Received: 17 June 2022 | Accepted: 29 August 2022

DOI: 10.1111/1365-2745.14020

Journal of Ecology | BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Dispersal and coastal geomorphology limit potential for mangrove range expansion under climate change

Jacqueline L. Raw[1,2] | Tom Van der Stocken[3,4] | Dustin Carroll[4,5] | Linda R. Harris[2] | Anusha Rajkaran[6] | Lara Van Niekerk[2,7] | Janine B. Adams[1,2]

[1]DSI-NRF Research Chair in Shallow Water Ecosystems, Department of Botany, Nelson Mandela University, Gqeberha, South Africa; [2]Institute for Coastal and Marine Research, Nelson Mandela University, Gqeberha, South Africa; [3]Ecology and Biodiversity Research Group, Biology Department, Vrije Universiteit Brussel, Brussels, Belgium; [4]Jet Propulsion Laboratory, California Institute of Technology, Pasadena, California, USA; [5]Moss Landing Marine Laboratories, San José State University, Moss Landing, California, USA; [6]Department of Biodiversity and Conservation Biology, University of the Western Cape, Cape Town, South Africa and [7]Coastal Systems and Earth Observation, Council for Scientific and Industrial Research (CSIR), Stellenbosch, South Africa

Correspondence
Jacqueline L. Raw
Email: jackie.raw33@gmail.com

Funding information
DSI-CSIR Parliamentary Grant; National Research Foundation, Grant/Award Number: UID: 120701 and UID: 84375; Nelson Mandela University; Water Research Commission, Grant/Award Number: K5/2769; EU Horizon 2020 Framework Programme for Research and Innovation, Grant/Award Number: 896888

Handling Editor: A. Randall Hughes

Abstract

1. Latitudinal range limits for mangroves on high-energy, wave-dominated coasts are controlled by geomorphological features and estuarine dynamics. Mangroves reach a southern global range limit along the South African coastline, but the distribution is patchy, with stands occurring in only 16% of the estuaries in the region. Yet, the persistence of forests planted >50 years ago beyond the natural distribution limit suggests that additional estuaries could support mangroves. Understanding regional drivers is necessary to inform global-scale estimates for how this important ecosystem is predicted to respond to climate change.
2. Here, we combine species distribution modelling (MaxEnt), Lagrangian particle tracking using an eddy- and tide-resolving numerical ocean model, and connectivity matrices, to identify suitable mangrove habitats along the South African coastline at present, as well as under the IPCC RCP4.5 and RCP8.5 climate scenarios.
3. Within the current South African distribution range (±900 km), eight more estuaries were identified to be suitable under contemporary conditions. When considering potential range extension (±110 km), an additional 14 suitable estuaries were identified. Connectivity matrices suggest limited long-distance dispersal, stranding mostly at or near the release location, and a decreased probability of connectivity towards the range limit. Under both future climate scenarios, 30% of estuaries currently supporting mangroves are predicted to become unsuitable, while an additional six estuaries beyond the current distribution are predicted to become suitable. However, there is limited connectivity between these new sites and established forests.
4. *Synthesis*. This study shows that dispersal substantially limits mangrove distribution at the southern African range limit and highlights the importance of including this process in species distribution models. Ultimately, our results provide

new insight into mangrove conservation and management at range limits that are not controlled predominantly by temperature, as it has been assumed that mangroves will largely expand to higher latitudes under climate change.

KEYWORDS
Avicennia marina, climate change, coastal wetland, dispersal limitation, Lagrangian particle tracking, range expansion, South Africa, species distribution modelling

1 | INTRODUCTION

Mangroves are typically tropical ecosystems with a global distribution range delineated by the 20°C winter isotherm for sea-surface temperature (Duke et al., 1998). Rising global temperatures over recent decades have allowed for mangrove range expansions to higher latitudes at five of the continental limits that are characterised by subtropical to warm-temperate transition zones (Gabler et al., 2017; Saintilan et al., 2014). Mangrove range expansion occurs by propagule establishment and subsequent growth and encroachment into areas occupied by salt marsh (Whitt et al., 2020; Yando et al., 2021). The shift from herbaceous or succulent salt marsh to woody shrubs and trees leads to habitat changes that may represent a substantial change in ecosystem-level processes and functions such as altered rates of nutrient and carbon cycling, soil diagenesis and biodiversity patterns (Cavanaugh et al., 2019; Kelleway et al., 2017). Both mangroves and salt marshes are valued for their ecosystem services, particularly in relation to climate change mitigation and adaptation (Duarte et al., 2013; Murdiyarso et al., 2015; Serrano et al., 2019). Research that can predict mangrove range expansions at regional and local scales is therefore needed to inform mitigation and conservation strategies for future decades (Osland et al., 2022).

Regional controls on mangrove distribution are variable between the different latitudinal range limits around the world (Hickey et al., 2017; Osland et al., 2017). Freeze events and absolute winter temperature minima are the most significant controls on mangrove distribution at some northern hemisphere range limits (eastern US, western Gulf of Mexico, northeast China) (Cavanaugh et al., 2014; Osland et al., 2013). However, at southern hemisphere range limits (Brazil, South Africa, Australia, New Zealand), the role of climate is less pronounced, and instead, the physical and geomorphological features of these coastlines limit the distribution of mangroves (Raw, Godbold, et al., 2019; Ximenes et al., 2018). Predicting regional mangrove range expansion therefore requires a quantitative approach to incorporate multiple interacting environmental variables, which can be achieved using species distribution models (SDMs) (Peterson et al., 2015).

SDMs are based on ecological niche theory in that they correlate the optimal ecological conditions for a species to occurrence locations (Melo-Merino et al., 2020). Correlative models are the most common type of SDM and are developed by relating known locations of a species to the environmental conditions at those locations so that ecological requirements can be estimated (Araújo & Guisan, 2006; Melo-Merino et al., 2020). As SDMs generally do not account for interactions with other species, it has been argued that they can only provide an approximation of the fundamental niche, rather than the realised niche (Araújo & Guisan, 2006). The geographical range of a species is determined by interactions between (1) suitable abiotic conditions, (2) biotic interactions such as competition and predation and (3) the area that a species can access by movement or dispersal (Soberón & Peterson, 2005). Therefore, when applying these models at range limits, it is important to include dispersal as a key process that may restrict range expansion alongside the species' physiological limits and the availability of suitable habitats. This allows for a more accurate prediction of the species' real-world distribution (approaching the realised niche). Furthermore, dispersal capabilities can be variable across the distribution range of a species, and so there is a need to specifically determine whether there are limitations at the edges when considering the potential for range expansions in response to climate change.

For mangroves, dispersal trajectories are influenced by factors at local, regional and global scales that together control temporal variability and observed connectivity patterns between and among mangrove forests (Van der Stocken et al., 2019). Dispersal limitation, as indicated by reduced genetic connectivity, has been identified at the African continental range limit along the east coast of South Africa (De Ryck et al., 2016). As mangroves produce hydrochorous seeds and fruits (hereafter referred to as 'propagules'), coastal hydrodynamics play an important role in dispersal and therefore recruitment and establishment into suitable areas. In this regard, recently developed high-resolution, eddy- and tide-resolving numerical ocean models have been used to simulate patterns of propagule dispersal and connectivity between mangrove occurrence locations (Van der Stocken et al., 2019). Ocean surface currents along the east coast of southern Africa are characterised by the Agulhas Current which flows south-westward from 27°S along the shelf edge and eventually retroflects eastward between 40 and 42°S into the Agulhas Return Current at the tip of the Agulhas Bank. The coastline is also characterised by high wave energy and microtidal conditions; thus, mangroves are limited to occurring in sheltered estuaries. Strong wave action and highly mobile sediments often constrict estuary inlets, and during periods of low river flow these systems can remain closed to the sea (Van Niekerk et al., 2020), thus creating barriers for mangrove propagule dispersal and establishment. Despite these challenges, previous research has shown that climate change will likely create suitable sites for mangroves beyond the current

range limit in this region, but less is known about how the suitability of areas currently occupied by mangroves may be impacted (Quisthoudt et al., 2013). This coastline therefore allows one to test the potential for mangrove range expansion in response to climate change in a region characterised by dynamic coastal conditions that could drive dispersal limitations. High-energy conditions also occur at other southern hemisphere range limits for mangroves in New Zealand, southeast Australia and Brazil (Morrisey et al., 2010; Roy et al., 2001; Schaeffer-Novelli et al., 1990).

The fragmented distribution of mangroves at the southern African range limit cannot be explained by climate variables alone. This is a freeze-free coastline, and the rainfall gradient is not a significant predictor of mangrove distribution as shown by previous quantitative studies (Quisthoudt et al., 2013; Raw, Godbold, et al., 2019). This is affirmed by the long-term (>50 years) survival of mangroves planted beyond their natural geographical range (Hoppe-Speer et al., 2015). Dispersal limitations due to coastal and open-ocean processes could leave suitable habitats unoccupied. If environmental conditions within the current distribution range become unsuitable under climate change, this could lead to net loss of mangroves and a possible contraction at this range limit. This has implications for global-scale assumptions on the response of this important ecosystem type to climate change.

The aim of this study is to determine the potential for mangrove range expansion and propagule dispersal limitation at the southern African distribution limit under current and future climate scenarios. Our objectives are to (1) determine the suitability of estuaries for mangroves within and beyond the current distribution range under contemporary climate conditions using mangrove occurrence locations and estuarine environmental conditions to build SDMs with MaxEnt; (2) predict the suitability of estuaries for mangroves under future (2050) projected environmental conditions (RCP4.5 and RCP8.5) using the MaxEnt species distribution modelling software; (3) examine the potential connectivity from propagule dispersal between predicted current; and (4) future suitable mangrove habitat and established mangrove forests, using high-resolution (1/48°×1/48°) regional ocean surface current data and a Lagrangian particle-tracking model. The potential for estuaries with suitable conditions (at present and by 2050) to be colonised from established mangrove populations via propagule dispersal will indicate whether this process is limiting range expansion in the region.

2 | MATERIALS AND METHODS

2.1 | Study site description

Mangroves occur in 31 of the 192 estuaries along the east coast of South Africa, over a tropical to warm-temperate biogeographical transition zone (latitudinal range of 26°53′42.6″ −33°13′32.8″S) (Figure 1). The coastline is relatively straight and exposed and is characterised by high wave energy and microtidal conditions (<2 m tidal range). In the tropical biogeographical region, rocky headlands and promontories allow for the formation of log-spiral bays. The shores between the estuaries in this region are diverse, comprising rocky, mixed and sandy beaches, with increasing proportions of rocky shores and cliffs in the southern half of the mangrove distribution (Harris et al., 2011, 2019).

2.2 | Mangrove data

The two dominant mangrove tree species in South Africa are *Avicennia marina* (Forssk.) Vierh. and *Bruguiera gymnorrhiza* (L.) Lam., each of which occur in 27 estuaries (i.e. mostly co-occurring but some estuaries have records for only one of these species), while *Rhizophora mucronata* Poir. occurs in 16 estuaries. Three tropical species, *Ceriops tagal* (Perr.) C.B. Robinson, *Lumnitzera racemosa* Willd. and *Xylocarpus granatum* J. Koenig, are found exclusively at the northernmost (tropical) location—the Kosi Estuary (Adams & Rajkaran, 2021).

Data for mangrove area cover (ha) in South African estuaries were collated from the National Estuarine Botanical Database (updated in 2019; http://bgis.sanbi.org/SpatialDataset/Detail/2687; Adams & Rajkaran, 2021). The MaxEnt SDMs are therefore not species specific, but rather characterise environmental conditions of extant mangrove habitat in this region—although this generally is dominated by the pioneer species, *A. marina*. Estuaries with mangrove habitat area >0.5 ha ($n = 29$) were selected from the database so that only established forests would be used to represent occurrence locations, thereby focusing on forests that are appropriate sources of propagules and reflecting conditions that allow successful establishment, growth, survival and therefore persistence of mangrove trees. Established forests in this region have been reported to have adult tree to seedling ratios ranging from 17:1 to 1:3, but this can be variable due to anthropogenic pressures such as harvesting (Hoppe-Speer, 2013).

2.3 | Estuarine environmental data

For the development of SDMs, environmental data are needed from the occurrence locations (as part of the background data), as well as from locations where mangroves do not occur (as part of the landscape data). As mangroves are restricted to estuaries, only environmental data from estuaries (and not areas along the open coast) were included in the model.

The estuarine environmental drivers of mangrove distribution along the South African coastline have previously been identified by Raw, Godbold, et al. (2019). This study used quantitative structural equation models (Grace et al., 2012) to consider observable abiotic variables as causal links and evaluate relationships between them using a combination of statistical models that limit model complexity while accounting for variability. Floodplain area, estuary mouth state and the flow regime of the estuary were identified as significant predictors of mangrove area in the model (Raw, Godbold, et al., 2019).

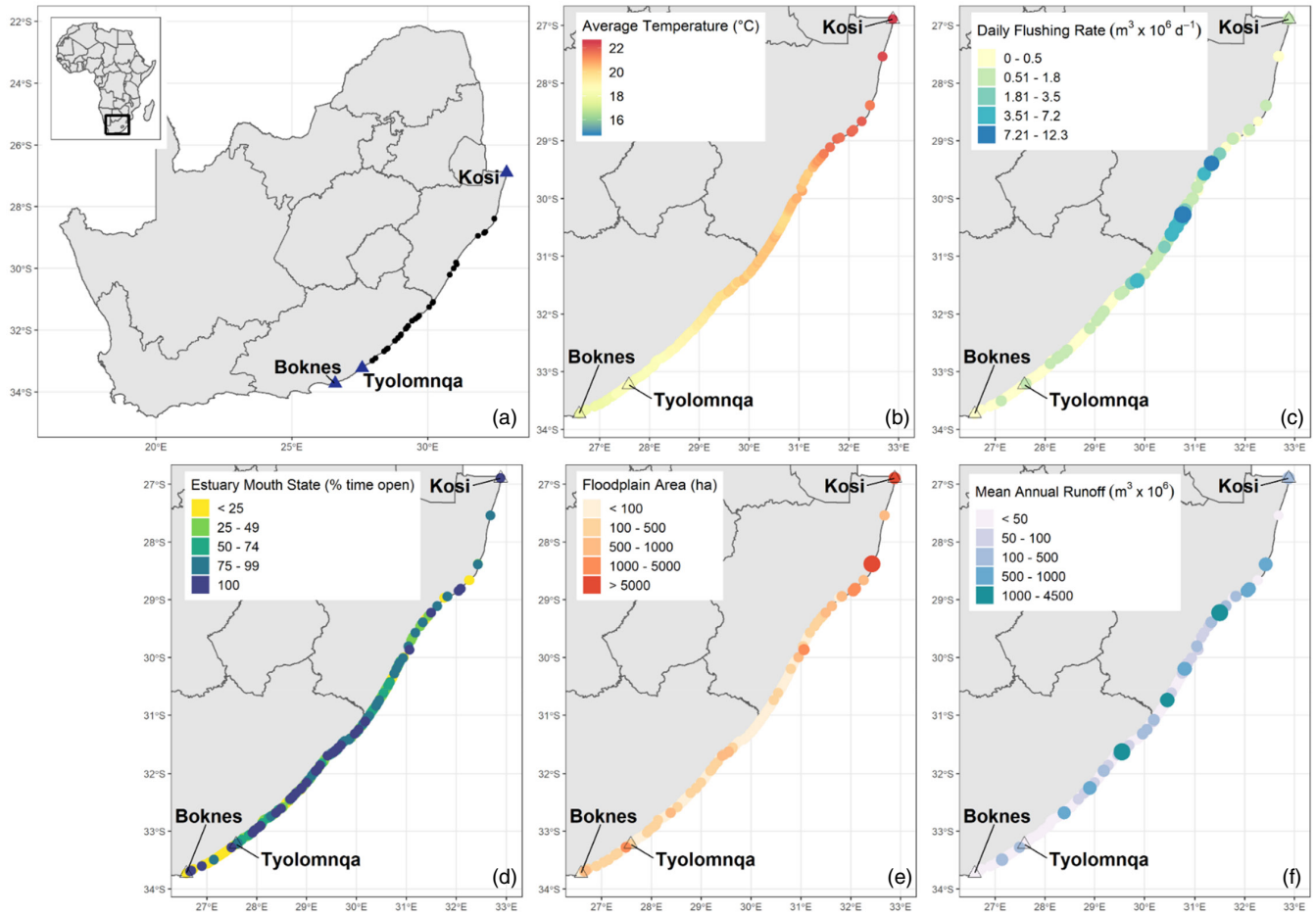

FIGURE 1 Estuaries along the South African coastline that support mangroves and boundary locations used to define the current (Kosi to Tyolomnqa) and potential (Kosi to Boknes) ranges for the species distribution models (SDMs) (a), and ranges of environmental variables: Average annual land temperature (°C) (b), daily flushing rate ($m^3 \times 10^6.d^{-1}$) (c), estuary mouth state (% time estuary is open to the ocean) (d), floodplain area (ha) (e) and mean annual runoff ($m^3 \times 10^6$) (f) for individual estuaries that were included in the SDMs.

This previous study considered a range of temperature variables, including both summer and winter land and sea temperatures, but found that average annual land temperature was the strongest temperature predictor of mangrove distribution. Similarly, while rainfall is variable along this stretch of the South African coastline where mangroves occur across the tropical to subtropical to warm-temperate biogeographical zones, there is not a strong rainfall gradient. The entire east coast of South Africa is characterised by rainfall in the mid- to late summer with mean annual precipitation ranges of 400–800 mm in the warm-temperate to subtropical transition zone, 600–1200 mm in the subtropical zone and 900 mm in the tropical zone (Van Niekerk et al., 2020). Although rainfall was not identified as a variable that drives mangrove distribution patterns, the related estuarine variable—mean annual runoff (MAR)—was significant (Raw, Godbold, et al., 2019).

The following variables were therefore used as the basis for the SDMs in this study: average annual land temperature (°C), floodplain area (ha), MAR ($m^3 \times 10^6$), daily flushing rate ($m^3 \times 10^6\, d^{-1}$) and estuary mouth state (% time that the estuary is connected to the ocean) (Figure 1). Data for these variables were obtained from the Council of Scientific and Industrial Research national database (updated in 2019) for the physical characteristics of South Africa's estuaries (Van Niekerk et al., 2017). This dataset consists of a combination of published, observed data (>20 years) and modelled data. For example, given the paucity of measured river inflow along the South African coast, MAR is based on modelled values over more than 50 years. Daily flushing rate is calculated from estimated MAR, mapped open water extent and average estuary depth. Environmental data were provided in tabular format for all estuaries along the east coast of South Africa, from Kosi Estuary in the north, to Boknes Estuary in the south (~1000 km, $n = 214$; Figure 1a).

The environmental variables for the 2050 projection models were developed by extracting temperature and rainfall projections for South Africa under the IPCC Representative Concentration Pathway (RCP) scenarios which consist of rectangular rasters at a spatial resolution of 8 km^2 for each municipality (Engelbrecht et al., 2019). Because South African estuaries are relatively small, in most cases they were matched one-to-one with these grid cells. Furthermore, given the limited mangrove extent inland from estuary mouths, changes predicted within the first grid cell adjacent to the

coast were considered the most relevant, even for longer estuaries. We considered two RCP scenarios, namely RCP4.5 and RCP8.5. RCPs each define a different possible climate scenario based on greenhouse gas concentration trajectories for the 21st century and are labelled based on radiative forcing values by the year 2100 (2.6, 4.5, 6.0, and 8.5 W m^{-2} for each respective scenario). RCP4.5 is an intermediate scenario where emissions are projected to peak by 2040 and then decline towards 2100. In RCP8.5, emissions are projected to continue to rise throughout the 21st century, it is considered a worst-case, yet realistic, climate scenario.

The projected 2050 temperature and rainfall data were extracted for the geographical location of each estuary. The average temperature increase and average predicted change in rainfall (in mm) by 2050 were calculated for each scenario from the 10th and 90th percentile predictions. For temperature, the value for 2050 was calculated by adding the predicted increase to the current mean annual land temperature. This value ranged from 1.35 to 1.78°C under RCP4.5 and 1.73 to 2.13°C under RCP 8.5. For rainfall, the percent difference in the predicted value from the current rainfall was calculated and used to scale MAR, daily flushing rate and estuary mouth state variables for 2050. Change in rainfall was calculated to range from a 7.8% decrease to a 3.3% increase under RCP4.5, while under RCP8.5 it was calculated to range from a 10.4% decrease to a 4.2% increase. Floodplain area was assumed to remain unchanged by 2050.

2.4 | Modelling mangrove distribution with MaxEnt

MaxEnt is an open-source software that uses the principles of maximum entropy for modelling spatial species distributions from presence-only species records and environmental factors (predictor variables) that are relevant for the species' habitat suitability (Phillips et al., 2019). This is achieved by MaxEnt randomly sampling background locations (i.e. where presence of the species is unknown) within the user-defined model domain (study area) and comparing characteristics of the predictor variables with environmental characteristics at the recorded occurrence locations. Areas of suitable habitat beyond the current occurrence locations can then be identified. The distribution model can be projected to new locations or under new environmental conditions (Figure 2).

An initial model (Model 1) was built to assess the prediction accuracy of MaxEnt and identify whether additional estuaries within the current mangrove distribution range (from Kosi Estuary to Tyolomnqa Estuary) have suitable environmental conditions for the habitat to occur. To determine whether estuaries beyond the current mangrove distribution are environmentally suitable, the modelling landscape was extended southwards by ~110 km (Model 2) (from Kosi Estuary to Boknes Estuary) (Figure 1a, extended distribution range). To predict the suitability of estuaries for mangroves under

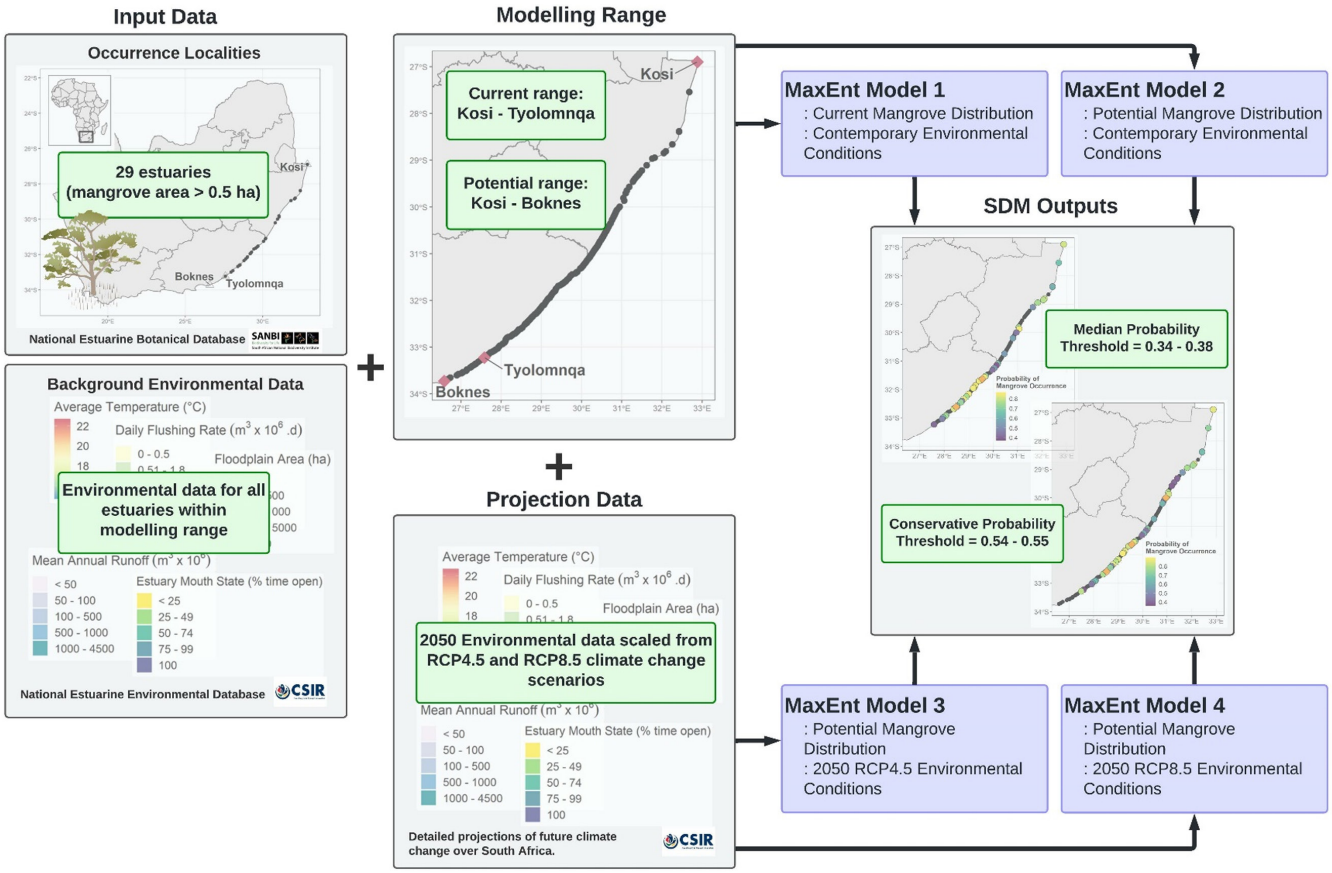

FIGURE 2 Schematic of the inputs to species distribution models developed in MaxEnt to predict habitat suitability of estuaries for mangroves along the east coast of South Africa.

climate change in 2050, projection models were built in MaxEnt for the IPCC RCP4.5 (Model 3) and RCP8.5 (Model 4) future scenarios.

For the projection models, the current mangrove occurrence locations and distribution range (from Model 1) were used as the baseline simulation. The extended distribution range (Model 2 domain) was used as the landscape projection (Figure 2).

All models were run in MaxEnt v. 3.4.1 (Phillips et al., 2019) initially with the data randomly partitioned into a 75% training set and a 25% testing set. After evaluating model fit, the models were re-run using the whole dataset as the testing set. The species-with-data format was used, as both the occurrence localities and environmental data were derived for individual estuaries and can therefore be represented as point-attributes (Elith et al., 2011). The models were run with linear, quadratic and hinge features, which were selected based on prior defined relationships between the environmental variables and mangrove area (Raw, Godbold, et al., 2019). Jack-knife tests of variable importance were used in each model and the area under curve (AUC) statistic was used as a measure of model performance.

To compare mangrove suitability between estuaries, the 'cloglog' output from the MaxEnt models was extracted; this provided an estimate for probability of occurrence between 0 and 1. The 'optimal.thresholds' function from the PresenceAbsence package in R v. 3.6.3 was then used to calculate a range of probability thresholds (Freeman & Moisen, 2008; R Core Team, 2020). The median threshold was calculated from this range. The threshold was used as a cut-off point to identify estuaries with a statistically significant probability of supporting mangroves based on the suite of environmental variables. Additionally, the most conservative threshold was identified for application in the propagule dispersal model. Threshold-dependent statistics (model sensitivity, model specificity, Cohen's kappa statistic and the true test skill statistic [TSS]) were then calculated to evaluate the accuracy of the distribution models under the associated probability thresholds (Allouche et al., 2006). Probability maps of mangrove occurrence for each estuary (and for each MaxEnt model) were generated in R v. 3.6.3.

2.5 | Modelling mangrove propagule dispersal

Connectivity matrices were generated by combining MaxEnt modelling outputs with simulated mangrove propagule dispersal trajectories computed from a high-resolution regional ocean model. These were used to assess whether suitable estuaries under contemporary (MaxEnt Model 2) and future (MaxEnt Models 3 and 4) conditions could be colonised by floating propagules from the 29 estuaries with 'confirmed' mangrove presence.

The hourly ocean surface current data used as input for the particle-tracking model were obtained from the LLC4320 configuration of the Massachusetts Institute of Technology general ocean circulation model (MITgcm; Hill et al., 2007). The ocean simulation includes tidal forcing, allowing for an improved representation of coastal and nearshore dynamics. LLC4320 has a nominal 1/48° (~2 km at the equator) horizontal grid resolution and 90 vertical levels; vertical grid cell thickness near the surface is 1 m. The simulation was initialised from a data-constrained global-ocean and sea-ice solution provided by the Estimating the Circulation and Climate of the Ocean, Phase II (ECCO2) project (Menemenlis et al., 2008). The high spatiotemporal resolution of the model resolves mesoscale-to-submesoscale processes, such as eddies and coherent structures, fronts and filaments. Surface boundary conditions were taken from the 6 hourly, 0.14° (~15 km) European Centre for Medium-Range Weather Forecast atmospheric reanalysis.

Dispersal trajectories were computed using a Lagrangian particle-tracking method that computes particle trajectories by linearly interpolating the LLC4320 surface-ocean velocities (Van der Stocken et al., 2019); trajectories were time stepped using a first-order Euler method. Vertical motion was not considered, which is a reasonable assumption as mangrove propagules float passively at the surface. Particles were released hourly from 1 March 2012 to 31 May 2012, based on reported propagule presence in the field (Steinke, 1986; Steinke & Charles, 1986; Steinke & Ward, 1988, 1990, 2003) and were tracked for 150 days (i.e. floating period). Release locations were the 29 estuaries in which mangroves occur today, whereas potential propagule stranding sites were selected based on the suitability of each estuary as indicated from the respective MaxEnt models and conservative probability thresholds. Though adequate data for floating periods is lacking, the value considered for this variable corresponds to the longer floating periods reported for *A. marina* in the literature (Clarke, 1993). This value was used to represent propagules with high-dispersal capacity that determine large-scale processes, such as the colonisation of unoccupied distant habitats (Nathan et al., 2008). All hourly particle trajectories were aggregated (i.e. bin-summed) on a grid with 1/48° resolution (i.e. the native ocean model LLC 1/48° grid) and normalised by the bin area. This yielded a particle concentration map showing the distribution patterns of dispersal in the region.

Connectivity matrices were generated to assess potential gene flow between populations and potential colonisation of suitable habitats from current mangrove populations. To accomplish this, a stranding algorithm was included in the dispersal model to evaluate whether or not a particle had (1) stranded within the maximum floating period of 150 days and (2) floated for a specified minimum period. The minimum floating period was included to avoid immediate stranding at the release site, and it allowed particles to embark on the so-called long-distance dispersal. As the value of this parameter is arbitrary, we performed a Monte Carlo simulation generating random minimum floating period values between 1 and 5 days and a simulation with a minimum floating period of 1 day, that is, time-scales that suffice for dispersal outside of the local system. The stranding computation considers the location of a dispersing particle and evaluates whether any of the eight connected cells (i.e. a bounding box) is a land grid cell that is designated 'suitable' based on the MaxEnt model output—this is the condition for stranding. A stranded particle is removed from the simulation, that is, we did not allow for multiple stranding events by a single particle.

3 | RESULTS

3.1 | Realised and potential distribution ranges for South African mangroves

Modelling the current distribution range of mangroves (Model 1, Figure 3a) allowed for a validation of the MaxEnt approach, as the occurrence and absence locations are known. The jack-knife analysis of variable importance showed that Floodplain Area yields the highest contribution towards model fit (as indicated by the regularised gain) and explains the majority of model variability (Table 1). The model performance (Table 2) had a strong measure of separability with AUC of 0.909. This indicates that the model can distinguish presence locations with high certainty as models with AUC >0.75 are considered useful, and <0.5 are considered random (Phillips et al., 2019). Almost all the threshold-dependent statistics were also >0.8, and often >0.9, further confirming high certainty in the models.

Model sensitivity (true positive rate, indicating omission errors) is higher for the median threshold compared to that for the conservative threshold, but the inverse is true for model specificity (true negative rate). The median threshold is, therefore, better at predicting true presence, despite returning some false positives. For example, eight 'non-mangrove' estuaries were predicted to be suitable based on environmental conditions (Table S1). However, one of these estuaries has a record of mangrove occurrence in the National Estuarine Botanical Database (Gqunube) (but less than the 0.5 ha cut-off used to define an established forest in this study), while one other (uMgobezeleni Estuary) has lost mangrove area after a bridge was built that altered the estuarine hydrodynamics (Taylor, 2016). The model also predicted suitability for the Qora Estuary, which was subsequently confirmed as a 'new' occurrence location for mangroves in the National Database. The selection of these estuaries further supports the accuracy and strength of the predictive model. In comparison, the conservative threshold best predicts estuaries without mangroves, despite also returning some false negatives. For both thresholds, specificity was higher than sensitivity, more so for the conservative threshold, hence the higher kappa value because prevalence is relatively low (Allouche et al., 2006). However, when prevalence is accounted for in the TSS, the median threshold is considered a marginally better threshold overall. Given these results, the conservative threshold was preferred for the connectivity modelling because it has a higher true negative rate, is more conservative in estimating presence and had values >0.8 for both kappa and TSS.

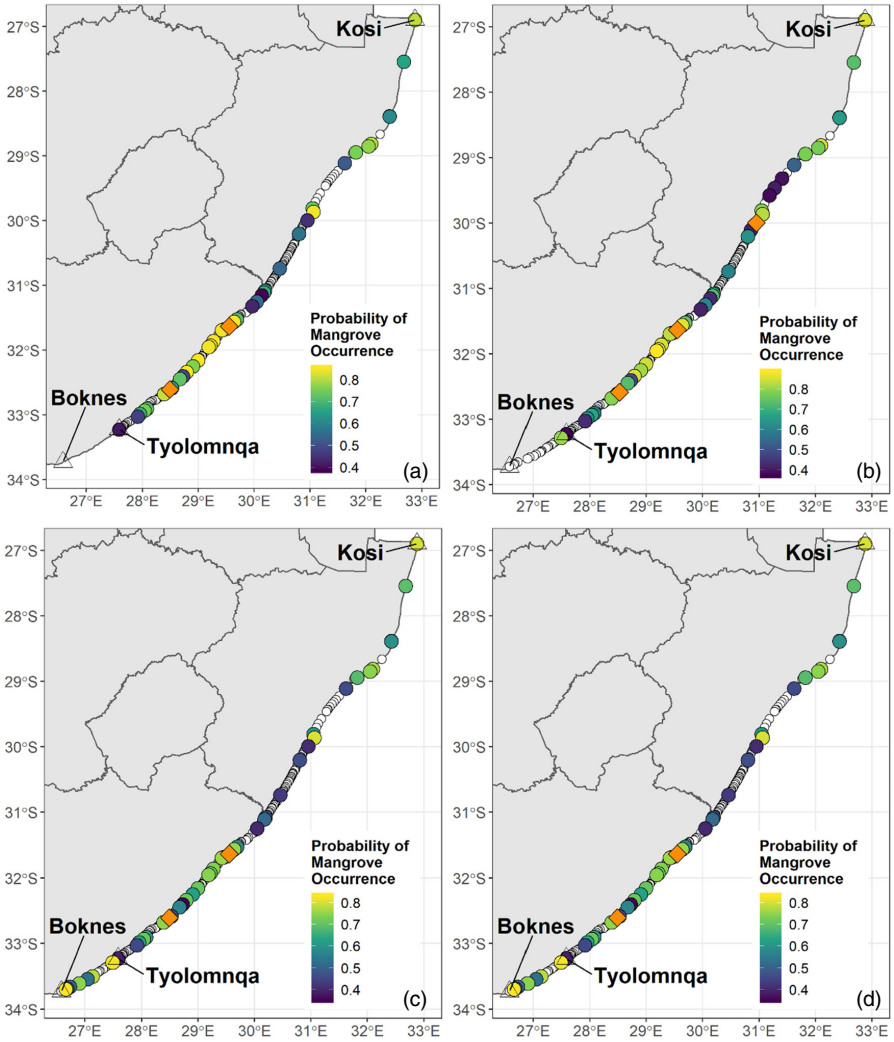

FIGURE 3 Probability of mangrove occurrence in estuaries along the South African coastline as predicted by MaxEnt species distribution models. The current distribution range from Kosi to Tyolomnqa (a) is compared to a potential extended distribution range from Kosi to Boknes under contemporary environmental conditions (b) as well as under RCP4.5 (c) and RCP8.5 (d) IPCC climate change projections. Orange diamonds indicate estuaries where mangroves are known to occur, but for which the probability of occurrence was found to be below the median thresholds in the models (a = 0.38, b = 0.34, c = 0.35, d = 0.35). White circles represent 'non-mangrove' estuaries with probability of occurrence below the same respective thresholds.

TABLE 1 MaxEnt species distribution model results for mangroves along the South African coastline

Variable	Regularised gain with variable	Percent contribution	Permutation importance
Model 1: Current distribution range			
Average annual temperature	0.061	0	0.4
Daily flushing rate	0.023	2.6	9.3
Floodplain area	0.989	38.4	67.0
Estuary mouth state	0.726	18.0	13.6
Mean annual runoff	0.963	40.9	9.6
Model 2: Extended distribution range			
Average annual temperature	0.109	2.7	2.6
Daily flushing rate	0.023	2.4	2.8
Floodplain area	0.909	26.8	70.0
Estuary mouth state	0.991	15.5	13.5
Mean annual runoff	0.712	52.6	11.1

TABLE 2 MaxEnt species distribution model performance metrics for mangroves along the South African coastline. Sensitivity, specificity, Cohen's kappa and true skill statistic (TSS) are reported for median and conservative probability thresholds

Model 1: Current distribution range					
Model performance	**Area under curve (AUC)**				
	0.909				
Probability threshold	**Value**	**Sensitivity**	**Specificity**	**Cohen's kappa**	**TSS**
Median	0.380	0.931	0.938	0.781	0.869
Conservative	0.545	0.862	0.975	0.837	0.837
Model 2: Extended distribution range					
Model performance	**AUC**				
	0.914				
Probability threshold	**Value**	**Sensitivity**	**Specificity**	**Cohen's kappa**	**TSS**
Median	0.335	0.897	0.914	0.681	0.810
Conservative	0.550	0.862	0.973	0.823	0.835

Extending the potential distribution range ~100km southwards along the coast (Model 2) increased the number of estuaries predicted to have suitable environmental conditions for mangroves. The jack-knife analysis of variable importance showed Estuary Mouth State makes the highest contribution towards model fit (Table 1). However, the variability in the model was still best explained by Floodplain Area (indicated by permutation importance, Table 1). Model performance metrics indicated high certainty in predictions, with an AUC of 0.914 (Table 2). Three mangrove estuaries were estimated to have a probability of occurrence lower than the median threshold (Figure 3b). An additional 14 estuaries where mangroves presently do not occur or occurred in the past and were lost were predicted to be suitable under Model 2.

3.2 | Projected distribution ranges for South African mangroves under climate change

The projected SDMs (Models 3 and 4) used the current distribution range (Model 1) as the background data extent and the potential distribution range (Model 2) as the projected data extent. The results from the jack-knife analyses of variable importance, as well as the model performance indicated by the AUC, are the same as that recorded for Model 1 (Tables 1 and 3). The other model performance metrics (sensitivity, specificity, Cohen's kappa and TSS) were lower than those for Models 1 and 2 (Table 3).

Modelling the projected mangrove distribution by 2050 under both the RCP4.5 (Model 3, Figure 3c) and RCP8.5 (Model 4, Figure 3d) climate scenarios showed an increase in the probability of occurrence for mangroves along the southern extended range. Under both projected models, two mangrove estuaries were estimated to have a probability of occurrence lower than the median threshold. An additional 16 estuaries where mangroves do not occur were predicted to be suitable.

3.3 | Propagule dispersal and connectivity between South African mangrove estuaries

High along-shore particle concentrations were observed in the dispersal model. The bulk of the particles are carried along the

TABLE 3 MaxEnt species distribution model performance metrics for mangroves along the South African coastline under projected climate change. Sensitivity, specificity, Cohen's kappa and true skill statistic (TSS) are reported for models under median and conservative probability thresholds

Model 3: RCP4.5 projected distribution range					
Model performance	**Area under curve (AUC)**				
	0.909				
Probability threshold	**Value**	**Sensitivity**	**Specificity**	**Cohen's kappa**	**TSS**
Median	0.350	0.931	0.919	0.715	0.850
Conservative	0.525	0.690	0.957	0.656	0.646
Model 4: RCP8.5 projected distribution range					
Model performance	**AUC**				
	0.909				
Probability threshold	**Value**	**Sensitivity**	**Specificity**	**Cohen's kappa**	**TSS**
Median	0.345	0.931	0.919	0.715	0.850
Conservative	0.495	0.690	0.951	0.641	0.641

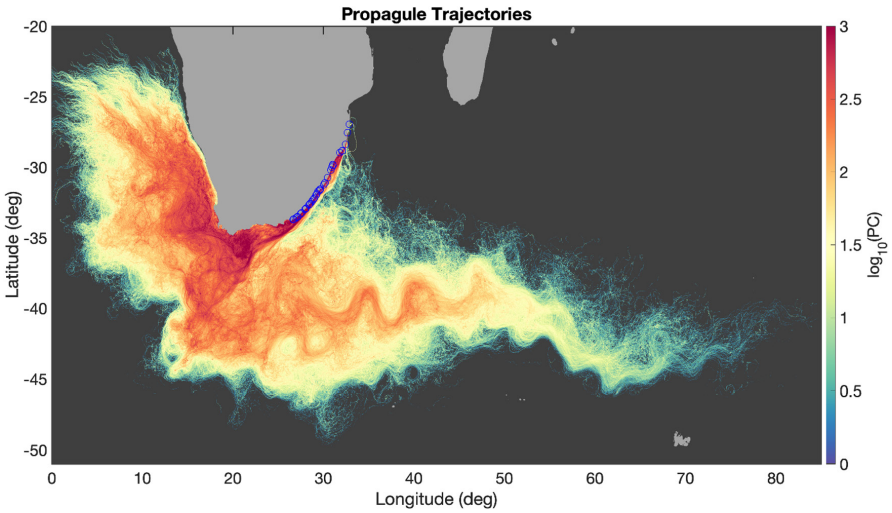

FIGURE 4 Distribution and patterns of mangrove dispersal around southern Africa. The particle concentration map is based on simulated Lagrangian trajectories for particles released hourly from the 29 South African mangrove estuaries (indicated by blue circles) from 1 January 2012 to 30 May 2012 and tracked for 3 months. Trajectories were bin summed to yield particle concentration (PC).

centrelines of the major ocean circulation features in this region, that is, the Agulhas Current System (including the retroflection and return current), as indicated by high propagule density (red colours) in Figure 4. The trajectories cover a broad expanse of both the Atlantic and Indian Oceans surrounding southern Africa.

The connectivity matrices used to assess potential colonisation from current mangrove populations to suitable sites showed high site fidelity. Overall, the Monte-Carlo approach showed dominant stranding at, or near to the release site with limited examples of longer distance connectivity, as indicated by high saturation in the matrices (Figure 5, diagonal). There was a dominant northeast-to-southwest directionality, with a few exceptions showing a northeastward connectivity (Figure 5, below diagonal). The probability of connectivity decreases southwards, as indicated by the decreased colour saturation from the upper right to lower left in the respective matrices. The furthest connection in the simulations covered >470 km and consisted of particles released at uMhlathuze Estuary (28°50′55.95″S) that stranded towards the south-west at Mbashe Estuary (32°14′59.95″S).

Some estuaries identified as suitable by MaxEnt, but which at present do not support mangrove forests >0.5 ha (Figure 5a, *x*-axis: uMgobezeleni, uMzimkhulu and Qora), had low connectivity with established mangrove forests, while others could potentially receive propagules from nearby systems (Figure 5a, *x*-axis: Gqunube). Under the current model setup, various mangrove estuaries appear isolated from other estuaries in the region (i.e. they do not exchange propagules with other populations). Some forests showed high levels of local stranding, either within the same system (Figure 5a, diagonal: Kosi and uMlalazi) or to a system in very close proximity (Figure 5a, near diagonal: uMngeni to Durban Bay). For some forests (Figure 5a, *y*-axis: Xora, Nqabara/Nqabarana and Nxaxo/Ngqusi), propagules were transported away from the estuary and did not strand at any coastal site, either locally or remotely as indicated by the lightly shaded rows.

By 2050, some mangrove estuaries within the current distribution range are predicted to be unsuitable by MaxEnt as indicated by white columns in the connectivity matrices (Figure 5b,c). Under both RCP4.5 (Figure 5b) and RCP8.5 (Figure 5c), several estuaries along a continuous stretch (*x*-axis: Mtentu to iSiphingo) are modelled

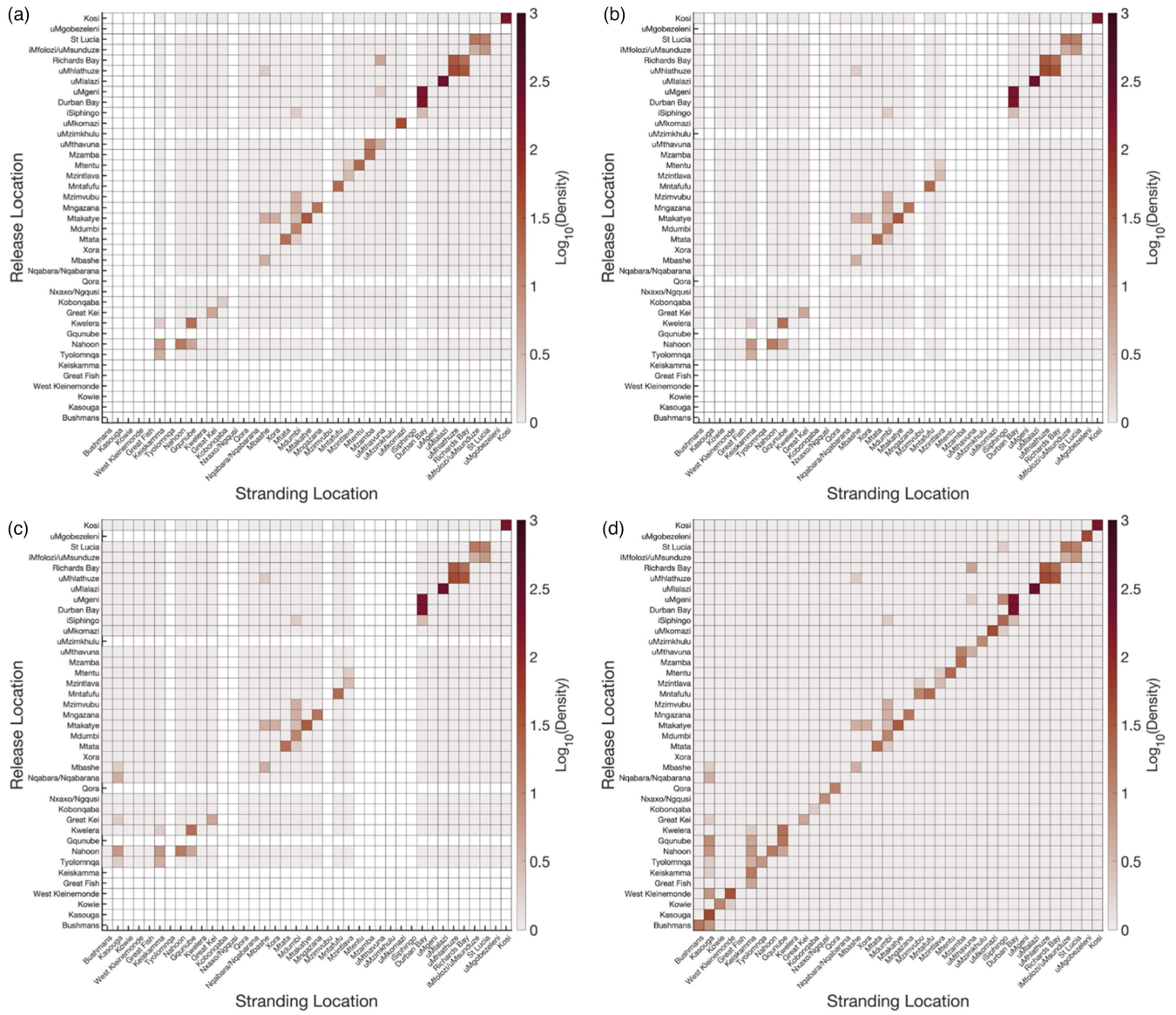

FIGURE 5 Matrices of potential connectivity between mangrove estuaries (*y*-axis, listed top to bottom, latitudinal range N-S) and estuaries with suitable conditions (*x*-axis, listed right to left, N-S) as predicted with the dispersal model and MaxEnt for contemporary (a) and future (2050) conditions under RCP4.5 (b) and RCP8.5 (c). White *rows* (*y*-axis) indicate sites where mangroves currently do not occur (not used as release locations in the dispersal model). White *columns* (*x*-axis) indicate sites projected to be unsuitable for mangroves based on the conservative probability threshold from MaxEnt. Simulations were also run to consider all sites identified as suitable in at least one of the MaxEnt models (d). Simulated propagules were stranded after reaching a land grid cell within 150 days. The minimum floating period was 1–5 days.

to be unsuitable stranding locations, thus contributing to a break in connectivity. Most estuaries beyond the current mangrove distribution range (that were predicted to have suitable habitat under future climate scenarios) were shown to have limited connectivity to established mangrove forests, as indicated by light shading in the connectivity matrices (Figure 5b,c, *x*-axis: Bushmans to Keiskamma). There was one exception under RCP8.5 where a suitable estuary beyond the current distribution was predicted to receive propagules from forests located to the north-east (Figure 5c, *x*-axis: Kasouga). However, if mangroves were to establish in more southern estuaries (where conditions are currently suitable), connectivity matrices demonstrate that there could be local connectivity and potential for dispersal and stranding towards the northeast (Figure 5d, *y*-axis: Bushmans to Keiskamma).

4 | DISCUSSION

A generalised prediction of mangrove range expansion to higher latitudes in response to increasing global temperature is not appropriate, as other environmental variables exert significant controls on the distribution of this habitat type at regional scales (Osland

et al., 2016). Here we present a novel approach to combine SDMs and propagule dispersal modelling and thus provide a robust and quantitative assessment of the potential for regional mangrove range expansion in southern Africa under climate change. Additional estuaries both within and beyond the current distribution range were found to have suitable conditions for mangroves under contemporary environmental conditions and under the IPCC RCP4.5 and RCP8.5 scenarios to 2050. Assessing the connectivity between estuaries with established mangrove forests and others with suitable environmental conditions indicated that the current distribution, and therefore the potential for range expansion under climate change, is limited by propagule dispersal.

4.1 | Predicting mangrove range expansion at the southern African distribution limit

Propagule dispersal in south-east Africa occurs predominantly in a south-westward direction, which reflects the primary flow direction of the Agulhas Current, while the few northward tracks represent the prevailing direction of longshore drift (Lutjeharms, 2007). Similar dispersal patterns have been observed for drifting plastic nurdles (Schumann et al., 2019) and plastic drift cards that were used in a field study to estimate dispersal and transport rates for *A. marina* propagules along the South African coastline (Steinke & Ward, 2003). Overall, there is high potential for along-shore connectivity between estuarine mangroves in the region, as shown by the particle concentration map and the report of drift cards being transported rapidly southwards (~600 km in 3 weeks). The particle concentration map also shows the potential for propagules to be transported around the Cape and towards the west coast of southern Africa. Mangroves do not occur along this coastline as the climatic conditions which are regulated by the cold water Benguela Current flowing up from Antarctica are unsuitable. The range limit for mangroves on the west coast of Africa is in Angola at Rio Longa (Diop et al., 2002), and is represented by Atlantic species such as *Avicennia germinans* (L.) L. Continental and oceanographic processes maintain the break between mangrove species on either side of the African continent (Van der Stocken et al., 2019). Connectivity is therefore limited when examining the matrices, with most particles stranding near their release point and indicating that mangroves largely recruit locally. The high probability for local dispersal and nearby connectivity suggests that potential establishment at new suitable sites may be governed by local- to regional-scale coastal and estuarine dynamics.

The high-energy and wave-dominated characteristics of this coastline drive estuary mouth closure for some systems when marine sediments are deposited at the inlet to form a barrier which is then breached by increased freshwater inflow from upstream (seasonal rainfall) or by storms that drive large wave events (Van Niekerk et al., 2020). This recurrent closure would constrain the exchange of propagules between mangrove populations directly by preventing inflow and outflow. Propagule recruitment to new locations may also be complicated by the reduced chances of entering an estuary where the location and size of the mouth are changing over seasonal and subseasonal timescales. Additionally, mangroves can experience dieback due to inundation stress if closed periods persist for up to 3 months (Mbense et al., 2016), reducing the net source of propagules available for dispersal between populations. The dispersal model does not resolve the sinking processes of propagules and only assumes surface-level transport. Upon sinking, a propagule is eliminated from the dispersing cohort in the simulation, therefore although there is realistically potential for re-floating (due to change in density gradients), this is not accounted for in the dispersal model. Propagule quality and buoyancy could therefore also be limiting dispersal or promoting self-seeding as has been observed for *A. marina* at some southern estuaries in this region (Steinke, 1986). Peak propagule production occurs in the summer months (November to January) for subtropical estuaries, with peak release periods in autumn (March to May) coinciding with equinox tides (Steinke, 1986; Steinke & Charles, 1986; Steinke & Ward, 1988). At warm-temperate estuaries, propagules have been reported to be present throughout the year, but also with a peak release in the autumn months (Steinke & Ward, 1990). This is an important aspect of the dispersal process that needs additional research. In addition to this, the potential for colonisation at range edges is generally much less than at the centre, thus resulting in observed pulses of pioneers into new territories (Whitfield et al., 2016). For biota relying on passive dispersal, the number of recruits that can find suitable settling areas is lower over greater distances.

Other localised physical processes such as tidal fluctuations and submesoscale features such as eddies, filaments and fronts or coastal configurations where estuary mouths open into bay areas with small circulation cells can all influence propagule dispersal, and thus either aid or restrict potential range expansion. Such local-scale propagule dispersal patterns have been reported for *A. marina* propagules modelled on the east African coastline between Kenya and Tanzania (Triest et al., 2021). At the scale of individual estuaries, king tides and overtopping by wave events can transport propagules into zones within an estuary that would not be accessible during typical conditions. This is evident in the mangrove population structure within some estuaries that indicate a single successful recruitment event along a flood line (Adams & Rajkaran, 2021). Local estuarine geomorphic settings, such as intertidal gradients and surface elevation, can also influence successful propagule establishment (Oh et al., 2017). Unfortunately, elevation data at appropriate spatial resolution are not currently available for all estuaries this region so surface elevation could not be included as a driver in the MaxEnt model. As the first-pass attempt to consider suitability based on surface elevation, we cross-referenced records of lower intertidal salt marsh species (i.e. *Salicornia meyeriana* Moss, *S. pachystachya* Bunge ex Ung.-Sternb., *Cotula filifolia* Thunb., *Salicornia tegetaria* S. Steffen, Mucina & G. Kadereit, *Salicornia natalensis* (Bunge ex Ung.-Sternb.) A.J.Scott, *Spartina maritima* (Curtis) Fernald, *Triglochin bulbosa* L., *Triglochin striata* Ruiz & Pav.) at estuaries that the MaxEnt model identified as suitable for mangroves. These plant species represent substrate

and hydrokinetic energy (tidal and wave) conditions suitable for mangroves as they would occur within similar intertidal zones, at an elevation range less than 1.5 m AMSL (Adams, 2020). This is also supported by increasing evidence of mangrove encroachment into salt marshes (Kelleway et al., 2017; Osland et al., 2013; Raw, Julie, et al., 2019; Saintilan et al., 2014; Whitt et al., 2020). We found that all estuaries identified as suitable by MaxEnt that are south of the current distribution range for mangroves had records of lower intertidal salt marsh plant species, indicating that surface elevation should not limit establishment at these sites. Overall, there is limited potential for range expansion at the southern African distribution limit due to near-shore currents, intermittent connectivity of estuary inlets and the along-coast distance between estuaries with established mangrove forests and those with suitable environmental conditions.

Up to nine estuaries that currently support mangroves in this region were predicted to become unsuitable by 2050 (Table S1). These are mostly small-sized to medium-sized systems and are located from the middle to the edge of the distribution range. Range edges have been characterised by genetic isolation and variability in individual and population fitness in comparison to core locations within a species' distribution. Limited gene flow has been recorded for southern African edge populations of *A. marina* compared to core populations in East Africa (De Ryck et al., 2016). The potential for reduced genetic diversity to constrain adaptation at range limits has been tested for *A. germinans* across the Atlantic coast of its distribution in the United States where it is limited by freeze events and winter temperature minima (Kennedy et al., 2020). Here reduced genetic variation did not constrain functional trait variation, as *A. germinans* occurring at range limits exhibited functional traits that were better adapted for cold tolerance. In comparison, at the southern African range limit, MAR was found to be the variable that contributes most to explaining model fit and variability in the 2050 projection models. Estimates for MAR in 2050 were derived from predicted changes in precipitation under the RCP4.5 and 8.5 scenarios, indicating the importance of rainfall in determining habitat suitability for mangroves under climate change (Gabler et al., 2017). In the quantitative model, MAR interacts with floodplain area to influence daily flushing rate which, in turn, impacts the state of the estuary mouth as open or closed as the interplay between nearshore energy as well as tidal and fluvial mechanisms determines whether an estuary is wave dominated or tide dominated (Raw, Godbold, et al., 2019). Changes in MAR under climate change due to increases or decreases in predicted rainfall will influence the suitability of estuaries for mangroves by changing freshwater availability, but also flushing rates that could either drive erosion or promote open mouth conditions, thus facilitating mangrove establishment (Adams & Rajkaran, 2021).

It is therefore unlikely that *A. marina* populations at the southern African range limit could adapt to these environmental changes that are predicted to make habitats unsuitable by 2050. Loss of mangrove forests in this region would lead to fragmentation of the distribution range, further loss in already limited connectivity, and thus the possibility for a contraction in the range limit. As mangroves are valued for their biodiversity contribution in South Africa, management approaches need to focus on preventing further degradation to extant forests in light of the existing pressures on these ecosystems (Adams & Rajkaran, 2021).

4.2 | Broader applications of the method

Understanding regional drivers of range expansions is important as these collectively influence global-scale distribution patterns. For mangroves, the potential for range expansion is variable between different range limits, depending on which factors control regional and local distributions (Hickey et al., 2017). Global mangrove range limits that are directly controlled by rainfall thresholds occur in semi-arid and arid biogeographical regions in northwest Africa, east-central Africa, west-central Africa, the Middle East, western Australia, western North America, western Gulf of Mexico and western South America (Osland et al., 2017). However, this study has demonstrated that the potential for mangrove range expansion under climate change is more complex than simple extrapolation to new locations based on changing environmental conditions. Fundamental niches may not be realised due to local factors and processes, and these should be taken into account when interpreting SDMs. For example, recent work to compare the physiological limits of mangrove propagules to climatic conditions at their range limits on both the Atlantic and Pacific coasts of North America found contrasting results between species and locations (*A. germinans* and *Rhizophora mangle* L.; Bardou et al., 2021).

There are multiple methods and approaches for modelling species distributions, many of which have been applied to mangroves to understand their occurrence patterns and potential distributions under climate change (Clarke, 2014). These include BIOMOD which uses presence/absence values and binomial variance (Record et al., 2013), or other statistical approaches that incorporate generalised linear models (Quisthoudt et al., 2013) or generalised additive models (Rioja-Nieto et al., 2017). MaxEnt has been more widely adopted since it was released as open-source software in 2017, along with an accompanying package (maxnet) to perform the analyses on the R statistical platform as an alternative (Phillips et al., 2017). This approach has since been quickly adopted for mangrove research and has been used for example to (i) identify areas for conservation and reforestation of mangroves (Hu et al., 2020), (ii) simulate impacts of climate change on mangrove forest inventories (John et al., 2020), and (iii) examine habitat suitability for mangrove plantation initiatives (Forouzannia & Chamani, 2022). Spatial data for mangroves and accompanying environmental data are generally available, and as these ecosystems are increasingly recognised for their multiple valuable benefits, MaxEnt provides researchers with an easily accessible tool for addressing a variety of distribution-related research questions.

MaxEnt is also a preferred option because the software provides a straightforward interface for use and it has been shown to have a greater predictive accuracy than other methods (Merow

et al., 2013). However, when using MaxEnt, it is important to (1) select appropriate evaluation data, (2) assess model fit and (3) apply the appropriate settings to optimise model complexity (Radosavljevic & Anderson, 2014). In this study, we used true presence/absence values for occurrence because only established forests with an area >0.5 ha were considered. Our occurrence locations were based on mapped habitat areas and therefore represent an unbiased sampling approach. Using the default configuration of MaxEnt can lead to non-optimal models which provide inaccurate estimates of the size and location of suitable areas (Morales et al., 2017). Model complexity needs to be optimised to appropriately assess variable importance and to produce a robust model that can be projected to different conditions or time periods. To assess model fit and optimise model complexity, we adjusted the configuration settings in MaxEnt to align with predefined relationships between the input environmental variables. This approach provided a robust initial model for subsequent projections. Including the dispersal model in our approach has also addressed an important gap that is prevalent in SDMs by incorporating an aspect of the realised niche as only areas that can be accessed are considered to be available (Soberón & Peterson, 2005). These constraints on mangrove distribution and propagule dispersal should be considered at other range limit locations with complex coastal geomorphological and hydrodynamic settings when making regional or global-scale comparisons on the potential for range expansions.

4.3 | Future research

Future research could consider other local-scale drivers or controls on mangrove occurrence that could also be incorporated to refine SDMs for mangroves if sufficient data are available. These could include site-specific environmental conditions, such as sediment characteristics, as well as geomorphic settings such as intertidal gradients, accommodation space and surface elevation. Other components of the realised niche could also be included, such as biotic interactions (potential facilitation or competition with salt marsh vegetation, or predation of propagules by crabs), as well as site-specific environmental conditions (sediment or nutrient properties). This information should also be related to propagule recruitment and survival success for dominant species in the region. Field studies are needed to document the distribution and abundance of mangrove propagules that strand along unsuitable stretches of the coast—including sandy beaches and rocky shores. Other climate change impacts could also be considered for projected SDMs. Sea-level rise or an increase in sea storms could influence areas available within estuaries for mangrove establishment, as well as estuary mouth dynamics. Current estimates of sea-level rise for the east coast of the country are +2.74 mm. $year^{-1}$, and preliminary data from in situ measurements of surface elevation change at specific sites indicate mangroves could be responding and keeping pace with current rates, but more long-term data are needed to properly assess this trend. Mangroves are also expected to be impacted by sea-level rise indirectly as a result of coastal squeeze as many estuaries have incised floodplains. In comparison, an increase in CO_2 would favour mangrove growth and productivity and although temperature does not define the South African distribution limit for the mangrove ecotype, it is possible that increased temperature with climate change could allow for more typically tropical mangrove species to expand their ranges further south. However, their potential for dispersal and recruitment would be under the same physical and environmental constraints.

Global climate change projections for the east coast of South Africa include an increased intensity and frequency of extreme storms. Within this region, coastal storms caused by cut-off low pressure systems have coincided with equinox spring high tides and the astronomical tidal cycle to create significant wave events (average wave heights of 8.5 m, peaking at 14 m; Smith et al., 2007). The region is also periodically exposed to tropical cyclones that form in the Mozambique channel. However, the relatively constricted mouths of most South African estuaries provide some protection against direct impacts of coastal storms and cyclones. While previous events have had some detrimental effects on mangroves, they could possibly facilitate dispersal to new locations to some degree.

In addition to the impacts of climate change, mangroves also face anthropogenic pressures in this region. Adams and Rajkaran (2021) provided a recent assessment on the state of mangroves in South Africa and found that both direct pressures (land-use change, harvesting, cattle browsing) and indirect pressures (increased freshwater abstraction, pollution) are escalating. While large losses of mangrove habitat occurred with the development of the port at Durban Bay (the busiest shipping terminal in southern Africa, and the fourth largest container terminal in the southern hemisphere), the greatest increases in mangrove area have occurred at uMhlathuze Estuary following the development of the port at Richards Bay—as a result of increased tidal range. Smaller mangrove forests have been irreversibly lost following construction of roads and bridges across estuary inlets. Mangrove forests are considered a rare and an indigenous forest type in South Africa and are therefore protected under the National Forests Act (No. 84 of 1998). However, most mangroves are not within formal protected areas, and different approaches towards their management, such as stewardship programmes, are likely to yield better results in reducing the pressures on these ecosystems. Rural areas also require different management approaches (e.g. community-based monitoring, payment for ecosystem services) from urban areas that can largely be controlled through formal protection or estuary management plans that focus on zonation.

5 | CONCLUSIONS

In conclusion, studies that predict range expansions of mangroves are important given the increasing global awareness of the multiple

key ecosystem services that they provide. As we have demonstrated, predicting changes in mangrove distribution can be far more complex than what can be interpreted from SDMs alone. Although studies, including ours, indicate there is suitable habitat beyond the current range limit in southern Africa, much of this habitat is not actually accessible due to limitations in dispersal and connectivity between estuaries with established forests and those with suitable areas. Consequently, there seems to be limited potential for range expansion along the east coast of southern Africa. We therefore encourage those predicting mangrove range extensions in other regions to take cognisance of additional factors like dispersal and climate change interactions because it may alter the outputs substantially. Furthermore, by applying our novel combination of methods, it can help to prioritise which estuaries and associated mangrove forests are important to safeguard through appropriate conservation, restoration and management measures. These measures would give mangroves the best possible chance of expanding their ranges naturally in response to climate change.

AUTHOR CONTRIBUTIONS

Jacqueline L. Raw, Tom Van der Stocken and Janine B. Adams conceived the ideas and formulated the overarching research aims of the study. Jacqueline L. Raw, Tom Van der Stocken, Dustin Carroll and Linda R. Harris developed and designed the methodology and created the models that have been applied. Jacqueline L. Raw, Tom Van der Stocken and Dustin Carroll conducted the formal statistical and computational analyses of the data. Jacqueline L. Raw, Anusha Rajkaran, Lara Van Niekerk and Janine B. Adams contributed to the research investigation process through data collection, collation and curation. Jacqueline L. Raw, Tom Van der Stocken and Dustin Carroll created the data visualisations. Jacqueline L. Raw and Tom Van der Stocken led the writing of the original draft, all authors contributed critically to the drafts and gave final approval for submission of the paper for publication.

ACKNOWLEDGEMENTS

The authors thank the reviewers and associate editor for their valuable and helpful comments on this manuscript. This research received funding from the Water Research Commission (WRC) of South Africa (Project K5/2769), the South African Department of Science and Innovation (DSI)—National Research Foundation (NRF) Research Chair in Shallow Water Ecosystems (UID: 84375), and the Nelson Mandela University. High-end computing resources were provided by the NASA Advanced Supercomputing (NAS) Division of the Ames Research Center. J.L.R. is supported by a DSI-NRF Innovation Postdoctoral Fellowship (UID: 120701). T.V.d.S. is supported by the EU Horizon 2020 Framework Programme for Research and Innovation under the Marie Skłodowska-Curie actions Individual Fellowship (MSCA-IF) with grant agreement No. 896888 (GLOMAC). L.V.N. is supported by the DSI-CSIR Parliamentary Grant. The funders played no role in the design of the study, collection or analysis of the data, writing the manuscript, or the decision to publish.

CONFLICT OF INTEREST

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The mangrove occurrence data presented in this manuscript are available from the South African National Estuarine Botanical Database hosted by the South African National Biodiversity Institute (SANBI): http://bgis.sanbi.org/SpatialDataset/Detail/2687 (Adams, 2019). The estuarine environmental data used in the MaxEnt models were extracted from Van Niekerk et al. (2017) and Engelbrecht et al. (2019). These data, along with the final results from the MaxEnt models, are available for download from the Dryad Data Repository https://doi.org/10.5061/dryad.4qrfj6qd7 Raw (2022).

ORCID

Jacqueline L. Raw https://orcid.org/0000-0002-5270-032X
Tom Van der Stocken https://orcid.org/0000-0002-1820-9123
Dustin Carroll https://orcid.org/0000-0003-1686-5255
Linda R. Harris https://orcid.org/0000-0003-4719-0481
Anusha Rajkaran https://orcid.org/0000-0001-7360-3660
Lara Van Niekerk https://orcid.org/0000-0001-5761-1337
Janine B. Adams https://orcid.org/0000-0001-7204-123X

REFERENCES

Adams, J. B. (2019). South African National Estuarine Botanical Database: Habitats. *SANBI Biodiversity GIS Repository*. http://bgis.sanbi.org/SpatialDataset/Detail/2687

Adams, J. B. (2020). Salt marsh at the tip of Africa: Patterns, processes and changes in response to climate change. *Estuarine, Coastal and Shelf Science*, *237*, 106650. https://doi.org/10.1016/j.ecss.2020.106650

Adams, J. B., & Rajkaran, A. (2021). Changes in mangroves at their southernmost African distribution limit. *Estuarine, Coastal and Shelf Science*, *248*, 107158. https://doi.org/10.1016/j.ecss.2020.107158

Allouche, O., Tsoar, A., & Kadmon, R. (2006). Assessing the accuracy of species distribution models: Prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology*, *43*, 1223–1232. https://doi.org/10.1111/j.1365-2664.2006.01214.x

Araújo, M. B., & Guisan, A. (2006). Five (or so) challenges for species distribution modelling. *Journal of Biogeography*, *33*, 1677–1688. https://doi.org/10.1111/j.1365-2699.2006.01584.x

Bardou, R., Parker, J. D., Feller, I. C., & Cavanaugh, K. C. (2021). Variability in the fundamental versus realized niches of north American mangroves. *Journal of Biogeography*, *48*, 160–175. https://doi.org/10.1111/jbi.13990

Cavanaugh, K. C., Dangremond, E. M., Doughty, C. L., Parker, J. D., Hayes, M. A., Rodriguez, W., & Feller, I. C. (2019). Climate-driven regime shifts in a mangrove–salt marsh ecotone over the past 250 years. *Proceedings of the National Academy of Sciences of the United States of America*, *116*, 21602–21608. https://doi.org/10.1073/pnas.1902181116

Cavanaugh, K. C., Kellner, J. R., Forde, A. J., Gruner, D. S., Parker, J. D., Rodriguez, W., & Feller, I. C. (2014). Poleward expansion of mangroves is a threshold response to decreased frequency of extreme cold events. *Proceedings of the National Academy of Sciences of the United States of America*, *111*, 723–727. https://doi.org/10.1073/pnas.1315800111

Clarke, P. J. (1993). Dispersal of grey mangrove (*Avicennia marina*) propagules in southeastern Australia. *Aquatic Botany*, *45*, 195–204. https://doi.org/10.1016/0304-3770(93)90021-N

Clarke, P. J. (2014). Seeking global generality: A critique for mangrove modellers. *Marine and Freshwater Research*, *65*, 930–933. https://doi.org/10.1071/MF13326

De Ryck, D. J. R., Koedam, N., Van der Stocken, T., van der Ven, R. M., Adams, J. B., & Triest, L. (2016). Dispersal limitation of the mangrove *Avicennia marina* at its south African range limit in strong contrast to connectivity in its core east African region. *Marine Ecology Progress Series*, *545*, 123–134. https://doi.org/10.3354/meps11581

Diop, E. S., Gordon, C., Semesi, A. K., Soumaré, A., Diallo, N., Guissé, A., Diouf, M., & Ayivor, J. S. (2002). Mangroves of Africa. In L. D. de Lacerda (Ed.), *Mangrove ecosystems: Function and management. Environmental science* (pp. 63–121). Springer. https://doi.org/10.1007/978-3-662-04713-2_2

Duarte, C. M., Losada, I. J., Hendriks, I. E., Mazarrasa, I., & Marbà, N. (2013). The role of coastal plant communities for climate change mitigation and adaptation. *Nature Climate Change*, *3*, 961–968. https://doi.org/10.1038/nclimate1970

Duke, N. C., Ball, M. C., & Ellison, J. C. (1998). Factors influencing biodiversity and distributional gradients in mangroves. *Global Ecology and Biogeography Letters*, *7*, 27–47. https://doi.org/10.1111/j.1466-8238.1998.00269.x

Elith, J., Phillips, S. J., Hastie, T., Dudík, M., Chee, Y. E., & Yates, C. J. (2011). A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*, *17*, 43–57. https://doi.org/10.1111/j.1472-4642.2010.00725.x

Engelbrecht, F., Le Roux, A., Arnold, K., & Malherbe, J. (2019). *Detailed projections of future climate change over South Africa*. CSIR. https://pta-gis-2-web1.csir.co.za/portal/apps/GBCascade/index.html?appid=b161b2f892194ed5938374fe2192e537

Forouzannia, M., & Chamani, A. (2022). Mangrove habitat suitability modelling: Implications for multi-species plantation in an arid estuarine environment. *Environmental Monitoring and Assessment*, *194*, 552. https://doi.org/10.1007/s10661-022-10194-6

Freeman, E. A., & Moisen, G. (2008). PresenceAbsence: An R package for presence-absence model analysis. *Journal of Statistical Software*, *23*, 1–31. https://doi.org/10.18637/jss.v023.i11

Gabler, C. A., Osland, M. J., Grace, J. B., Stagg, C. L., Day, R. H., Hartley, S. B., Enwright, N. M., From, A. S., McCoy, M. L., & McLeod, J. L. (2017). Macroclimatic change expected to transform coastal wetland ecosystems this century. *Nature Climate Change*, *7*, 142–147. https://doi.org/10.1038/nclimate3203

Grace, J. B., Schoolmaster, D. R., Guntenspergen, G. R., Little, A. M., Mitchell, B. R., Miller, K. M., & Schweiger, E. W. (2012). Guidelines for a graph-theoretic implementation of structural equation modelling. *Ecosphere*, *3*, 1–44. https://doi.org/10.1890/ES12-00048.1

Harris, L. R., Bessinger, M., Dayaram, A., Holness, S., Kirkman, S., Livingstone, T.-C., Lombard, A. T., Lück-Vogel, M., Pfaff, M., Sink, K. J., Skowno, A. L., & Van Niekerk, L. (2019). Advancing land-sea integration for ecologically meaningful coastal conservation and management. *Biological Conservation*, *237*, 81–89. https://doi.org/10.1016/j.biocon.2019.06.020

Harris, L. R., Nel, R., & Schoeman, D. S. (2011). Mapping beach morphodynamics remotely: A novel application tested on south African sandy shores. *Estuarine, Coastal and Shelf Science*, *92*, 78–89. https://doi.org/10.1016/j.ecss.2010.12.013

Hickey, S. M., Phinn, S. R., Callow, N. J., Niel, K. P. V., Hansen, J. E., & Duarte, C. M. (2017). Is climate change shifting the poleward limit of mangroves? *Estuaries and Coasts*, *40*, 1215–1226. https://doi.org/10.1007/s12237-017-0211-8

Hill, C., Menemenlis, D., Ciotti, B., & Henze, C. (2007). Investigating solution convergence in a global ocean model using a 2048-processor cluster of distributed shared memory machines. *Scientific Programming*, *15*, 107–115.

Hoppe-Speer, S. C. L. (2013). *Response of mangroves in South Africa to anthropogenic and natural impacts. PhD* (p. 191). Nelson Mandela Metropolitan University.

Hoppe-Speer, S. C. L., Adams, J. B., & Rajkaran, A. (2015). Mangrove expansion and population structure at a planted site, East London, South Africa. *Southern Forests*, *77*, 131–139. https://doi.org/10.2989/20702620.2014.1001622

Hu, W., Wang, Y., Dong, P., Zhang, D., Yu, W., Ma, Z., Chen, G., Liu, Z., Du, J., Chen, B., & Lei, G. (2020). Predicting potential mangrove distributions at the global northern distribution margin using an ecological niche model: Determining conservation and reforestation involvement. *Forest Ecology and Management*, *478*, 118517. https://doi.org/10.1016/j.foreco.2020.118517

John, E., Bunting, P., Hardy, A., Roberts, O., Giliba, R., & Silayo, D. S. (2020). Modelling the impact of climate change on Tanzanian forests. *Diversity and Distributions*, *26*, 1663–1686. https://doi.org/10.1111/ddi.13152

Kelleway, J. J., Cavanaugh, K. C., Rogers, K., Feller, I. C., Ens, E., Doughty, C., & Saintilan, N. (2017). Review of the ecosystem service implications of mangrove encroachment into salt marshes. *Global Change Biology*, *23*, 3967–3983. https://doi.org/10.1111/gcb.13727

Kennedy, J. P., Preziosi, R. F., Rowntree, J. K., & Feller, I. C. (2020). Is the central-marginal hypothesis a general rule? Evidence from three distributions of an expanding mangrove species, *Avicennia germinans* (L.) L. *Molecular Ecology*, *29*, 704–719. https://doi.org/10.1111/mec.15365

Lutjeharms, J. R. E. (2007). Three decades of research on the greater Agulhas current. *Ocean Science*, *3*, 129–147. https://doi.org/10.5194/os-3-129-2007

Mbense, S. P., Rajkaran, A., Bolosha, U., & Adams, J. B. (2016). Rapid colonization of degraded mangrove habitat by succulent salt marsh. *South African Journal of Botany*, *107*, 129–136. https://doi.org/10.1016/j.sajb.2016.06.011

Melo-Merino, S. M., Reyes-Bonilla, H., & Lira-Noriega, A. (2020). Ecological niche models and species distribution models in marine environments: A literature review and spatial analysis of evidence. *Ecological Modelling*, *415*, 108837. https://doi.org/10.1016/j.ecolmodel.2019.108837

Menemenlis, D., Campin, J., Heimbach, P., Hill, C., Lee, T., Nguyen, A., Schodlok, M., & Zhang, H. (2008). ECCO2: High resolution Global Ocean and sea ice data synthesis. *AGU Fall Meeting Abstracts*, *31*, OS31C–1292.

Merow, C., Smith, M. J., & Silander, J. A. (2013). A practical guide to MaxEnt for modeling species' distributions: What it does, and why inputs and settings matter. *Ecography*, *36*, 1058–1069. https://doi.org/10.1111/j.1600-0587.2013.07872.x

Morales, N. S., Fernández, I. C., & Baca-González, V. (2017). MaxEnt's parameter configuration and small samples: Are we paying attention to recommendations? A systematic review. *PeerJ*, *5*, e3093. https://doi.org/10.7717/peerj.3093

Morrisey, D. J., Swales, A., Dittmann, S., Morrison, M. A., Lovelock, C. E., & Beard, C. M. (2010). The ecology and management of temperate mangroves. *Annual Review of Oceanography and Marine Biology*, *48*, 43–160.

Murdiyarso, D., Purbopuspito, J., Kauffman, J. B., Warren, M. W., Sasmito, S. D., Donato, D. C., Manuri, S., Krisnawati, H., Taberima, S., & Kunianto, S. (2015). The potential of Indonesian mangrove forests for global climate change mitigation. *Nature Climate Change*, *5*, 1089–1092. https://doi.org/10.1038/nclimate2734

Nathan, R., Schurr, F. M., Spiegel, O., Steinitz, O., Trakhtenbrot, A., & Tsoar, A. (2008). Mechanisms of long-distance seed dispersal. *Trends in Ecology & Evolution*, *23*, 638–647. https://doi.org/10.1016/j.tree.2008.08.003

Oh, R. R., Friess, D. A., & Brown, B. M. (2017). The role of surface elevation in rehabilitation of abandoned aquaculture ponds to mangrove forests, Sulawesi, Indonesia. *Ecological Engineering*, *100*, 325–334. https://doi.org/10.1016/j.ecoleng.2016.12.021

Osland, M. J., Enwright, N., Day, R. H., & Doyle, T. W. (2013). Winter climate change and coastal wetland foundation species: Salt

marshes vs. mangrove forests in the southeastern United States. *Global Change Biology*, *19*, 1482–1494. https://doi.org/10.1111/gcb.12126

Osland, M. J., Enwright, N. M., Day, R. H., Gabler, C. A., Stagg, C. L., & Grace, J. B. (2016). Beyond just sea-level rise: Considering macroclimatic drivers within coastal wetland vulnerability assessments to climate change. *Global Change Biology*, *22*, 1–11. https://doi.org/10.1111/gcb.13084

Osland, M. J., Feher, L. C., Griffith, K. T., Cavanaugh, K. C., Enwright, N. M., Day, R. H., Stagg, C. L., Krauss, K. W., Howard, R. J., Grace, J. B., & Rogers, K. (2017). Climatic controls on the global distribution, abundance, and species richness of mangrove forests. *Ecological Monographs*, *87*, 341–359. https://doi.org/10.1002/ecm.1248

Osland, M. J., Hughes, A. R., Armitage, A. R., Scyphers, S. B., Cebrian, J., Swinea, S. H., Shepard, C. C., Allen, M. S., Feher, L. C., Nelson, J. A., O'Brien, C. L., Sanspree, C. R., Snyder, C. M., Stetter, A. P., Stevens, P. W., Swanson, K. M., Williams, L. H., Brush, J. M., Marchionno, J., & Bardou, R. (2022). The impacts of mangrove range expansion on wetland ecosystem services in the southeastern United States: Current understanding, knowledge gaps, and emerging research needs. *Global Change Biology*, *28*, 3163–3187. https://doi.org/10.1111/gcb.16111

Peterson, A. T., Papeş, M., & Soberón, J. (2015). Mechanistic and correlative models of ecological niches. *European Journal of Ecology*, *1*, 28–38. https://doi.org/10.1515/eje-2015-0014

Phillips, S. J., Anderson, R. P., Dudík, M., Schapire, R. E., & Blair, M. E. (2017). Opening the black box: An open-source release of Maxent. *Ecography*, *40*, 887–893. https://doi.org/10.1111/ecog.03049

Phillips, S. J., Dudík, M., & Schapire, R. E. (2019). *Maxent software for modeling species niches and distributions* (Version 3.4.1). https://biodiversityinformatics.amnh.org/open_source/maxent/

Quisthoudt, K., Adams, J. B., Rajkaran, A., Dahdouh-Guebas, F., Koedam, N., & Randin, C. (2013). Disentangling the effects of global climate and regional land-use change on the current and future distribution of mangroves in South Africa. *Biodiversity and Conservation*, *22*, 1369–1390. https://doi.org/10.1007/s10531-013-0478-4

R Core Team. (2020). *R: A language and environment for statistical computing (3.6.3) [computer software]*. R Foundation for Statistical Computing. https://www.R-project.org/

Radosavljevic, A., & Anderson, R. P. (2014). Making better Maxent models of species distributions: Complexity, overfitting and evaluation. *Journal of Biogeography*, *41*, 629–643. https://doi.org/10.1111/jbi.12227

Raw, J. L. (2022). Dispersal and coastal geomorphology limit potential for mangrove range expansion under climate change. *Dryad*, *Digital Repository*. https://doi.org/10.5061/dryad.4qrfj6qd7

Raw, J. L., Godbold, J. A., Van Niekerk, L., & Adams, J. B. (2019). Drivers of mangrove distribution at the high-energy, wave-dominated, southern African range limit. *Estuarine*, *Coastal and Shelf Science*, *226*, 106296. https://doi.org/10.1016/j.ecss.2019.106296

Raw, J. L., Julie, C. L., & Adams, J. B. (2019). A comparison of soil carbon pools across a mangrove-salt marsh ecotone at the southern African warm-temperate range limit. *South African Journal of Botany*, *127*, 301–307. https://doi.org/10.1016/j.sajb.2019.11.005

Record, S., Charney, N. D., Zakaria, R. M., & Ellison, A. M. (2013). Projecting global mangrove species and community distributions under climate change. *Ecosphere*, *4*, 1–23. https://doi.org/10.1890/ES12-00296.1

Rioja-Nieto, R., Barrera-Falcón, E., Torres-Irineo, E., Mendoza-González, G., & Cuervo-Robayo, A. (2017). Environmental drivers of decadal change of a mangrove forest in the north coast of the Yucatan peninsula, Mexico. *Journal of Coastal Conservation*, *21*, 167–175. https://doi.org/10.1007/s11852-016-0486-0

Roy, P. S., Williams, R. J., Jones, A. R., Yassini, I., Gibbs, P. J., Coates, B., West, R. J., Scanes, P. R., Hudson, J. P., & Nichol, S. (2001). Structure and function of south-east Australian estuaries. *Estuarine*, *Coastal and Shelf Science*, *53*, 351–384. https://doi.org/10.1006/ecss.2001.0796

Saintilan, N., Wilson, N. C., Rogers, K., Rajkaran, A., & Krauss, K. W. (2014). Mangrove expansion and salt marsh decline at mangrove poleward limits. *Global Change Biology*, *20*, 147–157. https://doi.org/10.1111/gcb.12341

Schaeffer-Novelli, Y., Cintrón-Molero, G., Adaime, R. R., & de Camargo, T. M. (1990). Variability of mangrove ecosystems along the Brazilian coast. *Estuaries*, *13*, 204–218. https://doi.org/10.2307/1351590

Schumann, E. H., MacKay, C. F., & Strydom, N. A. (2019). Nurdle drifters around South Africa as indicators of ocean structures and dispersion. *South African Journal of Science*, *115*, 1–9. https://doi.org/10.17159/sajs.2019/5372

Serrano, O., Lovelock, C. E., Atwood, T. B., Macreadie, P. I., Canto, R., Phinn, S., Arias-Ortiz, A., Bai, L., Baldock, J., Bedulli, C., Carnell, P., Connolly, R. M., Donaldson, P., Esteban, A., Lewis Ewers, C. J., Eyre, B. D., Hayes, M. A., Horwitz, P., Hutley, L. B., … Duarte, C. M. (2019). Australian vegetated coastal ecosystems as global hotspots for climate change mitigation. *Nature Communications*, *10*, 4313. https://doi.org/10.1038/s41467-019-12176-8

Smith, A., Guastella, L., Bundy, S., & Mather, A. A. (2007). Combined marine storm and saros spring high tide erosion events along the KwaZulu-Natal coast in march 2007. *South African Journal of Science*, *103*, 274–276. https://doi.org/10.10520/EJC96710

Soberón, J., & Peterson, A. T. (2005). Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodiversity Informatics*, *2*, 1–10. https://doi.org/10.17161/bi.v2i0.4

Steinke, T. D. (1986). A preliminary study of buoyancy behaviour in *Avicennia marina* propagules. *South African Journal of Botany*, *52*, 559–565. https://doi.org/10.1016/S0254-6299(16)31492-2

Steinke, T. D., & Charles, L. M. (1986). Litter production by mangroves. I: Mgeni estuary. *South African Journal of Botany*, *52*, 552–558. https://doi.org/10.1016/S0254-6299(16)31491-0

Steinke, T. D., & Ward, C. J. (1988). Litter production by mangroves. II. St Lucia and Richards Bay. *South African Journal of Botany*, *54*(5), 445–454. https://doi.org/10.1016/S0254-6299(16)31276-5

Steinke, T. D., & Ward, C. J. (1990). Litter production by mangroves. III. Wavecrest (Transkei) with predictions for other Transkei estuaries. *South African Journal of Botany*, *56*, 514–519. https://doi.org/10.1016/S0254-6299(16)31017-1

Steinke, T. D., & Ward, C. J. (2003). Use of plastic drift cards as indicators of possible dispersal of propagules of the mangrove *Avicennia marina* by ocean currents. *African Journal of Marine Science*, *25*, 169–176. https://doi.org/10.2989/18142320309504007

Taylor, R. H. (2016). Dynamics of the macrophyte vegetation of the Mgobezeleni floodplain and estuary, northern KwaZulu-Natal. *South African Journal of Botany*, *107*, 170–178. https://doi.org/10.1016/j.sajb.2016.08.022

Triest, L., Van der Stocken, T., Sierens, T., Deus, E. K., Mangora, M. M., & Koedam, N. (2021). Connectivity of *Avicennia marina* populations within a proposed marine transboundary conservation area between Kenya and Tanzania. *Biological Conservation*, *256*, 109040. https://doi.org/10.1016/j.biocon.2021.109040

Van der Stocken, T., Carroll, D., Menemenlis, D., Simard, M., & Koedam, N. (2019). Global-scale dispersal and connectivity in mangroves. *Proceedings of the National Academy of Sciences of the United States of America*, *116*, 915–922. https://doi.org/10.1073/pnas.1812470116

Van Niekerk, L., Adams, J. B., James, N. C., Lamberth, S. J., MacKay, C. F., Turpie, J. K., Rajkaran, A., Weerts, S. P., & Whitfield, A. K. (2020). An estuary ecosystem classification that encompasses biogeography and a high diversity of types in support of protection and management. *African Journal of Aquatic Science*, *45*, 199–216. https://doi.org/10.2989/16085914.2019.1685934

Van Niekerk, L., Taljaard, S., Ramjukadh, C.-L., Adams, J. B., Lamberth, S. J., Weerts, S. P., Petersen, C., Audouin, M., & Maherry, A. (2017). *A multi-sector resource planning platform for South Africa's estuaries*. (Water Research Commission Report K5/2464). Water Research Commission.

Whitfield, A. K., James, N. C., Lamberth, S. J., Adams, J. B., Perissinotto, R., Rajkaran, A., & Bornman, T. G. (2016). The role of pioneers as indicators of biogeographic range expansion caused by global change in southern African coastal waters. *Estuarine, Coastal and Shelf Science*, *172*, 138–153. https://doi.org/10.1016/j.ecss.2016.02.008

Whitt, A. A., Coleman, R., Lovelock, C. E., Gillies, C., Ierodiaconou, D., Liyanapathirana, M., & Macreadie, P. I. (2020). March of the mangroves: Drivers of encroachment into southern temperate saltmarsh. *Estuarine, Coastal and Shelf Science*, *240*, 106776. https://doi.org/10.1016/j.ecss.2020.106776

Ximenes, A. C., Ponsoni, L., Lira, C. F., Koedam, N., & Dahdouh-Guebas, F. (2018). Does sea surface temperature contribute to determining range limits and expansion of mangroves in eastern South America (Brazil)? *Remote Sensing*, *10*, 1787. https://doi.org/10.3390/rs10111787

Yando, E. S., Jones, S. F., & Hester, M. W. (2021). Limited mangrove propagule retention at a latitudinal range limit: Spatiotemporal patterns at the patch scale. *Estuaries and Coasts*, *44*, 834–845. https://doi.org/10.1007/s12237-020-00805-1

SUPPORTING INFORMATION

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

How to cite this article: Raw, J. L., Van der Stocken, T., Carroll, D., Harris, L. R., Rajkaran, A., Van Niekerk, L., & Adams, J. B. (2023). Dispersal and coastal geomorphology limit potential for mangrove range expansion under climate change. *Journal of Ecology*, *111*, 139–155. https://doi.org/10.1111/1365-2745.14020