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Mapping distributions, threats and opportunities to conserve the greater glider by integrating biophysical and spatially-explicit population models

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Executive summary

Predicting climate change impacts on extinction risk is challenging because it usually involves novel environments and always involves interactions with other threatening processes. Current approaches have limited capacity to include such complexities but they could strongly alter the effectiveness of proposed management actions and decisions about where and how to allocate management resources. We here demonstrate how the integration of state-of-the-art biophysical, distribution and population modelling approaches can account for the interactions between climate change and parallel threats while minimising extrapolation risk. We illustrate the approach using a threatened arboreal mammal, the Greater Glider, in the Central Highlands of Victoria, Australia. Our framework enabled us to combine the effects of wildfire, logging, and habitat fragmentation on populations, while accounting for physiological responses to climate change and their effect on vital rates. Our results suggest additional population declines that would not be explicitly captured in other modelling methods. These methods are not specific to a particular taxa or location and may be applied anywhere in the world using open-source, and freely available, software. A major anticipated application of the framework is to identify appropriate management actions to conserve populations and assess their likely effectiveness through simulations.

Introduction

A range of strategies exist for modelling the distribution and abundance of species as a function of environmental conditions, and they vary according to the extent that processes are made explicit (Briscoe et al, 2019). At one extreme are correlative species distribution models (SDMs) which represent a statistical description of the association between occurrence and environment. At the other extreme are process-explicit models of individuals or populations that integrate theoretical and empirical knowledge of ecological systems. The increasing availability of data required for correlative SDMs and the ease of their implementation has made correlative SDMs a popular choice among researchers, environmental scientists, governments, and non-governmental organisations (Guissan et al. 2016). Correlative models are useful for broad characterisation of current (and future) species distributions but require careful consideration of data used to fit them to ensure appropriate use (Guillera-Arroita et al, 2015). Whilst correlative models are useful for broad characterisation of current (and future) species distributions, when used in isolation, they fail to explicitly consider biological processes (e.g. dispersal limits, species interactions) or anthropocentric impacts (e.g. habitat modification, roadkill). As modelling becomes more process-explicit, greater generality of inference and understanding is achieved but at the cost of greater data requirements. However, given the increasing complexity of managing species persistence in the face of climate change, land-use modification, and economic volatility, we must now look to model frameworks which incorporate processes in a practical yet meaningful manner.

Spatially explicit population modelling is a process-explicit method that can incorporate information about how populations change, interact with environmental effects, and disperse in a landscape (Dunning et al, 1995; Akçakaya et al. 2004, Wintle et al. 2005, Fordham et al, 2013). Such models have been used to better understand and predict the impacts on species persistence of dynamic land use change, including forest logging and fire, direct persecution of species, and climate change (Wintle et al. 2005, Bekessy et al. 2009, Keith et al. 2008, Fordham et al. 2013), and the relative benefits of alternative conservation actions (Southwell et al. 2008). In most cases, the use of population models entails the use of correlative SDM to characterise spatial and temporal variation in carrying capacity (Briscoe et al 2019). Biological input parameters to these models, particularly vital rates (e.g., survival and fecundity) are often sourced from historical empirical data and are therefore unknown for future conditions and often are assumed to be static or are modelled correlatively with environmental conditions. However, the link between environment and vital rates can be at least partially captured by explicitly modelling the physical processes by which physiology and environment interact to affect vital rates. For example, energy and mass balance equations from the field of biophysical ecology can be used to identify the fundamental niches of species with respect to their energy and water requirements for thermoregulation (Kearney and Porter 2009; Kearney et al., 2010). Such an approach can be used to more confidently predict future changes in vital rates (e.g. survival and fecundity) linked to changing climatic conditions.

Past model integration efforts have seen the linking of spatially explicit demographic models with correlative SDMs to predict impacts of land use and climate change (Wintle et al. 2005; Keith et al. 2008) and the potential to improve the robustness of such predictions by inferring demographic parameters from biophysical models has been identified (e.g. Buckley 2008, Kearney et al. 2010). However, this opportunity has yet to be properly exploited in the creation of spatially explicit population projections to better predict the impacts of climate and land use change (e.g. Buckley 2008, Kearney et al. 2010, Kearney 2012a). Here we demonstrate how linking biophysical models with models of landscape dynamics (LANDIS-II; Scheller et al., 2006) and population dynamics (STEPS; Visintin et al, 2020) can improve our understanding of future changes in species populations and inform management objectives. We demonstrate our modelling framework by projecting long-term persistence of the Australian arboreal marsupial glider in a changing climate and landscape.

Methods

Study species

Greater gliders (*Petauroides volans*) are a large (900-1700 grams), arboreal possum capable of extended aerial travel and are found in forests along the east coast of Australia. Greater gliders (hereafter 'gliders') are vulnerable to environmental change because they have slow life history characteristics, low thermoregulatory capacity and their dispersal is limited by the presence of tree canopy (Taylor et al, 2007). They also have specialist habitat requirements including, large tree hollows (and therefore mature forests) for nesting and nitrogen-rich leaves from specific eucalypt species for suitable forage (Wagner et al, 2021). They were recently listed as "vulnerable" under Australia's EPBC Act (Commonwealth of Australia 1999) based on data showing population declines (Lindenmayer and Sato, 2018) and loss of habitat. Gliders face the cumulative impacts of a range of threats including habitat loss, fire and climate change (Wagner et al, 2021).

Case study region

Our modelling landscape was the 11,320 square kilometre (1,132,000 ha) Central Highlands region of south-east Australia (Figure 1). The region is predominantly native forest and the total area is equally split, and managed, for both conservation and wood production. The landscape dynamics in the area are well-characterised by existing models (e.g. response of tree species to wildfire and timber harvesting). Gliders have been known to occur across the entire region but there have been reported population declines (SAC, 2017). Previous modelling suggested that the area will remain climatically suitable for gliders in the future (Kearney et al, 2010) but it was focused on long-term mean climate and did not account for extremes. However, the observed decline of gliders appears to be correlated with high night-time temperatures in the region (Wagner et al, 2021). Thus, models incorporating finer temporal resolution of climatic variation may reveal important physical limitations on the gliders (Kearney et al. 2012b).

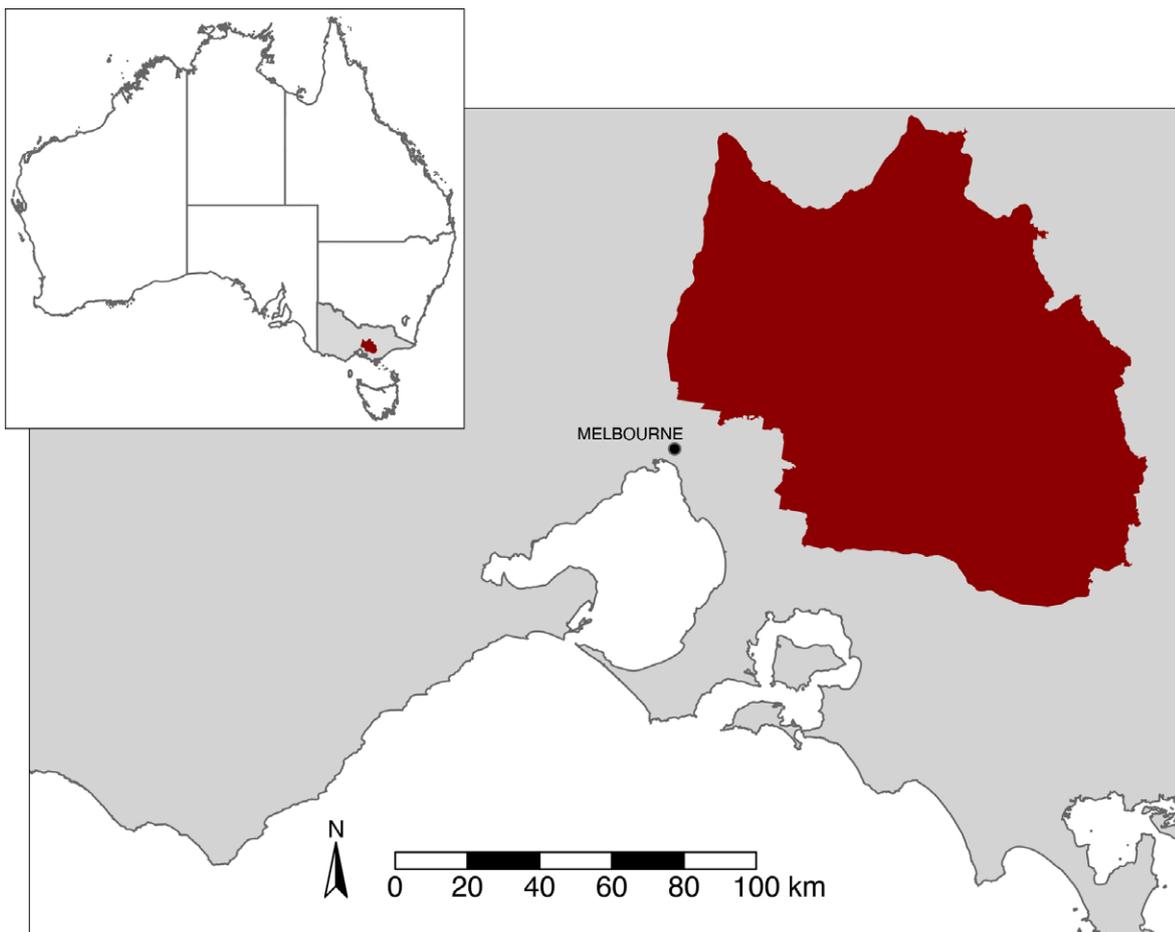


Figure 1. Central Highlands study area in Victoria, Australia. The area covers approximately one million hectares and is located within 40 kilometres of the Victorian capital city of Melbourne.

Spatial and temporal extent

We used two spatial resolutions across the study region in our modelling framework: 11,320 grid-based cells (one square kilometre resolution) represented habitat suitability, landscape information, and potential populations; 520 grid-based cells (twenty-five square kilometre resolution) represented information on future climate and predicted changes in survival and fecundity. The coarser biophysical modelling resolution was resampled to a finer resolution prior to use in the final population simulations. Biophysical simulations were made on hourly timesteps using disaggregated daily weather input data via a microclimate model, following Briscoe et al. (2016). All population simulations were based on annual timesteps spanning a 50-year time horizon, beginning in the year 2019 and going through the year 2069.

Weather data

We sourced daily climate projections from the Australian Commonwealth Scientific and Industrial Research Organisation (CSIRO) at 0.05 degree spatial resolution (Clarke et al, 2011) between the years 2016 and 2085 (which we clipped to our temporal extent of interest) for the Central Highlands region. Projections were based on the MIROC5 RCP8.5 model and included ambient air temperature (mean, minimum and maximum), relative humidity, precipitation, solar radiation, and air pressure. Wind speed was provided as mean monthly projections.

Landscape dynamics

Forest dynamics were modelled with LANDIS-II - used by Nitschke et al. (2020) to model the impact of fire, management and climate change on the critically endangered Leadbeater's possum in a subregion of the study landscape. For our study, the full Central Highlands landscape was similarly modelled following the approach of Wang et al. (2017). Predictions of total biomass and fire locations, frequencies and severities from the LANDIS-II simulation at one square kilometre resolution for each year in the simulation period were generated. The model included future climate projections (RCP8.5), simulated wildfires and planned burning, and prescribed timber harvesting until the year 2030 (a current target of the Victorian state government policy). Nitschke et al. (2020) provide a more detailed description of wildfire, planned burning and timber harvesting parameters used in the simulations.

Species distributions

Correlative SDMs were fitted to known glider presences and absences, and several climate and geographic environmental variables to provide spatially-explicit base information for our modelling framework. We used Boosted Regression Trees (Elith et al, 2008), a machine learning algorithm, to classify glider presences and absences based on both temporally-varying and static environmental variables. We then predicted relative habitat suitability for the species at one square kilometre resolution for each year in the simulation period. To estimate values for comparing to our population simulations, we multiplied the predicted suitability values by the maximum density of gliders (60) in each cell and summed the values across the landscape to generate a rough estimate of population change in each year.

Biophysical model

Physiological constraints on survival and reproduction of greater gliders were modelled using the R package NicheMapR (Kearney & Porter, 2017; Kearney & Porter, 2020). This is an R implementation of models initially developed by Porter et al. (1973, 2006), which were previously used to model the distribution of greater gliders across its Australian range (Kearney et al, 2010). A key advance is that we used the `endoR` function (Kearney et al. in review) to simulate responses to daily weather rather than long-term average monthly climate, as used in Kearney et al. (2010). This allowed us to account for the impact of weather extremes that can be important for understanding range dynamics of arboreal folivores (Briscoe et al. 2016; Wagner et al. 2020). Several parameters were also updated including fur and mass properties, which can vary geographically (Briscoe, unpublished data; McGregor et al, 2020).

Preliminary tests of the model against data presented in RübSamen et al, 1984 indicated reasonable agreement for both energy and water costs, as well as changes in core temperatures (Figure 2).

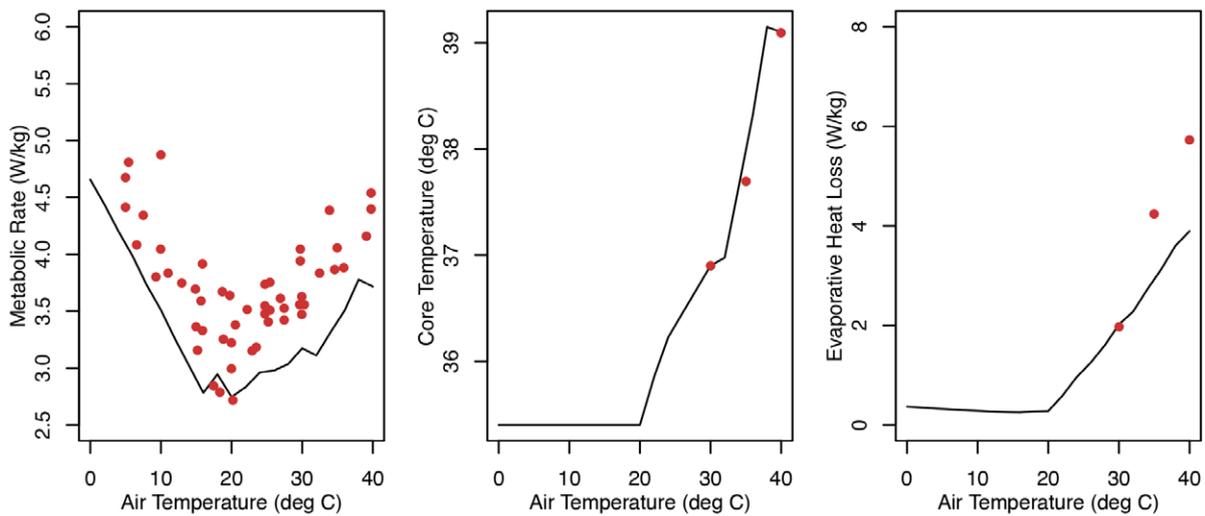


Figure 2. Predicted metabolic rate (W/kg), core temperature (°C) and evaporative heat loss (W/kg) of greater gliders at air temperatures of 0–40 °C. Lines represent our biophysical model predictions, red dots indicate observed data from Rübsamen et al. 1984.

Ambient hourly microclimate data were generated using a modified version of the *micro_aust* function in the NicheMapR package (Kearney & Porter, 2017) and the future climate data from CSIRO described previously. As no future predictions for daily wind data were available, we fitted splines to predicted monthly averages across all fifty years to impute daily values (i.e. cubic spline interpolation, see Wahba, 1990). We assumed gliders occupied habitats between 30–100% canopy cover, as they typically only occur in forests, and were exposed to wind because they forage near tree extremities that offer more preferable food quality (e.g. new foliage).

Greater gliders den in tree hollows during the day (Lindenmayer 2002), preferring large *Eucalyptus* species trees with diameters > 50cm (Smith et al, 2007). Temperatures within tree hollows are typically much more stable than ambient (Rowland et al, 2017) and so by using hollows in large trees gliders are likely to reduce thermoregulatory costs during weather extremes. To estimate the likely den temperatures in large, very buffered tree hollows we simulated hourly temperatures at a depth of 30cm into a shaded solid wood surface. We assumed a basic density of 580kg m⁻³ and moisture content of 120%, based on measurements of Mountain Ash (*Eucalyptus reglans*) trees in Victoria (Brown & Hillis, 1984). From this, we estimated a wood specific heat value of 3138 J kg⁻¹ K⁻¹ (Steinhagen, 1977), and thermal conductivity of 0.4017 W m⁻¹ °C⁻¹ (Wullschlegler et al. 2011). This approach neglects the heat effect of a glider on its own environment, which may be substantial (Kearney et al. 2011, Griffiths et al. 2017), and also ignores the effect of air flow from outside the hollow. To account for this second issue, we also ran models assuming that den conditions were similar to those in deep (100%) shade with no solar radiation and low windspeed (1% of interpolated speed).

For each of 520 spatial locations in our study area (25 square kilometre grid-cell resolution), we ran eight simulations to determine the energy and water requirements of greater gliders for every hour in our 50-year simulation period. Six simulations placed the glider outside of the den in 30%, 70% and 100% shade with interpolated wind velocities and either active foraging (metabolic rate of 7.08 W/kg) or inactive foraging (metabolic rate of 2.81 W/kg). The remaining two simulations assumed resting activities for the gliders; one in a tree hollow (with temperature influenced by the thermal properties of wood) and the other in a protected environment that tracked shaded ambient conditions. Both resting simulations assumed a metabolic rate of 2.81 W/kg, however, only the resting in a protected environment assumed low wind (i.e. free convection only, 1% of interpolated speed). All metabolic parameters were based on previous work done on greater gliders (Table 1).

Table 1: Energy costs as estimated by Foley et al. 1990

Cost kJ/kg/day	Cost (W/kg)	Activity (hours per day)	Original Source
205	2.37	Basal (24)	Foley, 1987
38	0.44	Digestion (24)	Rübsamen et al, 1984 & Foley, 1987
118	4.10	Feeding/grooming (8)	Hume, 1984 & Foley, 1987
5-10	0.17	Movement (8)	Robbins 1983

For each hour throughout the 50-year simulation period, we used selection rules to determine the most cost-effective action for a glider; for daytime it was the minimum energy cost from one of the two denning simulations, and for night-time it was the minimum energy cost from one of the six non-denning simulations, or from one of the denning simulations if the minimum energy costs exceeded a threshold indicated by a "panting" parameter in the model. We assumed that active gliders had increased minimum metabolic requirements (Table 1) but allowed heat from activity to pay additional thermoregulatory costs of keeping warm.

From the hourly estimates, we aggregated total daily energy and water costs based on two periods of time that the gliders were outside of the den; all night between dusk and dawn (7-11 hours of activity, see Lindenmayer et al, 2002) and a fixed period of four hours (suggested by empirical observations in Henry, 1985). The four final daily energy budget scenarios used in our analysis were:

- Scenario E1: Foraging when dark (zero solar radiation) and in shade (minimum exposure to open night sky) to minimise energy costs; active all hours of night; denning during day and, when breathing multiplier is maximum (panting), in a location that minimises energy costs; food intake based on active hours.
- Scenario E2: As for E1 but active only 4 hours of night.
- Scenario W1: As for E1 but minimising water rather than energy costs.
- Scenario W2: As for W1 but active only 4 hours of night.

For each scenario, we calculated daily energy and water gains based on time foraging. We based these calculations on empirical data detailing nutritional qualities of *Eucalyptus* leaves and physiological characteristics of gliders (e.g. digestive efficiencies). To determine daily energy/water balances, we then subtracted costs from gains. Positive values indicated surplus energy/water and negative values indicated deficits.

To determine the potential for gliders to reproduce in a year, we summed the daily energy and the daily water balances in the respective year, and used the minimum of the two to determine how many grams of baby glider could be produced (Kearney et al, 2010). Because gliders are known to only have one young per year and the calculated values are only meaningful as a relative measure, we rescaled the values across all years to be one at the maximum value of all simulations and all other values to be a proportion of the maximum (e.g. if 300g was the maximum and rescaled to 1.0, 200g would be rescaled to 0.67). To calculate survival for each year, we counted the total number of days exhibiting energy surpluses and water surpluses and selected the minimum of the two – this was then divided into 365 to represent the proportion of days that the animal met its energy requirements. We transferred survival and fecundity values to their respective locations in our study area for each simulation year and produced eight total stacks of rasters (gridded data), each with 50 layers (Figure 3).



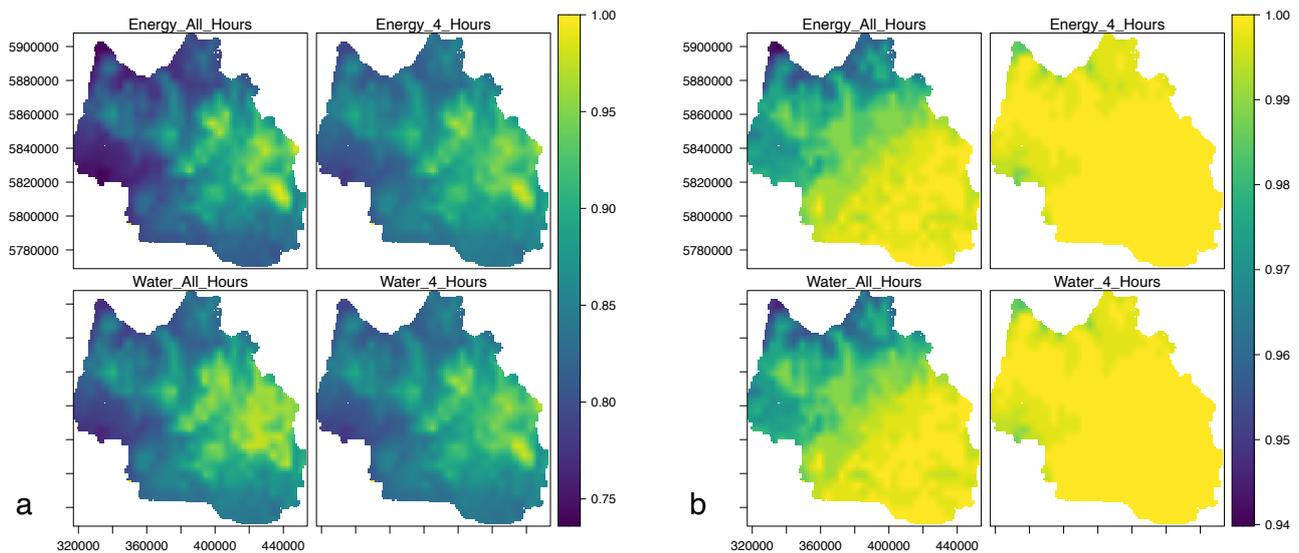


Figure 3: Example of spatially-explicit multipliers on fecundity (panel a), and survival (panel b), in the first year (2019) for all four scenarios; E1: foraging all hours with energy limiting activity (Energy_All_Hours), E2: foraging only four hours with energy limiting activity (Energy_4_Hours), W1: foraging all hours with water limiting activity (Water_All_Hours), and W2: foraging only four hours with water limiting activity (Water_4_Hours).

Population dynamics

We simulated population dynamics using open-source spatially-explicit population simulation software (steps – Visintin et al, 2020). Our simulations were based on a model framework that included the outputs of correlative SDM (habitat suitability), LANDIS-II (forest dynamics) models, and NicheMapR (biophysical) models described previously (Figure 4).

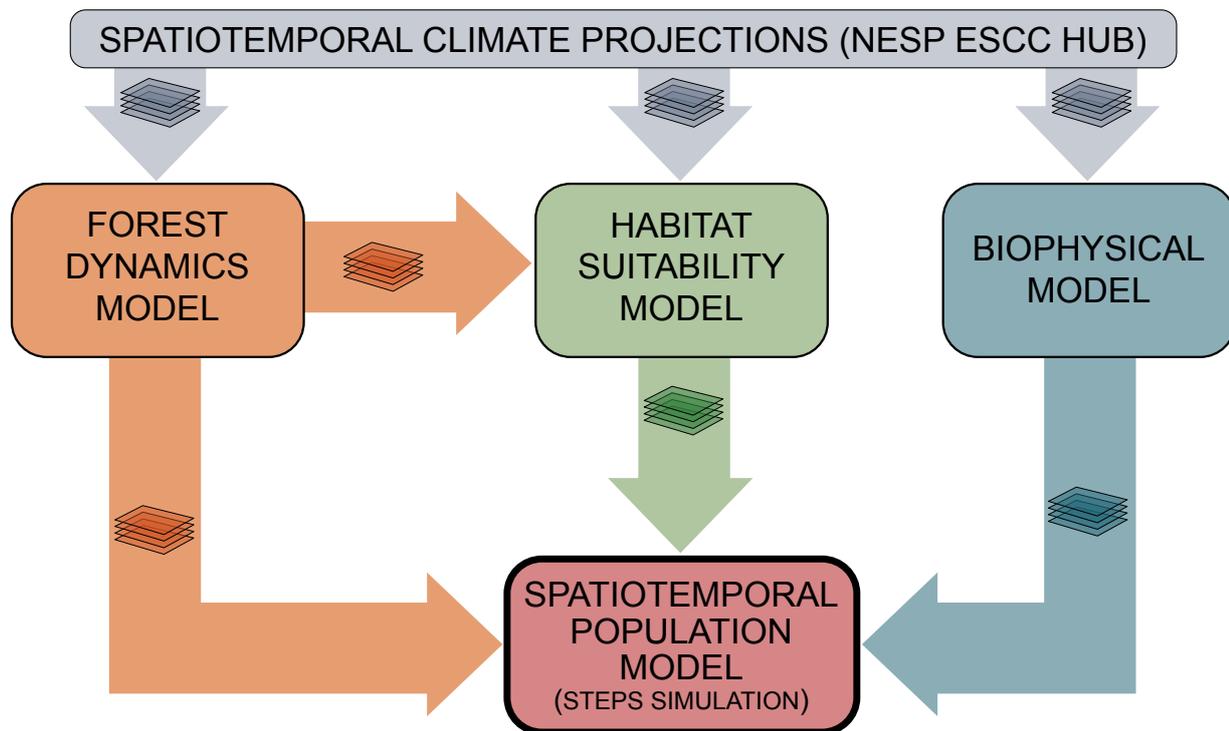


Figure 4: The simulation framework is comprised of; a habitat suitability (correlative species distribution) model, the LANDIS-II forest dynamics model, and the NicheMapR biophysical model. Climate projections from the National Environmental Science Program Earth Systems and Climate Change Hub were inputted into all the models.

For our initial parameters, we assumed three life stages (newborn, juvenile, adult) in an age-based transition matrix (adapted from Possingham et al, 1994) where the probability of survival for newborns was 0.5, for juveniles was 0.85, and for adults was 0.9. Only adults reproduced at a rate of 0.5 gliders per adult. We modelled only females and assumed a pre-breeding census - our intrinsic rate of population change (λ) was 1.08, indicating natural population growth. These baseline values were adjusted throughout the simulation based on outputs from the biophysical model.

Initial populations were generated using stable age distributions and totalled approximately 5,000 greater gliders across the study area. In randomly selected cells, glider abundances were assigned using a logistic function that related the number of individuals to habitat suitability – cells with higher suitability received more initial individuals up to the maximum carrying capacity of 60 individuals. This corresponded to 0.6 individuals per hectare which is the mid-range of previous estimates in similar habitats (Henry, 1985; McCarthy et al, 2001b; Jones et al, 2009). Initial populations were proportionally allocated across the three life-stages based on stable age distributions: newborns (~27%), juveniles (~13%), and adults (~60%).

Carrying capacity in each cell was controlled by a logistic function – as habitat suitability changed in space and time, the population limit changed accordingly. The functional shape was symmetric meaning that at habitat suitability values of 0.5, 30 individuals could be sustained in a population (50% of the maximum carrying capacity).

All juveniles in a population dispersed in the landscape and no other life stages were allowed to move between populations. We used individual-based cellular automaton movements based on random walks up to three cells (3 km). The movements were influenced by habitat suitability and carrying capacity – individuals were more likely to move into higher quality habitat with available carrying capacity.

Density dependence was represented in all simulations by reducing survival and fecundity in populations that approached carrying capacity – newborns were omitted from calculations of total cell populations. We also included demographic stochasticity (affecting small populations) and two levels environmental stochasticity (affecting survival and fecundity) in all of our models.

Disturbances in the landscape affected population abundance. Populations were reduced in each cell where fires occurred, with the magnitude of change varying with fire severity. Intense fires killed all individuals in a cell and lower-intensity fires reduced the populations by approximately 15%, with linear scaling between the maximum and minimum intensities. To approximate hollow recruitment – an important resource for gliders - populations were also modified by "time since logging" which varied between zero and 190 years and a threshold function was used to determine its effect on abundance. Time since logging values equal to or less than 100 years were set to zero carrying capacity; values above 100 were linearly scaled by dividing by 50 and subtracting 2; and values above 150 years were set to one indicating that the maximum carrying capacity specified by the SDM was not reduced due to the age of the forest, hence abundance was only modified in areas subject to logging within the last 150 years.

We ran fifty replicates of a baseline 50-year steps simulation without any modifications to survival and fecundity (i.e. ignoring the outputs of our biophysical model). We then ran four additional simulations of fifty replicates each for our biophysical model output scenarios – E1, E2, W1, and W2. To test our models' sensitivity to uncertainty, each set of five simulations were run using both low (0.02) and high (0.2) values of environmental stochasticity – the standard deviation on truncated random normal distributions around the values of the transition matrix (means).



Results

From our biophysical model, the predicted survival and fecundity multipliers ranged between 0.67 and 1 (Table 2). Fecundity was generally more impacted than survival due to biophysical stress across all four scenarios and all years. The spatial variation between the values was low within each scenario and year. All scenarios indicated seasonal, but generally decreasing trends across all years. Based on predictions from the biophysical models, the first year was predicted to be the best, whilst year 34 was predicted to be the worst. This suggested a possible range restriction to the south and to the east (Figure 5).

Table 2: Predicted multipliers on survival and fecundity from the four biophysical model scenarios.

Scenario	Minimum Fecundity Multiplier	Maximum Fecundity Multiplier	Minimum Survival Multiplier	Maximum Survival Multiplier
E1	0.600	1.0	0.868	1.0
E2	0.687	1.0	0.923	1.0
W1	0.624	1.0	0.877	1.0
W2	0.686	1.0	0.926	1.0

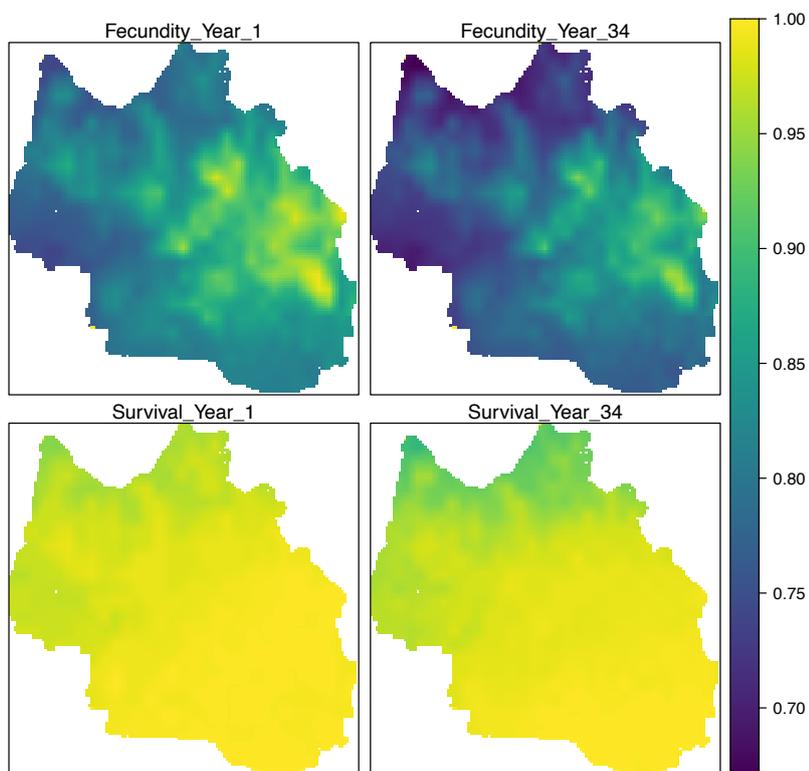


Figure 5: Spatially-explicit multipliers on fecundity (top), and survival (bottom), in the best (first) year and worse (thirty-fourth) year for the E1: foraging all hours with energy limiting activity scenario predicted by the biophysical model.

Our low stochasticity baseline simulation indicated a decreasing population trend with an initially strong decline and then gradual downward trend (Figure 6a). The mean population estimate in year 50 was approximately 1,060 gliders but the estimated expected minimum population across all simulation replicates was approximately 950 gliders, or 20% of the total initial population. The high stochasticity simulations indicated similar trends to the low stochasticity simulations but with more variation throughout years and lower expected minimum populations - approximately 540 gliders in year 50 and an expected minimum population of approximately 170 gliders throughout (Figure 6b).

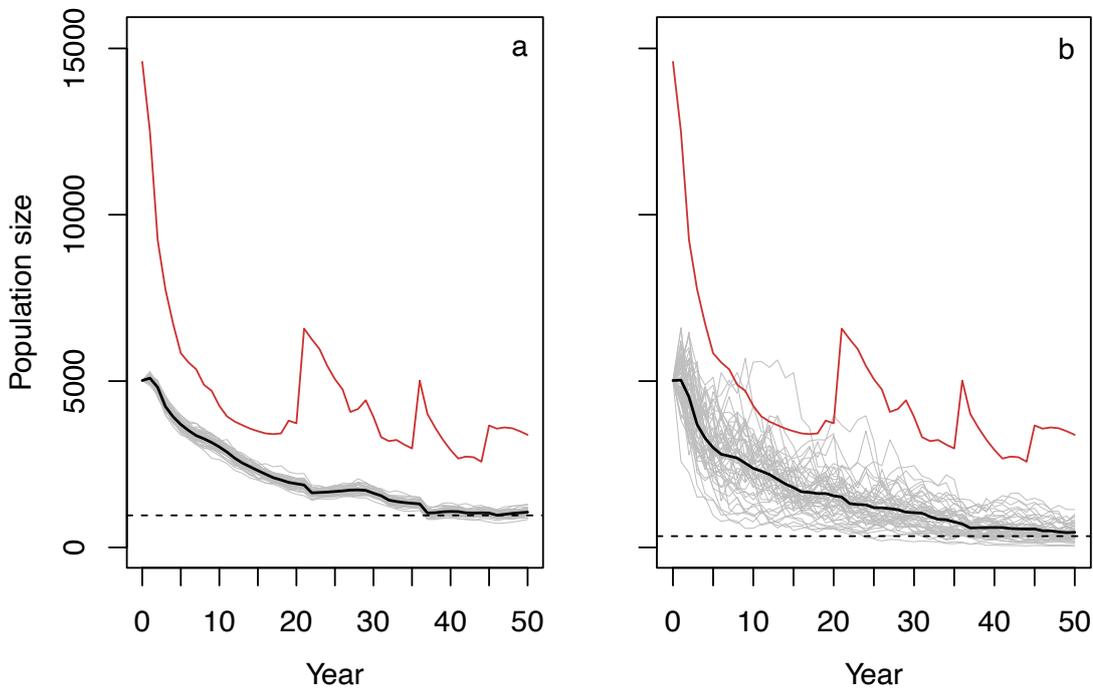


Figure 6: Simulated population trend over 50-year time period for the baseline scenario (i.e. excluding biophysical model outputs) for low (panel a) and high (panel b) environmental stochasticity. Gray lines represent each simulation replicate, the bold line indicates the mean population trajectory, and the dotted line indicates the expected minimum population (see McCarthy and Thompson, 2001a) of the simulation. The red line indicates the calculated carrying capacity from the correlative SDM predictions – i.e. maximum number of individuals (60) multiplied by the habitat suitability in each grid cell, summed across the landscape for each year. Note, simulated trends were similar for all scenarios with and without biophysical model outputs.

All of our simulations that included modifications to survival and fecundity based on outputs from the biophysical models also indicated declining populations but the expected minimum populations were consistently lower (Figure 7a & 7b). The additional uncertainty produced more overlap in the spreads of expected minimum populations (Figure 7b). The baseline simulation exhibited the most uncertainty in each level of stochasticity, followed by the energy limiting, four hours foraging scenario (E2).



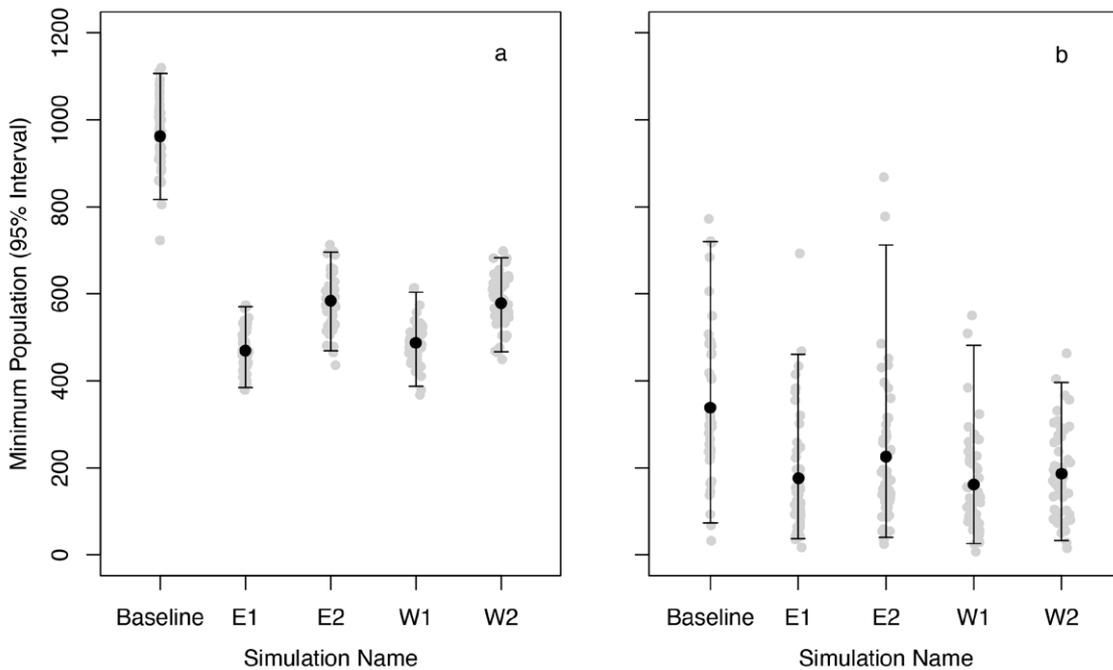


Figure 7: Expected minimum populations for low (panel a) and high (panel b) stochasticity simulated scenarios, with and without deterministic modifications to vital rates based on outputs from the biophysical models. The black dots represent expected minimum abundance across all 50 simulation replicates (each represented as a grey dot). The scenarios that include biophysical information are: E1: foraging all hours with energy limiting activity, E2: foraging only four hours with energy limiting activity, W1: foraging all hours with water limiting activity, and W2: foraging only four hours with water limiting activity.

The populations distributed themselves similarly between all of the scenarios in both the low and high environmental stochasticity variants (see Appendix). Summing the incidents that cells were occupied by populations in each timestep and replicate suggested important areas for conservation – the largest occurring in the southwestern portion of the study area (Figures 8-12).

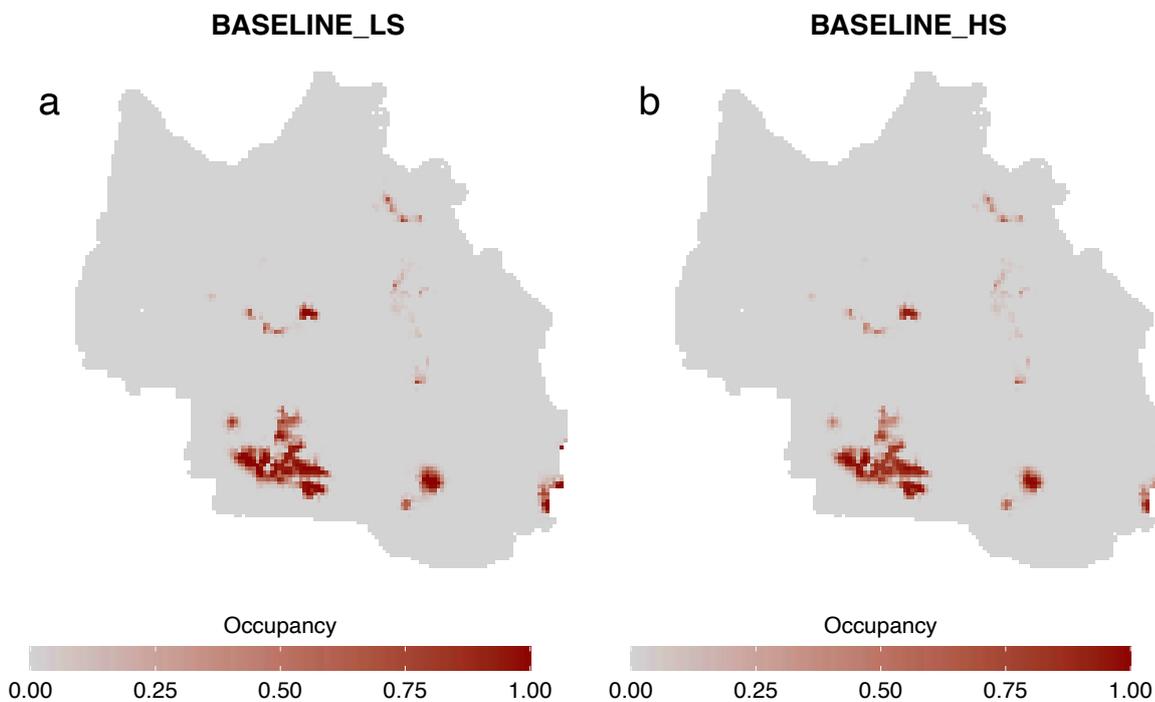


Figure 8: Spatial population distribution over the 50-year time period for the baseline scenario (i.e. excluding biophysical model outputs) for low (panel a) and high (panel b) levels of environmental stochasticity. Cell values represent the sums of instances where a cell has been occupied by a population over the entire simulation - rescaled to be between zero and one.

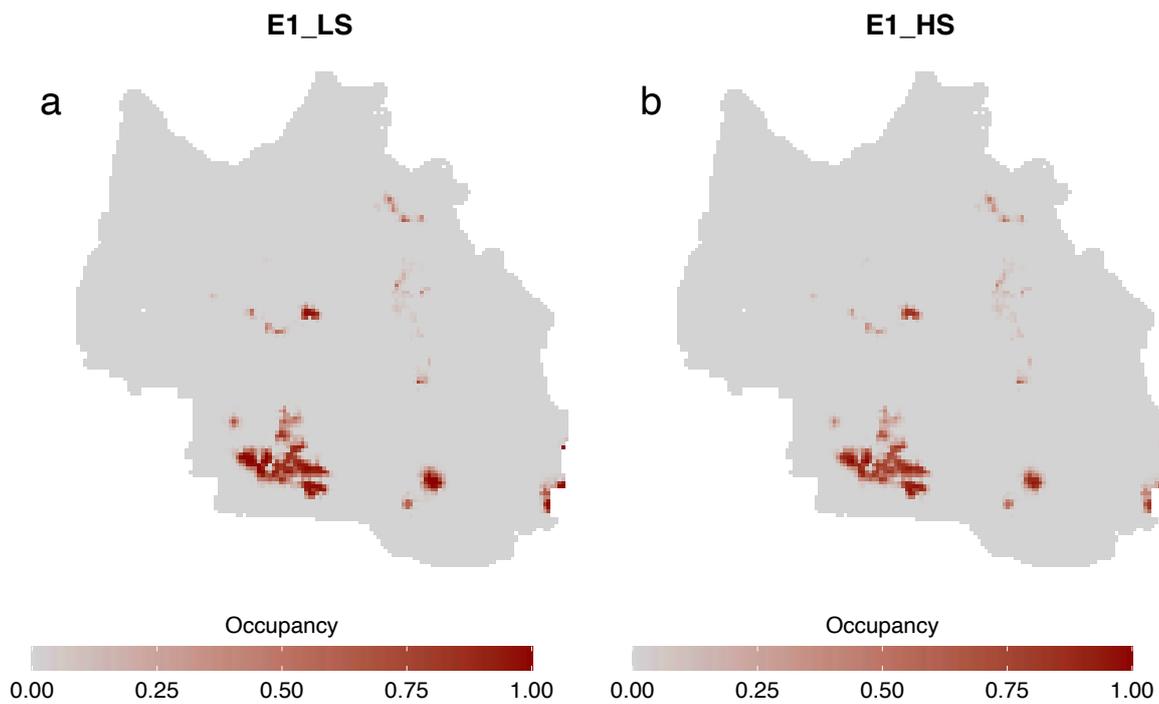


Figure 9: Spatial population distribution over the 50-year time period for the E1 scenario (including biophysical model outputs) for low (panel a) and high (panel b) levels of environmental stochasticity. Cell values represent the sums of instances where a cell has been occupied by a population over the entire simulation - rescaled to be between zero and one.

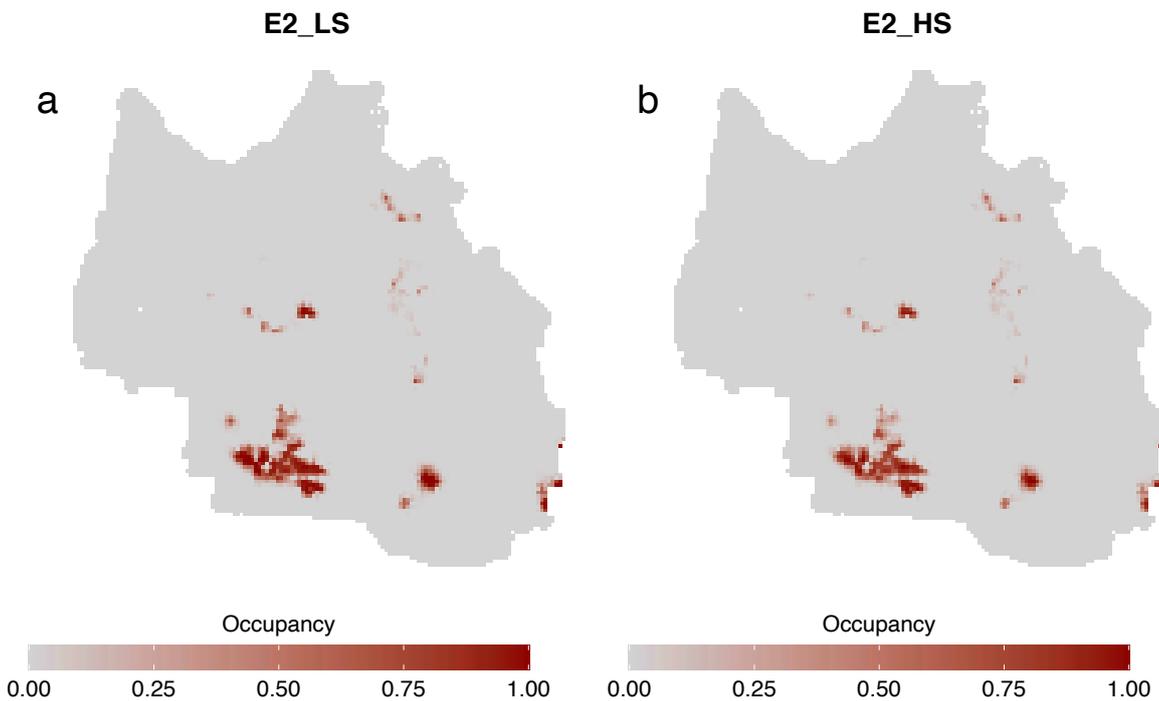


Figure 10: Spatial population distribution over the 50-year time period for the E2 scenario (including biophysical model outputs) for low (panel a) and high (panel b) levels of environmental stochasticity. Cell values represent the sums of instances where a cell has been occupied by a population over the entire simulation - rescaled to be between zero and one.

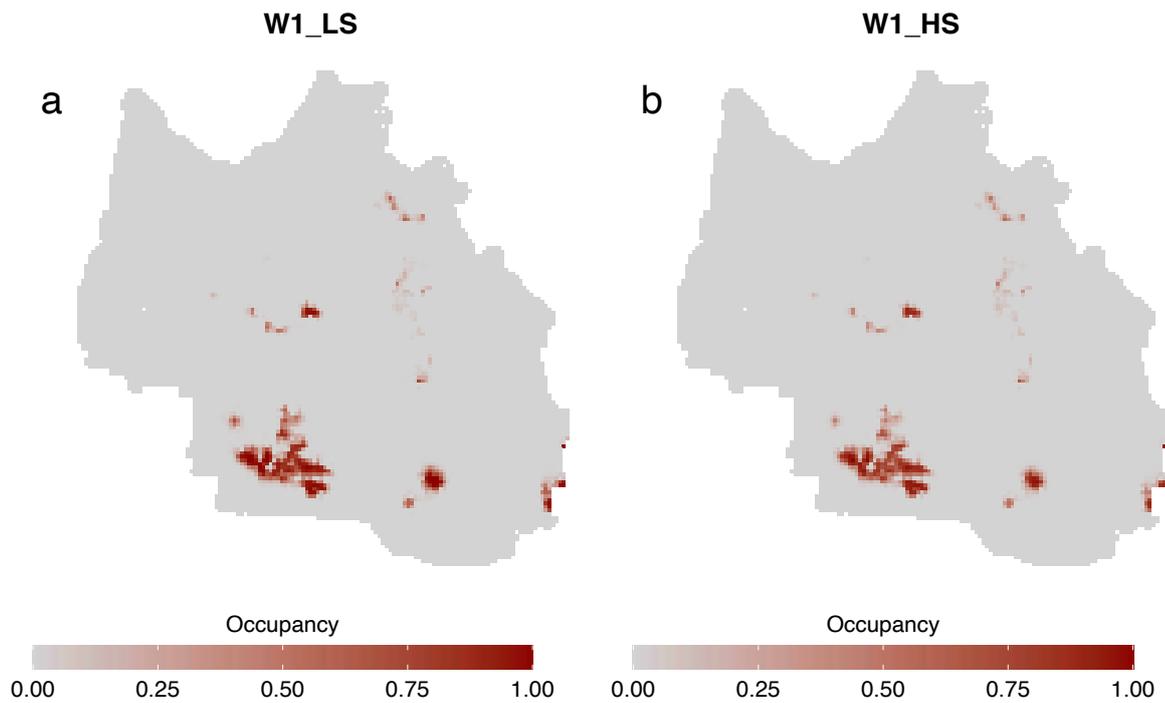


Figure 11: Spatial population distribution over the 50-year time period for the W1 scenario (including biophysical model outputs) for low (panel a) and high (panel b) levels of environmental stochasticity. Cell values represent the sums of instances where a cell has been occupied by a population over the entire simulation - rescaled to be between zero and one.

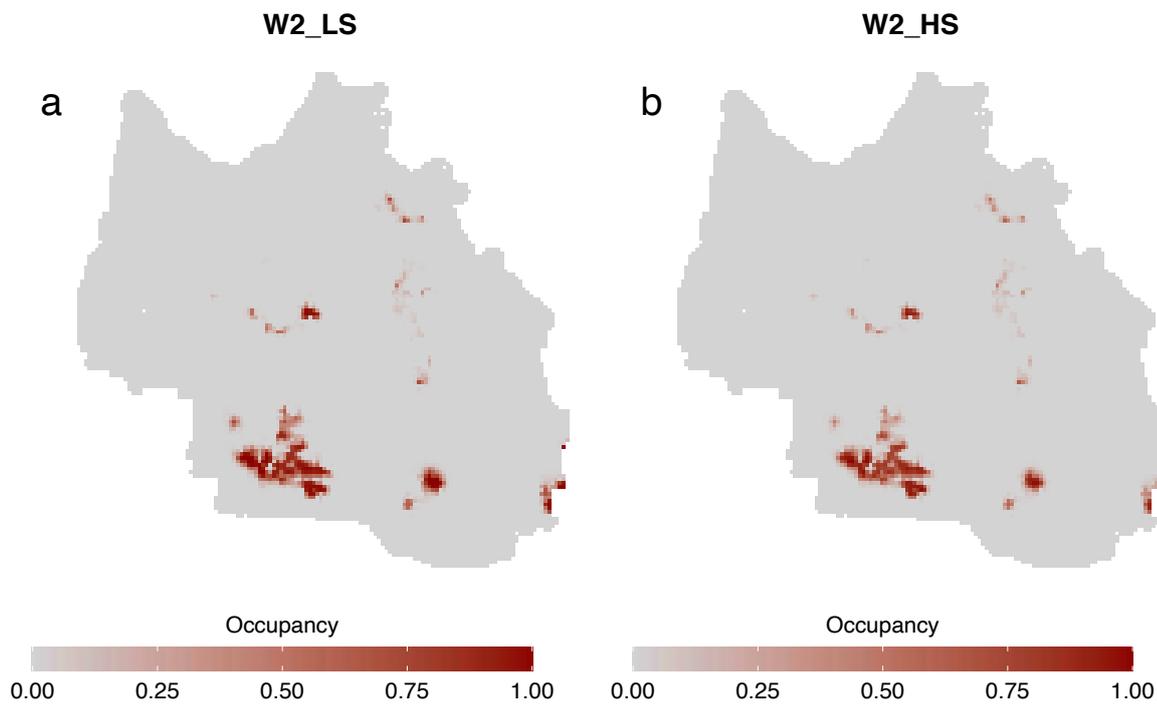


Figure 12: Spatial population distribution over the 50-year time period for the W2 scenario (including biophysical model outputs) for low (panel a) and high (panel b) levels of environmental stochasticity. Cell values represent the sums of instances where a cell has been occupied by a population over the entire simulation - rescaled to be between zero and one.

Discussion

Our study demonstrates a useful framework for incorporating projected vital rate changes into spatially-explicit population simulations. In contrast to correlative methods, our framework considers causal processes explicitly in the modelling. We found that incorporation of the biophysical impacts on survival and fecundity had a strong impact on the population outcomes for the greater glider with a reduction of approximately 25-50% in expected minimum abundance across the simulations including biophysical impacts (Figure 6). This is important for management as implicitly assuming that biophysical processes are adequately captured in modelling may provide false confidence in expected minimum populations – which could in actuality be considerably lower and below a threshold that wildlife managers deem to be acceptable.

Bringing population dynamics and biophysical constraints into our models had a substantial influence on projected outcomes for the greater glider. While carrying capacity based on land use, landscape (forest cover and age) and climate change showed a gradual decline over the simulation period, population size dropped much more dramatically through the latter half of the simulation period due to dispersal limitations and metabolic constraints (Figure 6). These impacts may not be captured in an analysis based solely on correlative SDMs and would certainly be more difficult to identify. It should be noted, however, that our SDM predictions took into account dynamically varying climate variables – also used as a basis for the biophysical model predictions. It may be argued that this method makes it difficult to disentangle carrying capacity from weather conditions given that carrying capacity is driven by our habitat suitability in the population simulations. Carrying capacity could actually be driven by the number of hollows and be a function of the static variables (non-climate) only. One method to test this assumption would be to repeat the SDM analysis excluding the dynamic climate variables – or using long-term climate not allowed to vary through time. This was excluded from our analysis, however, future work would benefit by adding this scope.

Our baseline population simulation resulted in a decreasing trend, which is commensurate with patterns suggested in other habitat modelling and surveys in the region (Lumsden et al, 2013; Lindenmayer et al, 2013; Berry et al, 2015; Wagner et al, 2020). However, other areas in Victoria have indicated insignificant or inconclusive changes in estimated populations (Nelson et al, 2018) signalling that our analysis may be usefully applied to these areas in an attempt to discover patterns that inform wider conservation efforts. Further, simulating historic population trends in other areas with good comparative survey data would help to calibrate parameter selection, but this was not included in the scope of this work.

The peaks and troughs shown in the carrying capacity (Figure 6) were most likely due to the forest dynamics modelled in the landscape model (i.e. LANDIS-II) that underpins the habitat suitability model (see Figure 4). As the model considered both disturbances (e.g. logging and fires) and regeneration (e.g. growth) in the landscape, we expect variation in the landscape quality and thus the number of individuals that can be supported in the landscape at each annual timestep. The population trends did not reflect these patterns because there was limited dispersal given our configuration of initial populations, simulation resolution, and species characteristics. Our initial populations were quite dispersed across the landscape (although more concentrated in areas of more suitable habitat), and given both the sedentary nature of gliders and our coarse grid cell resolution, did not move very far. The total carrying capacity calculations were determined across all cells regardless of containing populations of gliders. Plotting the total carrying capacity of all populated cells against the total populations across the landscape for each timestep would show a more consistent pattern.

As anticipated, including high stochasticity in model projections made little difference to mean expectations of future population size, but did dramatically increase the risk of falling to dangerously low levels. Our stochasticity parameterisation is based on plausible variation in parameter values under changing environments, and so provide a realistic characterisation of future risks that should be incorporated in land management and conservation decision making. The inflation of risks of extremely low population sizes or even local extinction under high stochasticity is well documented (McCarthy and Thompson 2001a) but is crucial to consider when avoiding extinction is demanded by society and risk-weighted decisions must be taken.

Although the differences between energy or water-limiting scenarios were negligible, both survival and fecundity were consistently lower in scenarios that simulated glider activity for the full duration of night. This suggests that food intake may not be adequate to support extended glider activities and that longer periods of denning are more advantageous (especially for predator avoidance). This is supported by other behavioural observations of greater gliders in this part of its range (Henry, 1985) which noted a consistent length of activity regardless of season. Observations of gliders in the other parts of its range suggest similarly consistent lengths of activity but over longer average night-time periods (Norton, 1988) - probably due to more conducive thermal conditions. This highlights the importance of choosing an appropriate set of input parameters that are based on empirical observations or controlled experiments that are representative of the local climatic conditions for which a biophysical model is being prepared.

Several other climate models exist and our choice of MIROC5 was based on early discussions with climate scientists, who considered this model to be the most appropriate for our study region. We did examine the outputs of three other climate models (RCP 8.5) and observed very similar overall predicted climate trends. Although comparing different representative concentration pathways was outside the scope of this study, our choice of "worst case" was notably conservative given the status of the target species. A key point is that our framework can easily accommodate predictions from any climate model making it applicable to many different spatial and temporal extents where data is available.

Converting biophysical model outputs into estimates of vital rate changes requires assumptions which are often context dependent and data driven. Although known information on the greater glider and associated food sources allowed us to prudently calculate grams of baby glider that would be produced given energy budgets, converting these estimates into expected impacts on fecundity is not trivial. We assumed that fecundity changed linearly with a reduction in the biophysical model predictions of energy available to reproduction, but alternative assumptions could be justified with experimental evidence.

Biophysical models have been around for several decades and their use has been primarily associated with understanding the behaviour and physiology of individual organisms (e.g. Porter et al, 1973). However, the use of biophysical modelling in conservation has only made slow progress over the past decade, likely driven by data and computational requirements. Our biophysical simulations ran for approximately 40 hours in a high-performance server environment. The fine-scale temporal resolution (hourly), reasonably long timespan (50 years), moderately large spatial extent (520 locations), and several variations (8 scenarios) resulted in nearly four billion data points that had to be stored for subsequent processing. The final estimates for daily energy and water use comprised approximately forty million records in a database. Nevertheless, with increasing advances in computational technology, we envision that this analysis will soon be run overnight on a standard laptop.

Our simulations were based on regular grids that spatially organised our input data and set the operational framework for a *steps* simulation. Because our framework used several different models and sources of input data, we were limited on the choice of modelling resolution. Grid cell size does, in fact, have an influence on population outcomes in a spatially-explicit simulation – especially when effects of demographic stochasticity (e.g. Allee effects) are included. This is because species attributes such as range size and activity patterns, and density dependence mechanisms, are explicitly represented in the modelling. We could have chosen a cell size that was closer to the observed 1.5 ha (~125m x ~125m grid cell) mean home range of Greater Gliders (Norton, 1988) but this would have amplified the effect of demographic stochasticity (the random fates of individuals) by only allowing a maximum of two animals in each grid cell. However, despite our larger cell sizes, the populations showed some initial decreases due to demographic stochasticity. Given a reasonably small area, analysts may opt to run several comparative simulations at different cell (i.e. patch) sizes.



Management implications

Estimating the effects of microclimates on an organism's vital rates through biophysical processes adds another dimension of information that may be used to help understand and predict outcomes of environmental change for species of conservation concern – and, as far as we are aware, combining these modelling methods, as in our framework, is a novel practice. Biophysical effects are often implied, assumed, or completely ignored in simulations; but variations in magnitudes of such impacts can be important for threatened species. For example, they may help in the prioritisation of targeted gene flow (Kelly and Phillips, 2016), especially where populations have known local adaptations to climate (e.g. pelt depth in the case of arboreal folivores, see Briscoe et al, 2014). Our study showed significant potential implications of climate and land use change mediated through population and biophysical processes, not necessarily captured in correlative analyses. This indicates that where possible, models used to support analysis of climate impacts and land use change should incorporate, or at least explicitly consider, population dynamics and biophysical processes.

Further, our framework may be used to identify at-risk areas that should be targeted for management actions. Due to its spatially-explicit nature, the framework is able to produce visual maps that indicate areas that may lose populations at greater rates. Simulating changes over time for many instances - each subject to environmental variation (or uncertainty) - creates more robust estimates and can help to discriminate between areas that support stable populations and those that are prone to extinctions.

The impacts of disturbances can be tested in the framework by changing parameters in the LANDIS-II model or the correlative SDM model, redefining the relationships between carrying capacity and habitat features used in the simulations, explicitly modifying the habitat suitability during the simulations, or a combination of all three. For example, in the model set up we have used for this work, we specified a timber harvesting scenario based on current state policy and standards set by VicForests. Model specifications can be changed, and new simulations run, to test different policy settings (or harvesting methods) to determine the impacts on species persistence. This type of analysis was completed for several species in Victoria as part of the Regional Forest Agreements review; a report detailing the methods is being finalised for the Victorian Department of Environment, Land, Water and Planning and should be released soon.

The choice of how "time since logging" values were applied to carrying capacity was a surrogate for tree hollow formation and thus habitat suitability. Any LANDIS-II model simulated logging in a cell triggered a recorded event that was used to determine the "time since logging" and assumed to not leave any large, potentially hollow-bearing trees that would be older than the recorded time. This method may be considered conservative, however, gliders have not been observed to persist in highly-fragmented remnants of forest and are highly sensitive to logging activities. Because the LANDIS-II model simulations output age and biomass information based on species, more sophisticated relationships between the projected forest characteristics and the carrying capacity can be defined. For example, carrying capacity could be affected by the dominant age class remaining in a cell rather than the time since logging. Unfortunately, computational power and data limitations preclude LANDIS-II simulations to be detailed enough to characterise individual trees in a forest landscape. Perhaps future advances will make this possible.

The density/abundance of hollow-bearing trees was inferred from the LANDIS-II modelling which provides spatially- and temporally-explicit age class distributions as outputs. It was assumed that cells with older trees above an age threshold would contain hollows and that the quality/density of hollows would be proportional to the forest age. These outputs were used as inputs to the correlative SDM to model the relative suitability of habitat across the landscape and therefore indirectly considered in the population simulations. More direct methods could employ survey information or estimations of hollow abundance (i.e. modelling) to affect the carrying capacity or the populations within STEPS simulations. For example, an analyst could use a comparison of estimated hollow density to population density to directly moderate the vital rates during a simulation.

Determining minimum patch sizes for viable populations is possible, but difficult, given the mechanics of the simulation framework. STEPS modelling requires an analyst to choose a grid cell size which will serve as the basis for discrete populations in space and time. As mentioned previously, the choice of this cell size has implications for some of the internal quantitative operations (e.g. demographic stochasticity). By specifying clusters of cells with suitable habitat surrounded by missing values in a spatial grid, a more classic patch-based metapopulation analysis can be emulated and would form the basis for investigating patch size effects on populations. It is recommended that a simulation is first specified from plausible parameter choices and generates a plausible population trend. Once this baseline simulation is established, an analyst may investigate changing the size of the patches by setting cells to missing values in the habitat suitability spatial layer and running additional simulations.

Our framework can be used to explore the effects of changes in landscape connectivity. STEPS features a cellular automata dispersal engine that considers individual-based movements and accounts for landscape permeability. This means it is possible to include spatial information that identifies barriers in a landscape and specify how much they will impede or support the movements of species. Further, the spatial information can be temporally-explicit and identify changes that occur at different intensities throughout a simulation timespan. For example, an analyst may specify that habitat that degrades below a suitability threshold (e.g. due to climate change) no longer permits movement and this would affect the ability of species to colonise new areas. By changing the information that defines the landscape permeability, analysts are able to target areas to improve connectivity and assess changes in projected population persistence. In a similar way, the framework may also be used to assess the effectiveness of strategies to stop undesirable movements (e.g. feral species).

Terminology used

Fundamental/environmental/ecological niche - any environmental state that would allow a species to persist indefinitely.

Life stages - identified functional stages of development for a species (e.g. juvenile, subadult, adult).

Parameters - configuration variables that can either be estimated by a model given a specific set of data or specified to control the behaviour of a simulation.

Sensitivity analysis - a technique used to understand how relative magnitudes of changes in model parameters change the performance or outputs of mathematical models.

Stochasticity - randomness or noise that is known to occur in nature and is explicitly incorporated into modelling using values drawn from statistical distributions and sets of random numbers.

Vital rates - a measurement of how fast vital statistics (births, deaths, growth rates) change for a species within demographic categories (age or sex).



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Appendix

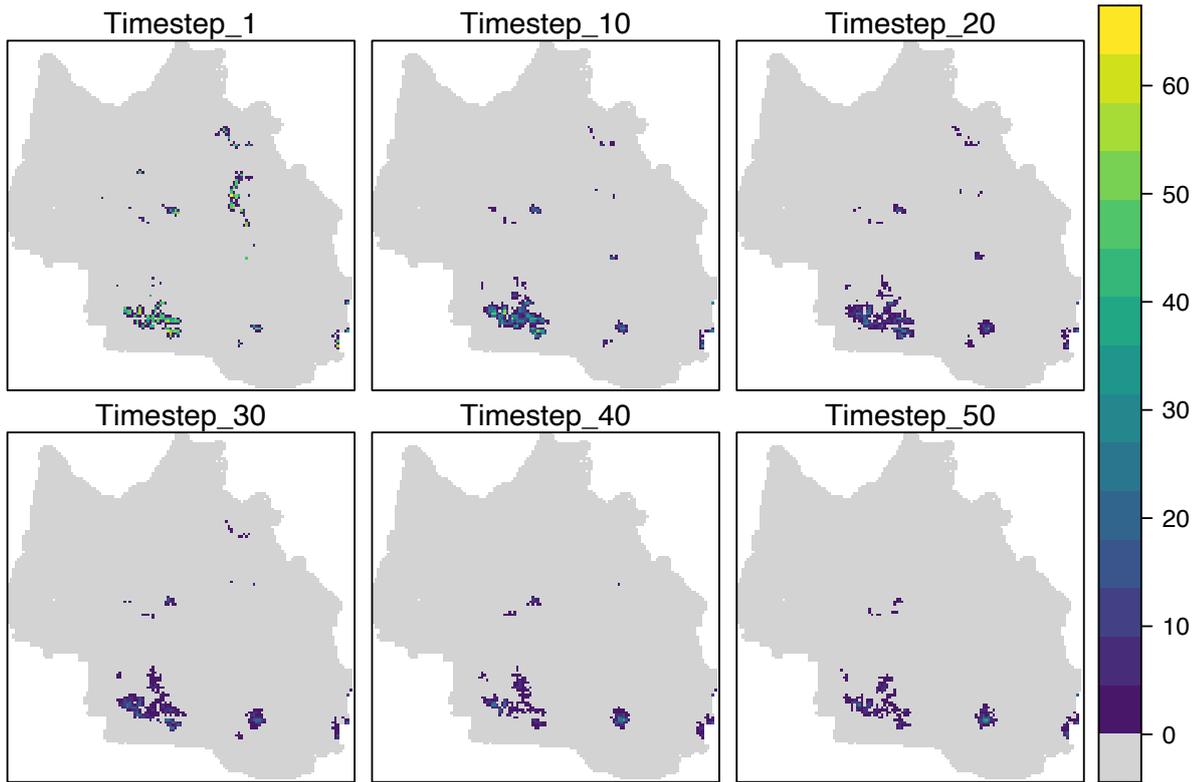


Figure A1: Spatially-explicit population distributions in select years (decades) based on the baseline scenario with low environmental stochasticity.

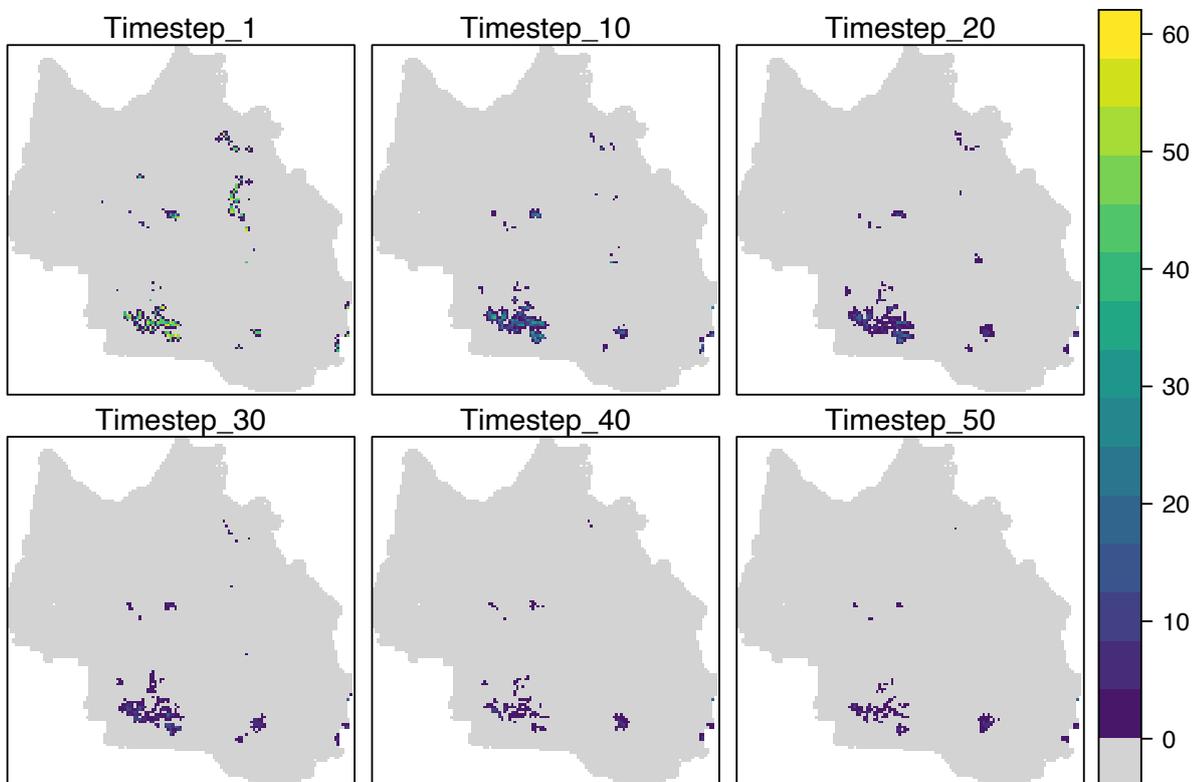


Figure A2: Spatially-explicit population distributions in select years (decades) based on the E1 scenario with low environmental stochasticity.

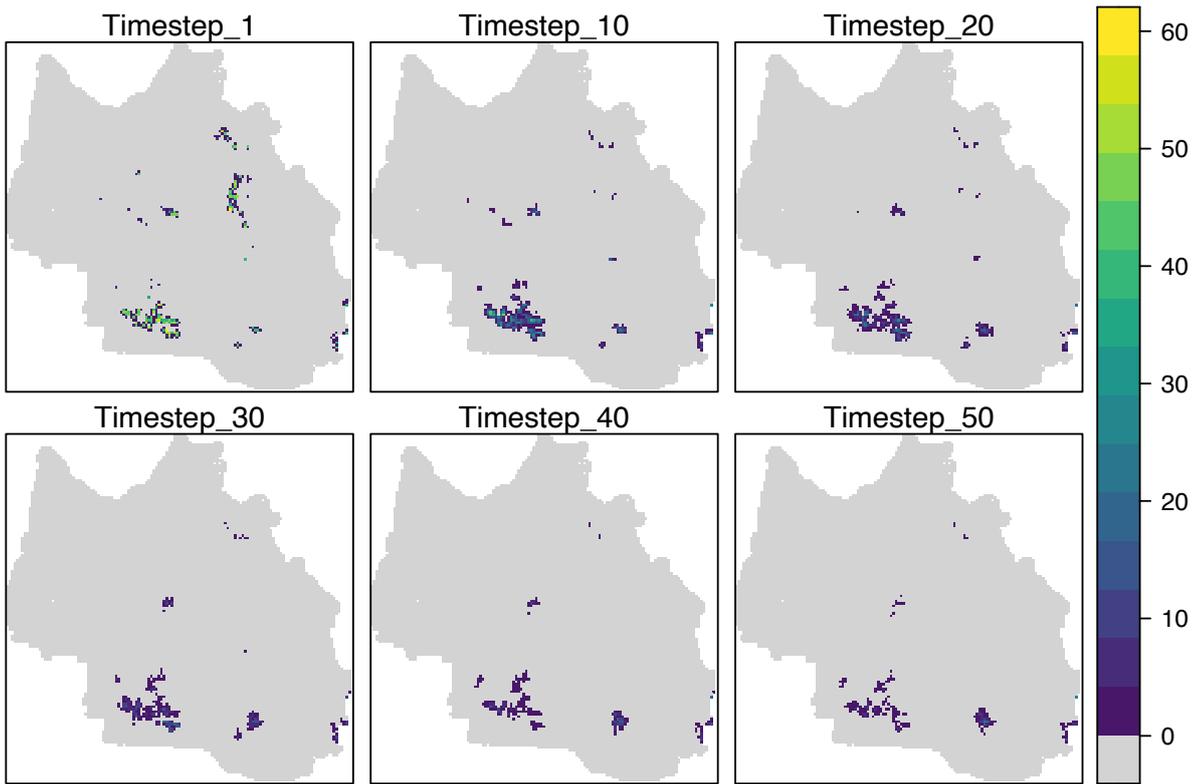


Figure A3: Spatially-explicit population distributions in select years (decades) based on the E2 scenario with low environmental stochasticity.

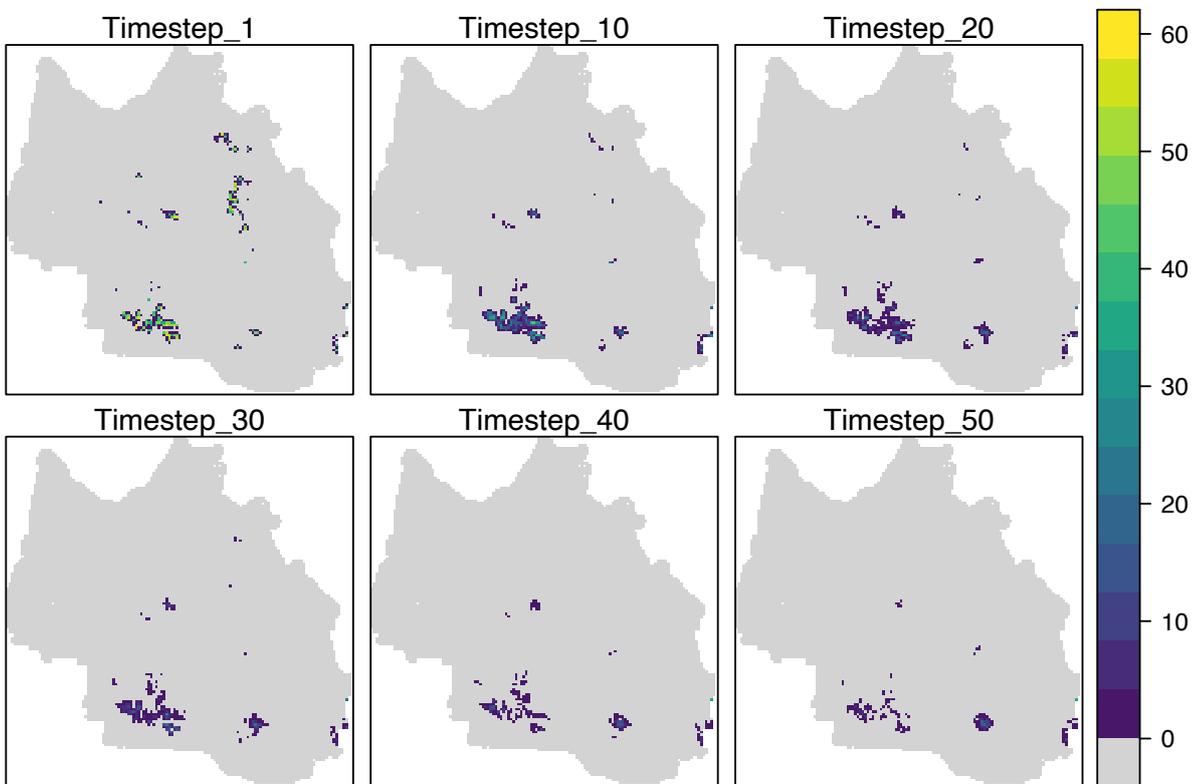


Figure A4: Spatially-explicit population distributions in select years (decades) based on the W1 scenario with low environmental stochasticity.

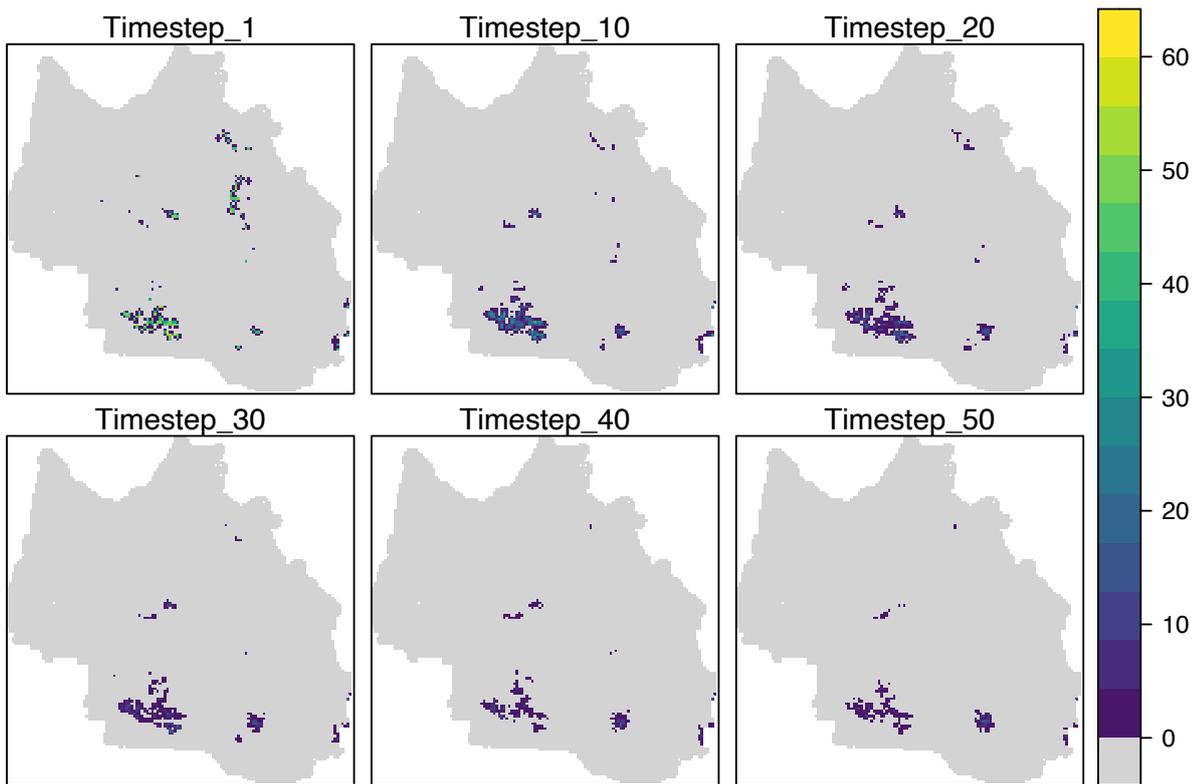


Figure A5: Spatially-explicit population distributions in select years (decades) based on the W2 scenario with low environmental stochasticity.

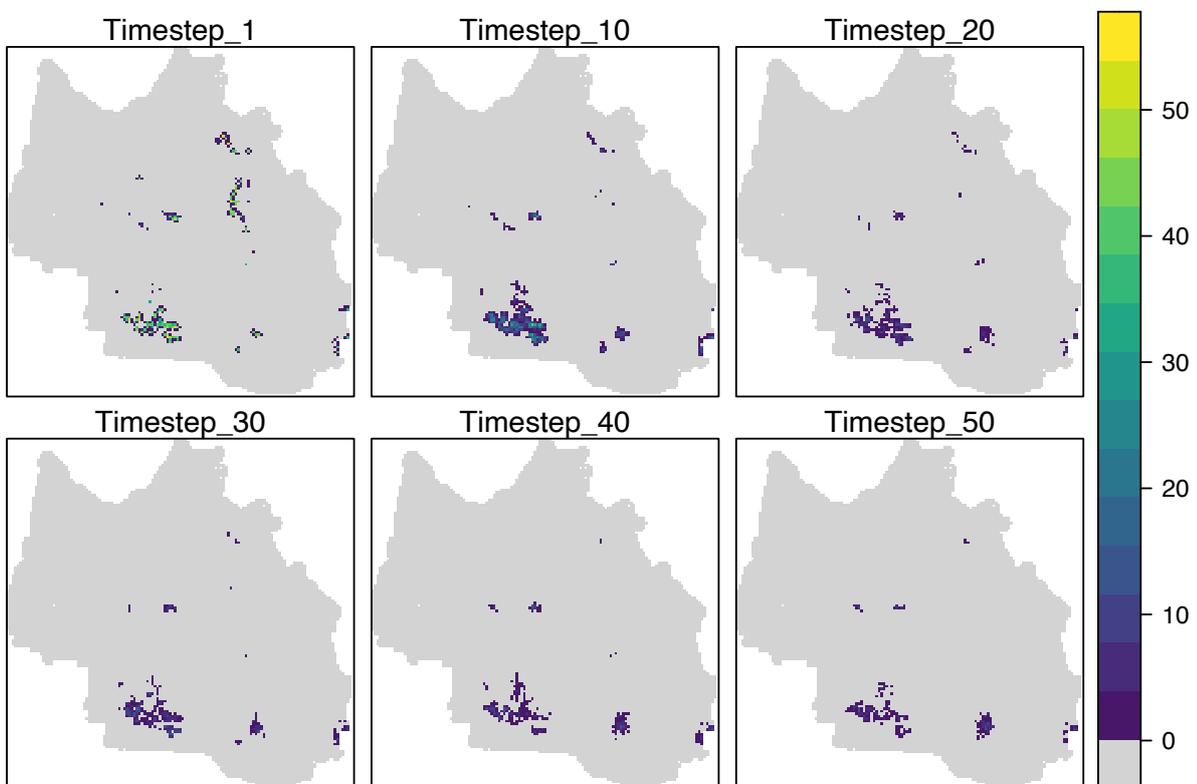


Figure A6: Spatially-explicit population distributions in select years (decades) based on the baseline scenario with high environmental stochasticity.

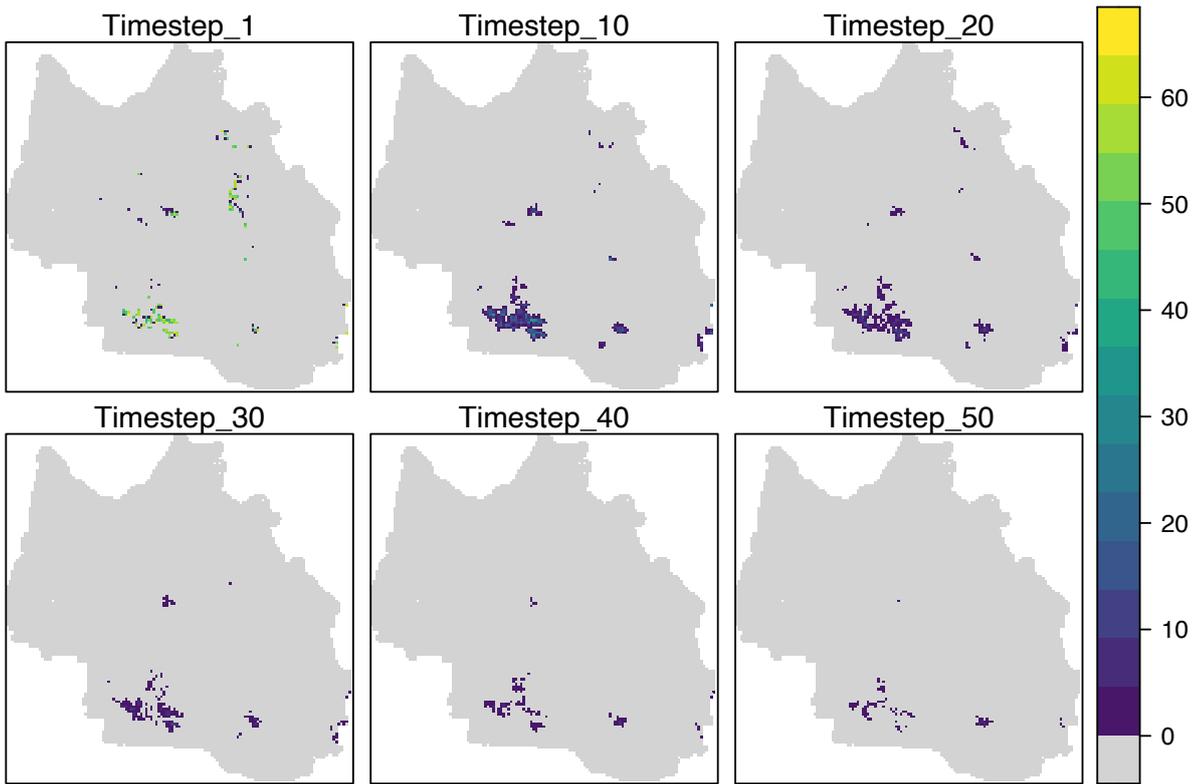


Figure A7: Spatially-explicit population distributions in select years (decades) based on the E1 scenario with high environmental stochasticity.

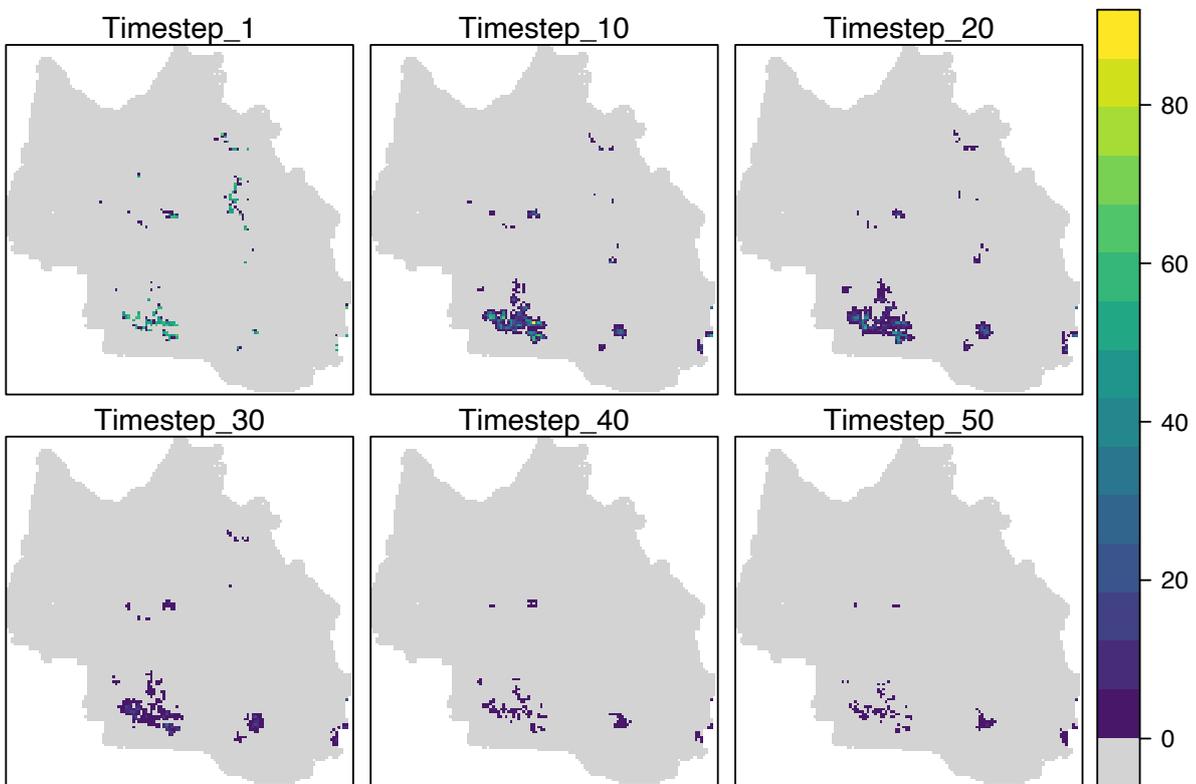


Figure A8: Spatially-explicit population distributions in select years (decades) based on the E2 scenario with high environmental stochasticity.

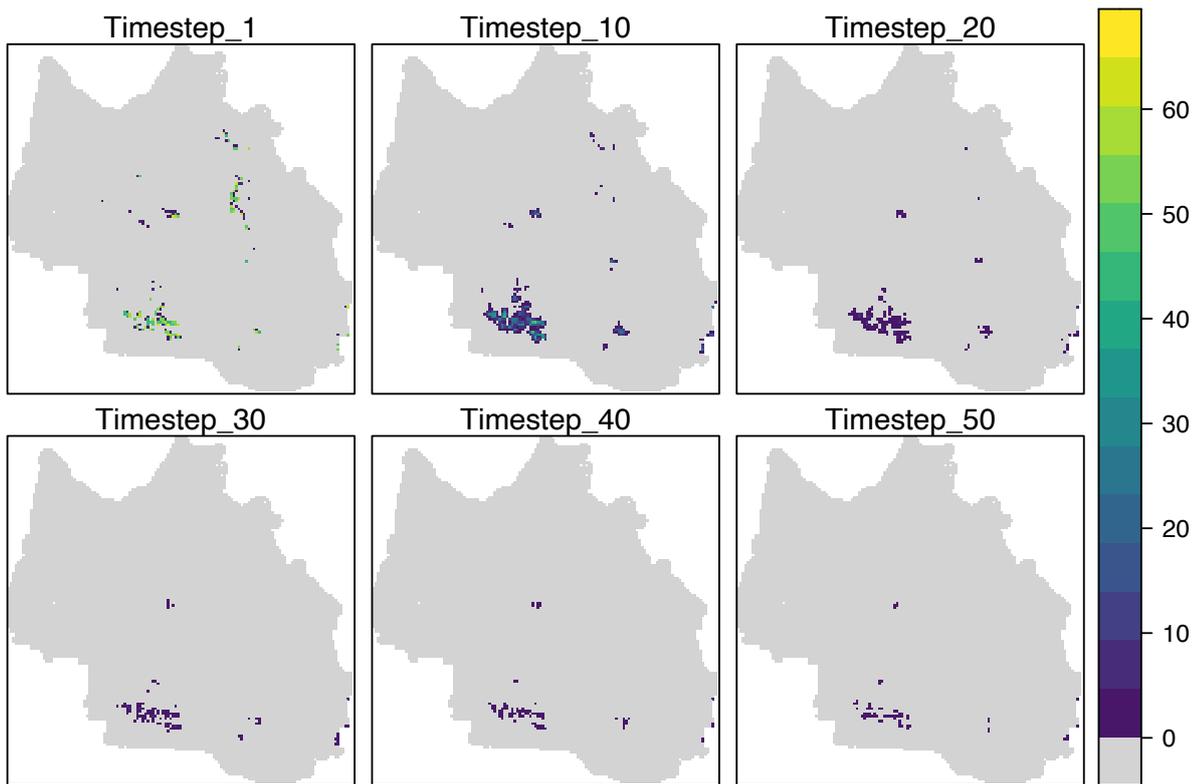


Figure A9: Spatially-explicit population distributions in select years (decades) based on the W1 scenario with high environmental stochasticity.

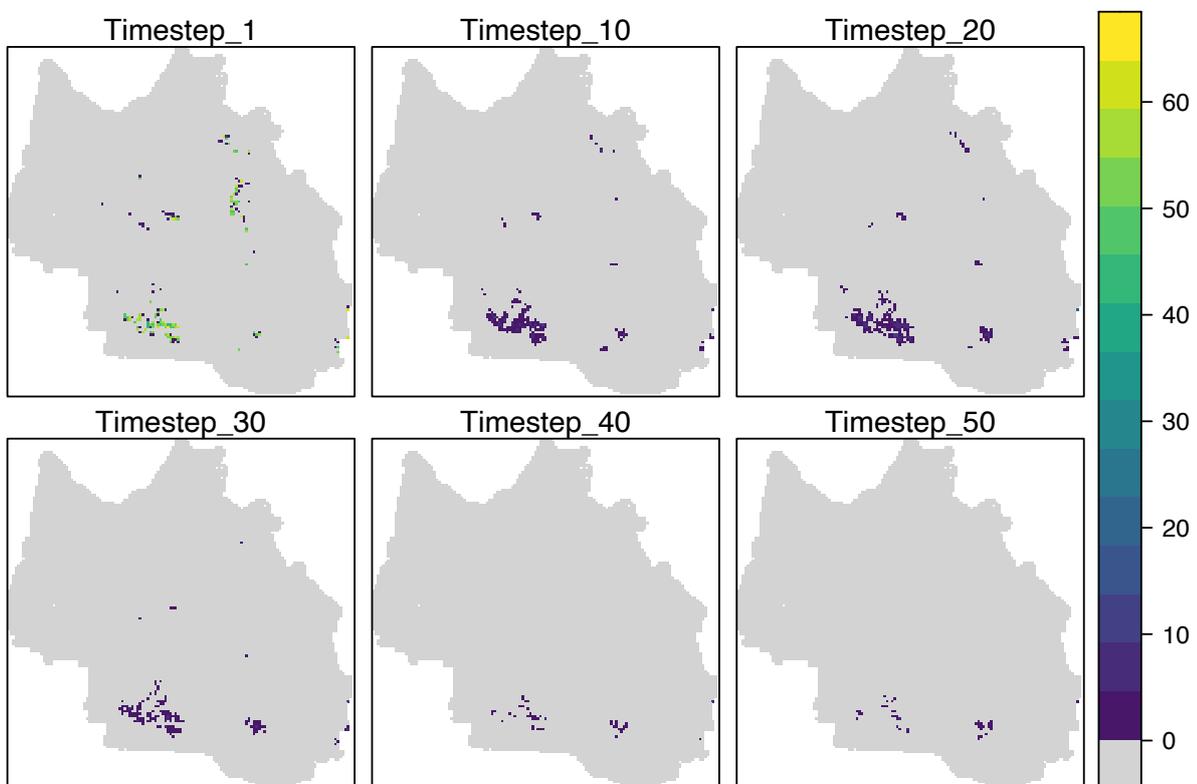


Figure A10: Spatially-explicit population distributions in select years (decades) based on the W2 scenario with high environmental stochasticity.

Further information:

<http://www.nespthreatenedspecies.edu.au>

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