced at least three growing seasons since it was last burnt (i.e. monsoon seasons; December–March). These layers depicted the conditions at the time Carpentarian Grasswren surveys were conducted (i.e. May in each year). After removing duplicates, two of the 115 occurrence records were located in cells that had been completely burnt over the previous 3 years. However, a fine scale (30 m) Landsat fire history dataset was available for a small section of the study area that corresponded with these two records. After crosschecking these records using the Landsat fire

scars, we found that the occupied cells did have a proportion of unburnt habitat that was not detected in the NAFI fire scar dataset. As such these records were not used to calibrate either of the Maxent models presented here and the total number of occurrences available for calibration was n = 113. We also constructed predictors for additional age classes (i.e. 4ysb, 6ysb and 8ysb), but found that the proportion of a pixel >3ysb was the best predictor and other similar classes were highly correlated.

Other attributes of fire scars (i.e. size and core area) may influence their suitability for Carpentarian Grasswren occupancy in the future if large homogenous fire scars challenge their dispersal capabilities. To assess the species relationship with proximal short-term fire refugium, we constructed another set of time-sliced fire history layers depicting the Euclidean distance to mature habitat, defined by habitat unburnt for at least six growing seasons, again capping the distance to a maximum of 5 km. To incorporate a similar distance variable into the static model, we constructed two layers depicting the Euclidean distance to pixels with a minimum fire frequency of three or less (i.e. burnt three times between 2000 and 2019), and a minimum fire frequency of zero. However, these variables were excluded from the final static model because they were strongly correlated and both had a permutation importance less than one when incorporated independently.

Pairwise Pearson correlation coefficients and Variable Inflation Factors were calculated for all variables, with all below the chosen thresholds of $\geq$0.7 and $\geq$ 10 respectively, demonstrating that all sets of predictors were suitable to include in models (Dormann et al., 2013; Pradhan 2016).

2.3. Species distribution models

We used maximum entropy species distribution modelling (MaxEnt) (Phillips et al., 2006) to predict Carpentarian Grasswren habitat suitability. The static model incorporated fire as a single fire frequency layer, while the dynamic model used temporally explicit fire history layers to produce twelve dynamic time-sliced predictions; one for each year from 2008 to 2019. The static approach matched all occurrences to the single long-term fire frequency layer whereas the dynamic model matched the occurrence records to the fire history layer unique to their year of collection.

MaxEnt requires background data to contrast the environmental conditions at presences with the environmental conditions found throughout the study area. Additionally, MaxEnt requires the assumption of random sampling (Kramer-Schadt et al., 2013; Merow et al., 2013) which is violated by spatial and temporal sampling biases inherent to the survey data used here. More specifically sampling density and extent were higher within and around the Buckley River sub-population, while northern sub-populations were represented by few occurrences. To refine the modelling process, we chose to account for sampling bias when generating background data (Fourcade et al., 2014; Vollering et al., 2019; Moua et al., 2020) using a stratified sampling approach that reflected sampling effort in space and time. This resulted in a background sample that concentrated around survey locations in proportion to survey location density per sampling period. For each sampling period (i.e. year) and sub-population, the successful and usuccessful surveys were used to produce a kernel density raster in ArcMap v10.5 (bandwidth 60 km). Kernel density rasters were then used to inform the sampling probability for background points, stratified by sampling period. Stratified background samples summed to 10,000, and the number drawn from each time-sliced layer was proportional to the number of successful and unsuccessful surveys unique to that sampling period and sub-population.

MaxEnt was implemented in R using the 'dismo' package in a 'samples with data' format (Hijmans et al., 2017; Team 2019). MaxEnt uses several different feature classes to fit relationships among the data, with the types of features and a regularization parameter known as the beta-multiplier specified by the user. We used Akaike Information Criterion corrected for small sample sizes (AICc) to select the optimal regularization parameter and feature classes because it allows a compromise between model goodness of fit and over-complexity (Galante et al., 2018). We used the 'trainMaxent' function from the 'enmSdm' package (Smith 2018) to select the most parsimonious model (fewest feature classes) with the lowest AICc (Morales et al., 2017). The static model used linear, product, quadratic and hinge features with a regularization multiplier of 2.8. The dynamic model used linear, quadratic and hinge features with a regularization parameter of 4.7. To assess the relative contribution of each variable to the model gain, a random k-fold cross-validation procedure with ten replicates was performed in conjunction with a jack-knife test of variable importance (Merow et al., 2013; Shcheglovitova and Anderson 2013). During k-fold cross-validation, ten folds representing independent subsets of the occurrence data (n = 12 test points) were set aside for testing the model. To discern the relative importance of each variable, the values of each variable were randomly permuted on the training data before reevaluating the model on the permuted data. The corresponding drop in training AUC, normalized as a percentage, gives the permutation importance of each variable, which has been found to better reflect ecological importance than other measures of variable importance (Searcy and Shaffer 2016). To further assess model performance, we conducted a spatial cross-validation procedure, using a checkerboard pattern, where presence-background data were split into spatially independent training and testing data (Muscarella et al., 2014). The 'test AUC' computed from each cross-validation procedure (averaged for the k-fold cross validation) gave a metric of model performance (Phillips et al., 2006; Merow et al., 2013).

2.4. Projections of suitable habitat

Models were projected onto stacked environmental layers to produce a predicted continuous surface of the logistic likelihood score based on the environmental conditions in each cell. The logistic predictions ranged between 0 and 1 and were interpreted as an indicator of habitat suitability (Pearson 2007; Norris 2014). Continuous surfaces were visualised in

both their natural continuous state, and as binary maps by applying the 10th percentile training presence threshold, meaning 10% of presence locations were predicted to contain unsuitable habitat. For the purpose of this research all cells above the chosen logistic threshold were considered 'suitable', and all below 'unsuitable'. The static model produced a single continuous prediction, and a single binary prediction using the threshold (0.326). A time-sliced prediction from the dynamic model was produced for each year from 2008 to 2019, depicting the habitat suitability at the end of May. To visualise spatio-temporal habitat dynamics, the continuous time-sliced predictions were converted to binary maps using the logistic threshold (0.27). The 12 binary maps were summed together to produce a single layer where cells were assigned values ranging from 0 to 12, representing the number of times a given cell was predicted to be suitable between 2008 and 2019. Additionally, the dynamic time-sliced predictions were visualised separately as binary maps.

To understand how Carpentarian Grasswren occurrence relates to each habitat map, we overlayed sub-population convex hulls using all known Carpentarian Grasswren records collected after the year 2000. Records prior to the year 2000 were excluded following current extent of occurrence (EOO) estimates by Harrington and Murphy (2016), who reported declines from historical sub-population EOO. For the Borroloola sub-population, we had to use pre-2000 records because this sub-population is thought to have gone extinct prior to 2000. Differences in the temporal continuity of habitat may help explain why Carpentarian Grasswren have disappeared from historical localities. We compared the availability and isolation of fire refugia surrounding historical and current sites from Borroloola and Wollogorang sub-populations. For each distinct patch of refuge habitat (i.e. habitat that was suitable every year between 2008 and 2019) the 'proximity index' metric was calculated using the spatial pattern analysis program FRAGSTATS (McGarigal 1995). Smaller proximity index values correspond with smaller, more isolated habitat patches.

3. Results

3.1. Model evaluation and variable importance

Both static and dynamic models appeared to have good discriminatory ability according to the average test AUC reported from the k-fold cross validation procedure (0.723 and 0.752 respectively; standard deviation 0.058 and 0.035 respectively) (Phillips et al., 2006; Merow et al., 2013); and both models showed the same difference between training and test AUC (−0.031). However, when the data were split into spatially independent training and testing sets, there was a larger difference between training AUC (0.75) and test AUC (0.70) for the static model. Conversely, the dynamic model retained its performance better as there was a smaller difference between training AUC (0.79) and test AUC (0.76), indicating a more general model that is less overfit to the training data.

The importance of variables used to represent fire differed considerably between models (Fig. 2). In the static model, fire frequency had a permutation importance of 18.6%, and was less important compared with distance to siliciclastic lithology and distance to topographic features (31% and 23.4% respectively). Conversely, fire gained importance in the dynamic model when incorporated as the proportion of habitat unburnt for at least three growing seasons, contributing more than all other predictors (35.5%).

3.2. Comparison of static and dynamic model predictions

Both static and dynamic models generally agreed on the distribution of suitable habitat. Nighty four percent of the static binary prediction (i.e. suitable habitat) corresponded with habitat that became suitable at least once according to the composite of dynamic binary predictions. However, there were important differences in how each approach depicts suitability based on different temporal fire patterns. The static model predicted 55,944 km^2 as suitable according to the binary prediction (Fig. 3a). This was less extensive than the total area that became suitable at least once during the 12-year period (95,122 km^2), according to a composite of all binary predictions from the dynamic model (Fig. 3b). The dynamic model predicted a larger area of suitable habitat in some years but less in others; dynamic predictions ranged from 28,806 km^2 (2013) to 69,527 km^2 (2017). The area and arrangement of suitable habitat reflects fire patterns in the preceding years. For example, habitat that was relatively extensive and connected in 2011 (Fig. 4a) experienced substantial contraction and fragmentation because of numerous widespread fires between 2011 and 2013 (Fig. 4b). Following this period of widespread fires, a decline in habitat availability in both 2012 (−14%) and 2013 (−45%) (% change relative to suitable habitat area in preceding year), was followed by a relative increase in suitable habitat in 2014 (56%) and 2015 (49%) and has remained relatively stable since.

3.3. Metapopulation structure

Static and dynamic model outputs revealed the most suitable and consistently suitable habitat closely matches current sub-population extent of occurrence, reflecting the metapopulation's fragmented nature (Fig. 5). The static outputs reflect suitability of long-term fire patterns and thus predict most of the suitable habitat in areas with fire frequencies less than five (Fig. 2C). Conversely, the nature of the time since fire layers allowed the dynamic model to predict snapshots of suitable habitat, and identified habitat that reached suitability after three growing seasons, regardless of its long-term suitability. Single maps produced as the sum of dynamic model predictions, where cell values represent the number of years suitable,

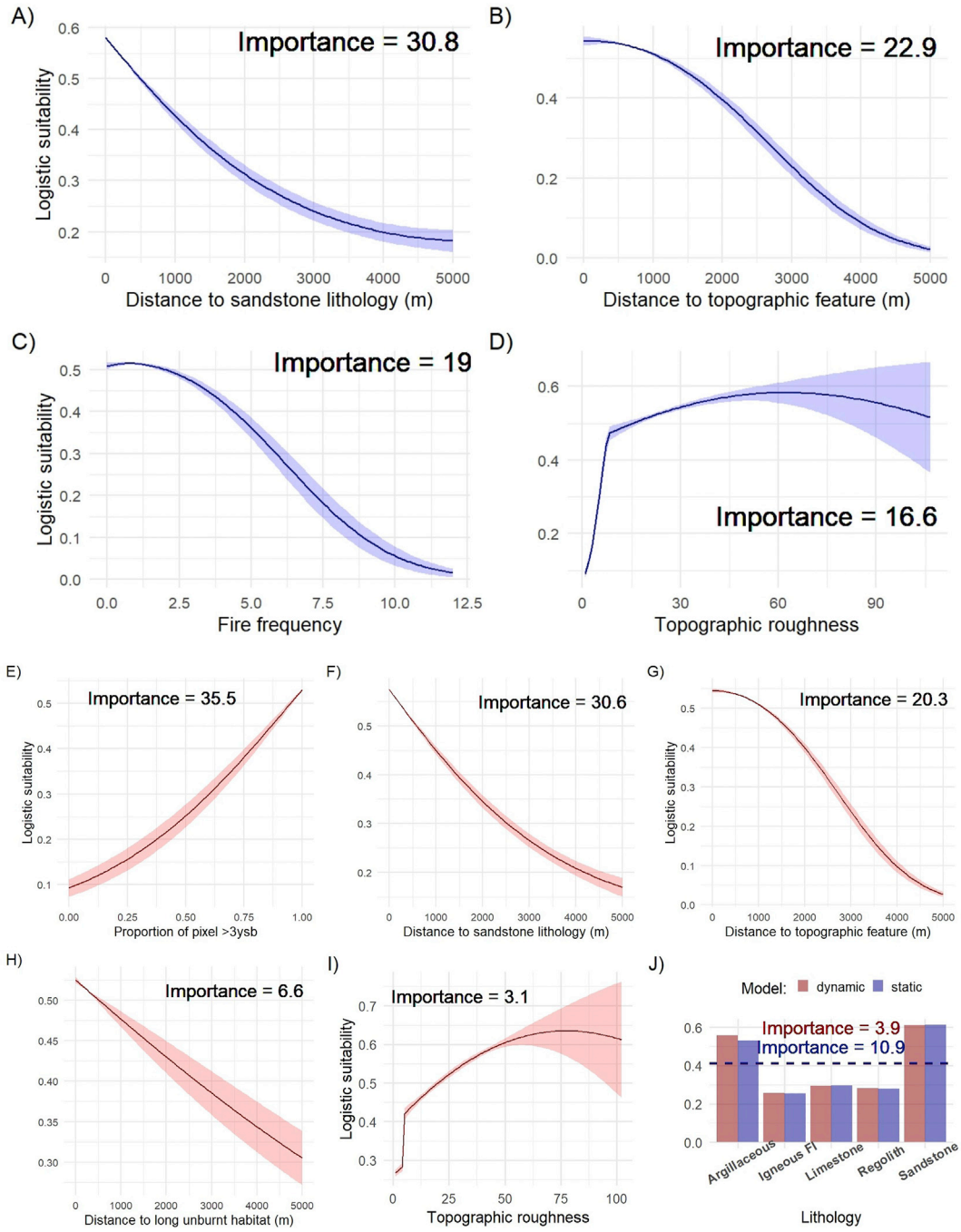

Fig. 2. Response curves from the dynamic model (red) and the static model (blue) show how logistic suitability responds to each variable. Shaded intervals represent the variation in each response over cross-validation replicates. The suitability level of other lithology classes not named in item J is represented by the dotted line (i.e. average for cross-validation replicates), and was almost identical for the dynamic model (0.413) and the static model (0.41). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

reflect the consistency of habitat availability from 2008 to 2019 (Fig. 5b). The areas of habitat that have remained suitable throughout the twelve-year period represent 'refuge habitat'. Generally, these areas are surrounded by other habitat which has been suitable for 10–11 years of 12 and we refer to these areas as 'consistently suitable habitat'. These predictions show that tracts between the three northern sub-populations do hold suitable habitat when fire is absent, though temporal continuity is generally low. Habitat consistency is lowest around the Borroloola region; and refuge and consistently suitable habitat are more limited and isolated. These results support the idea that fire regimes have caused the species disappearance

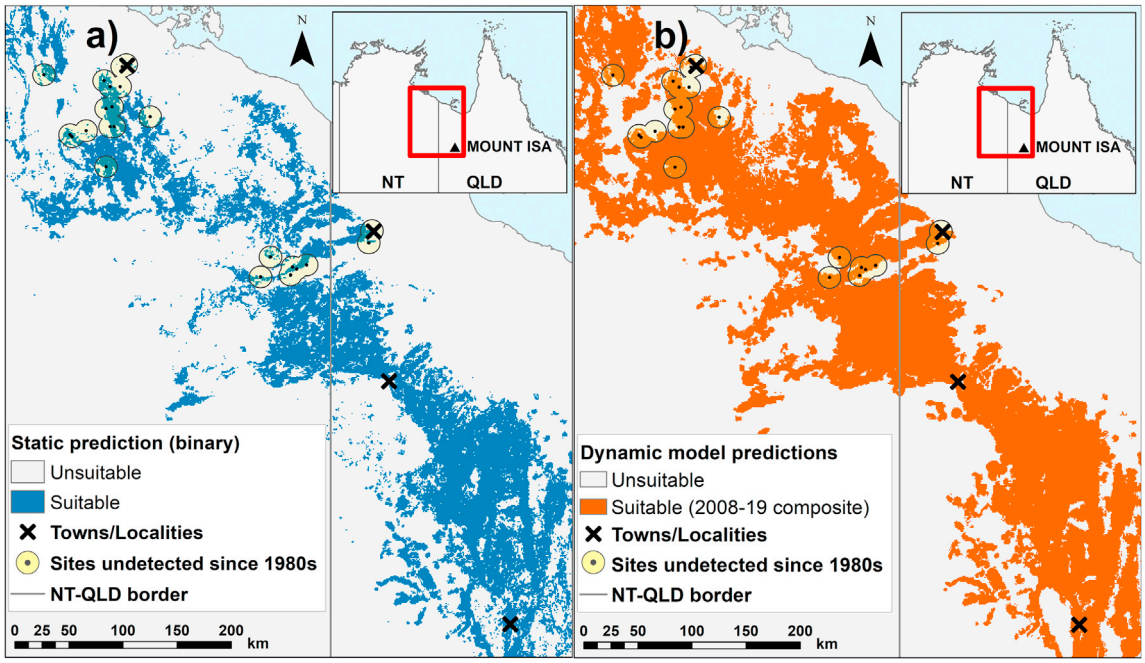

Fig. 3. The binary prediction from the static model (a) identified areas with relatively low fire frequency as suitable. A composite of all dynamic binary predictions shows where suitable habitat occurred at least once between 2009 and 2019 (b). Each binary map used the 10th percentile training presence threshold to define suitable and unsuitable habitat. Towns/Localities as per Fig. 1.

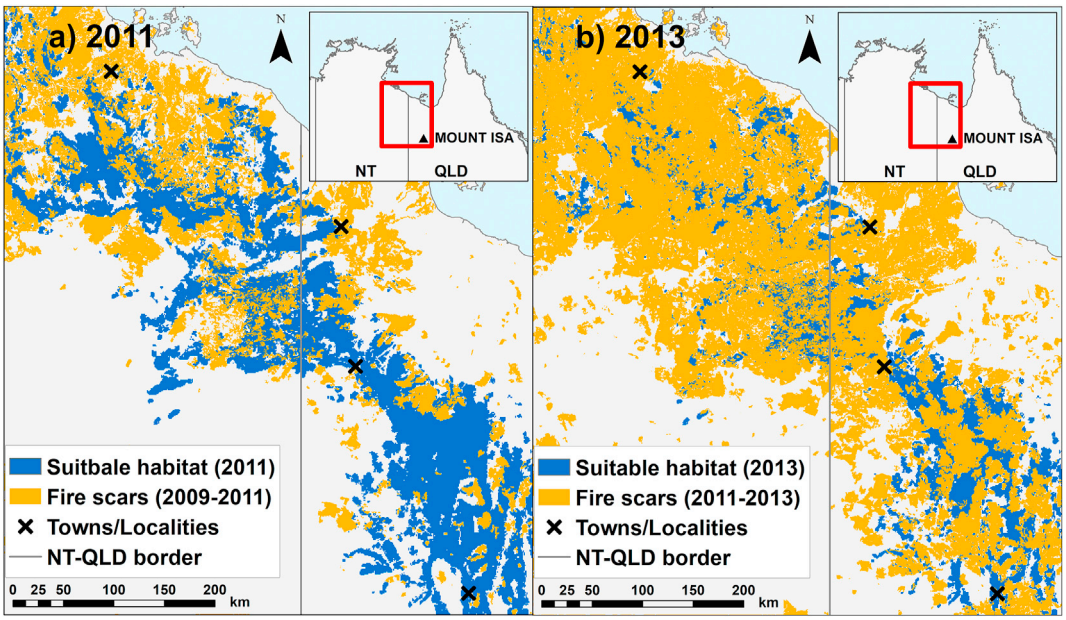

Fig. 4. The dynamic model predicted more extensive and connected habitat in 2011 (a) than in 2013 (b). Predictions are of suitable habitat at the end of May, defined from continuous logistic likelihood surfaces using the 10th percentile training presence threshold. The much reduced and fragmented habitat available in 2013 was the result of widespread fires in the preceding three years. Towns/Localities as per Fig. 1.

from this area (Harrington and Murphy, 2019). The fragmented arrangement of refuge and consistently suitable habitat corresponds with the fragmented nature of the species' metapopulation. However, both models failed to explain why there are no recent observations of the species between the two southern sub-population convex hulls. Despite a substantial amount of refuge habitat, Carpentarian Grasswren have not been observed in this 'corridor' since 2003. However, relatively

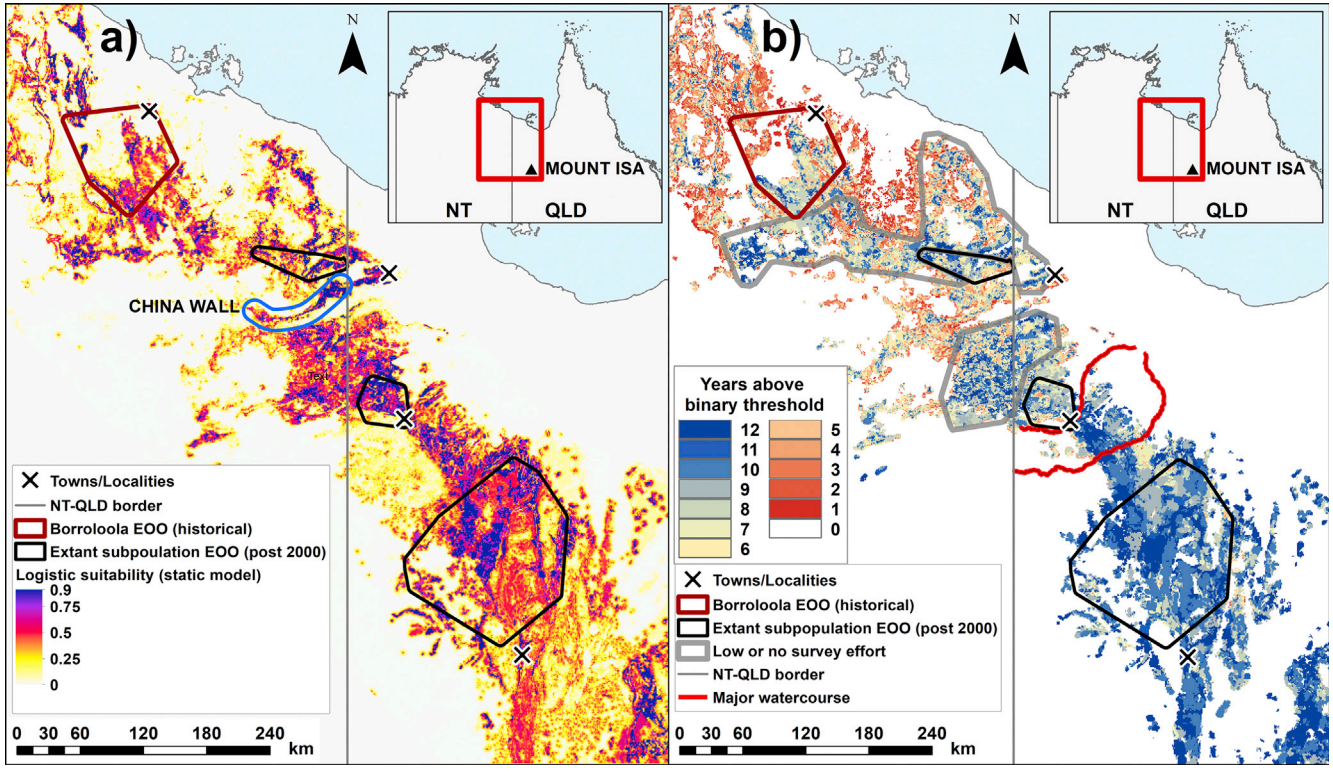

Fig. 5. The current extent of occurrence (EOO) for extant sub-populations are convex hulls constructed using all Carpentarian Grasswren records collected post 2000; Wollogorang (WOL), Boodjamulla (BDJ) and Buckley River (BKR) (refer to Fig. 1). The Borroloola (BOR) EOO is constructed using historical records. The static model prediction (a) depicts the logistic likelihood of cells (i.e. suitability). The sum of twelve dynamic model predictions (b) shows the number of years a cell has been suitable, according to the 10th percentile training presence threshold, and reflects the consistency of habitat availability. Grey polygons enclose areas containing consistently suitable habitat and refuge that have experienced little to no search effort. Towns/Localities as per Fig. 1.

few surveys (n = 20) were conducted in suitable habitat between the two major watercourses that isolate this area (Fig. 4b) and most sites have not been revisited to confirm the species absence. Furthermore, these two major watercourses (i.e. Gregory River and Lawn Hill Creek) may hinder Carpentarian Grasswren dispersal into the intervening area (Harrington and Murphy 2016), and as a result the species may occur in this 'corridor' at lower densities, especially if the fire history was unsuitable in the past.

Both models agree that the extent and consistency of suitable habitat proximate to the Boodjamulla and Wollogorang sub-populations is limited, and historical locations with no recent records reflect low suitability and consistency (e.g. China Wall & Borroloola) (Fig. 5). However, the models did identify areas with low fire frequency and consistent suitability outside current sub-population EOOs that have experienced little search effort, particularly in the centre of the species' potential range. (Fig. 5). Historical sites where the species has not been detected since the 1980s were predicted to contain suitable habitat (Fig. 3), despite the fact these localities were not represented in the training data (Fig. 1). However, in years following frequent and widespread fire habitat became severely reduced (i.e. Fig. 4b). Furthermore, refuge habitat around these historical sites was more limited and isolated in comparison with more recent sites. The average proximity index was low for patches of refuge habitat within 5 km of historical Wollogorang records (1.27) and Borroloola records (1.98). Patches of refuge within 5 km of current Wollogorang records were less isolated (average proximity index = 5.93). Additionally, only one patch of refuge had a proximity index >2.6 and this was still more isolated than the five largest patches within 5 km of recent Wollogorang occurences (proximity index = 8.32–16.19). Furthermore, within 5 km of historical Wollogorang sites, less than 4% of pixels were refuge habitat and 7% remained suitable for 11–12 years between 2008 and 2019. Within 5 km of historical Borroloola occurrences, 9% of pixels were refuge habitat and 11% remained suitable for 11–12 years. Conversely, at sites where the species is still persisting in the northern sector of the Wollogorang EOO (Fig. 1), 11% of pixels were refuge, and 22% were suitable for 11–12 years. Finally, extant EOOs (Fig. 5) contained more habitat that was suitable for 10–12 years (16–45%) compared with the apparently extinct Borroloola EOO (8%).

4. Discussion

4.1. Comparison of static and dynamic approaches

To better understand the potential habitat (and therefore distribution) of Carpentarian Grasswren, we incorporated the dynamic nature of fire into MaxEnt species distribution modelling. Accounting for the temporally explicit fire conditions when occurrence records were collected, by using a dynamic sequence of layers that reflected post-fire age, allowed for better models that assessed the species relationship with fire. The higher average test AUC of the dynamic model suggest that it performed well in comparison with the static approach. Moreover, the dynamic model retained its performance when crosschecked using spatial cross-validation, unlike the static model. Additionally, when incorporating fire in a dynamic manner, its relative importance in the model increased substantially, becoming the most important predictor.

The relatively low contribution of the fire frequency variable to static models likely results from an inferior explanation of Carpentarian Grasswren occurrence in comparison with time since fire. These findings support recent circumstantial inference that Carpentarian Grasswrens depend on relatively long unburnt habitat, and are threatened by unsuitable fire patterns (Harrington and Murphy 2016). Because the static model incorporates relatively long-term fire patterns, the single static prediction will better reflect areas where the species is more likely to persist than any single time sliced prediction from the dynamic model. However, once considered simultaneously, time-sliced predictions have a synergistic effect and the habitat dynamics they reveal can support ecological inference.

The mechanism driving the disjunct Carpentarian Grasswren distribution is unclear given that apparently suitable habitat is observed between sub-populations (Harrington and Murphy 2016). While the static model did confirm the fragmented nature of sub-populations, suggesting that high fire frequency might be the driver, the dynamic predictions revealed more detail about the mechanism. It showed that habitat availability fluctuates through time, with very limited areas of consistently suitable habitat. We suggest that these areas have been too small for too long to maintain remnant populations and too isolated too often for recolonisation to have occurred, especially by a species such as the grasswren, with their suspected limited dispersal capabilities.

In contrast, persistence in the extant sub-populations has been supported by the consistent presence of large areas of suitable habitat, including the availability of post-fire refugia which existed in spatial configurations more suited to the species' dispersal abilities. Assuming the importance of these characteristics for Carpentarian Grasswren occurrence, the species may have persisted undetected in a substantial amount of habitat to the west of the Boodjamulla EOO and to the north-east of the Wollogorang EOO. This habitat is within close proximity of habitat with recent records. The presence of fire refugia and lack of sampling in these areas suggests Carpentarian Grasswren presence may have gone undetected, given the species is cryptic and the habitat is difficult to access. The static model outputs corroborate this speculation; predicting suitable habitat in these unsurveyed areas. Additionally, further search effort is required in the habitat corridor between the Buckley River and Boodjamulla EOOs to confirm the species absence. An ample amount of refuge habitat suggests these sub-populations are connected. However, it is important to understand whether Carpentarian Grasswrens can colonise this area, from the north or south; the presence of two major watercourses (and the associated habitats) potentially challenge the species poor dispersal capabilities. Targeted surveys in refuge habitat and consistently suitable habitat will improve confidence in the species' presence or absence, and thus, confidence in the species' true distribution.

4.2. Implications for extinction risk and fire management

Our study has underscored the need to consider the dynamic nature of habitat availability, in this case driven by fire, when understanding species' distributions. Our dynamic model shows that large fire events that leave little unburnt refugia are likely to lead to local extinction, which is reflected in the absence of grasswrens from otherwise suitable habitat between each sub-population. While Carpentarian Grasswrens can use habitat within 3–4 years post-fire, the presence of long-term fire refugia in proximity to all sub-populations probably reflects a habitat requirement for population persistence, a theme that echoes a finding by Murphy et al. (2010). Sub-populations may be centred around long term refugia because these areas provide the only reliable source for dispersal and re-colonisation at a scale that is biologically relevant to grasswrens. Recolonisation into areas that have experienced repeated homogenous fires is likely to be very slow for Carpentarian Grasswrens, given their likely limited dispersal capabilities. Indeed, in the absence of active fire management to maintain unburnt refugia, we suggest that recolonisation is unlikely to occur.

We also argue that in some areas, recolonisation may be unlikely even if fire management improves because remnant populations are now so distant. In such cases, recolonisation may well rely on a combination of successful fire management and active re-introduction. Active fire management with prescribed burning at a regional scale in the cooler months of the year can increase availability of unburnt refugia during subsequent wildfire events (Legge et al., 2011). For management to actively protect refugia after widespread fire, dynamic predictions can help identify these priority areas if projection surfaces are updated as new fire data becomes available. Predicting habitat dynamics in response to fire, and identifying refugia, could have important implications for designing prescribed fire regimes (Reside et al., 2019). Adapting this research to consider multiple threatened species may enable management to formulate a more comprehensive approach to prescribed burning for conservation.

5. Conclusion

We provide a SDM approach that incorporates the dynamic nature of fire through the use of sequential, time sliced, fire history layers. Both static and dynamic approaches produced models that performed reasonably well, and were able to identify potentially suitable areas that should be surveyed to confirm the distribution of the Carpentarian Grasswren. However, incorporating fire into SDM using a dynamic modelling approach demonstrated that there are significant fluctuations in available habitat as a result of fire, and large areas of the species' potential distribution do not remain suitable consistently. This results in few refuges over time, and fragmentation of habitat, supporting the idea that inappropriate fire regimes are driving declines. This important detail is not captured by the static modelling approach that is widely used. Visualising fluctuations in habitat availability can assist in explaining metapopulation structure, and holds relevance for conservation management and real time monitoring of species' extinction risk. Field validation of model outputs will further assess the relevance of model outputs and improve confidence in the species' true distribution. While this research supports the use of dynamic modelling in relation to fire, the technique is potentially applicable to modelling any habitat that responds to a range of dynamic processes.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors. We thank BirdLife Northern Queensland for providing Carpentarian Grasswren occurrence data, and thank all those involved in its collection. We thank Southern Gulf NRM for their support of grasswren surveys. Gabriel Crowley and Lea Ezzy have made important contributions to grasswren monitoring and management, supporting the work that made this research possible. April Reside and Ayesha Tulloch provided advice and expertise in habitat modelling when developing the project's methodology.

References

Amatulli, G., Domisch, S., Tuanmu, M.-N., Parmentier, B., Ranipeta, A., Malczyk, J., Jetz, W., 2018. A suite of global, cross-scale topographic variables for environmental and biodiversity modeling. Scientific Data 5, 180040.

Andrew, M.E., Fox, E., 2020. Modelling species distributions in dynamic landscapes: the importance of the temporal dimension. J. Biogeogr. 47, 1510–1529.

Austin, M.P., Van Niel, K.P., 2011. Improving species distribution models for climate change studies: variable selection and scale. J. Biogeogr. 38, 1–8.

Australian Goveronment Department of the Environment, 2019. *Amytornis Dorotheae* in Species Profile and Threats Database. Department of the Environment, Canberra.

Bertola, L.V., Higgie, M., Hoskin, C.J., 2019. Resolving distribution and population fragmentation in two leaf-tailed gecko species of north-east Australia: key steps in the conservation of microendemic species. Aust. J. Zool. 66, 152–166.

Bradie, J., Leung, B., 2017. A quantitative synthesis of the importance of variables used in MaxEnt species distribution models. J. Biogeogr. 44, 1344–1361.

Clarke, M.F., 2008. Catering for the needs of fauna in fire management: science or just wishful thinking? Wildl. Res. 35, 385–394.

Cockburn, A., Osmond, H.L., Mulder, R.A., Green, D.J., Double, M.C., 2003. Divorce, dispersal and incest avoidance in the cooperatively breeding superb fairy-wren *Malurus cyaneus*. J. Anim. Ecol. 72, 189–202.
Connell, J., Watson, S.J., Taylor, R.S., Avitabile, S.C., Clarke, R.H., Bennett, A.F., Clarke, M.F., 2017. Testing the effects of a century of fires: requirements for post-fire succession predict the distribution of threatened bird species. Divers. Distrib. 23, 1078–1089.
Crase, B., Liedloff, A.C., Wintle, B.A., 2012. A new method for dealing with residual spatial autocorrelation in species distribution models. Ecography 35, 879–888.
Dormann, C.F., 2007. Effects of incorporating spatial autocorrelation into the analysis of species distribution data. Global Ecol. Biogeogr. 16, 129–138.
Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36, 27–46.
Fois, M., Cuena-Lombraña, A., Fenu, G., Bacchetta, G., 2018. Using species distribution models at local scale to guide the search of poorly known species: review, methodological issues and future directions. Ecol. Model. 385, 124–132.
Fourcade, Y., Engler, J.O., Rödder, D., Secondi, J., 2014. Mapping species distributions with MAXENT using a geographically biased sample of presence data: a performance assessment of methods for correcting sampling bias. PloS One 9, e97122.
Franklin, J., 2010. Moving beyond static species distribution models in support of conservation biogeography. Divers. Distrib. 16, 321–330.
Galante, P.J., Alade, B., Muscarella, R., Jansa, S.A., Goodman, S.M., Anderson, R.P., 2018. The challenge of modeling niches and distributions for data-poor species: a comprehensive approach to model complexity. Ecography 41, 726–736.
Garnett, S., Szabo, J., Dutson, G., 2011. The Action Plan for Australian Birds 2010. CSIRO Publishing.
Gibson, L., Barrett, B., Burbidge, A., 2007. Dealing with uncertain absences in habitat modelling: a case study of a rare ground-dwelling parrot. Divers. Distrib. 13, 704–713.
Harrington, G.N., Murphy, S.A., 2016. The distribution and conservation status of Carpentarian grasswrens (Amytornis dorotheae), with reference to prevailing fire patterns. Pac. Conserv. Biol. 21, 291–297.
Higgins, P.J., 2001. Handbook of Australian, New Zealand & antarctic birds. In: Tyrant-flycatchers to Chats, 5. Oxford University Press.
Hijmans, R.J., Phillips, S., Leathwick, J., Elith, J., Hijmans, M.R.J., 2017. Package 'dismo'. Circle 9, 1–68.
Horton, H., 2011. Of spinifex and grasswrens, with particular reference *to'Amytornis ballarae*', the kalkadoon grasswren. Queensl. Nat. 49, 3.
Kearney, M.R., Wintle, B.A., Porter, W.P., 2010. Correlative and mechanistic models of species distribution provide congruent forecasts under climate change. Conservation Letters 3, 203–213.
Kelly, L.T., Haslem, A., Holland, G.J., Leonard, S.W., MacHunter, J., Bassett, M., Bennett, A.F., Bruce, M.J., Chia, E.K., Christie, F.J., 2017. Fire regimes and environmental gradients shape vertebrate and plant distributions in temperate eucalypt forests. Ecosphere 8, e01781.
Kramer-Schadt, S., Niedballa, J., Pilgrim, J.D., Schröder, B., Lindenborn, J., Reinfelder, V., Stillfried, M., Heckmann, I., Scharf, A.K., Augeri, D.M., 2013. The importance of correcting for sampling bias in MaxEnt species distribution models. Divers. Distrib. 19, 1366–1379.
Kujala, H., Moilanen, A., Gordon, A., 2018. Spatial characteristics of species distributions as drivers in conservation prioritization. Methods in Ecology and Evolution 9, 1121–1132.
Kukkala, A.S., Moilanen, A., 2013. Core concepts of spatial prioritisation in systematic conservation planning. Biol. Rev. 88, 443–464.
Lee, A.T., Reeves, B., Wright, D.R., 2018. Hottentot buttonquail *Turnix hottentottus*: endangered or just overlooked? Bird. Conserv. Int. 1–8.
Legge, S., Murphy, S., Kingswood, R., Maher, B., Swan, D., 2011. EcoFire: restoring the biodiversity values of the Kimberley region by managing fire. Ecol. Manag. Restor. 12, 84–92.
Lu, N., Jia, C.-X., Lloyd, H., Sun, Y.-H., 2012. Species-specific habitat fragmentation assessment, considering the ecological niche requirements and dispersal capability. Biol. Conserv. 152, 102–109.
McGarigal, K., 1995. FRAGSTATS: Spatial Pattern Analysis Program for Quantifying Landscape Structure. US Department of Agriculture, Forest Service, Pacific Northwest Research Station.
Merow, C., Smith, M.J., Silander Jr., J.A., 2013. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. Ecography 36, 1058–1069.
Morales, N.S., Fernández, I.C., Baca-González, V., 2017. MaxEnt's parameter configuration and small samples: are we paying attention to recommendations? A systematic review. PeerJ 5, e3093.
Moua, Y., Roux, E., Seyler, F., Briolant, S., 2020. Correcting the effect of sampling bias in species distribution modeling–A new method in the case of a low number of presence data. Ecol. Inf. 101086.
Murphy, S.A., Legge, S.M., Heathcote, J., Mulder, E., 2010. The effects of early and late-season fires on mortality, dispersal, physiology and breeding of red-backed fairy-wrens (*Malurus melanocephalus*). Wildl. Res. 37, 145–155.
Murphy, S., Harrington, G., Felderhof, L., 2011. Preliminary Spatial Model Using Fire Scar Data to Monitor Carpentarian Grasswrens. Report by Map IT and Birds Australia North Queensland.
Muscarella, R., Galante, P.J., Soley-Guardia, M., Boria, R.A., Kass, J.M., Uriarte, M., Anderson, R.P., 2014. ENM eval: an R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. Methods in Ecology and Evolution 5, 1198–1205.
Norris, D., 2014. Model thresholds are more important than presence location type: understanding the distribution of lowland tapir (Tapirus terrestris) in a continuous Atlantic forest of southeast Brazil. Tropical Conservation Science 7, 529–547.
Osborne, P.E., Suárez-Seoane, S., 2007. Identifying core areas in a species' range using temporal suitability analysis: an example using little bustards *Tetrax tetrax L.* in Spain. Biodivers. Conserv. 16, 3505–3518.
Pearson, R.G., 2007. Species' distribution modeling for conservation educators and practitioners. Synthesis. American Museum of Natural History 50, 54–89.
Perry, J., Fisher, A., Palmer, C., 2011. Status and habitat of the carpentarian grasswren (*Amytornis dorotheae*) in the northern territory. Emu-Austral Ornithology 111, 155–161.
Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. Ecol. Model. 190, 231–259.
Pradhan, P., 2016. Strengthening MaxEnt modelling through screening of redundant explanatory bioclimatic variables with variance inflation factor analysis. Researcher 8, 29–34.
Purvis, A., Gittleman, J.L., Cowlishaw, G., Mace, G.M., 2000. Predicting extinction risk in declining species. Proc. Roy. Soc. Lond. B Biol. Sci. 267, 1947–1952.
Ray, D., Behera, M.D., Jacob, J., 2018. Evaluating ecological niche models: a comparison between Maxent and GARP for predicting distribution of Hevea brasiliensis in India. Proc. Natl. Acad. Sci. India B Biol. Sci. 88, 1337–1343.
Raymond, O., Liu, S., Gallagher, R., Zhang, W., Highet, L., 2012. Surface Geology of Australia 1: 1 Million Scale Dataset 2012 Edition. Commonwealth of Australia, Geoscience Australia.
Reside, A.E., Briscoe, N.J., Dickman, C.R., Greenville, A.C., Hradsky, B.A., Kark, S., Kearney, M.R., Kutt, A.S., Nimmo, D.G., Pavey, C.R., 2019. Persistence through tough times: fixed and shifting refuges in threatened species conservation. Biodivers. Conserv. 28, 1303–1330.
Reside, A.E., VanDerWal, J., Kutt, A., Watson, I., Williams, S., 2012a. Fire regime shifts affect bird species distributions. Divers. Distrib. 18, 213–225.
Reside, A.E., VanDerWal, J., Kutt, A.S., 2012b. Projected changes in distributions of Australian tropical savanna birds under climate change using three dispersal scenarios. Ecology and Evolution 2, 705–718.
Runge, C.A., Tulloch, A., Hammill, E., Possingham, H.P., Fuller, R.A., 2015. Geographic range size and extinction risk assessment in nomadic species. Conserv. Biol. 29, 865–876.
Russell-Smith, J., Edwards, A.C., 2006. Seasonality and fire severity in savanna landscapes of monsoonal northern Australia. Int. J. Wildland Fire 15, 541–550.
Russell-Smith, J., Yates, C., Edwards, A., Allan, G.E., Cook, G.D., Cooke, P., Craig, R., Heath, B., Smith, R., 2003. Contemporary fire regimes of northern Australia, 1997–2001: change since Aboriginal occupancy, challenges for sustainable management. Int. J. Wildland Fire 12, 283–297.
Searcy, C.A., Shaffer, H.B., 2016. Do ecological niche models accurately identify climatic determinants of species ranges? Am. Nat. 187, 423–435.

Shcheglovitova, M., Anderson, R.P., 2013. Estimating optimal complexity for ecological niche models: a jackknife approach for species with small sample sizes. Ecol. Model. 269, 9–17.
Smith, A., 2018. enmSdm: tools for modeling species niches and distributions. Rpackage version 0.2.
Team, R.C., 2019. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.
Thuiller, W., Münkemüller, T., 2010. Habitat suitability modeling. Effects of climate change on birds 77–85.
Tucker, C.M., Rebelo, A., Manne, L., 2012. Contribution of disturbance to distribution and abundance in a fire-adapted system. Ecography 35, 348–355.
Villero, D., Pla, M., Camps, D., Ruiz-Olmo, J., Brotons, L., 2017. Integrating species distribution modelling into decision-making to inform conservation actions. Biodivers. Conserv. 26, 251–271.
Vollering, J., Halvorsen, R., Auestad, I., Rydgren, K., 2019. Bunching up the background betters bias in species distribution models. Ecography.
Watson, S.J., Taylor, R.S., Nimmo, D.G., Kelly, L.T., Haslem, A., Clarke, M.F., Bennett, A.F., 2012. Effects of time since fire on birds: how informative are generalized fire response curves for conservation management? Ecol. Appl. 22, 685–696.
Webb, M.H., Terauds, A., Tulloch, A., Bell, P., Stojanovic, D., Heinsohn, R., 2017. The importance of incorporating functional habitats into conservation planning for highly mobile species in dynamic systems. Conserv. Biol. 31, 1018–1028.
Williams, H.M., Willemoes, M., Thorup, K., 2017a. A temporally explicit species distribution model for a long distance avian migrant, the common cuckoo. J. Avian Biol. 48, 1624–1636.
Williams, R., Cook, G., Liedloff, A., Bond, W., 2017b. Australia's tropical savannas: vast, ancient and rich landscapes. Australian Vegetation 368–388.
Woinarski, J.C., Legge, S., 2013. The impacts of fire on birds in Australia's tropical savannas. Emu-Austral Ornithology 113, 319–352.
Zurell, D., Thuiller, W., Pagel, J., Cabral, J.S., Münkemüller, T., Gravel, D., Dullinger, S., Normand, S., Schiffers, K.H., Moore, K.A., 2016. Benchmarking novel approaches for modelling species range dynamics. Global Change Biol. 22, 2651–2664.