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RESEARCH ARTICLE

Model predictions of key revegetation species response to climate change differ between correlative and mechanistic models: implications for adapting restoration

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Using native species to revegetate and restore areas of the landscape is important to redress habitat degradation and fragmentation resulting from land-use change. However, under a changing climate, the restoration of previously cleared land in urban and agricultural areas may be increasingly difficult as life history traits of plants, such as seed dormancy, stratification, germination, and seedling survival, could be impacted. Using 10 native species commonly used in revegetation projects in southeastern (SE) Australia and the Port Phillip and Westernport (PPWP) region, we compared correlative and mechanistic model predictions of how climate change could impact the climatic suitability of each of these species. We compared climatic suitability under projected future climate conditions for 2090 relative to current climatic suitability. The correlative models were substantial to excellent in predicting species occurrence and showed that in SE Australia and the PPWP region, all 10 species were at a moderate to extreme risk under the 2090 projection. Substantial divergence between the correlative and mechanistic modeling outputs was also evident, with species such as *Allocasuarina verticillata*, *Olearia lirata*, and *Bursaria spinosa* showing quite different responses for correlative versus mechanistic models. This was due to the species' response to water stress during germination and establishment. Differences between the correlative and mechanistic models highlight the need to consider both approaches when modeling a species' response to climate change.

Key words: climate modeling, correlative, habitat restoration, life history, mechanistic, resilience

Implications for Practice

- Ten commonly used revegetation species in southeastern Australia are at moderate to extreme risk of a changing climate by 2090.
- Water stress, both soil and atmospheric, are likely to reduce the area of suitable species habitat under future climate conditions.
- As correlative and mechanistic models represent different processes, predictions can differ substantially; however, both model types offered complementary guidance on areas of expected suitable habitat under projected future climates.
- Where model predictions concur, we might have higher confidence that projected future conditions at those locations are suitable for a given species.
- Where model predictions diverge, managers should consider ancillary site and species information to guide revegetation decisions.

Introduction

Native vegetation restoration is an important means of redressing habitat loss and fragmentation in modified landscapes where land has been cleared for agricultural development and urbanization. This restoration usually aims to maintain and improve biodiversity conservation, ecological functioning, socio-economic services, and cultural values that are reliant on these ecosystems (Pecl et al. 2017). Against a backdrop of time lags between planting, establishment, development, maturity, and self-regeneration, particularly of long-lived species (Vesk et al. 2008), is the present reality of already changing environmental conditions due to climate change (Jellinek et al. 2020). For instance, Allen et al. (2010) provided a global overview of tree mortality as a result of drought and high temperatures. There are also examples of established trees such as *Eucalyptus* sp. showing signs of dieback in Australia due to hotter and drier conditions and insect attacks (Calder & Kirkpatrick 2008). Revegetated areas in southeastern (SE) Australia can similarly

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be impacted by factors such as declining cool season and growing season rainfall, and increases in summer temperatures, affecting plant growth and survival in planted sites (Jellinek et al. 2020).

Vegetation restoration failures are not only costly but could have large-scale detrimental impacts for the faunal species reliant on these restored habitats, and the ecosystem services these areas provide (Mac Nally et al. 2009; Paquette & Messier 2010). Revegetation is likely to be negatively impacted by climate change, in particular from water stress, although few studies directly consider the effects of climate on plant survival (Palma & Laurance 2015). Revegetated areas have been shown to be detrimentally impacted by higher than average maximum mean temperatures in the hottest months and below average rainfall (Jellinek et al. 2020), but the effects of fire are also likely to counteract the benefits of plantings in some landscapes (Hermoso et al. 2021).

In the face of negative climate change impacts on restored areas, managers need forward planning to understand risks, weigh up alternatives and guide decisions that will maximize chances of revegetation success under future climate and environmental conditions (Hermoso et al. 2021). Some management questions include: Are species that are commonly used in revegetation works likely to tolerate future climates? Are there particular areas of the managed landscape that are likely to support native vegetation into the future? Or conversely, are there particular areas that may become inhospitable to native vegetation?

A common approach for exploring future climate suitability is to develop correlative, statistical species distribution models (SDMs) using species occurrence or abundance data and climate and environmental predictors, and to compare future predicted climatic suitability using climate projections to predicted climatic suitability under current climate conditions (Peterson et al. 2015; Shabani et al. 2016). While correlative SDMs are widely used due to the relative availability of biological and environmental data inputs and modeling methods (Elith & Leathwick 2009), few examples exist where correlative models have been used to predict future climatic suitability for revegetation species (Rossetto et al. 2019). Correlative SDMs also do not capture physiological and ecological processes that govern important life history stages that could be sensitive to climatic changes (Mok et al. 2012). For instance, seed dormancy, stratification, germination, and seedling survival are all critical for plant establishment and subsequent growth (Kildisheva et al. 2020), but these processes and how they are impacted under climatic variation are not explicitly represented in correlative SDMs. Mechanistic SDMs are a valuable tool for incorporating these critical processes but have been much less widely used due to their demanding data requirements (Stewart et al. 2022).

While it is widely argued that mechanistic models are more robust for predicting species responses under novel climates (Kearney et al. 2010; Briscoe et al. 2019; Higgins et al. 2020; Dorji et al. 2024), they do not necessarily perform better than correlative models in predicting current distributions (Buckley et al. 2010; Dorji et al. 2024). In particular, mechanistic models can struggle to accurately predict absences in a species' current range (Kearney et al. 2010; Rougier et al. 2015; Higgins et al. 2020). Correlative models can be as robust as mechanistic models, particularly where contemporary and projected future climate of the revegetation site is within the climate niche the correlative model is calibrated on (Higgins et al. 2020). As mechanistic and correlative models represent different niche concepts (Dorji et al. 2024), quantifying the sensitivity and response of species to climate change using both modeling approaches is one way that can provide complementary predictions that provide improved guidance for managers (Rougier et al. 2015).

In this study, we developed both correlative and mechanistic SDMs for key revegetation species used in restoration and revegetation projects in SE Australia. For mechanistic models, this involved seed ecology experiments to quantify germination and survival under different treatments in climate-controlled conditions. Response functions for stratification, temperature, and moisture/drought impacts on germination were then used to parametrize mechanistic models for each species using Tree and Climate Assessment Germination and Establishment Model (TACA-GEM) (Mok et al. 2012; Erickson et al. 2015; Mitchell et al. 2016).

Using correlative and mechanistic models for each species, predictions of climatic suitability were made under current climate conditions and projected future climate conditions (2090 under a high emissions scenario–representative concentration pathway [RCP] 8.5). Risk vulnerability of each species was then assessed on the basis of change in extent and severity of decline of predicted future climatic suitability relative to current climatic suitability. We discuss congruency and divergences between model outcomes, the risk vulnerability to climate change of each species, and then outline the management implications, limitations, and uncertainties.

Methods

Study Area and Context

Melbourne Water is a statutory water authority that manages and operates water supply and sewage systems for a population of approximately 5 million residents and cares for the land and waterways throughout the approximately 13,000 km^2 Port Phillip and Westernport (PPWP) region in the state of Victoria, Australia (Fig. 1). Current mean annual temperature in the region ranges from approximately 9°C in the northeast (Yarra Ranges) to approximately 16°C in the urban areas along the coast. Current mean annual rainfall ranges from a high of approximately 1400 mm in the northeast (Yarra Ranges) to a low of approximately 450 mm in the southwest of the region. Victoria's climate has warmed by about 1.2°C since 1910, and every decade since 1950 has been warmer than preceding decades (DEECA 2024). Over the last 30 years, Victoria's cool season rainfall has declined by greater than 10% compared to the 1961–1990 period, and this long-term trend of decrease is expected to continue in the future (DEECA 2024). The main land uses are for agriculture (44%) and urban areas (14%), the remainder being covered by native vegetation (42%) (Melbourne Water 2024). Melbourne Water has a strategic and operational lead role in protecting, conserving, and restoring native vegetation and ecosystems.

In consultation with Melbourne Water, we selected 10 native plant species that are regularly used in revegetation projects in southeastern Australia (hereafter, SE Australia) and the PPWP region (Fig. 1). These 10 species represent a range of lifeforms from a sedge to longer-lived shrubs and trees (Table 1). Each of these species has a broad current distribution in SE Australia, being found in Victoria and New South Wales, with some species extending into South Australia and Queensland.

Correlative SDMs

Presence data for each of the 10 species was collated from the Atlas of Living Australia (ALA 2022) (Table 1). The ALA presence data was cleaned to remove species records that were: outside of their natural range, not a direct observation, recorded before 1950, lacked information on year of observation; or, had a location uncertainty of ≥500 m (Miller et al. 2020). The range of the species was determined by the state boarders for Victoria and New South Wales. Pseudo-absence data were randomly generated with an equal number of presence and absence data points to reduce the impact of prevalence bias on model outcomes (Barbet-Massin et al. 2012; Wagner et al. 2020). To avoid spatial autocorrelation, presence and absence points were filtered to remove points within 5 km from each other (R Core Team 2023).

Bioclimatic predictor variables for model-building included: Annual Heat Moisture Index (AHMI), Maximum Temperature of the Warmest Month (MTWM), Temperature Seasonality (TS), Mean Annual Temperature (MAT), Isothermality (ISO), Mean Temperature of Wettest Quarter (MTWQ), Precipitation Seasonality (PS); and Minimum Temperature of Coldest Month (MTCM). Climate data used in the analyses were from WorldClim 2 (Fick & Hijmans 2017) with the exception of the AHMI, the aridity variable, which was calculated from the mean annual temperature and precipitation bioclimatic variables (Miller et al. 2020).

Correlative boosted regression tree (BRT) models were built and run following Miller et al. (2020), using accepted modeling practices (Hao et al. 2020). The presence/pseudo-absence data was split into a calibration (70%) and validation (30%) dataset. The calibration dataset was used to build the model and the independent validation dataset to test model performance. Model performance was measured using the area under the curve (AUC), Total Skill Statistic (TSS), Kappa, and deviance metrics.

Climate change projections were based on a high emission pathway (RCP 8.5) for the year 2090 using the ACCESS 1.0 model (Lewis 2013). ACCESS 1.0 represents historic climate in the region better than most other General Circulation Models (GCMs) and provides a model that aligns with the consensus of multiple GCM predictions.

Mechanistic SDMs (TAGA-GEM Models)

Mechanistic models that integrate species responses to climatic stresses at germination and seedling establishment phases capture a critical phase in plant demography and recruitment (Mok et al. 2012). The germination, growth, and survival of plants at this stage are known to be affected by multiple factors, including temperature and soil moisture (see Fig. for some of the factors influencing seed germination and survival).

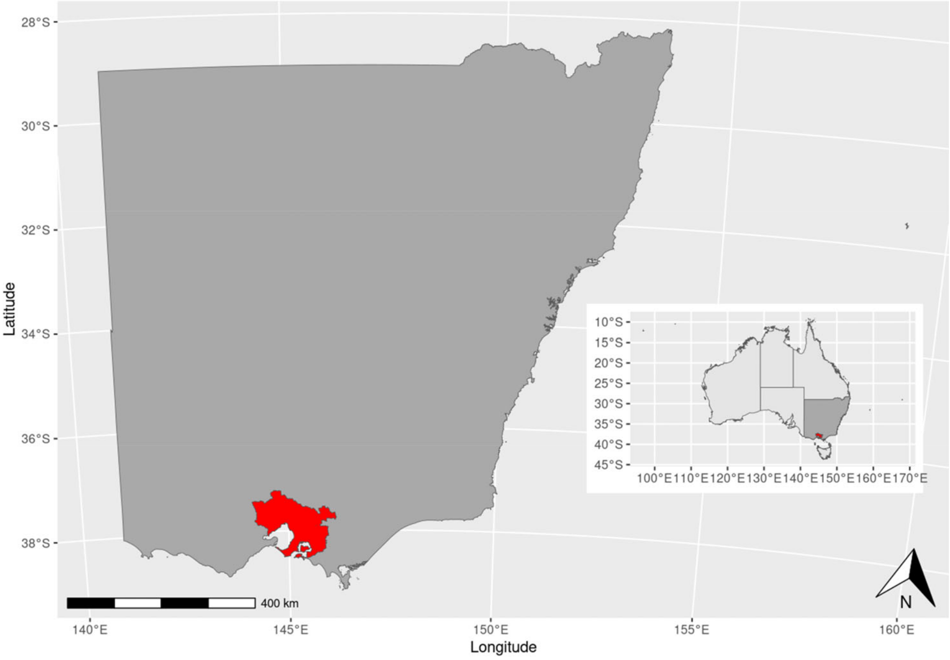

Figure 1. Map of the study area. The gray area represents the overall study region of southeastern Australia (NSW and Victoria), and the red area represents the Port Phillip and Westernport region, where finer-scale modeling was undertaken.

Table 1. Correlative and mechanistic model performance metrics for the 10 species of interest calculated on the validation dataset. Occurrence threshold represents the probability of occurrence value from the models that maximize predictability of species presence and absence. ALA, Atlas of Living Australia.

			Correlative model results					*Mechanistic model results*				
Species	*Common name*	*Type*	*Deviance explained (%)*	*AUC*	*TSS*	*Kappa*	*Occurrence Threshold*	*AUC*	*TSS*	*Kappa*	*Occurrence threshold*	*Presence points (ALA)*
Acacia dealbata	Silver wattle	Large shrub	0.74	0.98	0.85	0.85	0.54	0.90	0.74	0.74	0.15	988
A. implexa	Lightwood	Shrub	0.43	0.89	0.63	0.61	0.44	0.70	0.41	0.41	0.13	8284
A. mearnsii	Black wattle	Large shrub	0.72	0.97	0.87	0.87	0.44	0.89	0.76	0.76	0.18	1891
A. melanoxylon	Blackwood	Tree	0.70	0.97	0.85	0.85	0.32	0.95	0.83	0.83	0.08	3713
Allocasuarina verticillata	Drooping sheoak	Tree	0.64	0.96	0.79	0.79	0.22	0.61	0.37	0.36	0.02	11,398
Bursaria spinosa	Sweet Bursaria	Shrub	0.51	0.90	0.74	0.74	0.54	0.78	0.48	0.49	0.08	4217
Eucalyptus camaldulensis ssp. camaldulensis	River red-gum	Tree	0.66	0.96	0.89	0.81	0.81	0.72	0.45	0.45	0.1	2837
E. viminalis	Manna gum	Tree	0.71	0.97	0.87	0.87	0.39	0.92	0.78	0.78	0.22	2709
Gahnia sieberiana	Red-fruit Saw-sedge	Sedge	0.70	0.96	0.87	0.86	0.48	0.90	0.73	0.76	0.13	1368
Olearia lirata	Snowy daisy-bush	Small shrub	0.62	0.94	0.81	0.82	0.5	0.89	0.71	0.71	0.2	1129

Mechanistic models such as TACA-GEM use information on species germination and growth traits to model how climate change is likely to influence plant recruitment and occurrence. The TACA-GEM model simulates the impact of climate variability and change on the germination and establishment potential for plant species at a daily time step across multiple years and soil types (Mok et al. 2012; Mitchell et al. 2016). This mechanistic model was used to explore how the 10 species' sensitivities to climate factors at critical life stages propagate through to predicted suitable habitat under projected future conditions.

Germination processes were parametrized using growth cabinet measurements of seed stratification effects, germination timing, and quantity under different levels of moisture stress. Ecophysiological measures were recorded and implemented into TACA-GEM. Both germination and seedling survival measurements were done using replicated treatments and controls of different temperatures and moisture stress levels. For climate change modeling, we used the same projection data used in the correlative SDMs.

Seed Ecology Experiments. To capture the importance of climate change on species distributions, we used life history characteristics of each species, which were: water stress (drought) tolerance, frost and climate tolerance; germination phenology; physiological dormancy; germination based on growing degree days (GDD); and seed fall and seed viability (Table S1). Data from growth cabinet measurements of seed germination trials were used to parameterize TACA-GEM to better understand how germination and other physiological processes influenced the species' predicted distributions under observed and future (2090) climates. For this study, we conducted seed germination trials for six of the 10 species: Drooping sheoak (*Allocasuarina verticillata*—tree), Sweet Bursaria (*Bursaria spinosa*—shrub), River red-gum (*Eucalyptus camaldulensis ssp. camaldulensis*—tree), Red-fruit saw-sedge (*Gahnia sieberiana*—sedge), Snowy daisy-bush (*Olearia lirata*—shrub), and Lightwood (*Acacia implexa*—shrub). Data for the other four species: Silver wattle (*A. dealbata*—large shrub), Black wattle (*A. mearnsii*—large shrub), Blackwood (*A. melanoxylon*—large shrub/tree), and manna gum (*E. viminalis*—tree), were obtained from a previous study (Nitschke et al. 2020).

Four replicates for each treatment with 10 seeds per replicate were used. Seeds were placed in a petri dish with moist filter paper and sealed with parafilm wax. Germination response profiles for temperature were developed following Rawal et al. (2015). We used two 12-hour day–night temperature treatments of 20°C (day)—12°C (night) and 25°C (day)—12°C (night). We used a base threshold temperature of 5°C to calculate GDD and to calculate the heat sum from which germination began and ended.

To break physiological dormancies, we applied two stratification treatments: cool-moist stratification and gibberellic acid. Cool-moist stratification methods followed Rawal et al. (2015). Seeds were placed in a double layer of filter paper, moistened with deionized water, wrapped in aluminum foil, placed in zip lock bags, and stored at 4 ± 0.5°C for either 14 or 28 days. Gibberellic acid (200 mg/L) was applied to petri dishes to account for any underlying physiological dormancies (Baskin & Baskin 2004). An unstratified treatment was also implemented.

To test for physical dormancy, a heat treatment was used. For this treatment, seeds were placed in 100°C water for 5 minutes and then cooled for an hour before placing them into a well-watered petri dish (Burrows et al. 2009).

Polyethylene glycol (PEG) is a well-established technique for inducing water stress on seed germination (Emmerich & Hardegree 1990). Water stress treatments for germination were examined using three PEG-induced water potentials controlled using PEG-8000 (Sigma) solutions, calculated for the two temperature treatments (20 and 25°C) following the methods of Michel (1983). The four water potential solutions were 0, −0.05, −0.1, −0.5 MPa. Solutions were added to the petri dishes as required to prevent the seeds from drying out. All petri dishes in the germination trial were checked every other day and solution added as required.

TACA-GEM Model Parameters. The TACA-GEM model has three modules: habitat, phenology, and germination (Rawal et al. 2015). The habitat and phenology components influence the establishment process in the model and reflect the assumed fundamental climate niche of a species. The germination module focuses on the timing and abundance of germination. Key parameters for the habitat niche module are the AHMI, GDDs, frost days, frost tolerance, and lethal frost temperature. AHMI thresholds were calculated from the Australian Living Atlas (ALA 2022) and linked BIOCLIM data (Booth et al. 2014). GDDs were calculated following Pausas et al. (1997) using the ALA data (ALA 2022) and linked BIOCLIM data. The default base temperature from Pausas et al. (1997) was 4.44°C, which was applied to calculate GDD for each species unless information from other sources was available (see references in Supplement S1).

For each species, we used presence data to extract frost day parameters from raster grid maps displaying the average annual number of frost days (daily minimum below 0°C) for the 30-year period spanning 1976 to 2005 (BOM 2023). Annual average frost days from the BOM maps ranged from 1 to 24 and ranged from 0 to 21 across the weather stations used in the TACA modeling. Frost days in the study area were below all species thresholds. Lethal frost temperature parameters were based on species or genus-specific literature sources (see references in Supplement S1). The coldest single day temperature recorded in the dataset was −6°C with other minimum temperatures recorded ranging from −1.2 to −4.4°C. Frost tolerance parameters were based on descriptions of frost tolerance (e.g. low, moderate, and high) from literature sources and given a numeric value between zero and one following Mok et al. (2012) and Rawal et al. (2015). Turgor loss points (TLP) were sourced from species-specific literature and where unavailable, genus-based values were used (see references in Supplement S1).

Water stress tolerance parameters were estimated using reported relative water stress tolerances of species (e.g. low, moderate, and high) and converted to the proportion of the year a species can tolerate surviving when soil moisture is below the TLP. Water stress tolerance parameters for species modeled using TACA-GEM in Nitschke and Hickey (2007), Mok et al. (2012), Rawal et al. (2015), Mitchell et al. (2016) and Nitschke et al. (2020) were used as benchmarks for estimating this parameter. Calibration simulations were then done to compare species establishment potential across soil types and climate data from ecological vegetation classes where the species is reportedly present and absent to tune the water stress and frost tolerance parameters. Germination niche parameters were provided by the seed ecology experiments for six species in the present study. Germination niche parameters for the other four species were available from Nitschke et al. (2020) which used similar seed ecology experiment methods.

The impact of climate variability and change on the germination and establishment potential of each species was modeled based on daily time-step across multiple climate years ($n = 10$ years) that represent the variability in annual temperature and precipitation across the observed climate record (Mok et al. 2012). The daily climate data used in the model was extracted from six Bureau of Meteorology weather stations across the PPWP region (BOM 2023). Five soil types were parametrized for the study area based on the Australian soils layer (Viscarra et al. 2014). Climate change was implemented using a direct adjustment approach following Mok et al. (2012). The regeneration results from the TACA-GEM simulations were fit to a response function with AHMI for each soil type for extrapolation of the aspatial results to the PPWP region.

We did not have independent field data on regeneration success for the modeled species, so we tested the predictive ability of the mechanistic models against the presence/pseudo-absence dataset used to develop the correlative SDMs for the SE Australia study region. To do this, we extrapolated the soil-AHMI models described above to SE Australia and created a model-averaged ensemble spatial map. We then extracted the TACA-GEM suitability scores to the presence and absence points for each species and applied the same validation methods as used for the correlative models against 100% of the dataset, rather than the 30% used for the correlative models. Model performance was measured using the AUC, TSS, and Kappa statistics and compared to correlative model fit (sensu Robertson et al. 2003; Rougier et al. 2015). Following Buckley et al. (2010) and Higgins et al. (2020) we compared the specificity (i.e. the probability of the model to correctly predict an absence) and sensitivity (i.e. the probability of the model to correctly predict a presence) (Allouche et al. 2006) metrics of the correlative and mechanistic models and tested for significant differences in these metrics using a paired t test across all species models (Higgins et al. 2020).

Overlap Analysis and Risk Classification

We used a niche overlap analysis (Warren et al. 2008; Choden et al. 2021) to compare spatial maps of species occurrence between baseline (i.e. current) and climate change predictions. To classify vulnerability of species to climate change, the risk framework from Bland et al. (2018) was used. The Bland et al. (2018) framework uses two components to classify risk: change in extent and severity of decline. For this work, change in extent was the change in modeled extent of occurrence under the current climate compared to modeled extent under climate change (at 2090). Severity was measured as the change in the modeled probability of occurrence, derived from the weighted probability of occurrence between current and future climate. Weighted probability of occurrence was calculated from the amount of area in occurrence classes of 0 to 0.1, 0.1 to 0.3, 0.3 to 0.5, 0.5 to 0.7, 0.7 to 0.9, and 0.9 to 1.0 multiplied by the mid-point of the probability class (i.e. 0.05, 0.20, 0.40, 0.60, 0.80, and 0.95 respectively). For our purposes, the categories from Bland et al. (2018) were renamed to match with Nitschke and Innes (2008). This resulted in Critically Endangered = Extreme; Endangered = Very High, Vulnerable = High, Nil = Moderate and/or None.

Results

The correlative SDMs developed for the 10 species of interest had strong model performance as judged by the percentage of deviance explained, AUC, True Skill Statistic (TSS), and Kappa scores (Burley et al. 2019). Percentage of deviance explained values ranged from 0.51 to 0.74. AUC values ranged from 0.89 to 0.98, TSS values from 0.63 to 0.89, and Kappa values from 0.61 to 0.87 (Table 1). The mechanistic models developed for the 10 species also had moderate to strong model performance with AUC values ranging from 0.61 to 0.95, TSS values from 0.37 to 0.83, and Kappa values from 0.36 to 0.83 (Table 1). There was no significant difference in sensitivity between correlative SDMs and mechanistic models, suggesting that both models were equivalent in their ability to predict presence points (Table 2). The mechanistic models had significantly lower ($p < 0.001$) specificity than the correlative SDMs, highlighting that mechanistic models overpredicted absences compared to correlative SDMs. This means that the mechanistic models predicted that a species could occur in a wider climatic niche than the correlative models. The validation statistics of the mechanistic models were influenced by specificity for many species, particularly *Allocasuarina verticillata*, where mechanistic models were equivalent to or better than the correlative models in predicting species presence.

The correlative models indicated that for the SE Australia region most species were at high to very high risk of their current distributions being affected by climate change to 2090 (Table 3). In the PPWP region, correlative models showed that five species were at high or very high risk, four species were predicted to be moderately or neutrally at risk from climate change, and *Eucalyptus viminalis* was at extreme risk (Table 3). In comparison, the PPWP region mechanistic models showed that species were largely at high risk, with *Bursaria spinosa* being at moderate risk, *Acacia melanoxylon* being at very high risk and *Gahnia sieberiana* being at extreme risk (Table 3).

Table 2. Comparison of the sensitivity (the probability of the model to correctly predict a presence) and specificity (the probability of the model to correctly predict an absence) metrics of the correlative and mechanistic models.

	SDM	*TACA*	*SDM*	*TACA*
Species	*Sensitivity*	*Sensitivity*	*Specificity*	*Specificity*
Acacia dealbata	0.96	0.97	0.90	0.77
A. implexa	0.86	0.95	0.76	0.46
A. mearnsii	0.95	0.94	0.92	0.81
A. melanoxylon	0.97	0.97	0.87	0.86
Allocasuarina verticillata	0.93	0.93	0.87	0.44
Bursaria Spinosa	0.96	0.86	0.78	0.62
Eucalyptus camaldulensis	0.96	0.83	0.93	0.62
E. viminalis	0.96	0.97	0.90	0.82
Gahnia sieberia	0.96	0.97	0.90	0.76
Olearia lirata	0.95	0.94	0.86	0.76
Average probability	0.95	0.93	0.87	0.69
p Value	0.62		<0.001	

Table 3. Species risk assessments for two regions, southeastern Australia (SEA) and Port Phillip and Westernport region (PPWP), based on correlative and mechanistic species distribution models. Classes: Extreme (Ex), Very High (VH), High (H), Moderate (M), None (N).

Species	*SEA correlative model*	*PPWP correlative model*	*PPWP mechanistic model*
Acacia dealbata	VH	VH	H
A. implexa	VH	M	H
A. mearnsii	H	M	H
A. melanoxylon	H	H	VH
Allocasuarina verticillata	VH	N	H
Bursaria spinosa	VH	M	M
Eucalyptus camaldulensis ssp. camaldulensis	H	VH	H
E. viminalis	Ex	Ex	H
Gahnia sieberiana	H	H	Ex
Olearia lirata	H	VH	H

In the germination trial, all species, apart from *A. implexa* and *B. spinosa*, were most influenced by soil water stress followed by atmospheric water stress (represented by AHMI), whereas both *A. implexa* and *B. spinosa* were most influenced by stratification followed by soil water stress (Table S2). *Eucalyptus camaldulensis ssp. camaldulensis* and *A. mearnsii* were more influenced by GDD than by atmospheric water stress (Table S2).

Acacia dealbata, *A. mearnsii*, and *E. viminalis* seed germinated early (around 50 days), except for the high water stress trial (MPa −0.1), and then died before 200 days. Similarly, *A. melanoxylon*, *Olearia lirata*, *A. implexa*, and *B. spinosa* seed did not germinate in the MPa −0.1 high water stress treatments, and *G. sieberiana* seed did not germinate in either the low (MPa −0.05) or high (MPa −0.1) water stress treatments. Three species germinated faster in the stratification trials than in any other trials (*A. verticillata*, *B. spinosa*, and *E. camaldulensis ssp. camaldulensis*), and *A. verticillata* and *E. camaldulensis* spp. *camaldulensis* appeared to survive well in all trials (Fig. S2).

Examples of the spatial differences in probability of a species occurrence between baseline (i.e. current) and 2090s climate scenarios were mapped for illustration (Figs. 2–4 & S3–S9). These maps showed that in the current climate scenario, correlative models predicted species had a wider distribution in the PPWP region than those of the mechanistic models. However, mechanistic models predicted the extent of suitable habitat for all species would decline by 2090, whereas correlative models suggested that for some species, the extent of suitable habitat would increase.

For *A. verticillata*, its correlative model predicted that its extent of suitable habitat would increase across SE Australia and especially in the PPWP region (Fig. 2A & 2B, respectively). Conversely, the mechanistic model suggested that the extent of suitable habitat for *A. verticillata* would be reduced in the west and southeast of the PPWP region by 2090 (Fig. 2C), the inverse of the correlative model predictions. Similar results were observed in the models for *A. implexa* (Fig. S3). Interestingly, the congruence between the mechanistic and correlative models for these species was mixed based on model validation. The mechanistic model was equivalent to the correlative model for *A. verticillata* in its ability to predict occurrence but underpredicted absences. For *A. implexa*, the mechanistic model was better at predicting occurrence but also underpredicted absences.

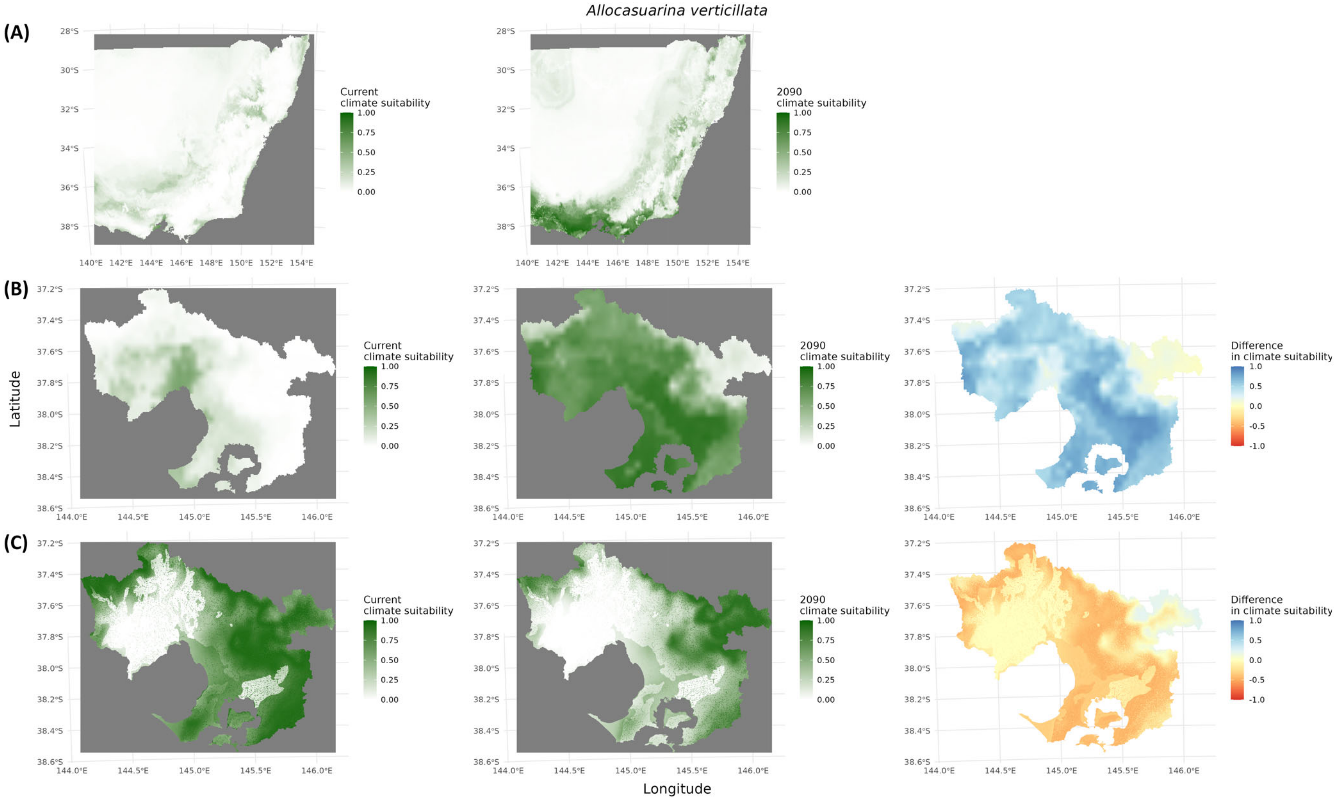

Figure 2. Species distribution modeling results for Drooping sheoak (*Allocasuarina verticillata*) showing: (A) the predicted current and 2090 future climate-impacted habitat suitability across southeastern Australia based on the correlative SDM, (B) the predicted current and 2090 habitat suitability across the Port Phillip and Westernport region and the difference between 2090 and current predictions based on the correlative SDM, and (C) the predicted current and 2090 habitat suitability across the Port Phillip and Westernport region and the difference between 2090 and current predictions based on the mechanistic SDM. In the left and center columns of maps, the deeper greens indicate areas of increased climate suitability. In the difference maps (right column), areas with deeper blues indicate increased climate suitability and deeper reds indicate reduced climate suitability.

The correlative and mechanistic models for *O. lirata* predicted that suitable habitat would reduce across SE Australia and the PPWP region by 2090 (Fig. 3A–C). In the PPWP region, the correlative model for *O. lirata* suggested a drastic reduction in suitable habitat by 2090 (Fig. 3B), while the reduction of suitable habitat by 2090 predicted by the mechanistic model was more modest (Fig. 3C). This aligns with the broader mechanistic model predictions of presence suggesting the species may have a wider climatic niche than represented by the correlative models. Our models also predicted similar results for *A. mearnsii* (Fig. S8) and *E. viminalis* (Fig. S9). Although correlative model predictions for *G. sieberiana* (Fig. S5) and to a lesser extent *A. melanoxylon* (Fig. S7) also showed reductions of suitable habitat in SE Australia and the PPWP region, mechanistic model predictions suggested these species would likely see greater reductions of suitable habitat across their range (Table 2). Interestingly, the *A. melanoxylon* mechanistic and correlative models were statistically equivalent in model validation, indicating the models are likely representing different niche processes.

Bursaria spinosa is currently widespread in SE Australia, but correlative model predictions show that by 2090 suitable habitat in north and central SE Australia will reduce substantively (Fig. 4A). In the PPWP region, the correlative model predictions show a broad reduction in climatic suitability across the region by 2090 (Fig. 4B). It also predicts that pockets of currently low suitability habitat may become more suitable in 2090 (Yarra Ranges in the northeast of the PPWP region, Fig. 4B). *Acacia dealbata* (Fig. S6) showed similar trends.

The correlative model for *E. camaldulensis ssp. camaldulensis* suggests that in the central parts of the PPWP region the species will mostly persist in its current location, but climatic suitability may increase in the north, east, and northwest by 2090 (Fig. S4). The mechanistic model, however, suggests that *E. camaldulensis ssp. camaldulensis* is likely to have slightly reduced suitable habitat in the south by 2090 (Fig. S4).

Discussion

From the modeling undertaken, the 10 species are at moderate to extreme risk of a changing climate by 2090. The reduction in the climatic niche of the species studied here is consistent with other studies that suggest contractions and fragmentation of suitable habitat of individual species due to climate change (Hughes 2003; Miller et al. 2020). The reduction in the species regeneration niche was also consistent with other studies that found regeneration was very sensitive to variations in weather,

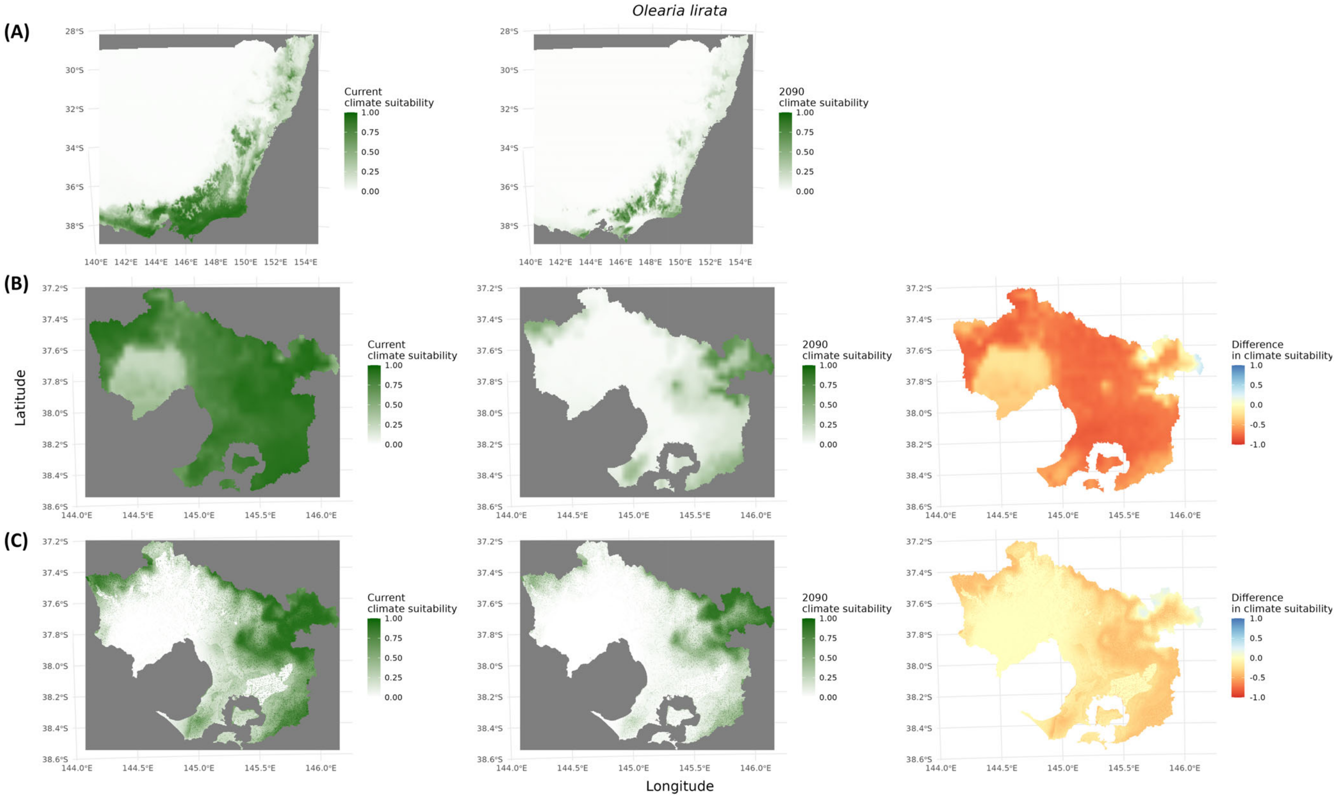

Figure 3. Species distribution modeling results for Snowy daisy-bush (*Olearia lirata*) showing: (A) the predicted current and 2090 future climate-impacted habitat suitability across SE Australia based on the correlative SDM, (B) the predicted current and 2090 habitat suitability across the Port Phillip and Westernport region and the difference between 2090 and current predictions based on the correlative SDM, and (C) the predicted current and 2090 habitat suitability across the Port Phillip and Westernport region and the difference between 2090 and current predictions based on the mechanistic SDM. In the left and center columns of maps, the deeper greens indicate areas of increased climate suitability. In the difference maps (right column), areas with deeper blues indicate increased climate suitability and deeper reds indicate reduced climate suitability.

climate, and soil moisture (Mok et al. 2012). While other factors such as disturbance and dispersal can impact species occurrence, climate is likely to have the greatest impact (Bouchard et al. 2019). Similarly, our modeling identified the importance of climate in shaping the distribution of individual species. A warming and drying climate will alter and shift species distributions which will ultimately impact the ability of land managers to use key revegetation species in the future in large parts of southeast Australia and in the PPWP region.

Though species risk to a changing climate was relatively consistent in our study, correlative and mechanistic modeling produced divergent results. In general, however, mechanistic models predicted overall declines of suitable habitat for all species by 2090, while correlative models predicted declines of suitable habitat for some species, but increases in suitable habitat for others. The mechanistic models overpredicted absences when tested against the current presence/absent dataset, indicating that the models were likely predicting a wider climatic tolerance for the species. However, when tested with climate change predictions the mechanistic models did not reflect this behavior (Buckley et al. 2010). In this study, the divergence between correlative and mechanistic model predictions regarding species absences may be the result of modeling the regeneration niche, which is more sensitive to environmental variability (Grubb 1977), and the inclusion of soil types in the mechanistic models that influence water availability to plants and impact regeneration success (Mok et al. 2012). Inclusion of soil properties into SDMs has been shown to result in different predictions under climate change when compared to climate only models (Ni & Vellend 2024). The predictions by the mechanistic model of increased potential of species occurrence in the absence dataset may seem contradictory to the narrower focus of the regeneration niche; however, this likely indicates that species can regenerate in areas outside of their contemporary range and may not occur there due to dispersal constraints, biotic constraints, or historical disturbances (Buckley et al. 2010; Briscoe et al. 2019). These factors can cause correlative models to underestimate potential habitat or carrying capacities in some environments (Briscoe et al. 2019) leading to a divergence in predictions between mechanistic and correlative models in measures of model specificity (Buckley et al. 2010). Our results are consistent with these lines of reasoning.

Allocasuarina verticillata had the largest divergence between model type outcomes, with the correlative model suggesting this species had larger areas of suitable habitat in SE Australia and the PPWP region under 2090 conditions, while its mechanistic

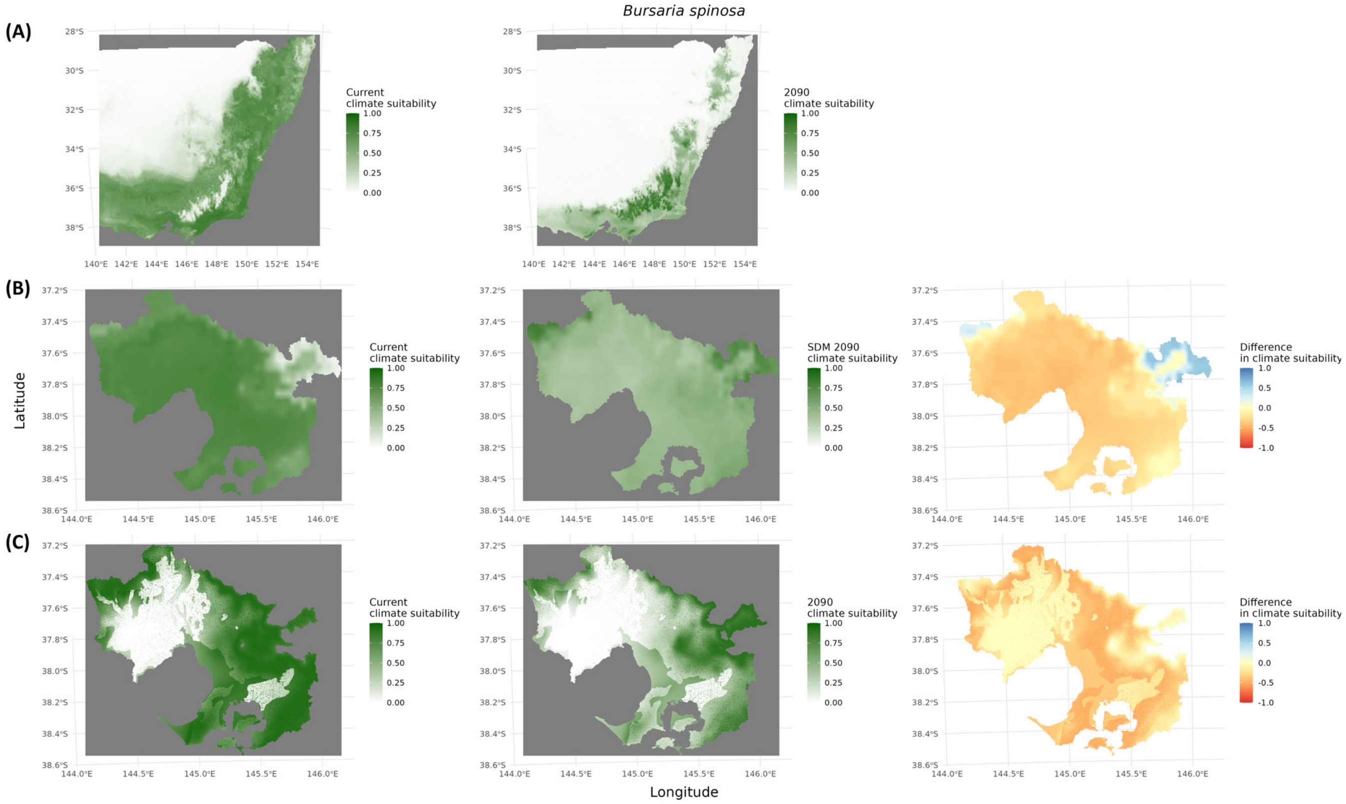

Figure 4. Species distribution modeling results for Prickly Bursaria (*Bursaria spinosa*) showing: (A) the predicted current and 2090 future climate-impacted distribution across SE Australia based on the correlative SDM, (B) the predicted current and 2090 habitat suitability across the Port Phillip and Westernport region and the difference between 2090 and current predictions based on the correlative SDM, and (C) the predicted current and 2090 habitat suitability across the Port Phillip and Westernport region and the difference between 2090 and current predictions based on the mechanistic SDM. In the left and center columns of maps, the deeper greens indicate areas of increased climate suitability. In the difference maps (right column), areas with deeper blues indicate increased climate suitability and deeper reds indicate reduced climate suitability.

model suggested that the species suitable habitat would reduce in some areas of this region. *Olearia lirata* and *Eucalyptus viminalis* showed the opposite effect, with correlative models suggesting that the species would not have suitable habitat in the PPWP region by 2090, and mechanistic models suggesting that they would only lose some of their current suitable habitat. Still other species, such as *Bursaria spinosa*, showed the differences between correlative and mechanistic models in the PPWP region were relatively small, with this species showing similar loss in suitable habitat across its range.

Since correlative and mechanistic models tended to diverge in their predictions related to climate change, differences in their risk vulnerability classification within the PPWP region resulted. These discrepant predictions of risk indicate that there is higher uncertainty of the future impact of climate change on a species habitat potential; however, as the models represent different niche concepts and potential ecological processes a precautionary approach can be taken to help reduce this risk. In practice, management interventions such as planting seedlings of long-lived species that are older and well-developed may help overcome or “leapfrog” vicissitudes of the regeneration stage. This divergence in model results highlights the importance of using both modeling approaches to improve our understanding of species risks to climate change (Rougier et al. 2015).

Contractions of a species’ suitable habitat creates a risk for species as they are likely to be subjected to increasing mortality rates and declining regeneration in their current ranges, while being reliant on dispersal to areas of future suitability. Increases in drought mortality are already occurring and are expected to increase in the future due to climate change (Allen et al. 2010), while declines in natural regeneration are already occurring in SE Australia (Singh et al. 2021) and globally (Allen et al. 2010). Areas where species climatic suitability is predicted to be maintained provides some assurance to and justification for managers electing to continue planting these species in those areas. It is important to note nevertheless, that these sites will still be exposed to the vagaries of climate extremes, disturbances (e.g. fires and floods) and insect and disease infestations.

As such, monitoring of planting sites as well as existing remnant vegetation is vital in order to identify changes in mortality and recruitment rates (Jellinek et al. 2020). Constant regeneration failures and/or increases in mortality of certain species will likely be an indicator of climate change-driven decline. As suggested by our results, water stress had the greatest impact on the species we studied so management interventions such as supplementary watering of newly planted species and other means of increasing vegetation survival and resilience may be required under changing climatic conditions. For example, planting climate adapted species through the use of climate adaptive provenancing and ensuring genetic diversity within species could allow some species to persist (Prober et al. 2018).

Differences between the correlative and mechanistic models highlight the importance of different perspectives when modeling a species' response to climate (Chown et al. 2010; Evans et al. 2015). Mechanistic models are expected to be more robust at modeling a species future distribution as they take into account physiological processes as well as demographic responses to environmental changes (Evans et al. 2015). However, they require a better understanding of a species physiological requirements, which is generally only known for common and well-studied species; and a consideration of what processes to include in the model to provide robust model outputs (Evans et al. 2015). This may result in mechanistic model predictions being confounded by a lack of understanding of species autecology. Another potential drawback is that the physiological data required may not be collected for a sufficient number of species before the climate has shifted (Schindler & Hilborn 2015). A way around this is to extrapolate physiological data collected in one species and use it for species that are closely related (Buckley & Kingsolver 2012). In support of this, our mechanistic modeling of *Acacia implexa* and *A. melanoxylon*, two strongly related species (Entwisle et al. 1996), showed that the current and future distributions of these species are very similar. In contrast, correlative models show substantially different responses, with *A. melanoxylon* having reduced suitable habitat, and *A. implexa* having increased suitable habitat expanding its range, possibly because the correlative models were not able to incorporate processes that influence germination and seedling survival for these species.

Though correlative and mechanistic models predicted differing extents of spatial contractions, suitable habitat predictions were congruent. For all species, water stress, both soil and atmospheric (represented by AHMI), played a major role in this response; however, other parameters such as GDD and stratification also influenced species responses. Similarly, in many areas, where a species' correlative model predicted occurrence, the mechanistic model predicted occurrence in the riparian areas, suggesting that water availability in these areas is important for species recruitment and persistence. The findings of the mechanistic modeling are in line with other studies suggesting that riparian areas are critical for buffering the impacts of climatic change (Rouget et al. 2003; Zhang et al. 2023) because they are located in natural depressions such as gullies or valleys where water is more permanent and where cold air drainage and fog formation occurs (McLaughlin et al. 2017). These mesic micro-environments thus act as climate refugia, so species may move into these wetter portions of the landscape as the climate warms and dries; however, in the warmest and driest parts of the PPWP region they did contract toward higher elevations even within riparian areas. Thus, monitoring vegetation survivorship, growth, and recruitment along riparian and upland gradients would provide an indication of potential climate change impacts and test the veracity of model assumptions.

The intent of this study was to explore future climatic suitability of commonly used revegetation species from two different perspectives—a bioclimatic perspective implemented using correlative modeling and a regeneration niche perspective implemented using mechanistic modeling. As the correlative and mechanistic models take into account different processes, it is important to recognize that there is no "point of truth". Nevertheless, mapped predictions from correlative and mechanistic models can offer some guidance on areas of expected suitable habitat under projected future climate conditions. Where correlative and mechanistic model predictions for a species concur, we might have higher confidence that projected future conditions at those locations are suitable for both bioclimatic and regeneration requirements for the given species. Where model predictions diverge, managers should consider ancillary data and knowledge about the species and the site to guide revegetation decisions.

Limitations and Future Research

Many studies suggest that correlative SDMs have a limited ability to predict a species occurrence as different climate models often provide different species distribution predictions (Shabani et al. 2016; Lee-Yaw et al. 2022). This is not necessarily the case as correlative models can be as accurate or more accurate than mechanistic models when evaluated within the data domain they were trained in (Higgins et al. 2020). That said, mechanistic models tend to perform better than correlative models when predicting into novel parameter spaces (Higgins et al. 2020). Results provided here may have differed substantially if another climate prediction model (other than the ACCESS 1.0) or another emissions scenario (other than RCP 8.5) was used. We also only used BRTs and WorldClim data, whereas different statistical approaches and climate datasets could lead to different spatial predictions of a species suitable habitat (Stewart et al. 2021, 2022). A more comprehensive approach to the SDM modeling would be to follow the approach of Stewart et al. (2022) and combine multiple climate datasets with multiple modeling approaches. Acknowledging these limitations, this study's aim was to compare a correlative SDM to a mechanistic model, and not to compare the results of different correlative model approaches.

The role of genetic variation and phenotypic plasticity is unknown for almost all plant species studied here, and uncertainties in genetics and ecology need to be better understood to improve our understanding of differences in correlative and mechanistic modeling outputs. Similarly, more work is needed to move towards mechanistic models that incorporate genetic variability for all species of interest (Escudero et al. 2003; Lee-Yaw et al. 2022).

Given the limitations and uncertainties associated with modeling outputs, and a non-stationary climate, opportunities to improve revegetation success will be best served by monitoring the survival, growth, and recruitment of the revegetation species and using these data to refine our understanding, models and practices.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Species life history parameters used in the mechanistic (TACA-GEM) models.

Table S2. Weighted responses of life history parameters used in the mechanistic models on modeled outcomes for each species.

Figure S1. Model design of TACA-GEM.

Figure S2. Response functions for the proportion of germinants implemented in the mechanistic model.

Figure S3. Species distribution modeling results for Lightwood (*Acacia implexa*).

Figure S4. Species distribution modeling results for River red-gum (*Eucalyptus camaldulensis ssp. camaldulensis*).

Figure S5. Species distribution modeling results for Red-fruit saw-sedge (*Gahnia sieberiana*).

Figure S6. Species distribution modeling results for Silver wattle (*Acacia dealbata*).

Figure S7. Species distribution modeling results for Blackwood (*Acacia melanoxylon*).

Figure S8. Species distribution modeling results for Black wattle (*Acacia mearnsii*).

Figure S9. Species distribution modeling results for Manna gum (*Eucalyptus viminalis*).

Supplement S1. Literature sources for mechanistic model parameterization.

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