Author/s:
Wagner, B;Baker, PJ;Stewart, SB;Lumsden, LF;Nelson, JL;Cripps, JK;Durkin, LK;Scroggie, MP;Nitschke, CR

Title:
Climate change drives habitat contraction of a nocturnal arboreal marsupial at its physiological limits

Date:
2020-10-01

Citation:
Wagner, B., Baker, P. J., Stewart, S. B., Lumsden, L. F., Nelson, J. L., Cripps, J. K., Durkin, L. K., Scroggie, M. P. & Nitschke, C. R. (2020). Climate change drives habitat contraction of a nocturnal arboreal marsupial at its physiological limits. ECOSPHERE, 11 (10), https://doi.org/10.1002/ecs2.3262.

esa ECOSPHERE

Climate change drives habitat contraction of a nocturnal arboreal marsupial at its physiological limits

BENJAMIN WAGNER,[1,†] PATRICK J. BAKER,[1] STEPHEN B. STEWART,[1,2] LINDA F. LUMSDEN,[3]
JENNY L. NELSON,[3] JEMMA K. CRIPPS,[3] LOUISE K. DURKIN,[3] MICHAEL P. SCROGGIE,[3,4] AND
CRAIG R. NITSCHKE[1]

[1]*School of Ecosystem and Forest Sciences, The University of Melbourne, 500 Yarra Boulevard, Richmond, Victoria 3121 Australia*
[2]*CSIRO Land and Water, College Road, Sandy Bay, Tasmania 7005 Australia*
[3]*Department of Environment, Land, Water and Planning, Arthur Rylah Institute for Environmental Research (ARI), P.O. Box 137, Heidelberg, Victoria 3084 Australia*
[4]*School of Biosciences, The University of Melbourne, Parkville, Victoria 3010 Australia*

Citation: Wagner, B., P. J. Baker, S. B. Stewart, L. F. Lumsden, J. L. Nelson, J. K. Cripps, L. K. Durkin, M. P. Scroggie, and C. R. Nitschke. 2020. Climate change drives habitat contraction of a nocturnal arboreal marsupial at its physiological limits. Ecosphere 11(10):e03262. 10.1002/ecs2.3262

Abstract. Increasing impacts of climatic change and anthropogenic disturbances on natural ecosystems are leading to population declines or extinctions of many species worldwide. In Australia, recent climatic change has caused population declines in some native fauna. The projected increase in mean annual temperature by up to 4°C by the end of the 21st century is expected to exacerbate these trends. The greater glider (*Petauroides volans*), Australia's largest gliding marsupial, is widely distributed along the eastern coast, but has recently experienced drastic declines in population numbers. Its association with hollow-bearing trees, used for nesting, has made it an important species for the conservation of old-growth forest ecosystems. Fires and timber harvesting have been identified as threats to the species. Greater gliders have disappeared however from areas that have experienced neither raising questions about the role of other factors in their decline. A unique physiology and strict *Eucalyptus* diet make them vulnerable to high temperatures and low water availability. As such, climatic conditions may drive habitat selection and recent climatic trends may be contributing to observed population declines. Using presence:absence data from across its distribution in Victoria, coupled with high spatial and temporal resolution climatic data and machine-learning modeling, we tested the influence of climatic, topographic, edaphic, biotic, and disturbance variables on greater glider occupancy and habitat suitability. We found that climatic variables, particularly those related to aridity and extreme weather conditions, such as number of nights warmer than 20°C, were highly significant predictors of greater glider occurrence. Climatic conditions associated with habitat suitability have changed over time, with increasing aridity across much of its southeastern distribution. These changes in climate are closely aligned with observed population declines across this region. At higher elevation, some areas where the greater glider is observed at high densities, conditions have become wetter, which is improving habitat quality. These areas are of growing significance to greater glider conservation as they will become increasingly important as climatic refugia in the coming decades. Protecting these areas of habitat will be critical for facilitating the conservation of greater gliders as the broader landscape becomes less hospitable under future climatic change.

Key words: aridity; Australia; climate; climatic change; conservation; distribution modeling; greater glider; habitat suitability; machine learning; marsupial; *Petauroides volans*; remote sensing; weather.

Received 29 June 2020; accepted 6 July 2020; final version received 12 August 2020. Corresponding Editor: Debra P. C. Peters.

† **E-mail:** bwagner@student.unimelb.edu.au

INTRODUCTION

The effects of climatic change and anthropogenic disturbances, such as land-use change, are negatively impacting biodiversity and altering ecological systems around the world (Stenseth et al. 2002, Walther et al. 2002). The increasing impacts of humans on natural ecosystems are leading to reductions in habitat area and quality for flora and fauna, which, in turn, lead to population declines, local extirpations, or extinctions (Diamond 1984, Lindenmayer et al. 2011, Youngentob et al. 2013). The rate of climatic change and the increase in occurrence of extreme events has had noticeable impacts on many global ecosystems and species (Hoegh-Guldberg et al. 2007, Cai et al. 2014, Iizumi et al. 2014, Moran-Ordonez et al. 2018). In Australia, the climate is projected to change drastically with increases in mean annual temperatures of up to 4°C by the end of the 21st century (CSIRO and Bureau of Meteorology 2015) and shifts in the amount and frequency of precipitation, as well as increases in the frequency of extreme events (Orlowsky and Seneviratne 2012). For southeastern Australia, these extreme events manifest as extended droughts and more frequent heat waves associated with increases in diurnal and nocturnal temperature maxima (Murphy and Timbal 2008).

Climatic change is already having profound effects on the populations and distributions of native fauna (Cork and Catling 1996, Fischer et al. 2001, Welbergen et al. 2007, Kearney et al. 2010) and flora (Hughes et al. 1996, Mok et al. 2012, Rawal et al. 2015*b*, *c*). Habitat suitability models that include climatic variables can provide insights into how species may respond to future climatic change (Zimmermann et al. 2009, Briscoe et al. 2016, Mathewson et al. 2017). These models however rarely account for local weather patterns and extremes, which can have important influences on species' populations and distributions (Reside et al. 2010, Bateman et al. 2012, Moran-Ordonez et al. 2018). As such, it is important to assess the climatic preferences and tolerances of species to identify potential refugia and to develop effective conservation strategies that can maintain stable populations in these areas over time. This requires understanding not only the direct and indirect impacts of climatic variability, but also their interactions with other factors; however, these have not been widely studied. Understanding how these various factors can affect species demography and habitat suitability is central to conservation planning and sustainable land management.

The greater glider (*Petauroides volans*), Australia's largest gliding marsupial, was once considered common but has recently experienced range-wide declines and local extinctions (Lindenmayer et al. 2011, Youngentob et al. 2013). The IUCN has classified the species as vulnerable (Burbidge and Woinarski 2020), and the species is listed as threatened nationally under the Environment Protection and Biodiversity Conservation Act, and within Victoria under the Flora Fauna Guarantee Act (Woinarski et al. 2014). In response, ~100,000 ha of old-growth forest in Victoria was protected in late 2019 (DELWP 2019). The conservation of these old-growth forests was due to its association with hollow-bearing trees that it uses for nesting (Lindenmayer et al. 1990). A range of studies have identified multiple factors that influence the habitat suitability of greater gliders at different scales, such as forest structure (Smith et al. 2007), disturbance (McLean et al. 2018), nutrient availability (Youngentob et al. 2011), and climate (Kearney et al. 2010). While the decline in greater glider populations has been variously attributed to timber harvesting, land-use change, bushfires, and planned burning (Possingham et al. 1994, Kavanagh 2000, Pope et al. 2004, Lindenmayer et al. 2013, Youngentob et al. 2013), declines and extinctions have also been observed in protected reserves, where forests have not been subject to logging nor have experienced recent fire (Lindenmayer et al. 2011). The broader decline in the species' populations in some parts of its distribution is likely the result of other environmental factors. Climate and weather are potential factors (see Kearney et al. 2010); however, few studies have explored how recent climatic change and extreme weather events impact the species. Changes to climate and weather patterns represent a potential systemic risk to greater gliders across their distribution as they have limited physiological flexibility—in particular, a narrow range of thermal tolerance (Rubsamen et al. 1984).

Unlike other mammals that have a thermoneutral zone of several degrees, the greater glider has a fixed thermoneutral point at 20°C, above which it becomes hyperthermic (Rubsamen et al. 1984). This makes it particularly sensitive to changes in ambient temperature and water availability (Cork and Catling 1996, McIlwee 2001). Consequently, greater gliders are commonly found in areas with mild, cool temperatures and high rainfall. In southeastern Australia, this is typically in mountainous areas >300 m asl, although greater gliders are most abundant above 700 m (Bennett et al. 1991). They are nocturnal animals that emerge at nighttime to feed; during the day, they shelter in tree hollows to remain cool and protected from predators. At temperatures >20°C, greater gliders expend considerable energy and water to cool themselves (Rubsamen et al. 1984). When nights are too hot, they remain in their insulated and cooler dens to conserve energy; however, this limits their ability to feed on *Eucalyptus* leaves, which are their primary source of nutrients and water (Marples 1973, Foley et al. 1990, Kavanagh and Lambert 1990). This physiological sensitivity suggests that a warming and drying climatic poses a threat to the greater glider at the warmer and drier margins of its distribution (Kearney et al. 2010).

In addition to the direct physiological effect of temperature on the greater glider, climatic change is also predicted to alter the nutritional value of one of their primary food resources (Lawler et al. 1997). *Eucalyptus* leaves have high levels of fiber, lipids, and phenols (Attiwill and Leeper 1987), but low protein and carbohydrate availability. This limits their nutritional value and reduces digestibility (Cork and Sanson 1990). Nitrogen is the primary source of protein for arboreal folivores; however, it typically only comprises 0.8–2.0% of dry matter in *Eucalyptus* leaves (Moore et al. 2004). Greater gliders have evolved a dietary preference for certain eucalypt species; they are found in greater abundance where eucalypt species with higher nitrogen content and digestibility are found at higher densities (Braithwaite et al. 1984, Kavanagh and Lambert 1990, Cork and Catling 1996, DeGabriel et al. 2009, Jensen et al. 2015). Foliar nutrition is influenced by topography and climate (Attiwill and Adams 1996). As ambient CO_2 levels rise, the C:N ratio of *Eucalyptus* foliage has been observed to increase, which results in lower levels of available nitrogen in the leaves (Lawler et al. 1997, Cotrufo et al. 1998, Kanowski 2001) and increasing leaf toxicity (Cork and Foley 1997, Moore et al. 2004), which could lead to further negative impacts on the greater glider.

In this study, we evaluated the influence of climate, disturbance, topography, edaphic, and forest structure variables on greater glider occupancy patterns within the southeastern part of its distribution. The primary aim was to identify the key variables associated with their habitat selection and the role that they may have played in the observed decline of the species. These variables were used to develop a species distribution model to predict areas of potentially suitable habitat to help guide landscape-scale forest management and conservation planning. Given the physiological constraints of the greater glider and their decline in areas where their main assumed threat, disturbance, is not a direct issue, we hypothesized that landscape-scale changes in habitat suitability are driven more by climate, topography, and edaphic factors than disturbance.

Materials and Methods

Study areas

Our study focused on three areas within the known distribution of the greater glider in Victoria, southeastern Australia: East Gippsland, the Central Highlands, and the Strathbogie Ranges. These areas were chosen due to the availability of presence and absence records and strong gradients of topography, climate, and vegetation communities across which the greater glider is known to occur (Appendix S1: Fig. S1).

East Gippsland includes approximately 1,200,000 ha of forests in far eastern Victoria (Dept. of Agriculture and Water Resources 2018). The vegetation ranges from open lowland forests dominated by a mix of *Eucalyptus* species (including *E. sieberi, E. tricarpa, E. globoidea)* and *Banksia* spp. to dense, high-elevation (>1000 m asl) sites dominated by *E. delegatensis* and other high-elevation mixed species (Opie et al. 1990, Sebire and Fagg 2009). *Eucalyptus obliqua* is the most abundant species, occurring across the entire elevational range of the region (Dept. of Conservation and Natural Resources 1995). Elevation ranges from sea level to ~1300 m asl. Annual rainfall across the region ranges between

648 and 1178 mm (average for 1981–2014; Stewart et al. 2020*b*) and mean annual temperature between 6° and 15.8°C (average for 1981–2014; Stewart and Nitschke 2017*b*). Greater gliders have been recorded at varying levels of abundance across the full range of elevation and in a variety of forest types. However, they are more abundant at higher elevations and in more closed forests (Henry 1984, Bennett et al. 1991, Van der Ree et al. 2004). Conservation-based prescriptions have been in place for over 20 yr in East Gippsland to protect areas with high densities of greater gliders from timber harvesting (Department of Conservation and Natural Resources 1995, Dept. of Natural Resources and Environment 1997).

The Victorian Central Highlands includes ~860,000 ha of forest to the east of Melbourne. Elevation ranges from 75 to 1600 m asl. Annual rainfall ranges between 564 and 2089 mm (Stewart et al. 2020*b*) and mean annual temperatures from 5.8° to 15.2°C (Stewart and Nitschke 2017*b*); however, local climatic conditions are heavily influenced by topography in this complex landscape. The main canopy tree species in the Central Highlands forests are *E. regnans, E. delegatensis*, and *E. obliqua* (Department of Natural Resources and Environment 1998). Surveys of arboreal marsupials, including the greater glider, have been conducted in the Central Highlands since the 1980s and have recently documented significant declines in their occurrence (Incoll et al. 2001, Lindenmayer et al. 2011, Lindenmayer and Sato 2018). Until late 2019, there were no timber harvesting prescriptions for conserving the species' habitat in the Central Highlands. The recently updated and implemented *Petauroides volans* Action Statement stipulates that a higher rate of tree retention must now occur where timber harvesting is permitted in areas of medium greater glider densities across all of Victoria. In addition, ~100,000 ha of key habitat across the entire state has been placed under immediate protection (see DELWP 2019).

The Strathbogie Ranges is an isolated landscape of approximately 44,000 ha of forest northeast of Melbourne. This is an area of typically steep slopes with native forests surrounded by agriculture and pine plantations in the lowlands. Elevation ranges from 300 to 1033 m asl; mean annual rainfall ranges from 718 to 1245 mm (Stewart et al. 2020*b*) and mean annual temperatures from 10.4° to 15°C (Stewart and Nitschke 2017*b*). The main tree species in the region are *E. radiata*, *E. globulus*, *E.dives*, and *E. dalrympleana* (Marshall 2007). Recent government and citizen science surveys for nocturnal fauna have identified an abundance of greater gliders in the region. A comparison with historical data from the 1980s provides no indication of population decline in the region, suggesting that this isolated forest landscape may be an important refuge for the species (Nelson et al. 2018).

Datasets and survey design

Observations from four surveys for arboreal, nocturnal fauna in mature forest, carried out between 2012 and 2019 in the three study areas, were combined into a dataset consisting of 725 sites. The survey dataset includes 233 sites where greater gliders were present. The survey sites ranged in elevation from 9 to 1508 m a.s.l (Table 1). All surveys were conducted at night using standard spotlighting survey methods to

Table 1. Overview of surveys used for this study.

Region (year)	Contributor	Total sites	*Petauroides volans* presences	Elevational gradient (m asl)	Survey effort (no. surveys/ site)	Minimum no. of surveyors/ survey
Central Highlands (2012)	Arthur Rylah Institute for Environmental Research	421	71	123–1508	2–3	1–2
East Gippsland (2015)	Department of Environment, Land, Water and Planning	164	94	9–1132	4	2
Strathbogie Ranges + Central Highlands (2017–2018)	Arthur Rylah Institute for Environmental Research	110	59	100–1400	1	2
East Gippsland (2018–2019)	This study	30	9	42–1200	1–2	2

detect nocturnal fauna while walking along forest tracks or through the forest, recording all species sighted using high-powered spotlights (Lumsden et al. 2013). The 2012 survey used 100-m transects to spotlight for arboreal species (Lumsden et al. 2013). The 2015–2019 surveys used transects of 1 km length on track or 500 m off track (Nelson et al. 2018). The 2012 surveys were surveyed twice by a single observer, while all the other surveys were surveyed at least once using two observers (Table 1). Double observer distance sampling has been found to increase detection probabilities (Kissling and Garton 2006). The different survey methods represent different levels of survey effort, which could influence detectability at non-presence sites (Watson et al. 2008). If one or more individuals of greater glider were spotted, the site was considered a presence site. Sites where gliders were not detected were classified as absence sites; however, because detection is imperfect for greater gliders (see Wintle et al. 2005), some absence sites may represent false-negative observations. The inclusion of too many false-negative sites can impact the performance of species habitat models by diluting or overestimating the influence of the predictor variable (Tyre et al. 2003). Greater gliders have high detectability given their small home ranges, low mobility, and high densities (Wintle et al. 2005). Wintle et al. (2005) found that two surveys had a greater than 60% detectability yielding low false-negative rates (<40%). Tyre et al. (2003) stated that for species with false-negative rates <50%, more sites should be sampled, as opposed to more visits to the same sites, to improve precision and reduce bias in habitat models. The approach used for the surveys considered in this study balanced multiple surveys to improve detectability at each site while increasing the number of independent sites to reduce potential bias in model estimates from false-negative observations. Other data recorded in all surveys included the following: location of observation, tree species on which an animal was observed, height on tree, behavior, fur color, time of observation, and distance and bearing to the animal.

Species distribution models built with balanced presence and absence points are more accurate and less likely to contain biases that may lead to model overfitting (McPherson et al. 2004, Liu et al. 2005). To ensure a balanced study design and avoid overrepresentation of absence sites from a single study region, we randomly selected absences from the 2012 Central Highlands surveys, where the target species was recorded at a lower proportion of sites. We did this to match the presence:absence ratio of the other two landscapes, which was 53%. Random sampling of absences was selected to avoid biasing the selection of absence sites under the assumption that, given the survey effort, the absence sites are true absences that represent a range of potential habitat suitability within areas of mature forest. All presences were used in the analysis. After balancing the presence: absence ratio, the final dataset used for modeling included 437 sites.

Independent variables

For all presence and absence sites, variables describing climate, topography, geology, forest structure, productivity, and soil chemistry, as well as past management and disturbance records, were compiled. The initial modeling dataset contained >150 variables across these categories, although climatic variables were most common (Appendix S1: Table S1). We reduced the total number of variables by first removing highly correlated variables and then low or non-significant variables through generalized linear models (GLM). Our final analysis included 12 variables.

Climatic data

All climatic variables were generated using daily gridded datasets. Variables used in the modeling were extracted at ~250 m resolution by interpolating weather station observations (Stewart and Nitschke 2017*a*, 2018, Fedrigo et al. 2019, Stewart et al. 2020*a*, *b*, *c*) and combining preexisting datasets (McVicar 2011). The generated data span the period from 1981 to 2014 (33 yr). These long, high-resolution time series of climatic data were developed specifically for ecological modeling across the state of Victoria and were used to calculate derived variables describing aridity, weather events, and climate. Variables used for modeling included daily maximum, minimum, and mean temperatures, diurnal temperature range, precipitation, potential evapotranspiration, vapor pressure deficit, and saturation vapor pressure (svp; Alduchov and Eskridge 1996; Eq. 1, e_s = saturation vapor pressure, T = temperature):

$$e_s(T) = 6.1094 \times \exp \frac{17.625 \times T}{243.04 \times T}. \tag{1}$$

From these data, the number of nights with temperatures >20°C (hot nights) and days with ≥25 mm of precipitation (wet days) was calculated. In addition, a daily condensation index (CI; Eq. 2, svp tmin = saturation vapor pressure at minimum temperature, vp9am = vapor pressure at 09:00 AM) was derived, with CI values < 0 used to calculate the number of days that condensation occurred. Climatic aridity for each site was calculated using the mean annual heat moisture index (AHMI; Eq. 3, MAT = mean annual temperature, MAP = mean annual precipitation; Wang et al. 2006, Paudel et al. 2016). A total of six climatic variables were used in the final model.

$$\mathrm{CI} = \mathrm{svp\,tmin} - \mathrm{vp9am} \tag{2}$$

$$\mathrm{AHMI} = \frac{(\mathrm{MAT} + 10)}{\left(\frac{\mathrm{MAP}}{1000}\right)} \tag{3}$$

Topographic, edaphic, and vegetative data

We used static variables describing topography (elevation, slope, aspect, geology), edaphic conditions (pH, soil type, terrain wetness index [TWI]), ecological context (ecological vegetation classes [EVC]), disturbance history, including number of past fires (both bushfires and planned burns) and number of timber harvesting operations, and the normalized difference vegetation index (NDVI) at survey date. These were collated for each site. All data are publicly available through open-source data portals DATA VIC (data.vic.gov.au) and TERN (portal.tern.org.au) or derived from freely available satellite imagery through NASA and USGS data portals (glovis.usgs.gov). For all sites, these data were extracted as spatial vector or raster layers in QGIS 3 (QGIS Development Team 2018).

Data preparation

All statistical analyses were conducted in R (R Core Development Team 2018) and the packages caret, dismo, effects, gbm, landscapemetrics, MuMIN, raster, ROCR, and SDMTools (Sing et al. 2005, Hijmans et al. 2017, Fox and Weisberg 2018, Barton 2019, Greenwell et al. 2019, Hesselbarth et al. 2019, Hijmans 2019, VanDerWal et al. 2019, Wing et al. 2019). Cumulative data for climatic events such as the total number of hot nights or condensation days across all 33 yr observed were divided by the total number of years (n = 33 for most variables) in the dataset to estimate mean annual values. Additionally, separate 11-yr datasets were developed, where the total number of cumulative events across the 11 yr observed was divided by $n = 11$. This allowed for comparisons of climate at approximately decadal time intervals. All variables were standardized prior to analysis.

Variable selection

The initial dataset included a wide range of variables that have been hypothesized to influence greater glider occupancy (Appendix S1: Table S1). To reduce the number of variables for analyses, we used a multi-step procedure. We first excluded variables when the Pearson's correlation coefficient was ≥0.7. The variable within a correlated pair that had more ecological relevance was kept. Variables that had multiple high intercorrelations with other variables of ecological meaning were also removed. This was particularly the case with elevation, which was correlated with most climatic variables. Elevation also represents a static proxy of climate making its inclusion for understanding the role of climatic variability relatively uninformative. We grouped the variables into seven categories (extreme events, climatic normals, structure/vegetation, topography, climatic indices, disturbance history, and soil) and used binomial GLMs to identify the strongest variables for predicting the presence or absence of greater gliders within each group. Only variables with significance of $P \leq 0.01$ were selected for inclusion in the final analyses. In cases where all variables within a given group had $P \leq 0.01$, the dredge function in MuMIN was used to build multiple models on all possible combinations of variables within that group. Only the significant variables in models with the highest AIC and delta ≤ 2.5 were selected for use in the machine-learning modeling (Anderson and Burnham 2004, Burnham and Anderson 2004). This process reduced the initial number of variables to 12 for further analysis (Table 2).

Table 2. Final modeling variables, their groups, and significance when fitted using GLM.

Group	Variable	Explanation	*P**
Extreme events	Hot nights	No. of nights with nighttime temperatures (tmin) ≥20°C	**
	Wet days	No. of days with precipitation (P) ≥ 25 mm	***
	Condensation events	No. of days with condensation index (CI) <0	*
Climatic normals	Potential evapotranspiration (et0)	Mean et0 of site	***
	Vapor pressure deficit (vpd)	Mean vpd of site	*
Structure/ vegetation	Forest type	Ecological vegetation classes (EVC)	***
	Normalized Difference Vegetation Index (NDVI)	NDVI value at survey date	*
Topography	slope	Slope in degrees	***
	TWI	Terrain wetness index	***
Climatic indices	AHMI	Annual heat moisture index	***
Disturbance history	Fires	No. of fires between 1981 and 2014	***
Soil	pH	Soil pH of organic layer	*

Note: Variables such as hot nights are cumulative over the 33-yr period, averaged per year.
$^{*}P \leq 0.01$, $^{**}P \leq 0.001$, $^{***}P \leq 0$.

Statistical modeling

We used boosted regression trees (BRTs) to identify variables associated with the occurrence of greater gliders and model habitat suitability. A machine-learning technique was selected because, unlike linear models, it allows for nonlinearities and interactions to be considered simultaneously (De'ath 2007, Elith et al. 2008). BRTs also allow for precise parameter control (such as learning rates and tree complexity) and an evaluation of interactions and variable thresholds within the final model. A learning rate of 0.001 was used with a bag fraction of 0.5 and a tree complexity of 5, to allow for interactions to be considered. The number of trees was chosen by error rate with minimum error as the selection criterion for model complexity (De'ath 2007). The full dataset was randomly split into training (70% of the data) and validation (30%) subsets. The models were built on training data only; model fit was tested using cross-validation (CV) and independent validation using the full dataset and the validation dataset, respectively. Multiple statistics were used to test model fit including CV correlation, deviance, accuracy, area under the curve (AUC), sensitivity (true-positive rate, TPR) and specificity (true-negative rate, TNR), and the true skill statistic (TSS), which, as compared to kappa, is not dependent on prevalence affecting predictive accuracy (Allouche et al. 2006). Cohen's kappa was instead used to determine the probability of occurrence threshold used to represent suitable habitat of the final habitat suitability model that maximized model fit (Elith et al. 2006, 2008, De'ath 2007). Additionally, the most important variable interactions were extracted. Interactions were based on the residual variance of a linear model fitted to determine the influence of the variable interaction on model variance. The interaction size expresses the relative strength of the interaction. If residual variance is 0, no interaction has occurred; the larger the interaction value, the stronger the observed interaction (see Elith et al. 2008).

Modeling spatial and temporal changes in greater glider habitat

We used the relationships between greater glider occurrence and environmental predictors to explore how these variables have changed over the last three decades and how this may have impacted the distribution of the species within the study landscapes. To do this, we developed rasterized data layers for each of the variables included in the final habitat suitability model. Important climatic variables were extracted for each ~250 m grid cell over the State of Victoria for two time frames. The first time frame was the entire 33 yr of climatic data; this was used to visualize the species distribution model. The second time frame was a series of 11-yr windows, which represented climate within the periods 1981–1992, 1992–2003, and 2003–2014 (climatic years were calculated from July to June). These 11-yr windows were used to test for changes in climate and variable patterns over time. Non-climatic variables were transformed into rasters and rescaled to 250-m resolution where necessary. Due to the lack of cloud-free satellite imagery for the entire State of Victoria for all survey periods, rasters were cropped to the forest areas of the three study landscapes. For these, all variable rasters were compiled into raster stacks using raster. Partial variable dependence plots were used to identify thresholds (i.e., variable values that lead to positive or negative impacts on habitat suitability) and extracted for each of the significant climatic predictors (i.e., AHMI, wet days, hot nights, VPD, and condensation). Using averaged rasters, we identified areas of suitable climatic conditions. Rasters representing all climatic variables for each 11-yr window were used to calculate the percentage of change in each climatic variable included in the model between the first (1981–1992) and last (2003–2014) period. We then analyzed the extent of currently suitable area by extracting area percentages and inter-period changes in habitat suitability using niche overlap and percentage of area of habitat suitability in either period, defined by variable thresholds according to Schoener and Gorman (1968) and Warren et al. (2008). The number and size of patches of suitable and unsuitable habitat were extracted by reclassifying prediction rasters based on the identified suitability threshold defined by Cohen's kappa and elevation to create landscape classes. These were then analyzed using calculate_lsm from the landscapemetrics package. We also used the data to identify changes in the area with suitable climatic conditions for greater gliders based on climatic variable-specific thresholds. Additionally, we used confirmed and verified historical records matching the earliest 11-yr window from the Victorian Biodiversity Atlas (VBA; vba.dse.vic.gov.au/vba) to explore whether the modeled declines in climatically suitable conditions for greater gliders were consistent with observed spatial patterns of declines in greater glider observations.

RESULTS

Model performance

Cross-validation and independent validation datasets suggest that the final boosted regression tree model performed with high classification accuracy in both evaluations. AUC was 0.93 for cross-validation and 0.82 for independent validation, respectively, and TSS was 0.71 and 0.5 (Table 3). In cross-validation, 90% of all presences and 81% of all absences were predicted correctly, while in independent validation, the model predicted 81% of all presences and 69% of all absences correctly. The best true-positive (TP) and true-negative (TN) predictions were achieved for the East Gippsland study region (Appendix S1: Figs. S2, S3). These results show that the models are robust and can be used as a predictive tool for greater glider occupancy across the studied landscapes.

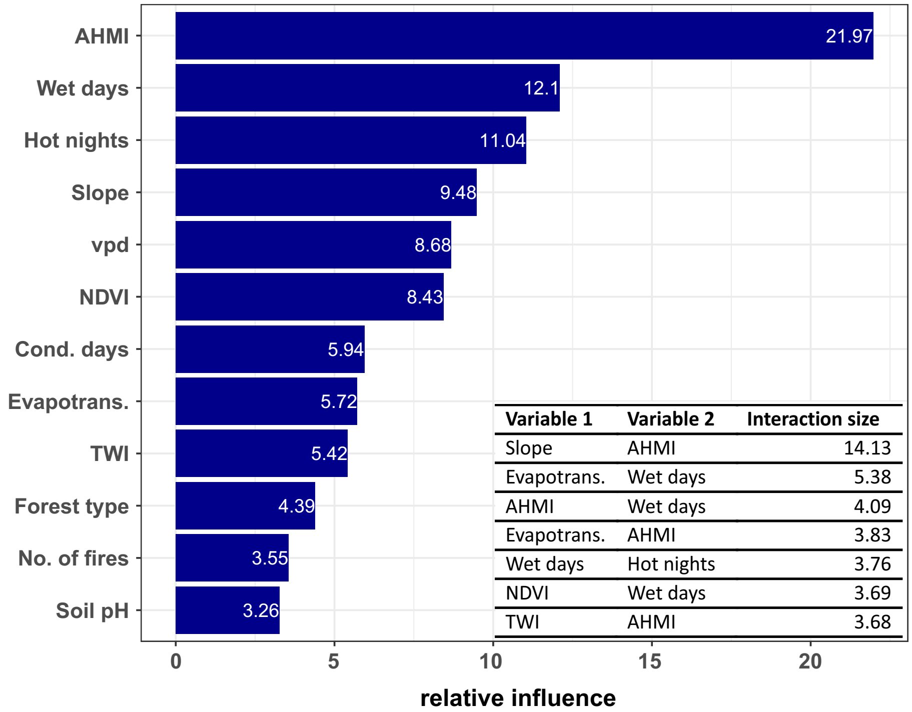
Variable importance

Aridity, weather events, and climate were the most important predictors of habitat suitability (Fig. 1). Non-climatic variables had less influence, although they still contributed to the model performance. Of the five most important variables, four were related to climate: AHMI (22% variable influence), number of wet days (12.1%), number of hot nights (11%), and vapor pressure deficit (8.7%). Other climatic variables had 5.9% (days with condensation) and 5.7% (evapotranspiration) variable influence, respectively. The performance of non-climatic variables in ranked order was slope (9.5%), NDVI (8.4%), TWI

Table 3. Summary of model evaluation.

Test	Kappa	Accuracy	AUC	Correlation	Sensitivity	Specificity	TSS	*P*
Cross-validation	0.71	0.86	0.93	0.74	0.81	0.90	0.71	<0.001
Independent validation	0.49	0.75	0.82	0.56	0.69	0.81	0.5	<0.001

Note: Both validations were based on a BRT model of 3300 trees with a deviance of 0.68.



Variable 1	Variable 2	Interaction size
Slope	AHMI	14.13
Evapotrans.	Wet days	5.38
AHMI	Wet days	4.09
Evapotrans.	AHMI	3.83
Wet days	Hot nights	3.76
NDVI	Wet days	3.69
TWI	AHMI	3.68

Fig. 1. Variable importance in percent and main interactions of final boosted regression tree (BRT) model for greater glider occupancy in eastern Victoria. See Table 2 for variable explanation.

(5.4%), EVC forest type (4.4%), number of fires (3.5%), and soil pH (3.3%). Partial dependencies were used to evaluate the influence (positive or negative) each variable had on the presence or absence of greater gliders (Fig. 2). Interactions were detected between both climatic and non-climatic variables. The strongest interaction was observed between slope and AHMI (interaction size: 14.13, Fig. 1; Appendix S1: Fig. S4).

Species distribution models

We predicted the location of high suitability habitat—areas most likely to have greater gliders present—in all three study regions (Fig. 3). High habitat suitability was defined based on the probability that maximized the kappa statistic (maximum TPR + TNR at 0.47). Areas below the threshold were considered unsuitable and unlikely to support greater gliders based on the model parameters. In East Gippsland, 16% (~200,000 ha) of the forest area was found to be high suitability habitat. In the Central Highlands and Strathbogie Ranges, 47% and 49% were high suitability habitat (~400,000 ha and ~20,000 ha, respectively; Fig. 3, Table 4). Elevations above 700 m were predominately classified as highly suitable across all regions (Appendix S1: Fig. S5); elevations above 500 m make up more than 50% of the total suitable area in all study regions (Appendix S1: Fig. S6).

Changes in climatic predictors and suitable habitat over time

Analyses of the climatic data and historic records suggested that climatic conditions over the past three decades have shifted, with extreme conditions such as hot nights increasing over time, particularly over the last five years of available data (Appendix S1: Fig. S7). In all sites within the three study regions, annual maximum summer nighttime temperatures have exceeded the thermoneutral point of 20°C since 1996. Additionally, we observed a trend of rising mean annual nighttime temperatures since the late 1980s across sites and regions (Appendix S1: Fig. S8). Analyzing changes in the area with suitable climatic conditions for greater gliders between 1981–1992 and 2003–2014 based on

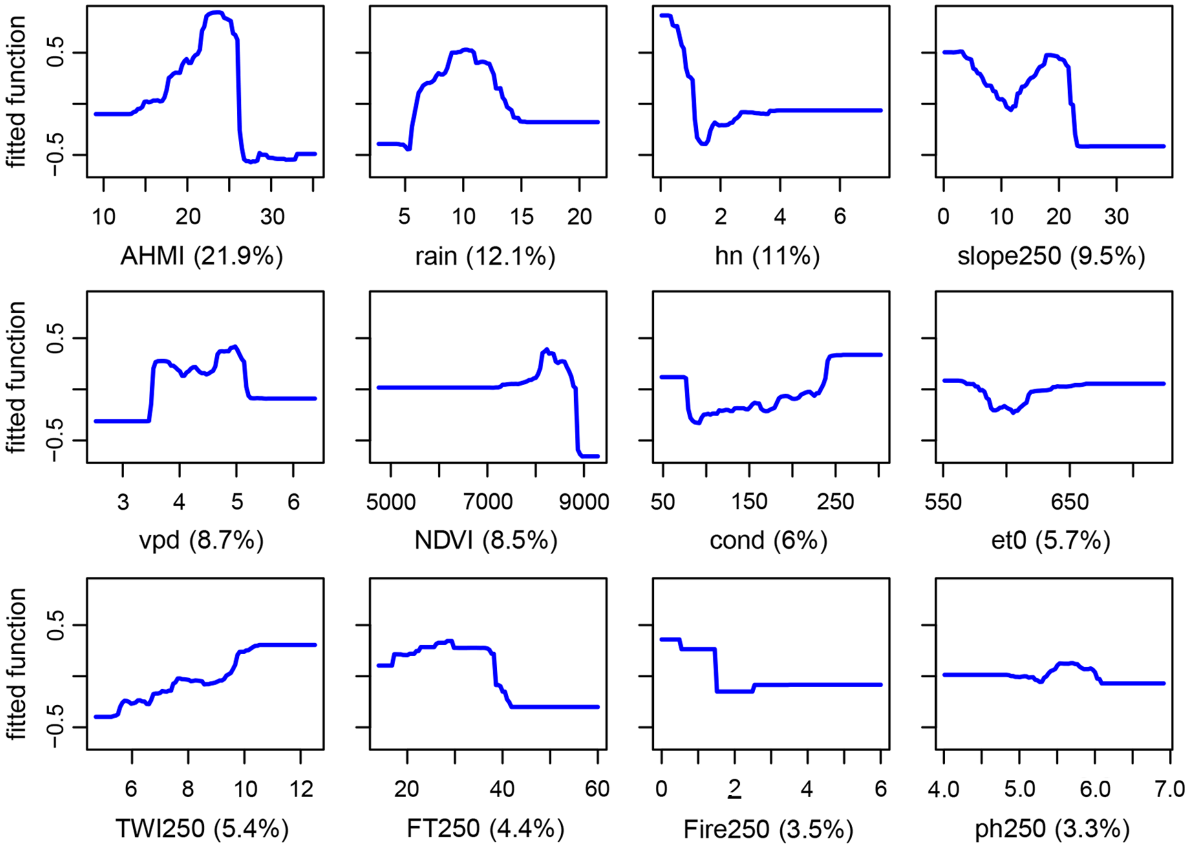


Fig. 2. Partial variable dependence plots for all 12 modeling variables and their variable importance in percent. Abbreviations are AHMI, annual heat moisture index; rain, number days with $P \geq 25$ mm; hn, number of nights with tmin ≥20°C; slope250, slope in degrees at 250-m resolution; vpd, vapor pressure deficit; NDVI, normalized difference vegetation index; cond, number of days with condensation index (CI) < 0; et0, potential evapotranspiration; TWI250, terrain wetness index at 250-m resolution; FT, forest type according to EVC; Fire250, number of forest fires between 1981 and 2014 at 250-m resolution; and ph250, soil pH at 250-m resolution.

climatic variable-specific thresholds, we found that the total area with suitable climatic conditions was highly responsive to decadal changes in climate across all three study regions and for all climatic variables. The most striking response was a decline in the area of suitable conditions associated with changes in the number of hot nights. The increasing frequency of hot nights was associated with a reduction in area with suitable climatic conditions from 63% (across all three regions) to 10%. For three variables (AHMI, wet days, and condensation days), an increase in the suitable area was detected in some regions. However, in most cases these changes were marginal (Table 5; Appendix S1: Fig. S9). Using single-variable suitable area extent and historic greater glider records from 1981 to 1992, we found, across the study regions, that the total area with suitable climatic conditions and greater glider observations was much greater in the 1980s and that the changes in observed occurrences by the late 2000s are consistent with observed changes in climatic conditions (Fig. 4). Studying the percentage change in AHMI between the first and last 11-yr period, we found that all study regions have generally become hotter and drier over time. These areas had higher average AHMI values in 2003–2014 compared with 1981–1992. Nevertheless, some areas in East Gippsland above 500-m elevation, experienced lower AHMI values between 2003 and 2014, suggesting a decline in aridity during this time period (Fig. 5).

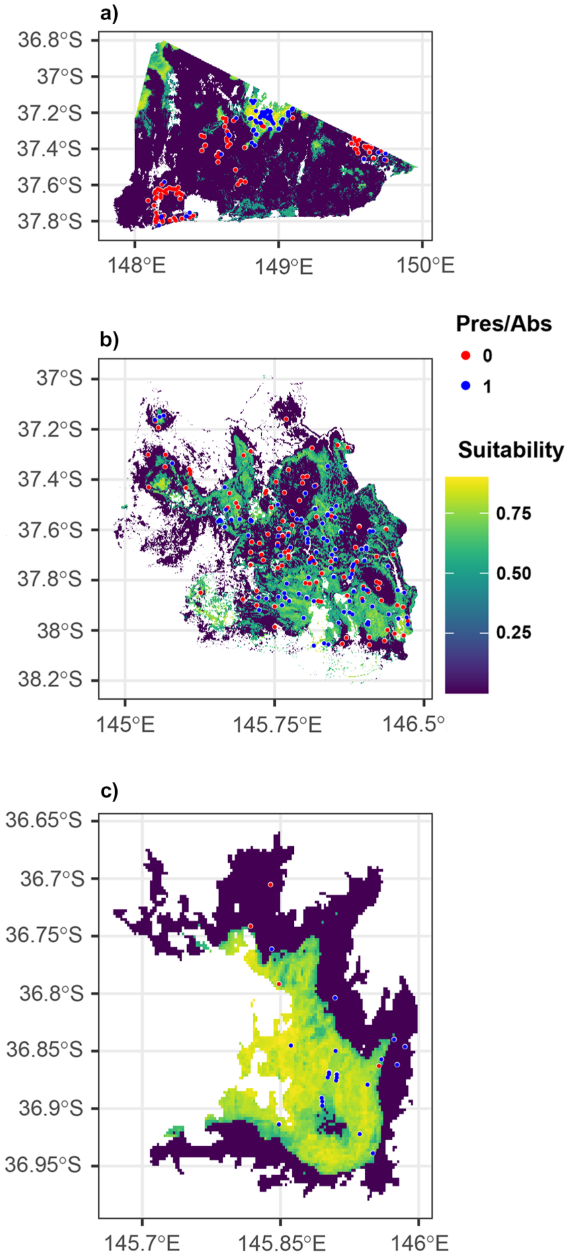


Fig. 3. Mapped habitat suitability for greater glider over forest areas of (a) East Gippsland, (b) Central Highlands, and (c) Strathbogie Ranges with survey site overlay (0/red = absence, 1/blue = presence site.

Discussion

Climatic change and weather extremes affect the quality and distribution of habitat for many animal species (Hughes et al. 1996, Reside et al. 2010, Bateman et al. 2012, Rawal et al. 2014, 2015*a*, Seidl et al. 2017). Using high-resolution, daily climatic datasets, we identified that the distribution of greater gliders in Victoria in southeastern Australia is primarily influenced by climatic variables that relate to their unique physiology; areas with cool nighttime temperatures and higher water availability were most suitable for greater gliders, and areas with high nighttime temperatures and arid conditions were least suitable. Importantly, we found that these climatic conditions have changed to such a degree over the last 30 yr that it has precipitated a landscape-scale contraction of wetter and cooler conditions to higher elevations. Our results have important implications for understanding the recent declines of greater glider populations in the region (see Lindenmayer et al. 2011, Lindenmayer and Sato 2018).

The greater glider's unique physiology and diet make it particularly vulnerable to high temperatures and low water availability (Rubsamen et al. 1984). Higher temperatures lead to heat dissipation through more rapid evaporation of saliva licked onto the animals' fur for cooling, as well as increased respiratory frequency and inefficient and excessive use of water for both processes. Foley et al. (1990) reported that free-living gliders obtained 58% of their water intake from water in leaves and only 18% from metabolic processes. Remaining water came from licking dew and rainwater on the surface of leaves, thus indirectly from their food source. Increasing aridity, more frequent hot nights, and decreasing numbers of wet days and days with condensation events all negatively impacted the area of potentially suitable habitat for greater gliders across a wide range of forests and forest conditions in southeastern Australia. Warmer nights (i.e., higher minimum temperatures) increase the water-holding capacity of the atmosphere (i.e., higher svp) and therefore reduce the amount of condensation available. When coupled with increasing aridity, these factors are likely to considerably reduce the amount of water available to the animal. Climate and weather variables accounted for ~65% of the variable influence in our model. Earlier studies demonstrated the influence of temperature on greater glider habitat suitability (Cork and Catling 1996) and suggested that climate is an important determinant

Table 4. Habitat suitability statistics based on landscape predictions for the three study regions.

Study region	Area suitable (ha)	Percentage of total area suitable	Mean suitability	SD	SE
East Gippsland	198,556	16	0.64	0.14	0.0008
Central Highlands	403,462	47	0.58	0.07	0.0003
Strathbogie Ranges	21,514	49	0.75	0.08	0.0014

Table 5. Area and overlap analysis results for each climatic variable in the three study regions.

Variable	Threshold	Region	Percentage of area suitable 1980s	Percentage of area suitable today	Percentage niche overlap
AHMI	14–25	EG	*4.5*	*6.9*	*62.3*
		CH	50.4	43.4	73.2
		SR	46.5	15.7	33.8
Wet days	>100 occasions per decade	EG	84.3	61.3	72
		CH	54.3	51.3	89.2
		SR	*98.2*	*99.4*	*98.7*
Hot nights	<50 occasions per decade	EG	85	9.1	10.7
		CH	65	18.9	29
		SR	39.5	4.1	10.3
vpd	3.5–5	EG	59	36.8	53.1
		CH	64.1	54.8	81.6
		SR	10	6.3	63
Condensation days	>200 occasions per year	EG	25	19.6	65.6
		CH	*46.2*	*46.3*	*96.3*
		SR	*8.6*	*8.7*	*93.8*

Notes: Values in italics indicate (marginal) increases in suitable habitat, all others are declines, based on variable thresholds. Region abbreviations are EG for East Gippsland; CH for the Central Highlands; SR for the Strathbogie Ranges. See Table 2 for variable explanation.

of the species' future distribution (Kearney et al. 2010).

Aridity, represented by AHMI, was the most influential variable in our model. High values of AHMI indicate increased atmospheric aridity in response to either warmer temperatures or low precipitation, which in turn influence site-level moisture availability (Paudel et al. 2016). Higher AHMI values had a negative influence on occupancy (Fig. 2). This suggests that long-term shifts in regional hydroclimate have the potential to significantly alter the distribution of the greater glider across the region. The observed change in aridity over the last 33 yr is consistent with observed declines of the species within the region. Interestingly, our analyses found that some high-elevation areas, particularly within East Gippsland, may have become less arid in recent years (Fig. 5). These areas were also modeled to be the most suitable for the greater glider. It is worth noting that AHMI does not account for the role of topography on water availability. To consider this, we included the terrain wetness index (TWI), which accounts for fine-scale effects of landform on soil moisture. It explained 5.4% of the influence in the model. Higher TWI values are associated with greater upslope drainage and thus higher soil moisture (Beven and Kirkby 1979). Steeper slopes were also found to positively influence the occupancy of the greater glider (Fig. 2). This may be due to the influence of steepness on soil runoff and microclimate. Steeper slopes tend to connect to areas with high TWI values in riparian areas, which are also areas with increased condensation and lower temperatures due to cold air drainage (Stewart and Nitschke 2017*b*). Additionally, the strong interaction between AHMI and slope (Appendix S1: Figs. S4, S10) suggests that in drier parts of the landscape, areas with flatter slopes have a higher likelihood of occupancy. These areas have lower temperatures (see Stewart and Nitschke 2017*b*), higher terrain wetness indices,

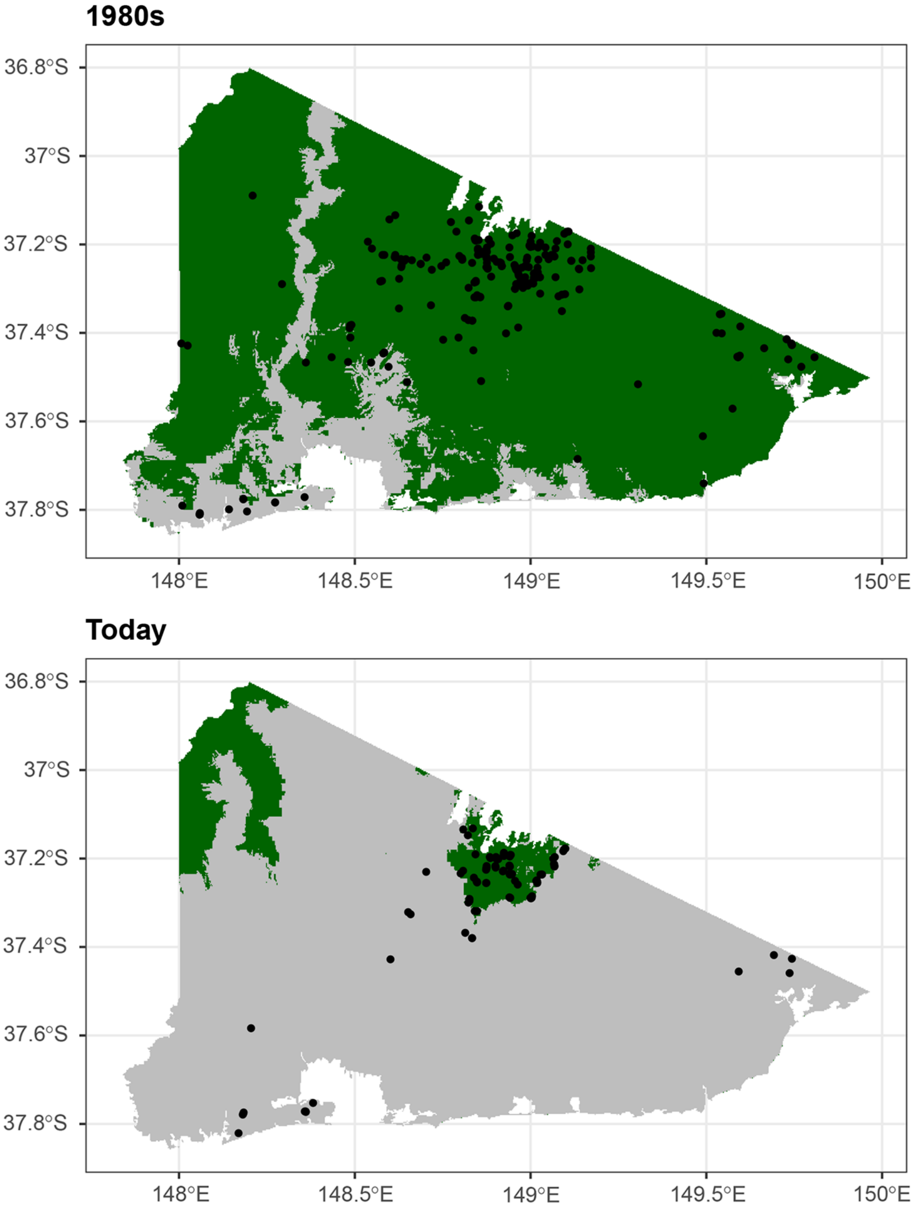


Fig. 4. Example of suitable habitat decrease for the variable hot nights (number of nights >20°C) according to variable threshold for 1981–1992 with historic records from the Victorian Biodiversity Atlas and 2003–2014 (today) with presence records from this study in East Gippsland. Dark green represents suitable-, gray represents unsuitable areas, and black dots are greater glider observations.

and higher levels of condensation. They are also typically dominated by riparian forests, where aridity is mediated by topographic influence. These results suggest that topographic complexity can provide microclimatic refugia in warmer and drier parts of the landscape, thus enabling the thermoregulatory threshold of greater gliders to be maintained. Many examples emphasize the importance of riparian and other stable habitat areas as refugia (Reside et al. 2019). Other species of Australian vertebrates, from the marsupial quokka (*Setonix brachyurus*) to woodland birds, are known to depend on these types of sites (De Tores et al. 2007, Bennett et al. 2014).

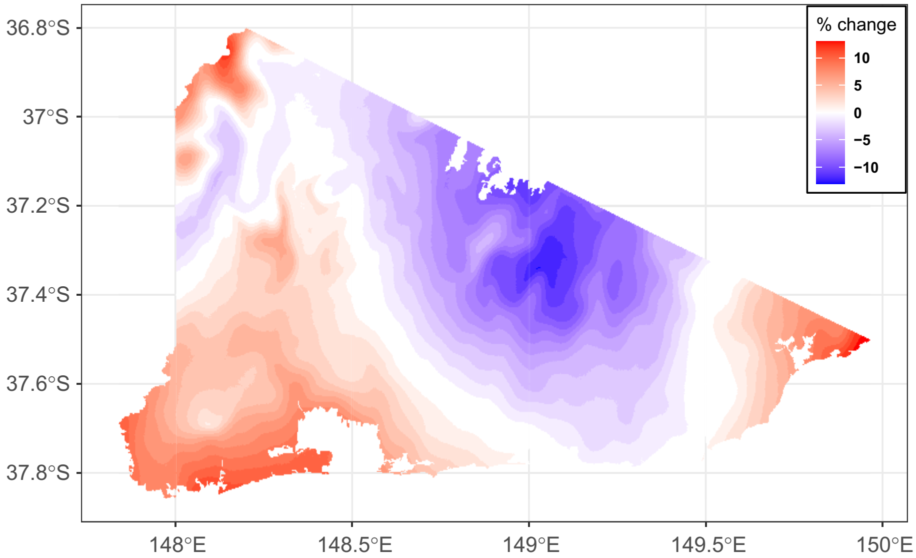


Fig. 5. Percent change in AHMI between 1981–1992 and 2003–2014 in the East Gippsland study region. Negative changes (blue colors) in AHMI indicate development of cooler and wetter conditions, suggesting the formation of climatic refugia for the greater glider. Positive changes (red colors) illustrate development of hotter and drier condition, likely reducing habitat suitability.

Several non-climatic variables relating directly or indirectly to vegetation quality were included in our final model of greater glider occurrence. The partial dependence plots of soil pH values suggest that sites with relatively neutral soils are preferred (Fig. 2). Soil pH may influence the nutritional content of the vegetation on which the species depends (Cork and Catling 1996). Soils with extreme pH values, whether too high or too low, generally have less plant-available nitrogen and other nutrients (Handreck et al. 2002). Cork (1992) showed that Australian eucalypt forests with leaf nitrogen content values below 10 mg/g are typically unfavorable for folivores. However, more research is needed to determine the relationship between soil pH and tree nutrition on greater glider habitat use. We also found that high NDVI values and certain forest types had a positive influence on occurrence (Fig. 2). In general, more productive forests (see Tucker 1979) with closed canopies were more likely to support the greater glider, which is consistent with early research by Kavanagh and Lambert (1990). NDVI has previously been identified as a useful predictor of greater glider abundance (Youngentob et al. 2015). These variables may be capturing the influence of soil and vegetation patterns on forest nutrition, which in turn influences the occurrence of greater gliders and other marsupial folivores. Closed-canopy forests in general also have a microclimatic effect and typically have cooler temperatures and higher moisture retention than open-canopy forests (Makarieva et al. 2006). These metrics may therefore represent a proxy for favorable microclimatic conditions within the landscape.

The lack of significant association with variables describing forest disturbance history (e.g., timber harvesting, forest fires, fire management practices) and the occurrence of greater gliders was surprising, as more than half of our sites had experienced some form of disturbance through fire or harvesting operations between 1980 and 2014 (Appendix S1: Fig. S11). Disturbance through fire and timber harvesting is generally considered the main threat to the species (Lindenmayer and Sato 2018, McLean et al. 2018). Timber harvesting, in particular, changes the structure of the forest, reducing nesting and foraging resources by replacing hollow-bearing trees with young regrowth or leaving relatively few habitable trees through retention, and thus poses a direct threat to the species at local scales (Lindenmayer and Sato 2018, McLean et al.

2018). However, the recently described local extinction of the greater glider at Booderee National Park, New South Wales, which has experienced neither logging nor severe fire over the period of observation, suggests that other factors may drive population fluctuations of the species (Lindenmayer et al. 2011). The lack of association between disturbance history and occurrence in our study may be, in part, due to the sampling design used to survey for greater glider and other arboreal marsupials. Typically, mature forests were targeted, and the survey technique detects animals when they are out foraging at night, rather than in their nesting habitat. However, the relatively small home ranges of greater gliders (Smith et al. 2007) may limit the importance of this as an issue. The species has often been detected adjacent to harvested areas. However, the harvested areas themselves are typically not directly targeted in arboreal marsupial surveys, nor are sites that have been recently burned. One reason for this is the dense vegetation that occurs in harvested and burnt areas, which limits detectability of animals in the forest canopy. Lindenmayer et al. (2013) found that the abundance of greater gliders declined when the amount of burned area around a survey point increased. The low importance of forest fires as a variable in our models suggests this response does not scale across the three study regions. Our analyses suggest that across mature forest stands, aridity and weather extremes are consistently more important than disturbance history in shaping the distribution of the species at the landscape-scale in southeastern Australia.

Only recently have the potential effects of heat stress and drought been considered as threat to greater gliders (see DELWP 2019). Modeled future climatic scenarios for southeastern Australia suggest that the climate will become warmer and drier with more extreme events in the coming decades (CSIRO and Bureau of Meteorology 2015). This may have important consequences for forests as habitat (Keenan and Nitschke 2016, Seidl et al. 2017). For the greater glider, predicted future climatic conditions will likely lead to more hot nights and less available water from rainfall and condensation. Indirect effects on forest nutrition and eucalypt species composition, preferred for foraging, may also lead to a reduction in habitat suitability. Our results suggest that the species has already experienced the impacts of climatic change and that these changes will be amplified as the climate becomes increasingly warmer and drier across southeastern Australia. Identifying and protecting bioclimatic refugia—that is, areas where suitable climatic conditions are likely to persist over the long term, within landscapes, is critical for the conservation of the greater glider. While many areas within the studied landscapes have become hotter and drier, some remained stable or have become less arid. Although observed aridity has increased throughout the entire Central Highlands and Strathbogie Ranges, mid- to high-elevation areas in East Gippsland have shown an opposite trend and may already be acting as climatic refugia for greater gliders (Fig. 5). These areas, where high densities of animals have been observed, are critical for the conservation of this species: In East Gippsland, more than 80% of suitable habitat lies above 500-m elevation and more than a third above 1000 m (Appendix S1: Fig. S6). In contrast, low-elevation sites, which have experienced the most drastic increases in AHMI, and which occur across all study regions, are likely to support fewer and fewer animals and will become increasingly unsuitable as habitat for the species. As the climate continues to change, low-elevation sites and other areas where the AHMI is likely to increase may become habitat traps—fragments of low-quality habitat that will eventually be unable to support greater gliders. Here, patch size of suitable habitat is already smaller and clumpiness of patches is lower, indicating more isolated habitat. In higher elevation areas, fewer but larger patches with higher clumpiness (close to maximum aggregation) indicate intact and interconnected habitat for the greater glider (Appendix S1: Table S2). Developing a network of bioclimatic refugia across these landscapes would be critical to the long-term viability of their populations in the region. Identifying these areas and protecting them will foster not only greater glider populations, but also with them a wide range of fauna and flora species relying on similar mature forest ecosystems and climatic conditions. All regions studied are covered by a complex and wide-ranging network of protected areas (Appendix S1: Figs. S12–S14). Recent conservation measures have added large areas to this protected network (DELWP 2019) and have led to the protection of additional crucial and climatically suitable habitat. As such, greater glider habitat in the Strathbogie Ranges forests is now widely protected (Appendix S1: Fig. S14). Nevertheless, large areas of suitable habitat in both East Gippsland and the Central Highlands study regions still lie outside any protected area, while areas with low or no suitability contribute large percentages to the protected area network. We found ~360,000 ha of currently suitable habitat for greater gliders across all three study regions to still be outside the protected area network (Appendix S1: Figs. S12–S14, Table S3).

The sensitivity of greater glider physiology to changes in climate and the potential impacts of recent climatic change on its distribution highlight significant challenges to the future conservation of some fauna. Conservation of these species is being challenged by both habitat loss and the direct impacts of climatic change on their physiology. The latter process may drive a contraction in population size or range extent, independent of habitat availability. The number of examples of mammal species being challenged by climatic change is increasing. Hoffmann et al. (2019) showed that the mountain pygmy possum (*Burramys parvus*) is increasingly threatened by the impacts of a warmer climate on its hibernation physiology, which may reduce overwintering survival. Rézouki et al. (2016) found that the recent trend to warmer winters and springs is increasing mortality rates in juvenile and older alpine marmots (*Marmota marmota*), due to interactions between marmot physiology, snow depth, and social structures. Recent climatic change is also considered as a potential cause in the contraction of moose (*Alces alces*) populations at the southern extent of their range due to heat stress (McCann et al. 2013). The broad conservation of habitat alone may not be enough to overcome the impacts of climatic change for these species. Understanding where both climatic and habitat refugia co-occur is critical for conserving these species under warmer future climatic conditions. For the greater glider and other species that are being pushed up to and beyond their physiological limits, recognizing the systemic impact of recent climatic change is critical to understanding and interpreting current population trends and designing conservation strategies that can facilitate their long-term protection. Although further work is needed to incorporate climatic change predictions into assessments of future habitat suitability for the greater glider in the region (e.g., Nitschke et al. 2020), our results demonstrate that the fingerprint of climatic change is already apparent across the warmer and drier portions of its distribution in southeastern Australia.

CONCLUSION

Climatic aridity and heat stress are primary drivers of greater glider habitat suitability in the studied regions and likely contribute to observed changes in greater glider populations over the past decades. Under a future of warming and drying climatic conditions, these observed declines are likely to continue as populations of greater gliders increasingly contract to bioclimatic refugia. Currently, the most suitable, stable, and least patchy habitat is found at higher elevations. However, these areas are not completely protected from future disturbances and climatic change. Targeted protection of current and future bioclimatic refugia will be important to ensure that viable populations of greater gliders can persist in southeastern Australia.

ACKNOWLEDGMENTS

This research was supported by the Australian Research Council (LP140100580 to CN and PJB, FT120100715 to PJB). BW was also supported by the University of Melbourne through a Melbourne Research Scholarship. Additional funding was generously provided to BW through from the Royal Zoological Society of New South Wales, the Foundation for Parks and Wildlife, and the Norman Wettenhall Foundation. Data collection (2012-2017) was funded by the Victorian Department of Environment, Land, Water and Planning (DELWP). CN was additionally funded through the Integrated Forest Ecosystem Research (IFER) program of DELWP. Lucas Bluff (DELWP) designed the 2015 East Gippsland surveys and carried out data collection with additional field assistance. We thank Lucas for his efforts and counsel and making his data available for this study. Field data collectors in 2012 for ARI included Ed McNabb (ARI staff) and contractors (Garry Cheers of G&B Cheers Flora & Fauna Consultants), Tamara Leitch, Aileen Collyer, Rolf Willig, and Jim Reside (Wildlife Unlimited). Luke

Emerson assisted with the 2017 Strathbogie Ranges and Central Highlands surveys. We thank field data collectors Tim Willersdorf (Parks Victoria), Diego Torres, Anu Singh, Ella Starkey, Steve Livesley (University of Melbourne), Edouard Sorin, Tom Ennes, and Florian Bourrel for their efforts in the 2018/2019 East Gippsland surveys. We further acknowledge and thank Raphael Trouvé and Anu Singh (University of Melbourne) for statistical and data analysis support. Finally, we would like to thank Natalie Briscoe (University of Melbourne), Ben Moore (Western Sydney University), Kara Youngentob (Australian National University), and Maria Cardoso (VicForests, Orbost) for advice and support. We want to thank the two anonymous reviewers for their thorough review of our research and the journal editors for helping in improving the quality of this manuscript. The authors have no competing interests to declare. Data were provided by co-authors and contributors to the project and used with their verbal or written permission. All authors conceived of the study. LL, JN, LD, JC, and MS designed and collected the field data for the ARI and DELWP studies with additional field assistance. BW and CN designed and collected field data for the 2018/2019 East Gippsland surveys with additional field assistance. SBS and CN provided data. BW analyzed the data and drafted the manuscript with contributions from CN and PJB. There are no conflicts of ethics to declare.

LITERATURE CITED

Alduchov, O. A., and R. E. Eskridge. 1996. Improved magnus form approximation of saturation vapor pressure. Journal of Applied Meteorology 35: 601–609.

Allouche, O., A. Tsoar, and R. Kadmon. 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). Journal of Applied Ecology 43:1223–1232.

Anderson, D., and K. Burnham. 2004. Model Selection and Multimodel Inference. Second edition. Springer-Verlag, New York, New York, USA.

Attiwill, P. M., and M. A. Adams. 1996. Nutrition of eucalypts. CSIRO Publishing, Clayton, Victoria, Australia.

Attiwill, P. M., and G. W. Leeper. 1987. Forest soils and nutrient cycles. Melbourne University Press, Beaverton, Carlton, Victoria, Australia.

Barton, K. 2019. MuMIn: multi-Model Inference. https://cran.r-project.org/package=MuMIn

Bateman, B. L., J. VanDerWal, and C. N. Johnson. 2012. Nice weather for bettongs: using weather events, not climate means, in species distribution models. Ecography 35:306–314.

Bennett, A. F., L. Lumsden, J. Alexander, P. Duncan, P. Johnson, P. Robertson, and C. Silveira. 1991. Habitat use by arboreal mammals along an environment gradient in north-eastern Victoria. Wildlife Research 18:125–146.

Bennett, A. F., D. G. Nimmo, and J. Q. Radford. 2014. Riparian vegetation has disproportionate benefits for landscape- scale conservation of woodland birds in highly modified environments. Journal of Applied Ecology 51:514–523.

Beven, K. J., and M. J. Kirkby. 1979. A physically based, variable contributing area model of basin hydrology/Un modèle à base physique de zone d'appel variable de l'hydrologie du bassin versant. Hydrological Sciences Journal 24:43–69.

Braithwaite, L. W., J. Turner, and J. Kelly. 1984. Studies on the arboreal marsupial fauna of eucalypt forests being harvested for wood pulp at Eden, Nsw Iii. Relationships between faunal densities, eucalypt occurrence and foliage nutrients, and soil parent materials. Wildlife Research 11:41–48.

Briscoe, N. J., M. R. Kearney, C. A. Taylor, and B. A. Wintle. 2016. Unpacking the mechanisms captured by a correlative species distribution model to improve predictions of climate refugia. Global Change Biology 22:2425–2439.

Burbidge, A. A., and J. Woinarski. 2020. *Petauroides volans* (amended version of 2016 assessment). The IUCN Red List of Threatened Species 2020: e. T40579A166500472. https://doi.org/10.2305/IUCN.UK.2020-1.RLTS.T40579A166500472.en. Downloaded on 01 October 2020.

Burnham, K. P., and D. R. Anderson. 2004. Multimodel inference - understanding AIC and BIC in model selection. Sociological Methods and Research 33:261–304.

Cai, W. J., et al. 2014. Increasing frequency of extreme El Nino events due to greenhouse warming. Nature Climate Change 4:111–116.

Cork, S. J. 1992. Polyphenols and the distribution of arboreal, folivorous marsupials in Eucalyptus forests of Australia. Pages 653–663 *in* Plant polyphenols. Springer, Boston, Massachusetts, USA.

Cork, S. J., and P. C. Catling. 1996. Modelling distributions of arboreal and ground-dwelling mammals in relation to climate, nutrients, plant chemical defences and vegetation structure in the eucalypt forests of southeastern Australia. Forest Ecology and Management 85:163–175.

Cork, S. J., and W. J. Foley. 1997. Digestive and metabolic adaptations of arboreal marsupials for dealing with plant antinutrients and toxins. Pages 204–226 *in* Marsupial biology: Recent research, new perspectives. University of New South Wales Press, Sydney, New South Wales, Australia.

Cork, S. J., and G. D. Sanson. 1990. Digestion and nutrition in the koala: a review. Pages 129–144 *in* A. K. Lee, K. A. Handasyde, and G. D. Sanson, editors. Biology of the Koala. Surrey Beatty, Sydney, New South Wales, Australia.

Cotrufo, M. F., P. Ineson, and A. Scott. 1998. Elevated CO_2 reduces the nitrogen concentration of plant tissues. Global Change Biology 4:43–54.

CSIRO, and Bureau of Meteorology. 2015. Climate change in Australia information for Australia's natural resource management regions: technical report. CSIRO and Bureau of Meteorology, Melbourne, Victoria, Australia.

De Tores, P. J., M. W. Hayward, M. J. Dillon, and R. I. Brazell. 2007. Review of the distribution, causes for the decline and recommendations for management of the quokka, Setonix brachyurus (Macropodidae: Marsupialia), an endemic macropodid marsupial from south-west Western Australia. Conservation Science Western Australia 6:13.

De'ath, G. 2007. Boosted trees for ecological modeling and prediction. Ecology 88:243–251.

DeGabriel, J. L., B. D. Moore, W. J. Foley, and C. N. Johnson. 2009. The effects of plant defensive chemistry on nutrient availability predict reproductive success in a mammal. Ecology 90:711–719.

DELWP. 2019. Greater Glider (*Petauroides volans* subsp. *volans*) Action statement No. 267 Flora Fauna Guarantee Act 1988 - Version 1.0. The State Department of Environment, Land, Water and Planning, East Melbourne, Victoria, Australia.

Department of Agriculture and Water Resources. 2018. Australia's State of the Forests Report 2018. Australian Bureau of Agricultural and Resource Economics and Sciences (ABARES), Canberra, Australian Capital Territory, Australia.

Department of Conservation and Natural Resources. 1995. Forest management plan for the East Gippsland Forest Management Area. Department of Conservation and Natural Resources, Canberra, Australian Capital Territory, Australia.

Department of Natural Resources and Environment. 1997. East Gippsland forest management plan amendment. Department of Natural Resources and Environment, Canberra, Australian Capital Territory, Australia.

Department of Natural Resources and Environment. 1998. Forest management plan for the Central Highlands. Department of Natural Resources and Environment, Canberra, Australian Capital Territory, Australia.

Diamond, J. 1984. "Normal" extinctions of isolated populations. Pages 191–246 *in* M. H. Nitecki, editor. Extinctions. University of Chicago Press, Chicago, Illinois, USA.

Elith, J., et al. 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29:129–151.

Elith, J., J. R. Leathwick, and T. Hastie. 2008. A working guide to boosted regression trees. Journal of Animal Ecology 77:802–813.

Fedrigo, M., S. B. Stewart, S. H. Roxburgh, S. Kasel, L. T. Bennett, H. Vickers, and C. R. Nitschke. 2019. Predictive ecosystem mapping of south-Eastern Australian temperate forests using Lidar-derived structural profiles and species distribution models. Remote Sensing 11:93.

Fischer, J., D. B. Lindenmayer, H. A. Nix, J. L. Stein, and J. A. Stein. 2001. Climate and animal distribution: a climatic analysis of the Australian marsupial Trichosurus caninus. Journal of Biogeography 28:293–304.

Foley, W. J., J. C. Kehl, K. A. Nagy, I. R. Kaplan, and A. C. Borsboom. 1990. Energy and water metabolism in free-living greater gliders, petauroides-volans. Australian Journal of Zoology 38:1–9.

Fox, J., and S. Weisberg. 2018. Visualizing fit and lack of fit in complex regression models with predictor effect plots and partial residuals. Journal of Statistical Software 87:1–27.

Greenwell, B., B. Boehmke, J. Cunningham, and G. Developers. 2019. gbm: generalized Boosted Regression Models. https://cran.r-project.org/package=gbm

Handreck, K. A., N. D. Black, and N. Black. 2002. Growing media for ornamental plants and turf. UNSW Press, Randwick, New South Wales, Australia.

Henry, S. 1984. Social organisation of the greater glider (*Petauroides volans*) in Victoria. Pages 221–228 *in* A. P. Smith and I. D. Hume, editors. Possums and Gliders'. Surrey Beatty and Sons, Chipping Norton, New South Wales, Australia.

Hesselbarth, M. H. K., M. Sciaini, K. A. With, K. Wiegand, and J. Nowosad. 2019. landscapemetrics: an open-source R tool to calculate landscape metrics. Ecography 42:1648–1657.

Hijmans, R. J. 2019. raster: geographic Data Analysis and Modeling. https://cran.r-project.org/web/packages/raster/index.html

Hijmans, R. J., S. Phillips, J. Leathwick, and J. Elith. 2017. dismo: species Distribution Modeling. https://cran.r-project.org/web/packages/dismo/index.html

Hoegh-Guldberg, O., et al. 2007. Coral reefs under rapid climate change and ocean acidification. Science 318:1737–1742.

Hoffmann, A. A., P. D. Rymer, M. Byrne, K. X. Ruthrof, J. Whinam, M. McGeoch, D. M. Bergstrom, G. R. Guerin, B. Sparrow, and L. Joseph. 2019. Impacts of recent climate change on terrestrial flora and fauna: some emerging Australian examples. Austral Ecology 44:3–27.

Hughes, L., E. M. Cawsey, and M. Westoby. 1996. Climatic range sizes of Eucalyptus species in relation to future climate change. Global Ecology and Biogeography Letters 5:23–29.

Iizumi, T., J. J. Luo, A. J. Challinor, G. Sakurai, M. Yokozawa, H. Sakuma, M. E. Brown, and T. Yamagata. 2014. Impacts of El Nino Southern Oscillation on the global yields of major crops. Nature Communications 5:3712.

Incoll, R. D., R. H. Loyn, S. J. Ward, R. B. Cunningham, and C. F. Donnelly. 2001. The occurrence of gliding possums in old-growth forest patches of mountain ash (*Eucalyptus regnans*) in the Central Highlands of Victoria. Biological Conservation 98:77–88.

Jensen, L. M., I. R. Wallis, and W. J. Foley. 2015. The relative concentrations of nutrients and toxins dictate feeding by a vertebrate browser, the greater glider *Petauroides volans*. PLOS ONE 10:e0121584.

Kanowski, J. 2001. Effects of elevated CO_2 on the foliar chemistry of seedlings of two rainforest trees from north-east Australia: implications for folivorous marsupials. Austral Ecology 26:165–172.

Kavanagh, R. P. 2000. Effects of variable-intensity logging and the influence of habitat variables on the distribution of the greater glider *Petauroides volans* in montane forest, southeastern New South Wales. Pacific Conservation Biology 6:18–30.

Kavanagh, R. P., and M. Lambert. 1990. Food selection by the greater glider, *Petauroides volans*: Is foliar nitrogen a determinant of habitat quality? Australian Wildlife Research 17:285–299.

Kearney, M. R., B. A. Wintle, and W. P. Porter. 2010. Correlative and mechanistic models of species distribution provide congruent forecasts under climate change. Conservation Letters 3:203–213.

Keenan, R. J., and C. R. Nitschke. 2016. Forest management options for adaptation to climate change: a case study of tall, wet eucalypt forests in Victoria's Central Highlands region. Australian Forestry 79:96–107.

Kissling, M. L., and E. O. Garton. 2006. Estimating detection probability and density from point-count surveys: a combination of distance and double-observer sampling. The Auk 123:735–752.

Lawler, I. R., W. J. Foley, I. E. Woodrow, and S. Cork. 1997. The effects of elevated CO_2 atmospheres on the nutritional quality of Eucalyptus foliage and its interaction with soil nutrient and light availability. Oecologia 109:59–68.

Lindenmayer, D. B., W. Blanchard, L. McBurney, D. Blair, S. C. Banks, D. Driscoll, A. L. Smith, and A. M. Gill. 2013. Fire severity and landscape context effects on arboreal marsupials. Biological Conservation 167:137–148.

Lindenmayer, D. B., R. B. Cunningham, M. T. Tanton, A. P. Smith, and H. A. Nix. 1990. Habitat requirements of the mountain Brushtail possum and the greater glider in the montane ash-type Eucalypt forests of the central highlands of Victoria. Australian Wildlife Research 17:467–478.

Lindenmayer, D. B., and C. Sato. 2018. Hidden collapse is driven by fire and logging in a socioecological forest ecosystem. Proceedings of the National Academy of Sciences of the United States of America 115:5181–5186.

Lindenmayer, D. B., J. T. Wood, L. McBurney, C. MacGregor, K. Youngentob, and S. C. Banks. 2011. How to make a common species rare: a case against conservation complacency. Biological Conservation 144:1663–1672.

Liu, C. R., P. M. Berry, T. P. Dawson, and R. G. Pearson. 2005. Selecting thresholds of occurrence in the prediction of species distributions. Ecography 28:385–393.

Lumsden, L., J. Nelson, C. Todd, M. Scroggie, E. McNabb, T. Raadik, S. Smith, S. Acevedo, G. Cheers, and M. Jemison. 2013. A new strategic approach to biodiversity management–research component. Arthur Rylah Institute for Environmental Research unpublished client report for the Department of Environment and Primary Industries, Melbourne, Victoria, Australia.

Makarieva, A. M., V. G. Gorshkov, and B.-L. Li. 2006. Conservation of water cycle on land via restoration of natural closed-canopy forests: implications for regional landscape planning. Ecological Research 21:897–906.

Marples, T. 1973. Studies on the Marsupial Glider, Schoinobates Volans (Kerr). 4. Feeding biology. Australian Journal of Zoology 21:213–216.

Marshall, R. 2007. Conservation plan for the strathbogie landscape: biodiversity action planning in the mid Goulburn. Department of Sustainability and Environment, East Melbourne, Victoria, Australia.

Mathewson, P. D., L. Moyer-Horner, E. A. Beever, N. J. Briscoe, M. Kearney, J. M. Yahn, and W. P. Porter. 2017. Mechanistic variables can enhance predictive models of endotherm distributions: the American pika under current, past, and future climates. Global Change Biology 23:1048–1064.

McCann, N., R. Moen, and T. Harris. 2013. Warm-season heat stress in moose (*Alces alces*). Canadian Journal of Zoology 91:893–898.

McIlwee, A. P. 2001. The distribution and abundance of arboreal folivores in response to variation in soil fertility, climate and the nutritional quality of eucalypt foliage. James Cook University, Townsville, North Queensland, Australia.

McLean, C. M., R. P. Kavanagh, T. Penman, and R. Bradstock. 2018. The threatened status of the hollow dependent arboreal marsupial, the Greater Glider (*Petauroides volans*), can be explained by impacts from wildfire and selective logging. Forest Ecology and Management 415:19–25.

McPherson, J. M., W. Jetz, and D. J. Rogers. 2004. The effects of species' range sizes on the accuracy of distribution models: Ecological phenomenon or statistical artefact? Journal of Applied Ecology 41:811–823.

McVicar, T. 2011. Near-Surface Wind Speed. v7. Data collection. CSIRO, Canberra, Australian Capital Territory, Australia.

Mok, H. F., S. K. Arndt, and C. R. Nitschke. 2012. Modelling the potential impact of climate variability and change on species regeneration potential in the temperate forests of South-Eastern Australia. Global Change Biology 18:1053–1072.

Moore, B. D., I. R. Wallis, K. J. Marsh, and W. J. Foley. 2004. The role of nutrition in the conservation of the marsupial folivores of eucalypt forests. Conservation of Australia's Forest Fauna 2:549–575.

Moran-Ordonez, A., N. J. Briscoe, and B. A. Wintle. 2018. Modelling species responses to extreme weather provides new insights into constraints on range and likely climate change impacts for Australian mammals. Ecography 41:308–320.

Murphy, B. F., and B. Timbal. 2008. A review of recent climate variability and climate change in southeastern Australia. International Journal of Climatology 28:859–879.

Nelson, J. L., M. P. Scroggie, L. K. Durkin, J. K. Cripps, D. S. Ramsey, and L. Lumsden. 2018. Estimating the density of the greater glider in the Strathbogie ranges, north east Victoria: with an Assessment of Coupes Scheduled for Timber Harvesting in 2018. Arthur Rylah Institute for Environmental Research, The State Department of Environment, Land, Water and Planning, Canberra, Australian Capital Territory, Australia.

Nitschke, C. R., R. Trouvé, L. F. Lumsden, L. T. Bennett, M. Fedrigo, A. P. Robinson, and P. J. Baker. 2020. Spatial and temporal dynamics of habitat availability and stability for a critically endangered arboreal marsupial: implications for conservation planning in a fire-prone landscape. Landscape Ecology 35:1553–1570.

Opie, A., G. Gillespie, S. Henry, V. Hurley, B. Lobert, and J. Westaway. 1990. Flora and Fauna Survey of the Coast Range Forest Block, (Southern Part), East Gippsland, Victoria. Department of Conservation, Forests & Lands. State Forests and Lands Service, Melbourne, Victoria, Australia.

Orlowsky, B., and S. I. Seneviratne. 2012. Global changes in extreme events: regional and seasonal dimension. Climatic Change 110:669–696.

Paudel, S. K., P. O. Waeber, S. W. Simard, J. L. Innes, and C. R. Nitschke. 2016. Multiple factors influence plant richness and diversity in the cold and dry boreal forest of southwest Yukon, Canada. Plant Ecology 217:505–519.

Pope, M. L., D. B. Lindenmayer, and R. B. Cunningham. 2004. Patch use by the greater glider (*Petauroides volans*) in a fragmented forest ecosystem. I. Home range size and movements. Wildlife Research 31:559–568.

Possingham, H. P., D. B. Lindenmayer, T. W. Norton, and I. Davies. 1994. Metapopulation viability analysis of the greater glider *Petauroides-volans* in a wood production area. Biological Conservation 70:227–236.

QGIS Development Team. 2018. QGIS Geographic Information System. Open Source Geospatial Foundation. https://www.qgis.org/en/site/

R Core Development Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rawal, D. S., S. Kasel, M. R. Keatley, C. Aponte, and C. R. Nitschke. 2014. Environmental effects on growth phenology of co-occurring Eucalyptus species. International Journal of Biometeorology 58: 427–442.

Rawal, D. S., S. Kasel, M. R. Keatley, and C. R. Nitschke. 2015*a*. Climatic and photoperiodic effects on flowering phenology of select eucalypts from south-eastern Australia. Agricultural and Forest Meteorology 214:231–242.

Rawal, D. S., S. Kasel, M. R. Keatley, and C. R. Nitschke. 2015*b*. Environmental effects on germination phenology of co-occurring eucalypts: implications for regeneration under climate change. International Journal of Biometeorology 59: 1237–1252.

Rawal, D. S., S. Kasel, M. R. Keatley, and C. R. Nitschke. 2015*c*. Herbarium records identify sensitivity of flowering phenology of eucalypts to climate: implications for species response to climate change. Austral Ecology 40:117–125.

Reside, A. E., et al. 2019. Persistence through tough times: fixed and shifting refuges in threatened species conservation. Biodiversity and Conservation 28:1303–1330.

Reside, A. E., J. J. Vanderwal, A. S. Kutt, and G. C. Perkins. 2010. Weather, not climate, defines distributions of vagile bird species. PLOS ONE 5:e13569.

Rézouki, C., M. Tafani, A. Cohas, A. Loison, J. M. Gaillard, D. Allainé, and C. Bonenfant. 2016. Socially mediated effects of climate change decrease survival of hibernating Alpine marmots. Journal of Animal Ecology 85:761–773.

Rubsamen, K., I. D. Hume, W. J. Foley, and U. Rubsamen. 1984. Implications of the large surface-area to body-mass ratio on the heat-balance of the greater glider (*Petauroides-volans-Marsupialia*). Journal of Comparative Physiology 154:105–111.

Schoener, T. W., and G. C. Gorman. 1968. Some niche differences in three Lesser Antillean lizards of the genus Anolis. Ecology 49:819–830.

Sebire, I., and P. C. Fagg. 2009. High elevation mixed species in Victoria's state forests. Department of Sustainability and Environment, East Melbourne, Victoria, Australia.

Seidl, R., et al. 2017. Forest disturbances under climate change. Nature Climate Change 7:395–402.

Sing, T., O. Sander, N. Beerenwinkel, and T. Lengauer. 2005. ROCR: visualizing classifier performance in R. Bioinformatics 21:3940–3941.

Smith, G. C., M. Mathieson, and L. Hogan. 2007. Home range and habitat use of a low-density population of greater gliders, *Petauroides volans* (Pseudocheiridae : Marsupialia), in a hollow-limiting environment. Wildlife Research 34:472–483.

Stenseth, N. C., A. Mysterud, G. Ottersen, J. W. Hurrell, K. S. Chan, and M. Lima. 2002. Ecological effects of climate fluctuations. Science 297:1292–1296.

Stewart, S. B., M. Fedrigo, S. H. Roxburgh, S. Kasel, and C. Nitschke. 2020*a*. Climate Victoria: 9am Vapour Pressure (9 second, approx. 250 m). v3. CSIRO. https://doi.org/10.25919/5e5701b5df4d8

Stewart, S. B., M. Fedrigo, S. H. Roxburgh, S. Kasel, and C. Nitschke. 2020*b*. Climate Victoria: precipitation (9 second, approx. 250 m). v1. CSIRO. https://doi.org/10.25919/5e3be5193e301

Stewart, S. B., M. Fedrigo, S. H. Roxburgh, S. Kasel, and C. Nitschke. 2020*c*. Climate Victoria: reference Evapotranspiration (FAO-56; 9 second, approx. 250 m). v1. CSIRO. https://doi.org/10.25919/5e3e4b6b309f2

Stewart, S. B., and C. Nitschke. 2017*a*. Climate Victoria: maximum Temperature (3DS; 9 second, approx. 250 m). v2. CSIRO. https://doi.org/10.25919/5e5d9c82c3b16

Stewart, S. B., and C. R. Nitschke. 2017*b*. Improving temperature interpolation using MODIS LST and local topography: a comparison of methods in south east Australia. International Journal of Climatology 37:3098–3110.

Stewart, S. B., and C. Nitschke. 2018. Climate Victoria: minimum Temperature (3DS-TM; 9 second, approx. 250 m). v2. CSIRO. https://doi.org/10.25919/5e5dc18621a12

Tucker, C. J. 1979. Red and photographic infrared linear combinations for monitoring vegetation. Remote Sensing of Environment 8:127–150.

Tyre, A. J., B. Tenhumberg, S. A. Field, D. Niejalke, K. Parris, and H. P. Possingham. 2003. Improving precision and reducing bias in biological surveys: estimating false-negative error rates. Ecological Applications 13:1790–1801.

Van der Ree, R., S. Ward, and K. Handasyde. 2004. Distribution and conservation status of possums and gliders in Victoria. Pages 91–110 *in* The biology of Australian possums and gliders. Surrey Beatty and Sons, Sydney, New South Wales, Australia.

VanDerWal, J., L. Falconi, S. Januchowski, L. Shoo, and C. Storlie. 2019. SDMTools: species Distribution Modelling Tools: tools for processing data associated with species distribution modelling exercises. https://www.rforge.net/SDMTools/

Walther, G. R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. Beebee, J. M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature 416: 389–395.

Wang, T., A. Hamann, A. Yanchuk, G. A. O'Neill, and S. N. Aitken. 2006. Use of response functions in selecting lodgepole pine populations for future climates. Global Change Biology 12:2404–2416.

Warren, D. L., R. E. Glor, and M. Turelli. 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution 62:2868–2883.

Watson, C., F. Weckerly, J. Hatfield, C. Farquhar, and P. Williamson. 2008. Presence–nonpresence surveys of golden-cheeked warblers: detection, occupancy and survey effort. Animal Conservation 11:484–492.

Welbergen, J. A., S. M. Klose, N. Markus, and P. Eby. 2007. Climate change and the effects of temperature extremes on Australian flying-foxes. Proceedings of the Royal Society B: Biological Sciences 275:419–425.

Wing, J., et al. 2019. caret: classification and Regression Training. http://caret.r-forge.r-project.org

Wintle, B. A., R. P. Kavanagh, M. A. McCarthy, and M. A. Burgman. 2005. Estimating and dealing with detectability in occupancy surveys for forest owls and arboreal marsupials. Journal of Wildlife Management 69:905–917.

Woinarski, J. C., A. A. Burbidge, and P. L. Harrison. 2014. The Action Plan for Australian Mammals 2012. CSIRO Publishing, Collingwood, Victoria, Australia.

Youngentob, K., I. R. Wallis, D. B. Lindenmayer, J. T. Wood, M. L. Pope, and W. J. Foley. 2011. Foliage chemistry influences tree choice and landscape use of a gliding marsupial folivore. Journal of Chemical Ecology 37:71–84.

Youngentob, K., J. T. Wood, and D. B. Lindenmayer. 2013. The response of arboreal marsupials to landscape context over time: a large-scale fragmentation study revisited. Journal of Biogeography 40:2082–2093.

Youngentob, K., H. J. Yoon, J. Stein, D. B. Lindenmayer, and A. A. Held. 2015. Where the wild things are: using remotely sensed forest productivity to assess arboreal marsupial species richness and abundance. Diversity and Distributions 21:977–990.

Zimmermann, N. E., N. G. Yoccoz, T. C. Jr Edwards, E. S. Meier, W. Thuiller, A. Guisan, D. R. Schmatz, and P. B. Pearman. 2009. Climatic extremes improve predictions of spatial patterns of tree species. Proceedings of the National Academy of Sciences of the United States of America 106:19723–19728.

DATA AVAILABILITY

Presence and absence data for *Petauroides volans* used in this study are available on the Victorian Biodiversity Atlas (https://vba.dse.vic.gov.au/vba/).

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3262/full