

# Predicting the past, present and future distributions of an endangered marsupial in a semi-arid environment

J. Riley<sup>1</sup> , M.R.K. Zeale<sup>1</sup>, O. Razgour<sup>2</sup>, J. Turpin<sup>3</sup> & G. Jones<sup>1</sup>

1 School of Biological Sciences, University of Bristol, Bristol, UK

2 University of Exeter, Exeter, UK

3 School of Environmental and Rural Science, University of New England, Armidale, NSW, Australia

## Keywords

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## Correspondence

Joanna Riley, School of Biological Sciences, University of Bristol, Bristol, BS8 1TQ, UK.  
Tel: +44 7872002087, Fax: +61 422973850  
Email: joriley999@gmail.com

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## Abstract

Globally, the impacts of anthropogenic climate change can displace species into more favourable climates. Semi-arid desert specialists, such as the sandhill dunnart, *Sminthopsis psammophila*, are typically susceptible to rainfall deficits, wildfires and extreme temperatures caused by anthropogenic climate change. We first used maximum entropy (MaxEnt) species distribution models (SDMs) to predict the current distribution of *S. psammophila*. Between 2016 and 2018, we ground validated the model's predictions throughout Western Australia, confirming *S. psammophila* in 18 locations in which it was predicted to occur. The predicted distribution of *S. psammophila* appears mostly constrained to within its known range. However, *S. psammophila* was verified 150 km north of its range in Western Australia and connectivity between the South Australian populations was correctly predicted. In 2019, we used updated occurrence data to project SDMs for *S. psammophila* during the mid-Holocene, present day and under two future representative concentration pathways (RCPs) of RCP 4.5 (an optimistic emissions scenario) and RCP 8.5 ("business as usual") for 2050 and 2070. By 2050 (RCP 8.5), almost all Western Australian Great Victoria Desert (WAGVD) habitat is predicted to be unsuitable for *S. psammophila*. By 2070 (RCP 8.5), the climates of the WAGVD and Yellabinna Regional Reserve populations are predicted to become unsuitable, and the species' geographical range is predicted to contract in Australia by 80%. However, the 2070 (RCP 4.5) scenario predicts that this contraction could be halved. As a sandy desert specialist, the distribution of *S. psammophila* is geographically limited at its southern bounds due to the cessation of suitable spinifex (*Triodia* spp.) habitats, and so further extension of the range southwards is not possible. Sympatric desert species may be similarly affected, and we suggest that SDMs will be a useful tool in helping to predict the effects of climate change on their distributions.

## Introduction

Globally, the distributions of many rare or threatened species remain unresolved and the future effects of climate change remain unknown. The geographical distribution of a species can provide insights into its ecology, evolution, population size and response to environmental change. However, data are often limited for less studied threatened species (e.g. Hending et al. 2020; Loiselle et al. 2003) or for those in remotely located regions such as deserts (e.g. Mohammadi et al. 2019).

In Australia, semi-arid and arid (arid zone) ecosystems occupy approximately 70% of the continent and are key conservation foci as they are resource-poor and particularly sensitive to environmental change (Smith & Morton 1990). Arid zone mammal species have suffered recent and rapid declines due to the displacement of the First Australians and the

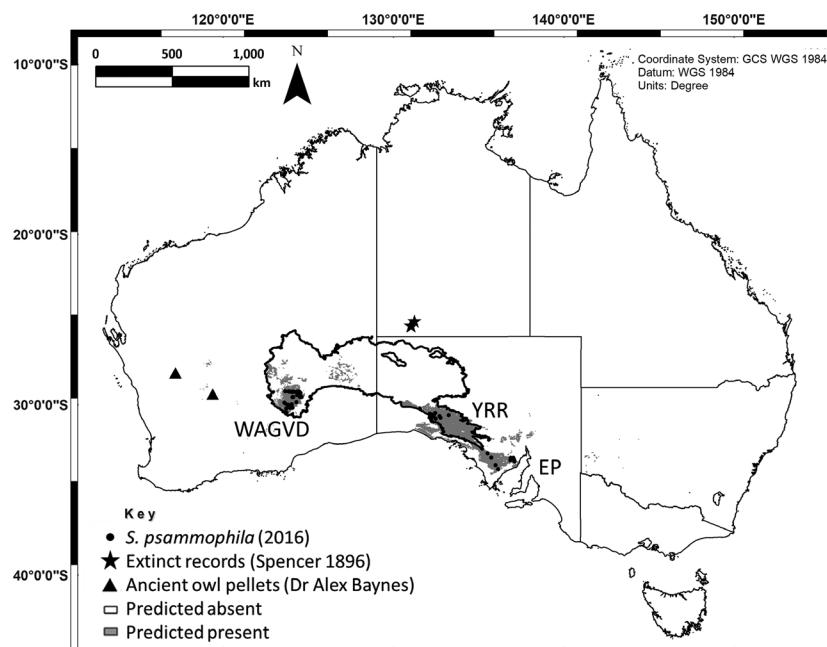
resulting changes in wildfire management, habitat availability and/or habitat densities (Burbidge et al. 1988; Gould 1971; Hallam 1985). The conversion of land to agriculture, industry and/or residence, competition from introduced herbivores and predation by the feral cat, *Felis catus*, and the introduced red fox, *Vulpes vulpes*, are recognized threats (Abbott 2008; Dickman 1996; King & Smith 1985; Short & Smith 1994; Woinarski et al. 2015, 2019). However, many threatened Australian mammals are also vulnerable to the rapid effects of anthropogenic climate change (Hughes 2003; Steffen 2009; McLean 2015, Arid Recovery Reserve 2019). Annual temperatures in Australia have warmed by over 1°C in the past century and in south-west Australia annual rainfall has decreased by up to 20% (Intergovernmental Panel on Climate Change (IPCC), 2014, Bureau of Meteorology (BOM), 2018) (Figure S1). As a result, Australia's biodiversity has been negatively affected, for example, the Bramble

Cay melomys, *Melomys rubicola* (Rodentia), is now extinct due to sea level rise, and species such as flying foxes, *Pteropus* spp. (Chiroptera), are experiencing sudden population crashes due to extreme heat events (Dexter et al., 1995; Hoffmann et al. 2019; Hughes 2003; Lindemayer et al. 2010; Waller et al. 2017; Welbergen et al. 2007). Recovery plans for Australia's threatened species typically address threats such as wildfires, invasive species and habitat loss. Yet, climate change – an ongoing and key threatening process – is rarely confronted (Stewart et al. 2018). Tracking of ecologically favourable climates has already been observed in the distributions of several Australian species. For example, an iconic Australian marsupial, the koala, *Phascolarctos cinereus*, is becoming increasingly restricted to its southern and eastern geographical range and is further threatened by mass die-offs due to wildfires (Adams-Hosking et al. 2011, Dickman 2020). Most species distribution models (SDMs) predict that we are committed to further extinctions due to past, ongoing and future emissions (IPCC 2014; Steffen 2009). However, general circulation models (GCMs) that are used for SDMs predict that the severity of the impacts of climate change can be reduced by reducing greenhouse gas emissions (Commonwealth Scientific & Industrial Research Organisation (CSIRO), 2015; IPCC 2014; Steffen 2009). Hence, there is a legitimate basis for an optimistic future viewpoint (Figueres & Rivett-Carnac 2020).

The sandhill dunnart, *Sminthopsis psammophila*, is listed as endangered nationally in Australia under the Environment Protection & Biodiversity Conservation (EPBC) Act, 1999. *Sminthopsis psammophila* was once widespread throughout

the Australian arid zone but is now known from three semi-arid, precarious and isolated populations only (Fig. 1). *Sminthopsis psammophila* is considered one of Australia's most rare but least studied species and is amongst the top five native species that are most likely to be killed by feral cats (Woolley et al. 2019). *Sminthopsis psammophila* was first recorded by Europeans in the Northern Territory during the Horn Expedition (Spencer, 1896), but subsequently presumed extinct until 1969 when individuals were captured on Eyre Peninsula (EP) in South Australia (Aitken 1971). Individuals were then located throughout EP, in the south-west Western Australian Great Victoria Desert (WAGVD) and within or near the Yellabinnia Regional Reserve (YRR) in the southern South Australian Great Victoria Desert (Copley & Kemper, 1992; Hart & Kitchener 1986; Pearson & Robinson 1990; Ward et al., 2008; Way 2008) (Fig. 1). Records of ancient (~50–500 years BP) *S. psammophila* bones were recently verified from near Yalgoo and Lake Barlee in Western Australia, 400–600 km west of the known WAGVD population (Dr Alex Baynes, pers. comm.) (Fig. 1). While surveys for *S. psammophila* have been undertaken in the Northern Territory, *S. psammophila* has not been recorded there and so appears to be regionally extinct (Churchill, 2001a).

*Sminthopsis psammophila* is regarded as difficult to detect as recent targeted surveys have repeatedly failed despite surveying in suitable sandy spinifex, *Triodia* spp. grassland habitats with deep pitfall traps (Brennan et al. 2012; Burbidge et al., 1976; Ecologia 2009; Gaikhorst & Lambert, 2008, 2009, 2014; GHD, 2010; Ninnox Wildlife Consulting, 2010). Due to the paucity of ecological knowledge on *S.*



**Figure 1** Extant and extinct *S. psammophila* occurrence records in Australia (compiled in 2016) with the binary presence (grey) and absence (white) predictions of MaxEnt 'Model 01: Present distribution'. The known *S. psammophila* populations are in the Western Australian Great Victoria Desert (WAGVD), Yellabinnia Regional Reserve (YRR) and Eyre Peninsula (EP). The Great Victoria Desert (GVD) bioregion border = thick black line and state borders = thin black lines

*psammophila*, providing a robust estimation of the species' distribution is essential for its conservation management.

The dense, southern semi-arid spinifex grassland habitats preferred by *S. psammophila* protect the species against predation but are highly flammable. The viability of remaining populations remains unknown and terrestrial fauna survey effort is low due to Australia's expansive geography (Churchill, 2001a; Woinarski & Burbidge 2016). As rainfall in southern Australia is predicted to continue to decline and become increasingly irregular, there is cause for concern for the future of its semi-arid habitats (BOM 2018). Further, under the "business as usual" future emissions scenario or representative concentration pathway (RCP) 8.5, Australia's annual average temperature relative to preindustrial temperatures is predicted to increase by up to 6°C by the end of the century (Hughes 2003; Steffen 2009). This will cause significant and rapid environmental change that many Australian arid zone species may not be able to adapt to.

Species Distribution Models (SDMs) are a useful tool in the conservation management of threatened species as they provide an evaluation of the relative importance of environmental variables that define the species' niche and are capable of producing robust predictions of geographical distributions (Jones *et al.* 2016). SDMs can be used to infer past or future distributions, assess variations in temporal and spatial biodiversity factors or to explore niche partitioning and interspecific competition (Russo *et al.* 2016). SDMs can also focus survey work on "high-value" areas, that is, areas with a high predicted presence for a threatened species, resulting in more targeted and cost-effective field surveys (Rebelo & Jones 2010; Russo *et al.* 2016). In addition, SDMs are beneficial for the discovery of new populations and are used globally to support a variety of conservation decisions (Guisan *et al.* 2013; Hending *et al.* 2020; Loiselle *et al.* 2003). Maximum entropy (MaxEnt) is a presence-only approach to model species distributions that is often preferred for the conservation management of rare species with limited occurrence records such as *S. psammophila*, as MaxEnt remains sensitive when only few training data are available (Guisan & Thuiller 2005; Razgour *et al.* 2011). MaxEnt consistently outperforms other model algorithms in its predictive performance and studies that ground validate MaxEnt model predictions show that its predicted distributions are realistic (e.g. Rebelo & Jones 2010). By using a presence-only occurrence record approach, MaxEnt negates the errors produced by using SDMs that also require absence records, which are often unreliable for rare and threatened species with detection difficulties.

Our study aims to identify factors limiting the distribution of an 'Endangered' (Environment Protection & Biodiversity Conservation (EPBC) Act, 1999) semi-arid mammal species in Australia and predicts how it will be affected by anthropogenic climate change. To address these aims we (i) first use SDMs to predict the current distribution of *S. psammophila* throughout Australia, (ii) ground validate the predictions from this model, (iii) use our updated occurrence records to refine our models to predict the species' past, present and future distributions, (iv) identify important

strongholds for *S. psammophila* under two future timescales of 2050 and 2070 and emissions scenarios of RCP 4.5 and RCP 8.5 and (v) propose conservation management strategies for threatened semi-arid specialists such as *S. psammophila*. In addition, we discuss historical occurrence records and the extent of the species' range prior to the arrival of Europeans.

## Materials and methods

### Study site

We first predicted the current distribution of *S. psammophila* in 2016 to determine whether there was suitable habitat outside the species' known range. The WAGVD and YRR populations are located in the southern GVD bioregion and the EP population is located in the adjacent semi-arid habitat in South Australia (Fig. 1). The southern GVD is an important natural refugial habitat for *S. psammophila*, as well as many mesic-influenced semi-arid xeric species, and is regarded as one of Australia's last pristine wildernesses as it has largely not been degraded by pastoralism or agriculture and supports many endemic and/or threatened species of flora and fauna (Madigan 1936; Sheard *et al.* 2006; Shephard, 1995).

### Model 01: Present distribution

We used MaxEnt v. 3.4.1. (Phillips *et al.* 2006) to model the current distribution of *S. psammophila* in 2016. Modelling procedures followed Merow *et al.* (2013). The extent of the study was all of Australia and the resolution (raster cell size) of the model was 2.5 arc minutes as mid-Holocene climatic layers are only available at a resolution of 2.5 arc minutes. To train Model 01, we used verified species occurrence records for *S. psammophila* ( $n = 51$ ) that were checked by experts (Table S1). Only records recorded between February 1969 and December 2016 were used as all *S. psammophila* records prior to 1969 are presumed to be from populations that are now extinct. These data were sourced from a combination of the Global Biodiversity Information Facility (GBIF, [www.gbif.org](http://www.gbif.org)), the Western Australian Department of Parks and Wildlife (NatureMap 2016), the Australian Government's National Collaborative Research Infrastructure Strategy and hosted by Commonwealth Scientific and Industrial Research Organisation (NCRIS and CSIRO, [www.ala.org.au](http://www.ala.org.au)) and recent field data collected largely by ourselves (Turpin & Lloyd 2014; Turpin & Riley 2017; Vimy Resources Limited, 2015) from Western Australia. Duplicate records within a single raster grid cell were removed. A kernel density bias file was created in SDMtoolbox v.2.0 (Brown *et al.* 2017) in ArcGIS v.10.5.1 (ESRI Inc. Redlands, CA, USA) and included in each model we ran to account for uneven sampling of occurrence data across the modelling extent (Hernandez *et al.* 2006; Legendre, 1993). The bias file was constructed as targeted *S. psammophila* surveys are often in areas that are near tracks or closer to human populations. We drew polygons with a 50–100 km buffer around all previous targeted *S. psammophila* survey areas (even if *S. psammophila* was not

found there). Environmental data were obtained from WorldClim (www.worldclim.org), Geoscience Australia (www.ga.gov.au) and the Department of Environment and Energy (www.environment.gov.au). Raster layers were formatted using SDMtoolbox in ArcGIS. Environmental layers were tested for collinearity and highly correlated layers ( $R > |0.75|$ ) were removed prior to model building. Variables considered to be more ecologically relevant to *S. psammophila* were retained. The final set of environmental layers used in Model 01 is described in Table 1. Categorical variables were reclassified to ten categories that were likely to influence habitat suitability for the species. Static variables were used in addition to bioclimatic layers to improve the predictive ability of the model as *S. psammophila* is restricted to sandy environments (Stanton et al. 2011).

Variables that contributed less than 1% to model predictions were removed in a step-wise procedure until five variables remained: Minimum temperature (°C) of the coldest month (Bio 06), Mean temperature (°C) of the wettest quarter (Bio 08), Precipitation (mm) in the wettest month (Bio 13), Surface Geology of Australia (Geology) and the Interim Biogeographic Regionalization for Australia (IBRA) subregion (Table 1). Optimal model parameters were determined by testing different combinations of regularization multiplier values (1, 1.5, 2 or 3) and model features (linear, quadratic, hinge, threshold and product), and comparing Akaike Information Criterion scores for small sample sizes (AICc) in ENMTools (Warren et al. 2010). The best-fit model with the lowest AICc score had a regularization value of '1' and used 'linear, quadratic, threshold and product' features. The final model is the average of the five-fold cross-validated models and was run using these parameters and the five environmental variables described above. Model performance was determined by threshold-independent statistical tests within MaxEnt [Area Under the Curve (AUC) of the Receiver Operating Characteristics (ROC) curve (Fielding & Bell 1997; Merow et al. 2013)]. A Jackknife analysis of the effect of environmental variables on training gain was generated within MaxEnt to assess their relative importance to the model (Phillips et al., 2009). Continuous MaxEnt scores (suitability) were converted to binary predictions for presence and absence using the threshold value that maximizes the sum of sensitivity and specificity (maxSSS), one of the best threshold selection methods for presence-only models (Liu

et al. 2013). *Sminthopsis psammophila* was predicted to be present in locations where suitability was  $\geq 0.59$  and absent in locations where suitability was  $< 0.59$ .

### Ground validation of Model 01: Present distribution

We ground validated the predictions of Model 01 between December 2016 and December 2018 by deploying 163 motion-sensing camera traps (maximum of one per raster grid cell) for the periods of 1 month in the best available long-unburned, spinifex grassland habitats in the WAGVD, Murchison and Coolgardie bioregions (Fig. 2).

Sixty-four locations were in raster grid cells that the model predicted *S. psammophila* to be present in, while 99 locations were in grid cells that were predicted as absent. More cameras were deployed in areas predicted as absent in an effort to detect *S. psammophila* outside its known range. Cameras were baited with peanut butter, rolled oats, sardines and fish oil within anchored bait tubes. Reconyx PC900 (Holmen, WI, USA) cameras were used in 90% of locations while Bushnell (Trophy Cam HD and Aggressor 20MP low glow, Overland Park, KS, USA), Little Acorn LTL-5610 (Oakleigh South, Vic., Australia) and Scoutguard SG880MK-8M (Molendinar, Qld, Australia) were used in the remaining 10% of locations. The different camera models were applied proportionately within areas predicted as present and absent to mitigate potential bias caused by differences in camera performance.

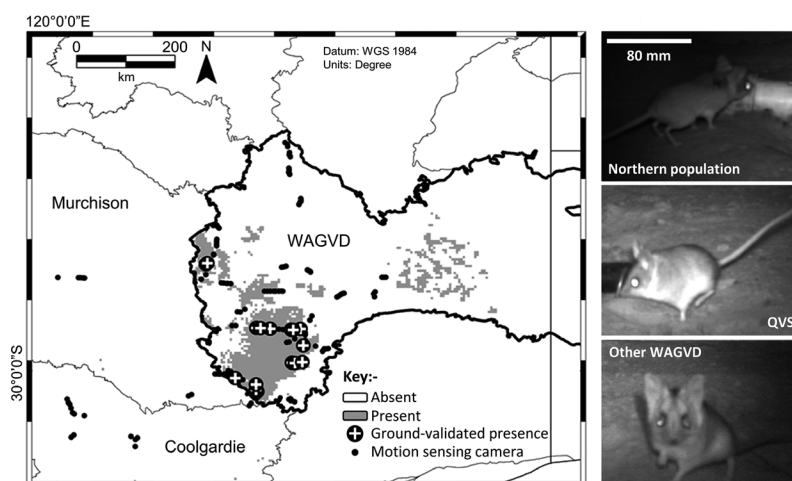
Following ground validation, we used a threshold-dependent statistical analysis to assess the predictive performance of the binary model based on the results of a confusion matrix (Fielding & Bell 1997) and the following performance scores:

- 1 Correct Classification Rate (CCR) = number of correctly predicted presence sites + number of correctly predicted absence sites/total number of sites;
- 2 Positive Predictive Power (PPP) = number of correctly predicted presence sites/sum of correctly and incorrectly predicted presence sites;
- 3 Negative Predictive Power (NPP) = number of correctly predicted absence sites/sum of correctly and incorrectly predicted absence sites.

All statistical analyses were performed in R v.3.5.1 (R Core Team 2018) and RStudio v.1.1.463 (R Core Team & RStudio Team, 2018).

**Table 1** Environmental variables, codes and descriptions used in 'Model 01: Present distribution' to predict the current distribution of *S. psammophila* in Australia using MaxEnt species distribution models. Cont. = continuous; Cat. = categorical variable

Variable code	Source	Type	Description	Percent contribution (%)	Permutation importance (%)
Bio 06	www.worldclim.org	Cont.	Minimum temperature (T <sup>c</sup> ) in the coldest month	28.5	40.7
Bio 08	www.worldclim.org	Cont.	Mean temperature (T <sup>c</sup> ) in the wettest quarter	21.4	1.7
Bio 13	www.worldclim.org	Cont.	Precipitation in the wettest month (mm)	5.3	46.6
Geology	www.ga.gov.au	Cat.	Surface Geology of Australia 1 M dataset 2012 (map symbol)	35.4	4.4
IBRA	www.environment.gov.au	Cont.	Interim Biogeographic Regionalization for Australia (IBRA, 2016) subregion	9.4	6.6



**Figure 2** Left: Ground-validated *S. psammophila* presence records ( $n = 18$ , white crosses in black circles) confirmed in the Western Australian Great Victoria Desert (WAGVD; thick black outline). Cameras ( $n = 163$ ; small black circles) were deployed in the WAGVD, Murchison and Coolgardie bioregions (thin black outline). Binary predictions of presence (grey) and absence (white) were made using MaxEnt 'Model 01: Present distribution' for *S. psammophila*. Right: examples of *S. psammophila* ground-validation images captured during April 2018 [sponsored by the Goldfields Environmental Management Group (GEMG)]

### Climate change SDMs

Using the updated occurrence records from ground validation, we used MaxEnt SDMs comprising all of Australia with a cell resolution of 2.5 arc minutes to refine our prediction of the present distribution of *S. psammophila*. We projected our model predictions for the current climate into the past using the mean of eight GCMs for the mid-Holocene, approximately 6 ka before present (BP), obtained from the WorldClim dataset (Table S2). To examine a range of future predictions, we assessed two future emissions scenarios (RCP 4.5 and RCP 8.5) for 2050 and 2070 timescales using the same eight GCMs as the present and mid-Holocene models. There are four commonly used future emissions scenarios (RCP 2.6, RCP 4.5, RCP 6 and RCP 8.5) that are selected for climate modelling and research, describing the different climate futures which are considered possible depending on the volume of greenhouse gases emitted during this century (IPCC 2014). The RCP 4.5 and RCP 8.5 emissions scenarios were selected as the RCP 2.6 pathway will likely be surpassed; hence, future greenhouse gas emissions will probably range between the RCP 4.5 and RCP 8.5 scenarios (depending on the scale of global greenhouse gas emissions reductions). Both 2050 and 2070 futures were modelled to support conservation management decisions for *S. psammophila*, particularly in Western Australia, where the effects of climate change are predicted to be more rapid and extreme than elsewhere in Australia (Hughes 2003).

Climate change modelling used our updated occurrence records for *S. psammophila* ( $n = 56$ ) recorded between February 1969 and August 2019. Occurrence data (Table S1) were supplemented with a record of a live capture between YRR and EP in 2017 (Brett Backhouse, pers. comm.) and four new spatially independent records determined during ground validation from the northern outlying population,

Queen Victoria Spring Nature Reserve and near the Nippon Highway in Western Australia. Environmental raster data processing and GIS protocols are given in Section 2.2. Surface 'Geology' was included with bioclimatic (WorldClim) data as this variable is ecologically influential for *S. psammophila*, that is, soil type strongly influences vegetation species, structure and density, particularly in Western Australia (Beard *et al.* 2000; Stewart *et al.* 2018). The final set of environmental variables used for climate change SDMs is described in Table 2 and included 'Annual mean temperature ( $^{\circ}\text{C}$ )' (Bio 01), 'Precipitation in the wettest month (mm)' (Bio 13) and 'Surface Geology of Australia' (Geology). Optimal model parameters were evaluated as per Section 2.2 and the bias file was updated using our new survey areas. The best-fit model with the lowest AICc score used a regularization value of '1' and 'linear, quadratic and hinge' features. A final five-fold cross-validated model was run using these parameters and the three environmental variables are described in Table 2. The geology variable was reclassified to ten categories that were likely to influence habitat suitability for the species.

Threshold-independent statistical testing of the climate change SDMs within MaxEnt followed the methods in Section 2.2 (Fielding & Bell 1997; Merow *et al.* 2013; Phillips *et al.*, 2009). Continuous MaxEnt suitability maps were converted to binary predictions using the maxSSS threshold and were either present ( $P \geq 0.142$ ) or absent ( $P < 0.142$ ) (Liu *et al.* 2013). The maxSSS threshold was lower than that of Model 01 because of the differing MaxEnt features and occurrence records used. GCMs within each time period (mid-Holocene, 2050 or 2070) and emissions scenario if applicable (RCP 4.5 or RCP 8.5) were averaged in ArcGIS using 'Cell Statistics' to produce a mean model of the output of the eight GCMs. We calculated percentage decreases in the size of habitat that were predicted as present using the binary threshold-dependent models and cell classifications

**Table 2** Final set of environmental variables, codes and descriptions used to assess the vulnerability of *S. psammophila* to climate change throughout Australia. Cont. = continuous; Cat. = categorical

Variable code	Source	Type	Description	Percent contribution (%)	Permutation importance (%)
Bio 01	www.worldclim.org	Cont.	Annual mean temperature (°C)	51.7	62.0
Geology	www.ga.gov.au	Cat.	Surface Geology of Australia; 1 M dataset 2012	44.8	35.3
Bio 13	www.worldclim.org	Cont.	Precipitation in the wettest month (mm)	3.5	2.7

within each model's 'Attribute Table' in ArcGIS. Null distributions of all model AUCs were performed to deem if predicted SDMs were statistically significantly better than random (Raes & ter Steege 2007).

## Results

### Model 01: Present distribution – performance and predictions

The statistical output of the final replicates of Model 01 demonstrated a good discriminative ability (mean  $\pm$  SD cross-validated AUC training score =  $0.990 \pm 0.005$  and AUC test score =  $0.977 \pm 0.0004$ ) (Figure S2). AUC values for *S. psammophila* fell above the highest 5% of the null distribution of AUCs (Figure S3). Model predictions indicated that suitable conditions for *S. psammophila* are mainly found within or near the current known range (Fig. 1). However, areas of suitable conditions were predicted outside these regions, including between the YRR and EP populations, and an area 150 km north-west of the recorded WAGVD range. In Western Australia, the highest suitability was in the south of Queen Victoria Spring Nature Reserve (0.99). In South Australia, the Cocata Conservation Park (0.99) and the Yumbarra Conservation Park (0.99) were highly suitable for *S. psammophila*. Hence, these protected areas were identified as areas of high value for the conservation of *S. psammophila*. The Model 01 Jackknife analysis showed that 'Geology' and two temperature variables (Bio 08 and Bio 06) were the most informative predictors of *S. psammophila* presence, contributing 35%, 29% and 21% to the model respectively (Table 1 and Figure S2). The Model 01 response curves indicated that the predicted probability of *S. psammophila* presence is highest in areas with a minimum temperature of the coldest month between 3 and 4°C and a mean temperature of the wettest quarter over approximately 23°C is not tolerated. Precipitation in the wettest month (Bio 13) had a peak response output at ~30 mm of rainfall and contributed significantly to the model with the highest permutation score. Surface geologies of 'Qd' (dunes, sandplain with dunes and swales; may include numerous interdune claypans; may be locally gypsiferous), 'Czs' (sand or gravel plains; may include some residual alluvium; quartz sand sheets commonly with ferruginous pisoliths or pebbles; local clay, calcrete, laterite, silcrete, silt, colluvium) and 'Ln' (Middleback subgroup: Jaspilite; quartzite; gneiss; quartz-mica schist; dolomitic marble) were important indicators for *S. psammophila* presence (Raymond et al., 2007).

### Ground validation of Model 01: Present distribution

During ground validation, *S. psammophila* was confirmed by 18 spatially independent cameras located in areas that were predicted by Model 01 to be present (Fig. 2). In April 2018, five cameras detected *S. psammophila* in Queen Victoria Spring Nature Reserve while ten images were captured by two cameras in an outlying region 150 km north of the known range of *S. psammophila* in Western Australia. The confusion matrix (Table 3) and threshold-dependent analysis showed that the model had a high Correct Classification Rate (CCR = 0.72) and a perfect Negative Predictive Power (NPP = 1.0), that is, no ground-validated presences were recorded in areas that were predicted as unsuitable by Model 01.

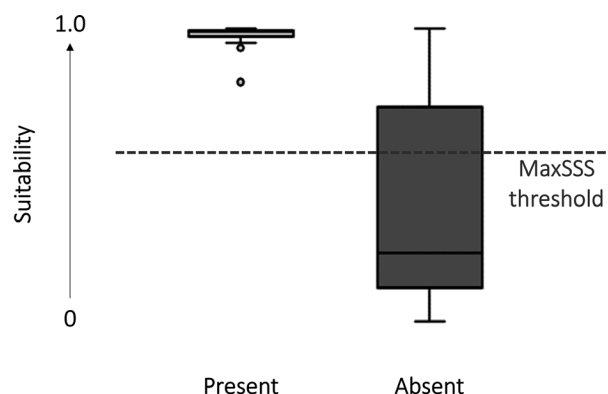
The low Positive Predictive Power (PPP = 0.28) suggested that although Model 01 performed well overall, it was better able to predict absences than presences. There is a high chance of false-negative results when surveying for elusive nocturnal marsupials, and this is likely a major contributing factor to the low PPP score. All ground-validated presence records had a predicted suitability above the maxSSS threshold (Fig. 3).

### Climate change SDMs

Our climate change models predicted that the range of *S. psammophila* will continue to contract southwards and eastwards over the next 30–50 years. In the worst-case "business as usual" emissions scenario, by 2050 (RCP 8.5), most WAGVD habitat may become unsuitable for *S. psammophila*, and by 2070 (RCP 8.5), all WAGVD habitat and the majority of YRR habitat are predicted to become

**Table 3** A confusion matrix (Fielding & Bell 1997) comparing 'MaxEnt Model 01: Present distribution' predicted presences and absences with ground-validated presences and absences for *S. psammophila* was used for the threshold-dependent statistical analysis

	Ground-validated presence	Ground-validated absence	Total
Predicted presence (Model 01)	18	46	64
Predicted absence (Model 01)	0	99	99
Total	18	145	163



**Figure 3** Threshold-dependent results comparing the habitat suitability of raster cells in MaxEnt 'Model 01: Present distribution' (y-axis) with camera trap ground-validation results where *S. psammophila* was either recorded (present) or not recorded (absent) in Western Australia (x-axis). MaxSSS = 0.59; the threshold that maximizes the sum of sensitivity and specificity (Liu *et al.* 2013)

unsuitable (Figs 4 and 5). Hence, both the WAGVD and YRR populations are at risk of extinction with no action on climate change. However, if there are global emissions reductions (RCP 4.5), *S. psammophila* may persist within the southern extremities of the WAGVD and a large area of YRR habitat is predicted to remain suitable. The EP population is predicted to contract in both future timescales and under both emissions scenarios; however, EP is identified as an important climatic refuge for *S. psammophila*. In the optimistic 2070 (RCP 4.5) emissions scenario (where greenhouse gas emissions peak in 2040 and then reduce), the predicted percentage decrease in area of the suitable distribution of *S. psammophila* in Australia is approximately half of the 2070 (RCP 8.5) "business as usual" or worst-case emissions scenario (where no action is taken on climate change) (Fig. 5).

Threshold-independent analysis of our climate change models determined that the present-day model had a mean  $\pm$  SD AUC training score of  $0.967 \pm 0.006$  and an AUC test score of  $0.950 \pm 0.049$ , indicating that the model had a high predictive performance (Figure S4). The climate change Jackknife analysis showed that 'Bio 01' and 'Geology' were the most informative predictors of *S. psammophila* presence, which contributed 52% and 45%, respectively, to the final model replicates (Table 2). The predicted suitability was highest in areas with a mean annual temperature (Bio 01) of up to 19°C; however, this declined sharply as mean annual temperature increased by as little as 1°C (Figure S4). The sandy surface geologies that were identified as important for *S. psammophila* presence remained the same as in Model 01 (see Section 3.1). The precipitation of the wettest month (Bio 13) response curve indicated that *S. psammophila* had the highest suitability in regions with ~30 mm of rainfall in the wettest month. In these MaxEnt models, the important environmental variables, maxSSS threshold and response curve outputs varied from those used in MaxEnt Model 01 due to the use of updated occurrence records, lack of the IBRA bioregion variable and the differing MaxEnt features

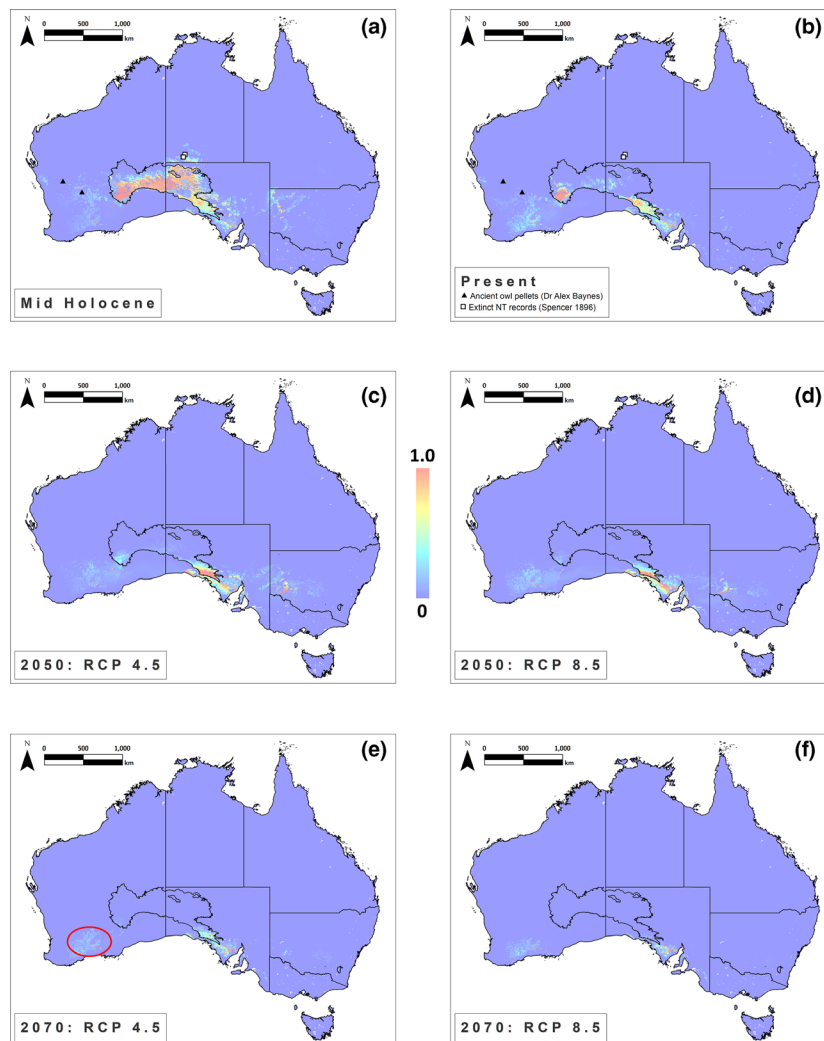
used for the most parsimonious models with the lowest AICc scores. However, these MaxEnt models demonstrate that mean annual temperature, winter rainfall and geology are important determinants of the distribution of *S. psammophila*.

## Discussion

### Species distribution models (SDMs) as conservation tools

Overall, the statistical output of MaxEnt demonstrated that the models performed well. Our ground-validation survey results provided confidence that our preliminary predictions in 2016 were robust, and we successfully confirmed the presence of *S. psammophila* in a remote region 150 km north-west of the known range. Although it was not possible to perform ground validation in South Australia, two new records were confirmed by Brett Backhouse (pers. comm.) in 2017 and Glen Murray (pers. comm.) in 2020 between the EP and YRR populations in habitats with high predicted suitability (0.98 and 0.78 respectively), thus further supporting our model predictions.

Limitations include that MaxEnt models do not predict the actual distribution, but rather suitable climatic and geographical space for *S. psammophila*. As *S. psammophila* prefers long unburned (32+ years seral stage) vegetation, its distribution is greatly affected by wildfire and is much further restricted within predicted envelopes (Riley 2020). Occurrence records are limited for *S. psammophila* as it is a rare desert-dwelling endangered species. Hence, model predictions may be improved with further field surveys. No false-positive presences were recorded – despite an increased effort to detect *S. psammophila* in regions predicted as absent. However, false-negative absences in areas that were predicted as present were common. This may be due to the low population density of *S. psammophila* and the influence of local rainfall, that is, rainfall deficits can correspondingly affect the population density of arid zone mammals (Masters 1993; McLean 2015). During our ground-validation surveys, the mean annual rainfall in the WAGVD region ranged from 200 to 400 mm (BOM 2018). We also used our knowledge of the preferred fire age (time since the last wildfire) and habitat preferences of *S. psammophila* in the WAGVD to deploy cameras within long-unburned, dense habitats, and this may have improved our detection success (Riley 2020). Dense habitats are essential for many Australian species as they provide natural protection against feral mesopredators, particularly feral cats that prefer hunting in open areas (McGregor *et al.*, 2015, McGregor *et al.* 2017). Dense vegetation also supports a greater abundance and diversity of invertebrate fauna, thus, yielding stable prey resources for carnivorous species such as *S. psammophila* (Reid & Hochuli 2007). To improve the model's Positive Predictive Power for rare species, additional survey methods should be used with camera traps, such as conservation detection dogs that are trained to locate threatened species, infrared cameras or environmental DNA analyses (Claridge *et al.* 2005; Long



**Figure 4** MaxEnt model predictions of the suitable distribution for *S. psammophila* during the (a) mid-Holocene, (b) present, (c) 2050 (RCP 4.5), (d) 2050 (RCP 8.5), (e) 2070 (RCP 4.5) and (f) 2070 (RCP 8.5) emissions scenarios. Suitability scores are given on a continuous scale from 1.0 (red) or very likely to occur to 0 (purple) or not likely to occur. RCP = representative concentration pathway. The Great Victoria Desert (GVD) bioregion and state boundaries are indicated by black lines. A potential ex-situ conservation area is indicated by a red oval in map e)

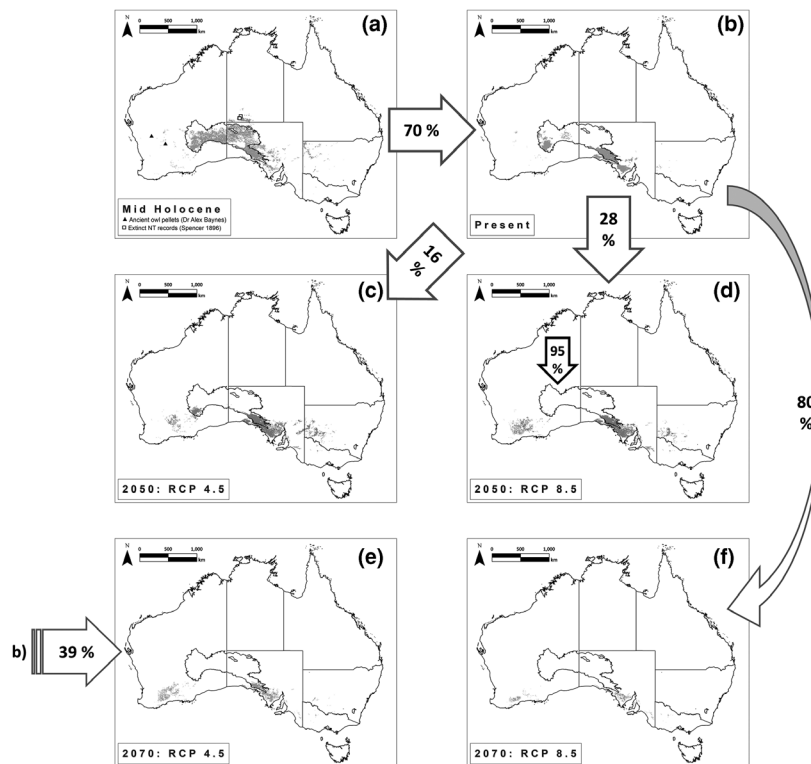
*et al.* 2007; Taberlet *et al.* 2012). An occupancy modelling approach that considers imperfect detection (MacKenzie *et al.*, 2017; Sollmann 2018) can also improve ecological understanding of poorly known and elusive species such as *S. psammophila* and could be applied to any type of systematically collected species detection/non-detection data.

### Factors affecting the distribution of arid zone species

The environmental variables used for all models support the hypothesis that the current distribution of *S. psammophila* is constrained by southern spinifex sand dune and plain habitats within yellow to orange sandy soils and a semi-arid climate that is influenced by winter rainfall. Our climate change models

showed that mean annual temperature and surface geology were the most informative predictors of *S. psammophila* presence and precipitation in the wettest month was an important predictive variable. Temperature and geology commonly limit species' ranges globally and, in Australia, strong rainfall and temperature gradients exist, with precipitation generally decreasing west to east and temperatures generally decreasing north to south (BOM 2018; Stewart *et al.* 2018). During the very windy conditions of the mid-Pleistocene in Australia, finer yellow to orange sand particles were deposited at higher elevations than heavier dark orange to red sand particles, causing heterogeneous soil landscapes within the arid zone (Madigan 1936; Sheard *et al.* 2006). These lighter yellow to orange sandy soils are preferred by *S. psammophila*; hence, surface geology soils are an informative indicator of presence. Conditions





**Figure 5** Binary predictions for *S. psammophila* presence (grey) and absence (white) were made using MaxEnt models and a maxSSS threshold of 0.142. (a) Mid-Holocene, (b) present, (c) 2050 (RCP 4.5), (d) 2050 (RCP 8.5), (e) 2070 (RCP 4.5) and (f) 2070 (RCP 8.5) emissions scenarios. Percentage decreases in suitable habitats for *S. psammophila* (large arrows) were calculated in ArcGIS. The percentage decrease in suitable habitat for the WAGVD *S. psammophila* population only from b) present to d) 2050 (RCP 8.5) is 95% (small arrow). RCP = representative concentration pathway. The Great Victoria Desert (GVD) bioregion and state boundaries are drawn with black lines. Binary model results were used in the confusion matrix analysis (Table 3) to assess the results of camera trap ground validation

remained windy in Australia between ~20 and 100 ka BP, thereafter, the winds calmed, and the densely vegetated, immobile, sand dune habitats of *S. psammophila* became stable (Hesse 2010; Williams, 2014). Therefore, the ‘Geology’ variable is useful for past (mid-Holocene; approximately 6 ka BP) and future (2050 and 2070) SDMs as conditions will not change by the end of the century as a result of climate change. The IBRA variable was not used for climate change projections as the IBRA boundaries will likely change over time (due to the changing climate which is a component of IBRA bioregional mapping) and are only suitable for present-day SDMs. When the static environmental variable of ‘Geology’ was included, this increased the predictive ability of the model (Figure S5). In accordance with Stanton et al. (2011), Sohl (2014) and Deb et al. (2019), we emphasize that it is important to include static and dynamic non-climate variables in addition to climate variables in species distribution models to predict future change in a species’ habitat or distribution as a result of climate change.

**Climate change in Australia**

In Australia, recent and rapid anthropogenic climate change has already caused mass population crashes, extirpations and

extinctions (Adams-Hosking et al. 2011; Holmgren et al. 2006; Hughes 2003; IPCC 2014; Steffen 2009; Waller et al. 2017; Welbergen et al. 2007). Some arid zone species, including *S. psammophila*, survived the most recent wave of mammal extinctions in Australia by exploiting dense habitats that provided natural protection against predators and extreme temperatures (Churchill, 2001b; Pavey et al. 2017). However, dense habitats, such as the southern, semi-arid natural refugial habitats of *S. psammophila*, typically rely upon more favourable climatic conditions (compared with the interior of the arid zone), that is, dense habitats are strongly influenced by lower temperatures and increased rainfall related El Niño–Southern Oscillation (ENSO) and Indian Ocean Dipole (IOD) effects (BOM 2018). Climate change is predicted to alter ENSO and IOD patterns, and the southern intermittent rainfall band that influences semi-arid desert regions is predicted to move further south (BOM 2018; Hughes 2003; Steffen 2009). Therefore, the last remaining refuges for many semi-arid specialists are precarious under future climate change.

**Looking back: The mid-Holocene model**

Our mid-Holocene model predicted that the WAGVD and YRR populations were previously well connected and

supports genetic analyses indicating that these populations share an ancestral haplotype (McLean et al. 2018). Further, the mid-Holocene model is indicative of the original distribution of *S. psammophila* at the time immediately before the European settlement of Australia. The predictions of presence by the mid-Holocene model agree with the locations of all known historical records (~50–500 years BP) in the Northern Territory and in Western Australia (Fig. 1). Hence, between ~50 and 500 years BP (the estimated age of historical records), *S. psammophila* appears to have rapidly contracted from a distribution resembling the mid-Holocene model to the restricted southern distribution known today.

Our climate change SDMs used bioclimatic and geographical data only and do not consider invasive predators, wildfires or habitat loss that have affected species' distributions throughout Australia. Hence, we propose that rapid anthropogenic climate change has been a major contributing factor affecting the contraction of *S. psammophila*. As many arid zone mammal species disappeared from the south first and then the north (tracking the displacement of the First Australians), the significant benefits of the indigenous management of the arid zone, for example, wildfire control and water (Gnamma) hole maintenance, are clearly demonstrated (Finlayson 1936, 1958, 1961; Latz & Griffin 1978; Burbidge et al. 1988; Bayly 1999; Johnson 2006). While climatic conditions in Australia became hotter and drier from the mid-Miocene, this was very gradual allowing species to naturally adapt, and synergistic extinction pressures were not present (Doherty et al. 2015). However, in a very short and recent window of time, the First Australians were removed, uncontrolled wildfires occurred and feral mesopredators became widespread. Many arid zone mammal species were not able to endure these extinction pressures. However, *S. psammophila* did not follow this south-to-north extinction pattern, implying some behavioural adaptation to the aforementioned extinction pressures. For example, the high mobility of *S. psammophila*, its preference for long-unburned dense habitats and use of concealed burrows may have allowed the species to persist while others perished (Riley 2020). We, therefore, propose that when the climate rapidly began to change due to an increase in global greenhouse gas emissions beginning in the industrial revolution (c.1760), this additional, significant climatic pressure caused the species to become restricted to dense habitats and favourable climates within Australia's southern and eastern deserts.

### The future distribution of *S. psammophila*

Under both the RCP 4.5 and RCP 8.5 future emissions scenarios, the distribution of *S. psammophila* is predicted to continue to contract southwards and eastwards as it tracks changes to Australia's temperature and rainfall. In the "business as usual" RCP 8.5 emissions scenario (our current emissions scenario), the areas holding the WAGVD and YRR populations are predicted to become unsuitable and the predicted distribution of *S. psammophila* may decrease by up to 80% in area throughout Australia. In addition, the increasing

frequency and severity of extreme events, such as droughts and wildfires, may cause sudden population crashes (Cai et al. 2014), as recently observed when at least 1.3 billion animals including mammals, birds and reptiles died in just a few months during the 2019/2020 eastern states wildfires (Dickman 2020). Extreme events were not modelled; hence, our predictions of decline may be optimistic. As *S. psammophila* is geographically restricted at its southern extent due to the cessation of appropriate soil types and semi-arid *Triodia* spp. habitats, and is climatically pressured at its northern extent, the habitable zone for *S. psammophila* will significantly decrease in the future. Further, within predicted suitable areas, *S. psammophila* is restricted to long-unburned habitats, implying that the species may be at an even greater risk of extinction.

### Conservation management recommendations

Our results strongly suggest that *S. psammophila* should remain listed as 'Endangered' throughout Australia (EPBC 1999). The WAGVD and YRR populations are at a higher climatic risk than the EP population; however, the EP population itself, although within a climatic refuge, is also predicted to contract in range in the future. Therefore, all populations should be monitored to detect distributional changes. Natural refugia and reserves within EP, Queen Victoria Spring Nature Reserve and the southern YRR, should be managed to conserve long-unburned, dense habitats. Arid zone conservation planners should consider the future climates of proposed fenced enclosures as northern and western habitats may become climatically unsuitable. We recommend that SDMs are used in conjunction with accurate fire mapping [e.g. Northern Australian Fire Information (NAFI) mapping, [www.firenorth.org.au](http://www.firenorth.org.au)] and/or fire ageing methods, for example, dendrochronology, for better informed decisions. In addition, the First Australians have 60+ ka of verbally conveyed knowledge regarding the changing climate, which is vital for threatened species conservation management (Green et al. 2010). Immediate protective measures controlling synergistic threats, for example, wildfires and feral mesopredators, are advised for key strongholds (Doherty et al. 2015). Conservation strategies should be specific to each population's habitat requirements. For example, in the WAGVD, the newly discovered northern population requires annual monitoring, and Queen Victoria Spring Nature Reserve requires priority protection as a long-term climate refuge. Regions of the far south-west of Western Australia (outside the arid zone) were indicated as climatic refuges by our SDMs. Translocations to artificial fenced reserves within such regions with transplanted soils, seeds and vegetation may be required to mitigate against further climate-related extinctions of arid zone species.

Overall, we demonstrate that SDMs can be used to improve the conservation management of species with few occurrence records. Our methods can be adapted (given an informed ecological understanding of the study species in question) to improve the conservation management of rare and threatened species worldwide.

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## Supporting information

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

**Figure S1.** Historical climate data from the nearest long-term weather station (Kalgoorlie-Boulder; BOM 2018) to the Western Australian Great Victoria Desert WAGVD) *S. psammophila* population.

**Figure S2.** Threshold-independent statistical output.

**Figure S3.** The AUC values for *S. psammophila* in all models fell above the highest 5% of the null distribution of AUCs.

**Figure S4.** Threshold-independent statistical output indicating model performance.

**Figure S5.** The prediction of ‘Model 01: Present distribution’ for *S. psammophila* in Australia if the environmental variable of ‘Geology’ is excluded. This highlights how non-climatic data can substantially improve a model’s predictive ability.

**Figure S6.** *Sminthopsis psammophila* photographs (possible cover images).

**Table S1.** *Sminthopsis psammophila* records ( $n = 51$ ) used for ‘Model 01: Present distribution’, with author and date recorded (Datum = WGS 1984).

**Table S2.** All bioclimatic data and general circulation models (GCMs) were sourced from WorldClim (www.worldclim.org). All GCMs were used by Australian climate change modellers and used in the Coupled Model Intercomparison Project (CMIP5) and the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC 2014).