

Projected direct and indirect effects of climate change on the Swift Parrot, an endangered migratory species

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Abstract. Assessing future changes in the suitability of the climate niche for interacting species across different trophic levels can identify direct and indirect effects of climate change that may be missed using single-species approaches. We use ensembles of species distribution models based on a dynamically down-scaled regional climate model to project the future suitability of climate for the Swift Parrot (*Lathamus discolor*), its primary food and habitat resources (Tasmanian Blue Gum (*Eucalyptus globulus*) and Swamp Gum (*E. ovata*)), and an introduced nest predator, the Sugar Glider (*Petaurus breviceps*). These results are combined with layers representing mature forest and fire danger to identify locations that may act as refuges for the Swift Parrot from fire, deforestation and predation under baseline and future climates. Almost a quarter of the nesting habitat of Swift Parrots is projected to become climatically unsuitable by the end of the 21st century, but large areas may remain climatically suitable for both Swift Parrots and their food trees. However, loss of forests and the presence of Sugar Gliders are likely to limit the availability of high-quality habitat. Offshore islands that the Sugar Glider is unable to colonise or where future climate is not projected to be suitable for the Sugar Glider may be the only places, in the near future, where the Swift Parrot will be protected from nest predation by this introduced species.

Additional keywords: Eucalypts, migratory bird, model ensemble, refugia, species distribution models, species interactions, Sugar Glider, trophic level.

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Introduction

Although climate is a direct determinant of the distributions of species, biotic interactions can also play an important role in determining the fate of species (Van der Putten *et al.* 2010). Changes to species interactions under a changing climate have been identified among the greatest threats to biodiversity (Tylianakis and Didham 2008) and recent studies have shown that many species respond idiosyncratically to climate change (VanDerWal *et al.* 2012). Given that any one species likely depends on several others for resources (e.g. food or shelter), cascading effects can indirectly affect species even if they themselves are tolerant of a changing climate. Both direct and indirect effects therefore need to be considered when assessing the potential impact of future climate change.

Conservation programs aiming to identify future refugia for threatened species need to identify areas that will remain

climatically suitable for the target species as well as for those species on which it depends. Ongoing conservation will be most successful in areas where these climate refugia coincide with refugia from other threatening processes, such as habitat loss and introduced species. Identifying where these refugia coincide in space should therefore be a priority when designing conservation programs for threatened species.

Species distribution models (SDMs) are commonly used to predict shifts in the distributions of species based on 'climate envelopes' (Elith *et al.* 2006; Araújo and New 2007), in recognition of the importance of climate in determining the geographical distributions of many plants and animals (Woodward 1987). More recently, the importance of considering species interactions in SDMs has been acknowledged (e.g. Araújo and Luoto 2007; Van der Putten *et al.* 2010; Romo and García-Barros 2014). However, the focus has remained on species within the same

trophic level, with few exceptions (see, for example, Giannini *et al.* 2013; Silva *et al.* 2014; Trainor and Schmitz 2014a, 2014b) and mobile or migratory species have rarely been considered (but see Heikkinen *et al.* 2007; Wisz *et al.* 2013).

The potential for mismatches in the climatic niche (Jackson *et al.* 2009) of interacting species of different trophic levels could be expected to be greater for migratory species (McKinney *et al.* 2012). Migrants respond to different climatic conditions and at broader spatial scales than any non-mobile species they interact with at the locations where they winter, stopover and breed. Additionally, the movements of migratory species expose them to a greater range of disturbances and threatening processes relative to those sedentary species are exposed to (Walther *et al.* 2002), and there is a need to improve management approaches for these species. We examine potential mismatches in the climatic niche (Jackson *et al.* 2009) of interacting species of different trophic levels for the endangered migratory Swift Parrot (*Lathamus discolor*) – a seasonal migrant that winters in mainland Australia but breeds only in the island of Tasmania

(Fig. 1) – the eucalypts it uses for food and breeding, and a nest predator, the Sugar Glider (*Petaurus breviceps*).

We use SDM ensembles to project the current (i.e. baseline) and future suitability of climate for Swift Parrots to identify potential mismatches in climatic suitability between three trophic levels (e.g. Swift Parrots, their predators and their food and nesting trees), and identify indirect effects of climate change. This set of interactions is representative of the difficulties that face conservation managers seeking to conserve species in a changing climate. We assess: (1) the extent and configuration of current and future suitable climate for breeding Swift Parrots in Tasmania; (2) the extent and configuration of current and future suitable climate for (a) food and nesting trees of the Swift Parrot, and (b) the Sugar Glider, an omnivorous and arboreal marsupial that depredates Swift Parrots, and is native to mainland Australia but was introduced to Tasmania in the 19th century; (3) the extant area of forest cover where current or future suitable climate occurs; (4) the extent to which the Parrots, their breeding habitat and their predators overlap in space; and (5) where

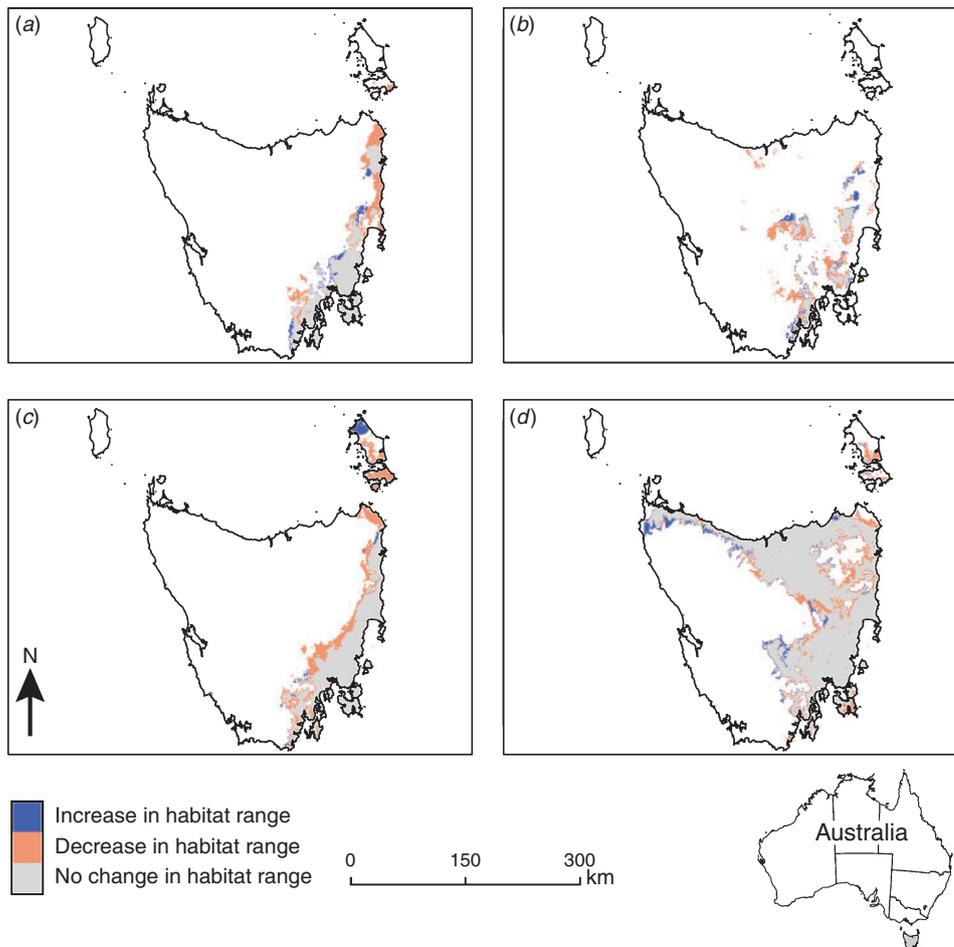


Fig. 1. Maps showing areas of agreement in the increase, decrease or no change in habitat range in Tasmania in for the period 2080 for (a) Swift Parrots; (b) Sugar Gliders; (c) *Eucalyptus globulus globulus*; and (d) *E. ovata*. The projections of habitat range are based on the results of the ensemble species distribution models using three dynamically downscaled GCMs. (For colour figure, see online version available at <http://www.publish.csiro.au/nid/17.htm>.)

resources, such as flowering trees and tree-hollows for nesting, will remain available for Swift Parrots with minimal future predation risk.

Methods

Study system

In Tasmania, Swift Parrots depend on two trees – *Eucalyptus globulus* (Tasmanian Blue Gum) and *E. ovata* (Swamp Gum) – for food and nesting habitat. They only breed in forests where either of these species occur in the canopy (Webb *et al.* 2014). These forests are concentrated along south-eastern Tasmania, but spatio-temporal patterns in flowering create discrete patches of food availability that vary from year to year (Webb *et al.* 2014), which Swift Parrots exploit to optimise their reproductive success (Stojanovic *et al.* 2015). However, there has been, and continues to be, extensive deforestation of Swift Parrot habitat across Tasmania, including its breeding range (Saunders and Tzaros 2011; Hansen *et al.* 2013). Swift Parrots have specific nest-cavity requirements, for hollows in mature trees, with small entrances, deep chambers and wide floors to the cavity; such cavities are rare, with as few as 5% of available cavities suitable as nests for Swift Parrots (Stojanovic *et al.* 2012). Species dependent on tree-cavities are disproportionately threatened by the loss of mature forest through anthropogenic land-use and stochastic events. Fire, the frequency and intensity of which is projected to increase in Tasmania under future climate change (Fox-Hughes *et al.* 2014), is an important cause of loss of Swift Parrot nest-cavities, and potentially reduces the availability of food resources in the short-term.

In addition to habitat loss, Swift Parrots are predicted to decline by >80% within three generations across mainland Tasmania as a result of predation of eggs, chicks and fledglings by Sugar Gliders (Heinsohn *et al.* 2015). It is believed that Sugar Gliders were introduced to Tasmania in the early decades of the 19th century, but the effect of predation on the Swift Parrot, which is greatest in disturbed forests (Stojanovic *et al.* 2014), may have increased over recent decades. Sugar Gliders are widespread in Swift Parrot nesting habitat (Stojanovic *et al.* 2014), and are tolerant of some anthropogenic habitat degradation (Suckling and Macfarlane 1983; Caryl *et al.* 2013).

Locality records

We used records of 531 independent Swift Parrot nests from a monitoring program that surveyed their entire potential breeding range over 4 years between 2010 and 2014 (for details, see Stojanovic *et al.* 2014; Webb *et al.* 2014). For our analyses, a 5-km buffer was placed around each Swift Parrot nest because this is the recommended scale at which management must be undertaken for logging operations near Swift Parrot nests. Sugar Gliders were not surveyed directly; records were obtained from detections by motion-activated cameras at Swift Parrot nests or when they were encountered during fieldwork. We also used 68 spatially validated records of Sugar Gliders from the Atlas of Living Australia, which incorporates the data collected by Stojanovic *et al.* (2014) (<http://biocache.ala.org.au/occurrences/search?taxa=sugar+glider>, accessed 31 May 2013) and covers the entire Tasmanian distribution of the species.

Records of the two critical *Eucalyptus* species were obtained from the Atlas of Living Australia (<http://collections.ala.org.au/>, accessed 22 March 2016). There were 3634 unique observations in Tasmania for *E. globulus* and 3246 observations for *E. ovata*. We did not use the full Australian distribution in the SDMs because, first Tasmanian *E. globulus* is a separate subspecies (*E. g. globulus*; Williams and Potts 1996) and, second, there is evidence of strong clinal variation in growth and survival traits in Tasmanian eucalypt species, sufficient to affect their response to changing climate (Dutkowski and Potts 1999).

We did not apply spatial thinning to the locality data, because we were confident that the records we used were not biased by taxonomic misidentification, inaccurate locational data or spatially biased sampling effort (Gould *et al.* 2014). All data were verified by a field ecologist (and coauthor in this study, D. Stojanovic) with extensive field-work over many years involving the target species across Tasmania.

Forecasting species distribution under baseline and future climates

SDM climatic envelopes for Swift Parrot nesting habitat, the two *Eucalyptus* species and the Sugar Glider were calculated using BIOMOD in the 'biomod2' package (Beaumont and Gallagher 2009; Thuiller *et al.* 2012) in the software R (R Core Team 2011). BIOMOD generates ensemble forecasting maps based on 10 statistical models including regression methods such as Generalised Linear Model (GLM), multivariate adaptive regression splines (MARS) and Generalised Additive Model (GAM); classification methods such as Classification Tree Analysis (CTA); maximum entropy (Maxent); flexible discriminant analysis (FDA); the machine learning techniques Artificial Neural Network (ANN), Random Forest (RF) and Generalised Boosting Model (GBM); and surface range envelope (SRE). We use consensus scenarios for the species using climatic data for two periods: 1976–2005 (the baseline period) and 2070–99 (hereafter 2080 period), under the A2 emissions scenario (Arnell 2004). The A2 emissions scenario is one of four qualitative storylines developed in the Special Report of the Intergovernmental Panel on Climate Change (IPCC) Working Group III (Nakicenovic and Swart 2000). The ensemble forecasting consensus approach has been advocated because it is often not possible to select one 'best' model (Burnham and Anderson 2002). Although statistical methods are often used to assess internal performance of a model, they cannot measure the ecological validity of one. Nor can an accurate representation of the current distribution be relied on to select the best model of future distribution because the relationship between the climatic variables and the distribution of species may change.

However, a limitation of using the BIOMOD ensemble is that the same number of pseudo-absences (or background points) is applied to all models. It has been recommended that a large number of randomly generated pseudo-absences be used for regression models, but fewer pseudo-absences may be more appropriate for classification and machine-learning techniques (Barbet-Massin *et al.* 2012). We compared the effect of different numbers of pseudo-absences for different models, and found that whereas individual model results changed slightly, the ensemble was not significantly affected overall. We used a

different number of randomly generated pseudo-absences for each species to reflect the different number of presence points (400 for the Swift Parrot, 400 for the Sugar Glider, 1500 for *E. globulus*, and 3000 for *E. ovata*).

We used 70% of the data to run the ensemble forecasting and the remaining 30% was used to run evaluation models. Models presented in this study were evaluated with a relative operating characteristic (ROC) (see online supplementary material).

The bioclimatic variables used in BIOMOD were selected using a principal component analysis (PCA) to identify uncorrelated variables ($R^2 < 0.6$) that accounted for >95% of the variance. Table 1 shows the bioclimatic variables used in the ensemble modelling for each species. We present the ensemble

SDMs as binary maps of climatic suitability, using a threshold value of 0.5 (Phillips and Dudík 2008); the full probability distribution for the studied species is presented in Fig. S1 in the online supplementary material. Since these models do not account for other environmental and ecological factors that influence the distributions of the species, they are intended to represent their potential climate domain, as opposed to ecological niche.

Climate change and climate models

We used future climate projections from a dynamically downscaled regional climate model, the Conformal Cubic Atmospheric

Table 1. The candidate set of 35 bioclimatic variables from which variables were selected using PCA to identify uncorrelated variables that accounted for >95% of the variance

The 35 candidate variables are commonly used in species distribution modelling (Porfirio *et al.* 2014b). The variables we used in BIOMOD for each species are marked with an 'X'

ID	Description	Swift Parrot	Sugar Glider	<i>E. globulus</i>	<i>E. ovata</i>
BIO1	Annual mean temperature				
BIO2	Mean diurnal range in temperature ^A		X		
BIO3 ^B	Isothermality (BIO2/BIO7)				
BIO4	Temperature seasonality (ANUCLIM coefficient of variation; BIOCLIM standard deviation)	X		X	
BIO5	Maximum temperature of warmest month				
BIO6	Minimum temperature of coldest month				X
BIO7	Annual temperature range (BIO5–BIO6)				
BIO8	Mean temperature of wettest quarter			X	
BIO9	Mean temperature of driest quarter				
BIO10	Mean temperature of warmest quarter		X		
BIO11	Mean temperature of coldest quarter				
BIO12	Annual precipitation		X		
BIO13	Precipitation of wettest month				
BIO14	Precipitation of driest month				
BIO15	Precipitation seasonality (coefficient of variation)	X	X		
BIO16	Precipitation of wettest quarter				
BIO17	Precipitation of driest quarter				
BIO18	Precipitation of warmest quarter				
BIO19	Precipitation of coldest quarter				
BIO20	Annual mean radiation				
BIO21	Highest month radiation				X
BIO22	Lowest month radiation				
BIO23	Radiation seasonality (coefficient of variation)				
BIO24	Radiation of wettest quarter				
BIO25	Radiation of driest quarter			X	X
BIO26	Radiation of warmest quarter				
BIO27	Radiation of coldest quarter				
BIO28	Annual mean moisture index				
BIO29	Highest month moisture index				X
BIO30	Lowest month moisture index				
BIO31 ^C	Moisture index seasonality (coefficient of variation)				
BIO32	Mean moisture index of highest quarter				
BIO33	Mean moisture index of lowest quarter				
BIO34	Mean moisture index of warmest quarter	X		X	X
BIO35	Mean moisture index of coldest quarter				

^AMeasure the variation between a high temperature and a low temperature that occur during the same day.

^BBIO3 (Isothermality) is the evenness of temperature over the course of a year, or a quantification of how large the day-to-night temperature oscillation is in comparison to the summer-to-winter oscillation.

^CBIO31, the coefficient of variation of the moisture index, was not used, because there was a large area in western Tasmania that could not be calculated due to standard deviation values of zero.

Model (CCAM) (Mcgregor and Dix 2001), developed by the CSIRO, Australia. Dynamically down-scaled climate models represent the climate processes that operate over small distances, in contrast to statistical down-scaling methods, which assume a statistical relationship between large-scale patterns of climate and local climate, or simple scaling techniques that interpolate coarse-scale model output to the local scale (Harris *et al.* 2014). They therefore have the potential to capture regional variation in the climate-change signal. This is particularly relevant in Tasmania, which has a complex topography and coastline, and a range of regional climatic influences.

The Climate Futures for Tasmania project used CCAM (Mcgregor and Dix 2001) to dynamically down-scale six global climate models (GCMs) to a resolution of ~10 km. We have used data from three of these down-scaled GCMs (GFDL-CM2.0, CSIRO MIROC3.2 (medres) and UKMO-HadCM3). These models were chosen because they represent current south-eastern Australian climate means and variability well (Smith and Chandler 2010), and cover the spread of projected changes to rainfall in south-eastern Australia present in the Phase 3 of the Coupled Model Inter-comparison Project (CMIP3) set of models (Christensen *et al.* 2007). Details of the modelling can be found in Corney *et al.* (2010), and the modelled projections are available through the Tasmanian Partnership for Advanced Computing (TPAC) portal (<https://dl.tpac.org.au/tpacportal/>).

ANUCLIM version 6.1 (Xu and Hutchinson 2011) was then used to interpolate statistically the output of the regional climate model from 10 km to 1 km and to generate monthly mean data for the bioclimatic variables in Table 1. We present results based on the A2 emissions scenario because global emissions are currently tracking at the higher level of this scenario (Peters *et al.* 2013). The A2 scenario is a high-emission scenario, broadly similar to the Representative Concentration Pathway (RCP) 8.5. In the fifth assessment report of the Intergovernmental Panel on Climate Change (IPCC) and Phase 5 of the Coupled Model Inter-comparison Project (CMIP5), the Special Report on Emissions Scenarios (known as SRES scenarios) were replaced by the RCPs scenarios. Regional comparisons of projections from the CMIP5 and CMIP3 models have found surface temperature, wind and rainfall patterns to be highly consistent between the archives (Irving *et al.* 2011; Markovic *et al.* 2013), so that release of the CMIP5 archive models has not made the CMIP3 models, used here, redundant.

Refuges for the Swift Parrot

We identified locations across Tasmania that may act as refuges from fire, deforestation and predation for the Swift Parrot under baseline and future climates. Fire danger was calculated as the absolute difference (90th percentile) of cumulative Forest Fire Danger Index (FFDI) between the baseline and future periods. The cumulative FFDI was calculated by Fox-Hughes *et al.* (2014) from the projections of the dynamically down-scaled regional climate model (<http://portal.sf.utas.edu.au/thredds/catalog.html>, accessed 3 March 2016). Forest loss and gain was based on the 'Global forest cover and changes since 2000' geographic information system (GIS) layer developed by Hansen *et al.* (2013), which identifies loss and gains in forest

cover from 2000 to 2013. We considered forest gain in Hansen *et al.* (2013) as unavailable habitat for Swift Parrots because young forests do not provide the tree-cavities required for nesting and young trees flower less prolifically than old trees (Brereton *et al.* 2004). It is important to note that the forest loss data do not include future scheduled forest loss and may therefore overestimate the amount of available habitat. The predation layer was based on the SDM ensembles for the Sugar Glider under baseline and future climates.

Available habitat resources were based on the SDMs for the Swift Parrot nesting habitat, the two *Eucalyptus* species, and the extent of mature forest. Current extent of mature forest was produced by reclassifying GIS data developed by the Biodiversity Conservation Branch, Department of Primary Industries, Parks, Water and Environment (DPIPWE) in Tasmania (DPIPWE 2010) into a binary file of mature or non-mature forests (Munks *et al.* 2007). We use the same mature forest layer for baseline and future extent while acknowledging that deforestation is continuing (Hansen *et al.* 2013). Future extent is unlikely to increase by 2080 given the time required for tree-hollows to develop in Australian forests (Gibbons and Lindenmayer 2002).

The set of modelled GIS data layers were analysed using the Multi Criteria Analysis Shell for Spatial Decision Support (MCAS-S) (Lesslie *et al.* 2008). The methods and the GIS data used in the MCAS-S analyses for the Swift Parrot, the Sugar Glider and the eucalypts are publicly and freely available from the National Environmental Research Program portal (<http://www.nerplandscapes.edu.au/data-packs>; Porfirio *et al.* 2014a). Future refuges are defined as being areas of mature forest where the future climate is suitable for the Swift Parrot and the two *Eucalyptus* species, but is not suitable for the Sugar Glider.

Results

Swift Parrot habitat resources

Baseline climate

We estimated the area climatically suitable for Swift Parrot nesting habitat under the baseline climate to be ~7946 km² (Table 2). Importantly, however, not all of this area is suitable nesting habitat, as only 53% of the Swift Parrot nesting habitat climatic envelope supports extant mature forests (Table 2). The ensemble maps based on each GCM are presented in Fig. S1.

The extent of climatically suitable area under the baseline climate is ~4011 km² for *E. globulus* and 11 789 km² for *E. ovata* (Table 2). A large proportion of the suitable area falls outside the reserve system in Tasmania (>70% for both species; Table 2). About half of the predicted suitable climatic range for the baseline climate for *E. globulus* and *E. ovata* is considered mature forest (51% and 46% respectively; Table 2). The area where projected suitable habitat for the Swift Parrot and mature eucalypts coincide is 3526 km², which is ~44% of the total area projected for the Parrot under baseline climate conditions.

Future climate

Our models project a reduction in area with a suitable climate for Swift Parrot nesting habitat of ~23% by 2080. This

Table 2. Area of predicted climatic suitability for the species for baseline climate projections

SP \cap nest-buffer = a subset of the total suitable habitat for Swift Parrot that co-occurs within the 5-km buffer zone; SP \cap eucalypts = areas where the distribution of Swift Parrots and the two eucalypts that are considered mature forest co-occur; SP \cap eucalypts \cap SG = areas where the distributions of Swift Parrot, the two eucalypts that are considered mature forest, and the Sugar Glider co-occur. Note: the numbers in the table may vary a little as data in the Swift Parrot data pack are updated

Species	Area of suitable habitat (km ²)	Proportion within private or public reserves	Proportion outside reserves	Proportion within mature forest
Swift Parrot	7946.74	0.31	0.69	0.53
SP \cap nest-buffer	1223.00	0.26	0.74	0.15
Sugar Glider	4011.83	0.22	0.78	0.54
<i>E. globulus</i>	785.79	0.28	0.72	0.51
<i>E. ovata</i>	11789.54	0.21	0.79	0.46
SP \cap eucalypts	3526.94	0.30	0.70	0.44
SP \cap eucalypts \cap SG	709.94	0.24	0.75	0.20

Table 3. Area of projected suitability for the species for future climate projections

Note: the numbers in the table may vary a little as data in the Swift Parrot data pack are updated

Species	Area of suitable habitat (km ²)	Proportion of change relative to baseline climate	Proportion within private or public reserves	Proportion outside reserves	Proportion within mature forests
Swift Parrot	6099	-0.23	0.28	0.72	0.53
Sugar Glider	3230	-0.19	0.22	0.78	0.57
<i>E. globulus</i>	9360	0.17	0.30	0.70	0.49
<i>E. ovata</i>	25023	1.12	0.17	0.83	0.38
SP \cap eucalypts ^A	2642	-0.25	0.37	0.62	0.40
SP \cap eucalypts \cap SG ^B	685.91	-0.03	0.28	0.71	0.25

^ASP \cap eucalypts = areas where the distribution of Swift Parrot and the two eucalypts that are considered mature forest co-occur.

^BSP \cap eucalypts \cap SG = areas where the distribution for Swift Parrot, the two eucalypts that are considered mature forest and the Sugar Glider co-occur.

loss is predominantly along the north-eastern coast of Tasmania (Table 3). However, although this area may be climatically suitable some parts may not support mature forest. When we filtered our projections of nesting habitat by 2080 using data on extant cover of mature forest across the study area, assuming that these forests will not be lost or degraded in the intervening period, the availability of potential habitat decreased by ~50% (Table 3). Approximately 28% of the future projected nesting habitat occurs within the present day reserve system (public and privately managed land; Table 3).

The climatically suitable area for the eucalypt forests dominated by *E. ovata* and *E. globulus* is projected to increase by 2080 (Table 3). However, a large proportion of the projected forest extent falls outside the Tasmanian reserve system (70% for *E. globulus*, 83% for *E. ovata*). The combination of the areas projected to be suitable for Swift Parrots, *E. globulus* and *E. ovata*, and mature forest (for the baseline period) provided an estimate of the total area of currently suitable habitat resources for the Swift Parrot of ~2642 km², which is ~40% of the range projected for Swift Parrot under the future climate projections (Table 3, Fig. 1).

Threats to and refuges of Swift Parrots

Our results show that, under the baseline climate conditions, 20% of potential (climatically suitable) Swift Parrot nesting habitat (accounting for the eucalypts classified as mature) of mainland Tasmania is also suitable for Sugar Gliders. The

remaining 80% could have a lower risk of predation for the Swift Parrot under baseline climate. Our projections based on the future climate for 2080 indicate that climatic suitability for Sugar Glider and Swift Parrot will be reduced by 20% and 23% respectively (Table 3), and that 25% of the potential Swift Parrot nesting habitat will also be suitable for Sugar Gliders by 2080. When the FFDI layer is included as a threat, there is only a 1% increase in the area considered as threatening for Swift Parrots in the future. Thus, the remaining 74–75%, with or without the FFDI layer, can be considered potential future refuges for Swift Parrot from predation and climate change for baseline and future climates (Fig. 2). However, our results indicate a significant change in climatic suitability of Swift Parrot habitat resources on Bruny Island, where Sugar Gliders do not occur, with a reduction of >50% in suitable habitat by 2080.

Discussion

By assessing changes to future climate suitability for interacting species across three trophic levels, we have highlighted the importance of direct and indirect effects of climate change on a migratory species. Swift Parrots are endangered and highly restricted in their breeding distribution, and our results indicate that they are likely to be affected by cumulative, synergistic effects of climate change on their food trees and main predator, in addition to ongoing deforestation. Identifying areas that in the future may be climatically suitable for the Swift Parrot

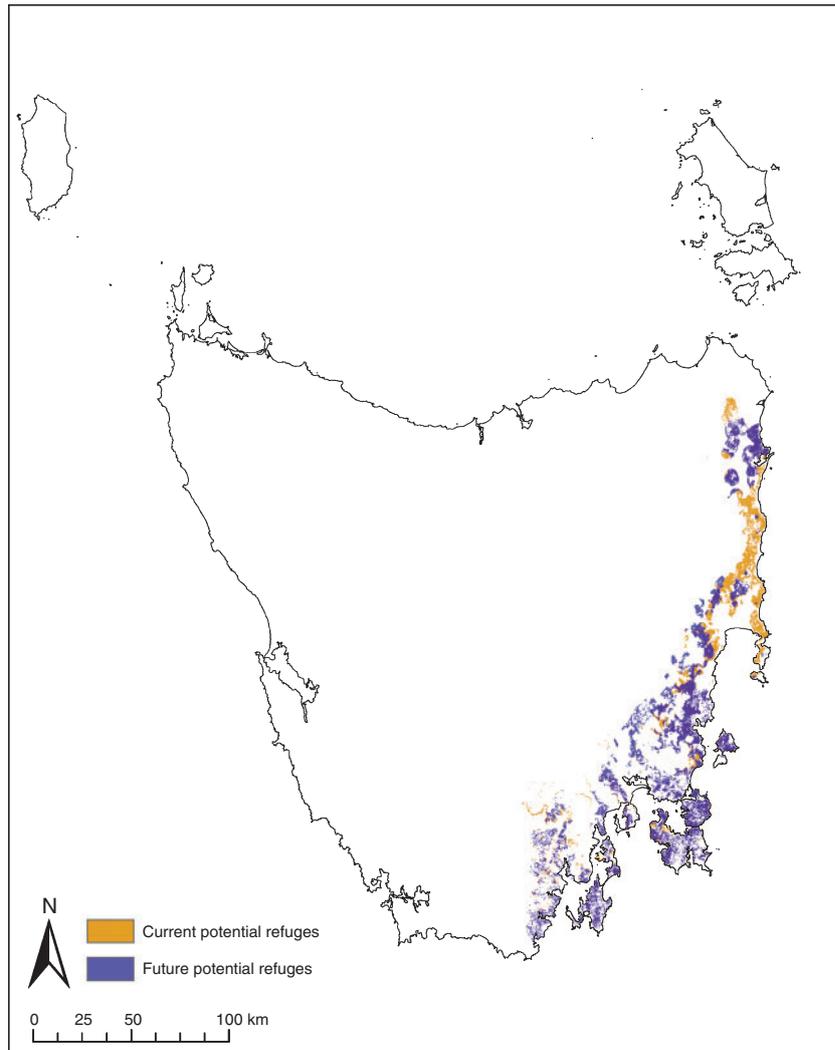


Fig. 2. Current and future potential refuges from climate and predation for the Swift Parrot. The layers and tutorials to reproduce this map are publicly and freely available from the National Environmental Research Program portal (<http://www.nerplandscapes.edu.au/data-packs>; Porfrio *et al.* 2014a). (For colour figure, see online version available at <http://www.publish.csiro.au/nid/17.htm>.)

and its food trees and also not suitable for Sugar Gliders is an important step towards identifying future refuges that could help improve the success of conservation programs for the species.

Our models show that almost a quarter of Swift Parrot nesting habitat is projected to become climatically unsuitable by the end of the century. This area is predominantly in the north-eastern part of Tasmania, an area that has been used for breeding in the past and is likely to be an important stepping stone for migration between the southern part of the breeding range and wintering range. This is a substantial direct threat to a species with such a restricted breeding range.

Minimising further loss of mature forest will be essential for the conservation of the Swift Parrot. A large proportion (77%) of current Swift Parrot nesting habitat is projected to remain climatically suitable under a changing climate, and 74% of

this area is projected to remain suitable for *E. globulus* and *E. ovata*. However, only 40% of this area currently occurs within public or private conservation reserves (Table 3). Areas of highest conservation priority should be those areas identified here as future refuges from predation and climate change, along with conservation of habitat known to be currently important. This is particularly pertinent given recent modelling that indicates the conservation status of Swift Parrots is substantially worse than previously thought (Heinsohn *et al.* 2015). Conservation of Swift Parrots depends on the preservation of high-quality habitat in the immediate term and persistence and expansion of such habitats into the future. Although we used current extent of mature forest in our analysis, future habitat loss caused by deforestation and fire will become more damaging as already diminished Swift Parrot nesting habitat becomes increasingly degraded.

The conservation of contiguous mature forest is also likely to minimise predation risk by Sugar Gliders relative to smaller habitat patches. The intensity of Sugar Glider predation has been linked to deforestation, with nest survival being highest in areas with high landscape cover of mature forest (Stojanovic *et al.* 2014). The area projected to be climatically suitable for the Sugar Glider declines by ~20% in the future. However, 27% of the area projected to remain suitable for Sugar Gliders overlaps with areas projected to be suitable for both the Swift Parrot and their food trees. In these areas, predation and competition for food and habitat resources will continue to be a threat to the Swift Parrot.

Offshore islands are currently important refuges from predation for the Swift Parrot. Even where the climate may be suitable for the Sugar Glider, they are unlikely to colonise islands without human intervention. However, the models for the future projections (the 2080 period) suggest a marked reduction in climatic suitability for the two *Eucalyptus* species used as food and nesting trees across much of the offshore islands. The climatic suitability of Bruny Island, which is currently recognised as an important breeding area for Swift Parrots (Webb *et al.* 2012), is projected to decline for both species of food tree by the end of the century. This represents a major threat to Swift Parrots given their reliance on *E. globulus* and *E. ovata* and the status of offshore islands as the only predator free habitat for breeding, although Maria Island remains suitable for both species. Long-lived trees such as these eucalypts may persist under suboptimal climatic conditions for many years, and hollows in dead trees could still be used for nesting by Swift Parrots. However, changes to flowering phenology and intensity could be one of the first responses to changing climate conditions (Root *et al.* 2003; Cleland *et al.* 2007). Flowering of Swift Parrot food trees is spatiotemporally highly variable (Webb *et al.* 2014) and strongly influenced by local conditions. Facultative movements between rich patches of flowering have a fitness payoff for nesting Swift Parrots under current climate scenarios (Stojanovic *et al.* 2015) but climate change might lead to deleterious mismatches in flowering phenology and the timing of migration or breeding.

Projections of future species distributions incorporate many sources of uncertainty, from the quality of observational data, to the choice of statistical model and its parameters (e.g. variable choice, number of pseudo-absences), in addition to emissions scenarios, ranges in global climate models and down-scaling technique (Araújo and Guisan 2006; Gould *et al.* 2014; Ekström *et al.* 2015). The assumption that the relationship between the distribution of a species and the environment will remain constant under future conditions is a limitation of all correlative SDMs, but particularly for models of invasive species, which are less likely to have reached equilibrium with their environment (Thuiller *et al.* 2005; Elith *et al.* 2010). Quantifying or removing all of this uncertainty is not possible (Harris *et al.* 2014) and the responses of species to changing conditions cannot be known with certainty. Conservation decisions will therefore continue to be made in the absence of accurate predictions of the future. Nevertheless, some knowledge of where climatically suitable habitat might persist under changing climatic conditions is essential for

conservation management, and SDMs remain an important tool in providing this information (Wiens *et al.* 2009). Just as climate projections are intended to represent the range of plausible climate futures, a range of SDMs can be considered to represent a range of possible future outcomes, at the same time as their limitations are acknowledged. By highlighting the range of plausible trajectories a species may be on, SDMs can help determine the priorities for monitoring populations and to track changes as they occur, an essential practical tool for adaptive management (Harris *et al.* 2013).

There are several approaches to incorporating species interactions into SDMs, and the method used can substantially affect the output (Leathwick and Austin 2001; Araújo and Luoto 2007; Anderson *et al.* 2009; Meier *et al.* 2011). One approach is to include the distribution of one species as a covariate in the SDM of another species (Giannini *et al.* 2013). However, this approach generally requires extensive data on species interactions and relies on the assumption that these interactions remain the same under changing climatic conditions (Hof *et al.* 2012). In the absence of such detailed knowledge, we used an alternative approach of identifying potential spatial mismatches in climatic suitability between interacting trophic levels by developing separate SDMs for each species. This approach could be further extended to include other important competitors like the Common Starling (*Sturnus vulgaris*) and the European Honeybee (*Apis mellifera*). Improved knowledge of species interactions, including spatial variability in the strength and effect of competition and predation, would improve the accuracy of the SDMs under current and future conditions (Giannini *et al.* 2013). Future SDM projections should include updated climatic projections, updated species observations and, if available, projected forest management.

Conclusions

Climate change is likely to have complex interacting effects, both direct and indirect, on individual species and on others with which they interact. We identify the multiple, synergistic threatening processes affecting the Swift Parrot, and consider how these may change under future climatic conditions. Although a large proportion of current Swift Parrot nesting habitat is projected to remain climatically suitable into the future, the extent of future refuges may be substantially reduced by deforestation, predation and declining climatic suitability for essential food and habitat resources. Identifying future refuges from these interacting threats is an important first step in determining priorities for habitat conservation for threatened species such as the Swift Parrot.

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