

Disentangling the effects of global climate and regional land-use change on the current and future distribution of mangroves in South Africa

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Abstract The mangrove distribution in South Africa is fragmented and restricted to small forest patches occupying only 16 % of the estuaries within the current range. In this study we used species distribution models to test (1) whether the absence of mangrove forest and its species (*Avicennia marina*, *Bruguiera gymnorrhiza* and *Rhizophora mucronata*) within their current range is driven by climate or by climate combined with human or geomorphic perturbation and (2) how climate change may potentially affect the latitudinal limit of the mangrove forests and its species in South Africa. We used three modelling techniques (generalized linear models, generalized additive models and gradient boosting machines) and a set of three climate-based predictive variables (minimum air temperature of the coldest month, waterbalance and growing-degree days) combined separately with an index of human or geomorphic perturbation. Climate variables for the future projections were derived from two general circulation models driven by two socio-economic scenarios (A2a

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and B2a). Within the range of the mangrove forest, the fragmented distribution of the mangroves in South Africa was not explained by our set of climate variables alone. The index of human perturbations slightly improved the predictions but the index of geomorphic perturbation did not. Climate change will create climatically suitable sites for the mangrove forest and the two species *A. marina* and *B. gymnorhiza* beyond their current limits, but model outcomes did not agree on the future potential distribution of *R. mucronata*. We were able to successfully predict range limits and to detect future climatically suitable sites beyond the current limits. Factors controlling mangrove distribution within its range are still to be identified although absences were partly explained by human perturbations.

Keywords Global change · Climate change · Human land use · Geomorphology · Cold edge · Latitude

Introduction

Mangroves are intertidal forests that are widely distributed along the coastlines of mainly tropical regions (Tomlinson 1986). Mangroves have a high rate of primary productivity and provide important ecological services such as food, nesting and nursery ground for many marine organisms, improved access to safe water and sanitation, protection against environmental stresses, carbon sequestration and goods for the surrounding human populations (Moberg and Ronnback 2003; Barbier 2007; Walters et al. 2008; Feagin et al. 2010; Barbier et al. 2011; Donato et al. 2011; Gedan et al. 2011; McLeod et al. 2011; Hopkins et al. 2012). Habitat change and destruction are so far the most important direct drivers of change in biodiversity and ecosystems (Millennium-Assessment 2005). In this context, mangrove forests are cleared for aquaculture and urbanization and indirectly deteriorate by pollution and upstream human activities. Collectively, these factors are currently causing their disappearance at a rate of 1–2 % per year (Duke et al. 2007). Climate change is an increasing threat to biodiversity and ecosystems worldwide and changes in temperature and precipitation patterns are expected to affect mangrove forest distribution (Gilman et al. 2008). Where rainfall decreases and evaporation increases, drought stress will increase, thus decreasing net primary productivity, growth and seedling survival. Under warmer conditions, mangrove ranges might expand to higher latitudes, where the range edges are limited by temperature but not by other factors, such as supply of propagules (Duke et al. 1998; Gilman et al. 2008). Therefore it is now urgent to provide reliable and robust spatial assessments of changes in distribution of mangrove forests driven by human land use and changing climate.

Range limits of plant species are primarily shaped by the direct relationships between environmental factors and individuals of a species and climate is the main driver of species distributions (Woodward and Williams 1987; Boucher-Lalonde et al. 2012). Mangroves have a very wide latitudinal extent and one of its genera, *Avicennia*, is the only one that shows some tolerance to frost (recorded down to -4 and -6.7 °C, Stevens et al. 2006) and yet, most latitudinal limits of *Avicennia* are completely frost-free. Therefore, frost is not a major driver of the mangrove distribution. Recently and in contrast to the conclusions of earlier studies (Macnae 1963; Chapman 1977; Barth 1982; Woodroffe and Grindrod 1991; Duke et al. 1998), Quisthoudt et al. (2012) found that temperature-based parameters at the latitudinal limits of the two dominant and widespread mangrove genera *Avicenna* and *Rhizophora* can be highly variable. Hence, temperature alone cannot explain the current

distribution of the mangroves. Aridity could be the second most important climate factor as it has been shown that mangroves require higher temperatures at latitudinal limits in extremely arid conditions than at other latitudinal limits (Quisthoudt et al. (2013, submitted for publication)). Historical contingency also shapes biogeographical ranges. Short- or long-term historical factors may indeed affect mangrove species ranges because of environmental changes: (1) locations are subjected to changes in geomorphology, climate and other abiotic factors through time and (2) environmental requirements can change throughout the evolution of the clades (Sax 2001; Morin et al. 2007; Pearman et al. 2008a). Disturbance-related factors (sensu Guisan and Thuiller 2005) such as wind, coastal hydrology (wave energy and tidal system) and coastal geomorphology (topography, substrate type and soil conditions including salinity and indirect effects on nutrient levels) and dispersal barriers can also locally limit the mangrove distribution. Limits of *Rhizophora* at lower latitudes due to unsuitable geomorphological settings further polewards or dispersal barriers have been reported in Japan, Mauritania, Bermuda, West-Mexico and Peru, and of *Avicennia*, in Japan and Bermuda (Sherrod and McMillan 1985; Quisthoudt et al. (2013, submitted for publication)).

In such context, mangrove forests of South Africa constitute an ideal regional study system. In South Africa, the mangrove distribution is an ensemble of fragmented, small forest patches restricted to estuaries, due to coastal geomorphology and wave action, from the border of Mozambique (26.9°S) to the southern latitudinal limit in Kobonqaba (32.6°S) (Steinke 1999; Adams et al. 2004). Along this 800 km long coastline, mangroves occur in only one-fifth of the 120 estuaries (Adams et al. 2004; Rajkaran et al. 2009; Van Niekerk and Turpie 2012). At least since 1982, mangroves have not colonized other estuaries (Adams et al. 2004; Rajkaran et al. 2009; Rajkaran 2011), although dispersal is physically possible, because we found viable mangrove propagules at estuaries without mangroves along the South African coastline. This fragmented distribution pattern makes the mangroves highly vulnerable: one extreme event (e.g. sea storm causing estuarine mouth closure and prolonged inundation of intertidal areas) can cause the loss of mangroves in a whole estuary. Since 1982, >40 % of the estuaries with mangroves in South Africa have lost their mangroves, resulting in only 24 estuaries with mangroves today (Adams et al. 2004; Rajkaran et al. 2009). Recently, the majority of the mangrove forest in Kobonqaba (Adams et al. 2010) and Bulungula Estuaries (32.1°S, Adams et al. 2004) disappeared due to a long term drowning event when the river mouths closed and the water level had rose above the pneumatophores. Temporarily closed river mouths are a common geomorphic perturbation in the South African estuaries. Studies in South Africa have shown that mangroves are intolerant of long-term inundation i.e. between 5 and 8 months (Breen and Hill 1969; Bruton 1980). More than 70 % of South Africa's estuaries are temporarily closed to the sea (Van Niekerk and Turpie 2012). Besides drowning, other processes that lead to (partial) loss of mangrove forests are siltation, harvesting, cattle (browsing and trampling) and infrastructure constructions (Rajkaran et al. 2009; Rajkaran and Adams 2010).

Species distribution models (hereafter referred to as 'SDMs') are powerful tools used to predict current and future potential distribution of species by relating environmental information with species' observations (Guisan and Thuiller 2005; Elith and Graham 2009). When compared to mechanistic and process-based models (e.g. TreeMig; Lischke et al. 2006), SDMs can provide faster and more cost-efficient assessments of potential species range changes. They can also be used for developing and testing theories (Shmueli 2010). However, the validity of SDM outputs relies on the assumption that a species' distribution limit is at equilibrium with the current climate (Guisan and Zimmermann 2000; Pearson and Dawson 2003). Species-climate equilibrium occurs when the

geographic observed species limit coincides with the potential species limit in the environmental space defined by the climatic niche (see Svenning and Skov 2004; Randin et al. 2013). Thus, plant species should be first in equilibrium with the current climate conditions in order to keep pace with future climate change. As a consequence, species that are not in equilibrium with the current climate conditions are most likely to be at risk and this can be detected by inconsistent model predictions (Araujo and Pearson 2005).

In this study, by using for the first time a set of SDM-based analyses with mangrove species at the regional scale, we investigated whether absences of mangrove species in >80 % of the estuaries within their current observed distribution ranges could be best explained by climate alone or by climate combined with human or geomorphic perturbations. We then assessed how climate change over the 21st century may potentially affect the current southern latitudinal limits of the mangrove forest and its associated species in South Africa as temperature will increase and precipitation patterns will change.

More specifically, we hypothesize here that:

H₁ If climate-based SDMs fail to predict accurately absences of mangrove forest and its species within their observed ranges, absences might be alternatively explained by either human-driven or geomorphic perturbations. Incorporating these two types of perturbations into climatically driven SDMs could therefore improve model predictions.

H₂ SDMs projections under climate change for the end of the 21st century forecast suitable areas for mangrove species beyond their current southern latitudinal limits in South Africa.

Methods

Study area and species dataset

The study area contained all 154 estuaries along the east coast of South Africa from 27°S to 34°S (Fig. 1). Today, the mangrove distribution is restricted to 24 estuaries. In 1982, there were 38 estuaries with mangroves as described by Steinke (1999). Changes in this distribution are reported by Adams et al. (2004) and Rajkaran et al. (2009) and allowed us to compile the mangrove distribution of 2011. In a first step, we modelled the distribution of the mangrove forest, restricted to the 24 estuaries. By doing this, we aimed at providing an assessment of the factors influencing the geographic distribution and changes of distribution at the level of mangrove communities. Secondly, we considered only the distribution of the most important tree species of mangrove forests. Six mangrove species have been initially identified in South Africa. In this study we focused on three species, *Avicennia marina*, *Rhizophora mucronata* and *Bruguiera gymnorhiza* (L.), because the other three species (*Ceriops tagal*, *Xylocarpus granatum* and *Lumnitzera racemosa*) have a very restricted geographic distribution in Kosi Bay, near the border with Mozambique. *A. marina*, *B. gymnorhiza* and *R. mucronata* are present in 21, 21 and 11 estuaries respectively. The following information has been digitized in the ArcGIS software (ESRI 2006) to extract the mangrove forest and mangrove species occurrences. Mangroves in South Africa are restricted to estuaries because the wave action along the South African coast is high and mangroves can only grow in low-energy tidal settings. Therefore we sampled absences in all the estuaries without mangroves and not the whole coastline. The grid size is 30 arc seconds resulting in a dataset of 1,106 pixels

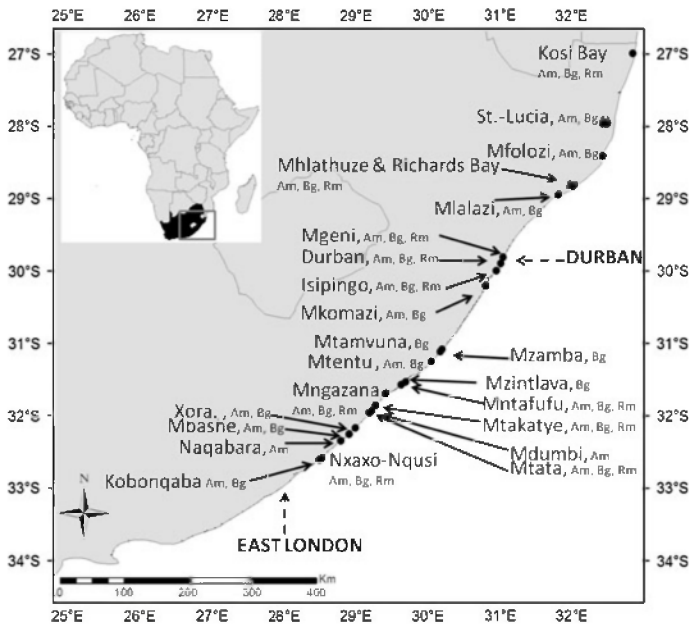


Fig. 1 Geographic location of the study area along the East Coast of South Africa (adapted from Steinke 1999; Adams et al. 2004; Rajkaran 2011). Estuaries with mangroves are named and indicated with *black dots*. The three common mangrove species of South-Africa are *Avicennia marina* (Am), *Bruguiera gymnorhiza* (Bg) and *Rhizophora mucronata* (Rm)

(see online resource 1 in electronic supplementary material for more details of the species dataset).

Model variables and model calibration

The following three climate variables were used for model calibration: (1) minimum temperature of the coldest month (TMIN), (2) growing-degree days (GDD) and (3) water balance (WBAL, see online resource 2 for calculation formula of GDD and WBAL). The TMIN is a proxy for extreme low winter temperatures that can cause direct damage to mangrove trees by chilling or freezing whereas GDD is a proxy for the period during which the species can grow and complete its lifecycle. Both TMIN and GDD are expected to be the main regulators (see Austin and Heyligers 1989 for terminology) at the high latitudinal limits (Sakai and Larcher 1987; Prentice et al. 1992) whereas WBAL is a proxy for relative humidity. Low relative humidity causes similar water stress as high soil salinity (Medina and Francisco 1997). As all mangrove species have the largest part of their distribution in the tropics, we calculated GDD by using a threshold value of 18 °C, which is the temperature that best defines the suitable envelope for tropical climate (Kottek et al. 2006; Peel et al. 2007). WBAL was derived from precipitation (P) and potential evapotranspiration (PET) (see online resource 2 for more details of environmental variable preparation and selection). The three predicting variables were derived from a global raster dataset (Worldclim, spatial resolution 30 arc seconds, Hijmans et al. 2005) adjusted to the period of our sampling by using the CRU TS3.1 climate dataset (Mitchell and Jones 2005). The Worldclim dataset is based on long-term monthly means of temperature and precipitation records for the standard period 1960–1990 (extended

to 1950–2000 when <10 years of observation; Hijmans et al. 2005). Because this time window did not match the more recent period of the mangrove forest inventory, we adjusted for our observation period by calculating anomalies between the period 1960–1999 and the period 1979–2009 for monthly mean temperature and precipitation values of the CRU TS3.1 climatic dataset (source: CRU Time Series high resolution gridded datasets, University of East Anglia Climate Research Unit, NCAS British Atmospheric Data Centre, available on <http://badc.nerc.ac.uk/view/>, spatial resolution: 0.5°, Mitchell and Jones 2005). We finally added these anomalies to the Worldclim climate data, after downscaling them to match with 30 arc seconds spatial resolution with an inverse distance weighted interpolation (polynomial function of order 2) in ArcGIS. Climate projections for the future time periods were obtained from two general circulation models (GCMs), the Hadley Centre Coupled Model v.3 (HadCM3, Carson 1999) and the model of Canadian Centre for Climate Modelling and Analysis (CCCMA, Flato et al. 2000), and based on two different regionally-oriented socio-economic storylines (A2a and B2a) provided by the IPCC (Nakicenovic and Swart 2000). The driving forces in the A2a scenario are a high rate of population growth, increased energy use, land-use changes and slow technological change whereas the B2a scenario contains an evolution towards environmental protection and social equity (IPCC 2007).

We derived a variable reflecting human perturbation based on the health status (explained below) and another variable reflecting geomorphic perturbation based on the river mouth condition of the inventory of the South African estuaries (hereafter designated as HP for the human perturbation index and RMC for the geomorphic perturbation index). This inventory was made by the South African National Spatial Biodiversity Assessment (NSBA) in 2011. The health status gives a score ranging from A (pristine) to F (degraded) to each estuary. This factor is built on the abiotic and biotic circumstances in the estuary (Van Niekerk and Turpie 2012). It is the most recent and complete dataset available on the estuaries of South Africa and it is used in the national policy and management of South African estuaries. We use this health status as a measure of human perturbation assuming that human pressure results in less healthy estuaries. From the same inventory, we derived two classes of RMC: “permanently open” versus “temporarily closed”.

Three different modelling techniques were calibrated using the Biomod package (Thuiller et al. 2009) in R (R 2.14.0, R-Development-Core-Team 2011) with presence/absence values and a binomial variance, using generalized linear models (GLM; McCullagh and Nelder 1989), and generalized additive models (GAM, Hastie and Tibshirani 1986) with a logistic link function and an iterative computer learning algorithm, called the gradient boosting machine (GBM; Ridgeway 1999; Friedman 2001; Ridgeway 2006) (see online resource 3 for more details of the modelling techniques). GLM and GBM have been shown to provide a good transferability of their predictive power in space (Randin et al. 2006) and in time (Pearman et al. 2008b). GAMs have a tendency to overfitting, thus reducing transferability (see Elith et al. 2006 for a detailed discussion on model performance). The predictive power of each model was evaluated through a repeated data-splitting procedure (for details, see Thuiller et al. 2009). A model was trained on 70 % of randomly-selected presences and absences and the predictive power of the models was evaluated on the remaining 30 % using the threshold-independent area under the curve (AUC) of a receiver-operating characteristic plot (ROC; Fielding and Bell 1997) (see online resource 4 for more details of AUC calculation). In order to assess the relevance of each predictor through all considered models, BIOMOD provides a measure of the relative importance of each variable, which is independent of the modelling technique and which is used with a permutation procedure (for more details see the documentation of the BIOMOD package). The variable importance was calculated as one minus the correlation score

between the original prediction and the prediction made with a permuted variable, and ranges between 0 (no importance) and 1 (high importance). After the internal training and evaluation, the outcome of the models is a probability. To produce informative maps of potentially suitable habitat, we reclassified the probabilistic projections of each modelling technique into binary values, representing either suitable or unsuitable habitat. This conversion required the selection of a threshold above which a pixel was reclassified as potentially suitable and unsuitable below. Predictions of models range between 0 and 1. Therefore we used an objective approach (*sensu* Liu et al. 2005) and selected a lowest presence decision threshold (LPT). LPT maximizes the sensitivity of model predictions and defines the smallest possible range of suitable habitat that includes all the occurrences of the calibration dataset (Pearson et al. 2007).

Spatial projections

We divided the modelling framework into three main parts: (1) model fitting, evaluation and projection under current conditions using climate variables only, (2) the same as in (1) but with an extra variable reflecting human or geomorphic perturbations and (3) spatial projections under future climate change with an ensemble approach. We used the same geographical domain for the projection of the current and future distributions as for the calibration of the models, i.e. the combined map of the current mangrove distribution and all estuaries along the east coast of South Africa from the border with Mozambique (27°S) to Gamtoos (34°S).

We first reclassified the probabilistic projections of mangrove forest and species according to the reclassification method explained previously for the three modelling techniques separately. Next, we used a synthetically combined consensus forecast as proposed and defined by Araujo and New (2007). We assigned a projected presence to a given pixel of the projection domain if this pixel was predicted as a presence by two out of the three models (MAJ) and by all the three models (CONS). Next, we assessed the effect of adding separately two predictors reflecting respectively human and geomorphic perturbations on the commission error rate (also designated as false positive rate; Fig. 2). This was done in estuaries located within the observed range of mangrove forests and species. Adding such predicting variables should decrease the commission error rate if the absence of mangrove species in estuaries is caused by these perturbations. We used the same procedure as for the climate-based SDMs for calibration and projection but the two perturbations variables were added separately as an ordinal factor into the climate-based models. Finally, a variance partitioning approach based on partial correlation analyses was used to quantify the independent amount of variance added by the HP or RMC variables and the joint contribution to the variance with climate. This approach allows partitioning of total variance into four identifiable fractions of deviance (Borcard et al. 1992; see Randin et al. 2009a for implementation): (1) pure contribution of the group of climate variables, (2) shared or joint contribution of the climatic and HP or RMC variables, (3) pure contribution of the HP or RMC variable and (4) unexplained variation. Here the adjusted geometric mean squared improvement R^2 was used as an estimator of the explained deviance without adjustment for the number of observations and predictors.

We projected the future distribution and southern latitudinal limits of the mangrove forests and its species for the years 2020, 2050 and 2080 for each GCM (HADCM3 and CCCMA), under the two scenarios (A2a and B2a) and, in a first step, for each modelling techniques separately by using the climate-based models. We also produced a consensus (ensemble) projection by assigning a presence to a cell if this cell was projected as

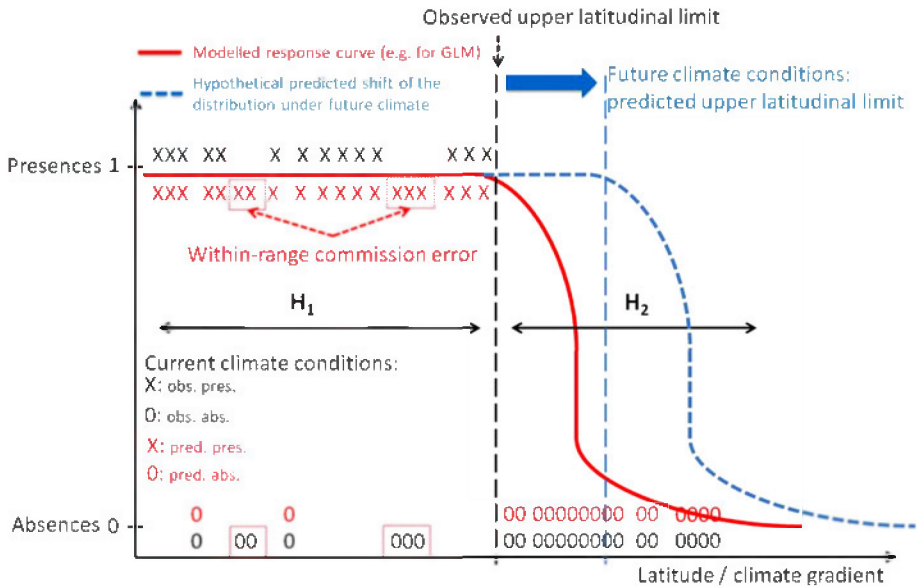


Fig. 2 Schematic view of the observed and modelled distribution of the mangrove forest and species in South Africa along the latitudinal gradient. The estuaries with and without observed mangroves are indicated with *black X* and *O* respectively; the estuaries with and without predicted mangroves under current climate conditions are related to our first working hypothesis (*projections in red*) whereas projections of the latitudinal limits under future climate conditions (*projections in blue*) are linked to our second working hypothesis. The first and second hypotheses are indicated on the figure as *H1* and *H2* respectively. (Color figure online)

presence by the majority of the six models (i.e. at least by four models of the two GCMs × three techniques) for each scenario (hereafter designated as MAJ-A2a for A2a and MAJ-B2a for B2a). All statistical analyses have been computed in R (R 2.14.0, R Development Core Team 2011) and all spatial analyses have been done in ArcGIS (ESRI 2006).

Results

Species distribution models performance

The predictive power of SDMs for the three species and the mangrove forest ranked between good to excellent when AUC of the three modelling techniques were evaluated by tenfold cross-validations (Table Online Resource 5). AUC values were interpreted using the classification of Araujo et al. (2005) and adapted from Swets (1988). We thus obtained useful models (according to Swets 1988) for deriving reliable projections under current and future climate conditions. All modelling techniques accurately predicted the current southern latitudinal limits of the mangrove species and forest (Fig. 3). However, over-prediction within the current distribution by the climate-based models was high, resulting in high commission errors (Table 1), although spatial projections of the current distribution revealed that the absences between Mkomazi and Mtamvuna were accurately predicted for all species and the mangrove forest (Fig. 3). GBMs also correctly predicted absences between Mtentu and Mzintlava. In addition, GBMs of *B. gymnorhiza* and the mangrove

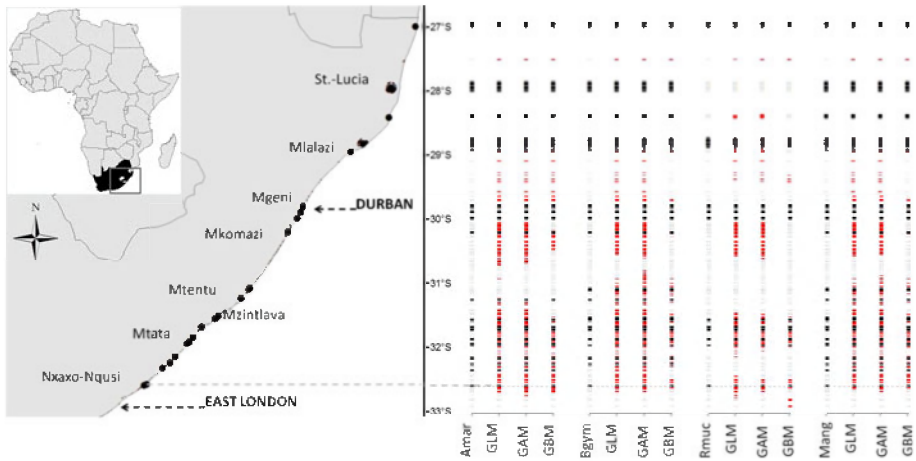


Fig. 3 Spatial projections of climate-based species distribution models for the mangrove forest (Mang) and for *Avicennia marina* (Amar), *Bruguiera gymnorrhiza* (Bgyrn) and *Rhizophora mucronata* (Rmuc). The current observations (above each acronym) and the projections of the different modelling techniques (GLM generalized linear models, GAM general additive models, GBM gradient boosting machines) are provided. True predicted presences are indicated in black, true predicted absences in light grey, false predicted presences (commission errors) in red. (Color figure online)

Table 1 (a) Commission errors of the climate model projections of the current distribution of each modelling technique (GLM, GAM, GBM) and the consensus outcomes MAJ and CONS. The predicting variables are 3 climate variables (CLIM). (b) Worsening (+) or improvement (–) of the commission error compared to the CLIM models (%) after adding a human perturbation factor (+HP) or a geomorphic perturbation factor (river mouth condition, +RMC) to the models

Predictors	Species	GLM	GAM	GBM	MAJ	CONS
(a) Commission error (%)						
CLIM	AMAR	81	79	50	78	48
	BGYM	81	92	38	80	30
	RMUC	54	50	19	47	15
	MANG	85	88	43	80	37
(b) Increase (+) or decrease (–) of the commission error compared to the CLIM models (%)						
CLIM + HP	AMAR	–3	–6	2	–7	2
	BGYM	16	–15	–3	–6	–2
	RMUC	7	1	–1	3	–2
	MANG	3	–10	–1	–8	–1
CLIM + RMC	AMAR	16	4	9	10	12
	BGYM	24	19	8	20	21
	RMUC	0	1	5	–1	–1
	MANG	20	16	13	21	16

AMAR *Avicennia marina*, BGYM *Bruguiera gymnorrhiza* (L.), RMUC *Rhizophora mucronata*, MANG the mangrove forest

forest correctly predicted absences between Mlalazi and Mgeni as well. Finally, all models of *R. mucronata* predicted the absence of the species in St-Lucia and between Mtata and Nxaxo-Nqusi. This could be attributed to waterbalance as it was a more important variable

in the models of *Rhizophora* compared to the other species. For all the estuaries, the predicted species occurrences by each modelling technique are given in Table online resource 6.

Does accounting for human or geomorphic perturbations in species distribution models improve predictions within mangrove forest and species current distribution ranges?

Overall, we found no consistent trend in the decrease of commission error among both species and modelling techniques when adding the HP or the RMC variable to the CLIM models (Table 1). Including the HP variable decreased commission errors of GAMs for *B. gymnorrhiza* and for the mangrove forest seriously by at least 10 % and resulted in a small decrease of the commission error of less than 6 % for the GLM and GAM of *A. marina* and the GBM of *R. mucronata* (Table 1). Hence, the improvement of the human perturbation to the model predictions within the ranges is both species- and technique-dependent while no improvement was shown when including the variable reflecting the geomorphic perturbations into the climatic models.

What is the relative importance of each predicting variable in the models and what is the independent contribution of climate compared to human or geomorphic perturbations?

The variable importance shown in Table 2 is a metric reflecting how a given variable contribute to the predictive accuracy of a model whereas variance partitioning shown in Table 3 allows calculating the independent contribution of a variable or group of variables in the total variance/deviance (model fit) of a model. In our case, variance partitioning separates the total variance of a model into (1) independent contribution of the climate variables, (2) shared or joint contribution of the climatic and HP/RMC variables, (3) independent contribution of the HP/RMC variable and (4) unexplained variation.

GDD was overall the most important variable for climate-based GAMs and GBMs with its relative importance ranging between 0.38 and 0.95 (Table 2). In contrast, the importance of TMIN and WBAL was on average low although TMIN was the most important variable for GLM of *A. marina* and the mangrove forest whereas WBAL was the most important variable for GLM and as important as GDD for GAM of *R. mucronata*. The importance of the climate variables in models including the HP variable was similar to models without it. However, the HP variable became the most important when included to climate models for which TMIN was the most important. RMC was the most important variable in models calibrated with climate and geomorphic perturbation for *A. marina*, *B. gymnorrhiza* and the mangrove forest. For models of *R. mucronata* including RMC, the most important variables were the same climate variable as for the climate-based models.

Variance partitioning showed that the contribution of the climate was always high compared to the contribution of the HP variable (Table 3). Models with the highest predictive power had a higher contribution of climate variables in comparison to the HP variable. However, the joint contribution of the HP variable and the climate variables reached high values. When accounting for RMC, the joint contribution of climate variables and RMC was high whereas the individual contribution of the climate variables was moderate and low for RMC. This pattern was different for *R. mucronata*, for this species the climate variables had the highest contribution whereas the individual contribution of RMC and the joint contribution were low. Most importantly, when comparing the results of variable importance and the variance partitioning (individual contribution of climate

Table 2 Variable importance of each predictor (TMIN, GDD, WBAL, HP and RMC) for the three modelling techniques (GLM, GAM and GBM), for the climate-based models (CLIM), the models with a human (+HP) and the models with a geomorphic (+RMC) perturbation index, for the mangrove forest and the three species

Species	Technique	CLIM					CLIM + HP					CLIM + RMC				
		TMIN	GDD	WBAL	TMIN	GDD	TMIN	GDD	WBAL	HP	TMIN	GDD	WBAL	RMC		
<i>Avicennia marina</i>	GLM	0.39	0.39	0.18	0.4	0.41	0.31	0.56	0	0.14	0.07	0.51				
	GAM	0.13	0.57	0.09	0.18	0.38	0.14	0.32	0.05	0.11	0.03	0.37				
	GBM	0.04	0.94	0.1	0.04	0.95	0.1	0	0.04	0.18	0.06	0.35				
<i>Bruguiera gymnorhiza</i>	GLM	0.45	0.51	0.12	0.06	0.63	0.25	0.59	0	0.25	0.08	0.48				
	GAM	0.1	0.7	0.03	0.16	0.48	0.1	0.33	0.03	0.24	0	0.34				
	GBM	0.06	0.95	0.07	0.05	0.89	0.07	0	0.01	0.37	0.02	0.38				
<i>Rhizophora mucronata</i>	GLM	0.19	0.63	0.76	0.16	0.59	0.86	0.18	0.19	0.53	0.67	0.17				
	GAM	0.12	0.66	0.66	0.1	0.65	0.67	0.03	0.14	0.52	0.56	0.22				
	GBM	0.08	0.71	0.39	0.01	0.73	0.26	0.21	0.08	0.64	0.34	0.03				
Mangrove forest	GLM	0.53	0.5	0.12	0.34	0.51	0.29	0.53	0	0.16	0.1	0.55				
	GAM	0.15	0.61	0.05	0.24	0.42	0.12	0.37	0.05	0.11	0.01	0.46				
	GBM	0.05	0.91	0.08	0.05	0.89	0.08	0	0.06	0.13	0.02	0.55				

The value of the most important predictor per model is indicated in bold

Table 3 Percentage of variance for the two fractions of variables (climatic and perturbations) for the models including climatic variables with human perturbations (CLIM + HP) and climatic variables with geomorphic perturbations (CLIM + RMC)

	CLIM + HP				CLIM + RMC			
	CLIM	HP	Joint	Unexpl.	CLIM	RMC	Joint	Unexpl.
<i>Avicennia marina</i>								
GLM	0.39	0.05	0.22	0.34	0.15	0.14	0.47	0.25
GAM	0.46	0.02	0.26	0.27	0.19	0.07	0.53	0.21
GBM	0.6	0	0.4	0.1	0.36	0.03	0.58	0.04
<i>Bruguiera gymnorhiza</i>								
GLM	0.38	0.05	0.21	0.36	0.14	0.13	0.45	0.28
GAM	0.45	0.01	0.24	0.3	0.18	0.07	0.51	0.24
GBM	0.6	0	0.3	0.1	0.37	0.03	0.56	0.05
<i>Rhizophora mucronata</i>								
GLM	0.36	0	0.1	0.54	0.32	0.02	0.14	0.52
GAM	0.75	0.01	0.01	0.24	0.64	0.04	0.12	0.2
GBM	0.7	0	0.3	0	0.82	0.01	0.15	0.02
Mangrove forest								
GLM	0.38	0.06	0.19	0.37	0.12	0.16	0.45	0.27
GAM	0.45	0.02	0.23	0.3	0.16	0.09	0.52	0.23
GBM	0.6	0	0.3	0.1	0.34	0.04	0.57	0.05

Fractions are the variance explained by the climate variables only (CLIM) and the human perturbation (HP) or the geomorphic index (RMC) separately, the joint contribution (Joint) and the unexplained variance (Unexpl.) of the models for the three modelling techniques (GLM, GAM and GBM) of the mangrove forest and the species

variables and perturbation variable), we found a consistent pattern of variation between these two metrics for the models with the human perturbation factor. However, for the models including geomorphic perturbation, a consistent pattern between these two metrics was only found for *Rhizophora* in contrast to the models of the mangrove forest and the other two species that showed the highest variable importance for RMC while the highest explained variance was due to the independent climate contribution.

How will the position of the latitudinal limit of the mangrove species and the mangrove forest change in the future?

The potential southern latitudinal limits of mangrove forest and all species were predicted to move only slightly towards higher latitudes until the 2020 period according to the majority projections (Fig. 4), with a maximum range expansion of 17 km south. Majority projections predicted larger range shifts (up to 68.6 km) towards the south of the current limits until the 2050 period. Finally, projections of shifts for the end of the 21st century (2080 period) ranged between 33 and 101 km. Surprisingly, a retreat from its current limit (up to 48.2 km) or a status quo was predicted by the consensus projections for *R. mucronata*.

The latitudinal limit of *A. marina* limit was predicted to steadily shift towards the south according to all models and both climate scenarios (Fig. 4) with a shift in average further

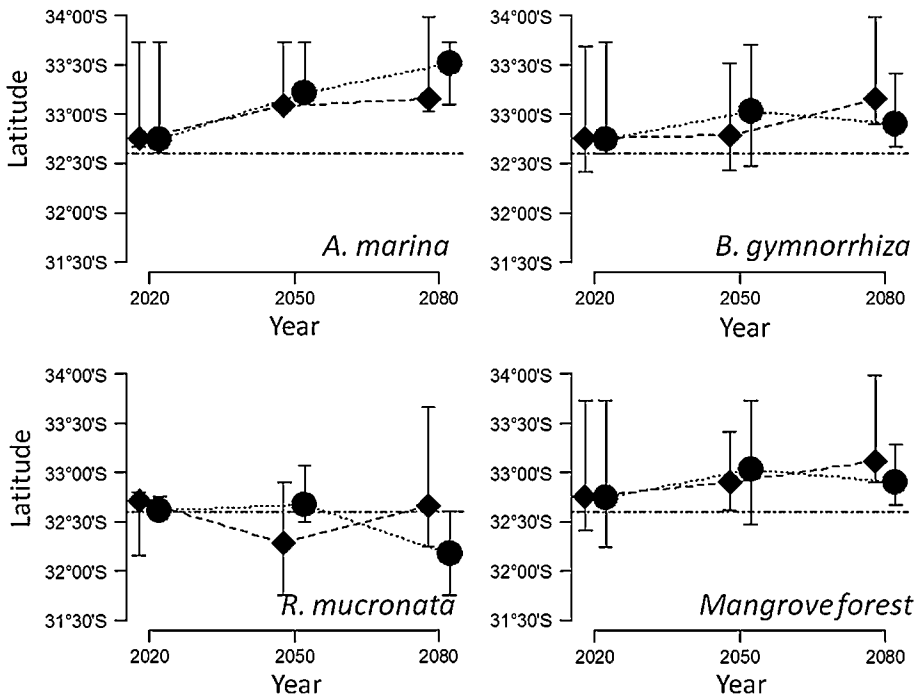


Fig. 4 Predictions of the future position of the latitudinal limits of the mangrove forest and its species in South-Africa. The positions of the limits given by the majority of the model predictions (majority is four out of six outcomes given by two GCMs × three modelling techniques) for each of the two climate scenarios is represented by *diamonds* for A2a and *circles* for B2a. The upper latitudinal limits of the most progressive and most conservative model predictions are indicated with the *error bars*. The current latitudinal limit is shown with a *horizontal dot-dash line*

south when compared to the mangrove forest around 2050. The majority of the models also projected a shift of *B. gymnorhiza*'s cold edge towards the south, although a status quo and a slight retreat were projected by the most conservative model for the 2020 and 2050 periods. Remarkably, after 2050 the majority and the most progressive model outcome for the B2a scenario showed a retreat of *B. gymnorhiza*. Based on the A2a scenario, the latitudinal limit of *R. mucronata* was predicted to slightly or not change until 2050 and then predicted to contract towards the equator until the 2080 period. Projections under B2a showed the opposite patterns: the latitudinal limit of *R. mucronata* was predicted to be closer to the equator than today for the period 2050 and then predicted to be the same as today for the period 2080 according to consensus projections. Range shift projections of the mangrove forest were similar to those of *B. gymnorhiza*.

Discussion

For the first time, a spatially explicit assessment of the current and future distribution of the mangroves at the regional scale is provided. Our modelling framework can be easily tested and expanded to other mangrove forest of other continents or at the global scale. All modelling techniques accurately predicted the current latitudinal limit of the mangrove

forest and its three species. These models were calibrated on a single latitudinal transect along the coast of South Africa, which increases the probability of isolating good relationships between species observations and environmental factors driven by latitude. However, our results suggest that the current southern latitudinal limits of both mangrove forest and mangrove species are well explained by climate-based SDMs. This allowed us to provide reliable projections of future range shifts over the 21st century. Here we showed that climate change might create climatically suitable sites beyond the current latitudinal limits of *A. marina* and *B. gymnorrhiza*. *A. marina* was predicted to shift in average further south than the mangrove forest around 2050, which confirms a species-specific range shift within species assemblages or communities (Walther 2003). Species-specific changes of distribution under climate change have also been predicted for benthic species such as seaweeds and might result in changes in species assemblages (Bartsch et al. 2012). Contrasted and diverging outcomes were projected by the set of the three modelling techniques and climate scenarios for the future distribution of *R. mucronata* and suggested a status quo of its leading edge. Water balance was a more important variable in the models to describe the current distribution of *R. mucronata* compared to the other species. The higher sensitivity of *R. mucronata* to drier conditions than *A. marina* and *B. gymnorrhiza* is well-known (Tomlinson 1986; Robert et al. 2009). However, variation of water balance is not directly related to changes in latitude. Future climate forecasts are more divergent on changes in water balance than temperature changes (Anderson et al. 2009), explaining the contrasted results we found for the future latitudinal limit of *R. mucronata*. Although growth conditions defined by abiotic factors apart from the limiting climate conditions appear to be suitable for *R. mucronata*, this species nevertheless never reaches dominance or even prevalence, except very locally, in the South African estuaries. This suggests other causes of its distribution. A possible one might be the apparent low competitive ability of *R. mucronata* against *B. gymnorrhiza*, in particular when reaching adult stages. *Bruguiera* trees taller than 2 m 50 have indeed a faster growth rate than *Rhizophora* trees of the same height in Mngazana, South Africa (Rajkaran 2011). Interactions among mangrove species at the same trophic level exist and will also affect their abundance and distributions in the future. Hence the auto-ecological response of the species and new interactions might lead to range shifts diverging from those produced by SDMs under the future changing climate.

Commission error rates within the current distribution were high for the climate-based models for all species. Consequently, the current distribution pattern within the latitudinal range of mangroves in South Africa could not be successfully explained by climate alone. Incorporating human driven perturbation into the models weakly improved the amount of over-prediction and no improvements were detected when adding the variable reflecting geomorphic perturbations.

Main drivers of the distribution of the mangrove forest and its species

Growing-degree days was the most important climatic predictor in the models for the forest and the three mangrove species. This is confirmed by other studies that also reported average temperature-based variables such as GDD or summer temperature to be the most important predictors for high latitudinal or altitudinal range limits of tree species (Morin et al. 2007; Mellert et al. 2011; Boucher-Lalonde et al. 2012). Hence, this suggests that the main driver of the mangrove latitudinal limits might be largely related to a minimum amount of heat limiting growth rather than extreme temperatures affecting the direct survival of the trees (killing plant tissues, flowers or leaves).

Predictions of absences within the observed distribution of mangrove species

Our results rejected the first hypothesis which was that human-driven or geomorphic perturbations explain the absence of mangroves in most estuaries within the distribution range. We did not test other alternative causes such as dispersal limitation. It is unlikely that South African mangroves are regionally limited by dispersal since mangrove propagules were found at several entrances of estuaries where mangroves were absent. However, limitation by dispersal and other historical factors should be tested at a larger scale. Since the human-driven perturbation factor only weakly improved model predictive power, our assumption that the list of health status based on the abiotic and biotic conditions reflects the anthropogenic impact on the estuary might be wrong. Alternatively, the anthropogenic impact that is captured in this health list might not be specific enough to be important for mangroves as it considers the whole estuary. This is an important result to be considered in the future use of the health list in management practices. In this context, we should also emphasize here that human pressure is high for many estuaries in South Africa and that major mangrove forests have disappeared due to clear-cutting when building harbours and other types of coastal infrastructures (Breen and Hill 1969; Moll et al. 1971; Bruton 1980; Begg 1984). Overall in South Africa, mangroves have already been under human pressure for a long time, at least since around 1900 (Moll et al. 1971; Rajkaran and Adams 2010), making absence of mangrove forest even more difficult to correlate with health status. Despite the weak improvement of predictive power found when including health status into SDMs of the mangrove species, this health status list might be adequate to capture mangrove degradation (i.e. changes in the abundance of species) rather than the loss of a whole species population in an estuary. It has already been demonstrated in the study of Randin et al. (2009a): they showed that a human perturbation variable that did not improve predictions of occurrences of mountain plant species by SDMs turns out to be an important variable when predicting the abundance of the same set of species. Unfortunately, information about abundance of species is not available for all South African mangrove forests.

When geomorphic perturbation was included in the models, it did not decrease the false positive error rate within the extent of the mangrove distribution compared to the models based on climate variables only. This could be explained mainly because we could not take into account the duration of river mouth closure: this is a more structuring factor and a continuous index rather than a simple categorical variable (two categories: “permanently open” and “temporarily closed” river mouths).

Although the independent contribution of the human and geomorphic perturbation (river mouth condition) in the models was low in average, the joint contribution of climate variables and of these factors was high up to 57 %. This may not necessarily result from a direct relationship between climate and human land use or river mouth condition. The co-variation between the climate and human perturbations might rather results from different histories and dominant land-use practices between the northern part of the study area (KwaZulu Natal), the central part (former Transkei) and the southern part (former Ciskei). This indeed could explain the north–south gradient of perturbations and the high correlation with the main climate variables. Over the last two centuries, agriculture was intensified, harbours were enlarged and highway and railway infrastructure was constructed along the coastline in KwaZulu Natal (Moll et al. 1971; Begg 1984; Rajkaran et al. 2009) resulting in a higher human disturbance (i.e. corresponding to HP categories 2 and 3), whereas in the former Transkei, extensive farming persisted, resulting in low human disturbances (HP categories 1 and 2). In the case of the geomorphic perturbation index, it has already been shown that the independent contribution of geomorphic-based variables is

weak on average and the joint contribution with climate is high (Randin et al. 2009b). This was due to the fact that climate could largely control the intensity of geomorphic perturbation, sometimes in combination with topography in complex terrains.

Range shifts for the 21st century

Our second hypothesis was that climate change creates climatically suitable sites for mangrove species south of their current latitudinal limits in South Africa over the 21st century. We showed that it might be the case for *A. marina* and *B. gymnorhiza* but not *R. mucronata*. The impact of climate change on the mangrove distribution is poorly studied (but see Alongi 2008; Gilman et al. 2008; Beaumont et al. 2011), besides for sea level rise (Di Nitto et al. 2008, 2010; Doyle et al. 2010; Loucks et al. 2010; McKee 2011; Traill et al. 2011). Our study on range shift of the latitudinal limits of mangrove forest and species did not incorporate sea level rise but is the first to address the potential effect of changing climate variables by global warming on mangrove latitudinal limits.

In the 70s, our three studied species have been planted in Nahoon Estuary (East-London, South Africa, 33°S). More recently, many seedlings of *A. marina* and some of *B. gymnorhiza* of those planted trees rapidly colonized the whole mudflat and tree height, up to 5–6 m, is at least 2 m higher than at today's natural latitudinal limit (maximum tree height: ± 3 m). This highlights (1) the importance of the dispersal process for establishing in new potential suitable estuaries and (2) the fact that recent warming may have already favoured establishment beyond the current latitudinal limits of these two species. Potential climatically suitable sites for *A. marina* and *B. gymnorhiza* at that latitude were predicted by our most progressive models from the period 2020 onwards. Moreover, all models predicted a suitable climate for *A. marina* in Nahoon from the period 2050 onwards. However, depending on the climate-scenario, the majority of the models predicted different outcomes about whether and when Nahoon will become climatically suitable for *B. gymnorhiza*.

At some other high latitudinal mangrove forests, recent expansion of forest area is reported mostly in mono-specific forests of *Avicennia* in South-East Australia, New Zealand and Florida (Saintilan and Williams 1999; Rogers et al. 2006; Morrissey et al. 2007, 2010; Stevens et al. 2006). These forest expansions have been attributed to many causes, e.g. estuary infilling and vertical accretion of tidal flats (Saintilan and Williams 1999, Ellis et al. 2004, Swales et al. 2007, Rogers et al. 2006), increased nutrient inputs (Saintilan and Williams 1999), changes in relative sea level due to sedimentation or subsidence (Rogers et al. 2006). Although so far these expansions did not result in a shift of the latitudinal limit polewards, their dynamics may lead to colonizations of new areas beyond the limits if climate become suitable and dispersal is possible.

Conservation opportunities for the future

From the point of view of mangrove conservation latitudinal expansion of the mangroves is desirable. However, expansion of mangroves might replace salt marsh areas which are plant species richer in South Africa (mangroves: max. 3 species; salt marshes: max. 5 species, Colloty et al. 2002). Besides, mangrove expansion might be in conflict with current anthropogenic land-use development strategies in these estuaries. Hence, it depends on regional management and policy choices whether mangrove expansion is desirable or not.

Here, we further discuss that before colonization of climatically suitable sites by *A. marina* and *B. gymnorhiza* can occur in a changing climate, two other requirements should be fulfilled: (i) mangrove propagules should be able to enter the potentially suitable

Table 4 Estuaries with their coordinates, health status (STATUS, ranging from A-pristine to F-degraded) and river mouth condition (RMC) (source: South African National Spatial Biodiversity Assessment (NSBA), 2011) beyond the present latitudinal limit of the mangrove forest in South-Africa that are climatically suitable for mangroves (MANG) and specifically for *Avicennia marina* and *Bruguiera gymnorhiza* in 2050 according to the majority of the model projections for each future climate scenario (A2a in grey and B2a in black)

Lat.	Lon.	Name	Status	RMC	AMAR	BGYM	MANG	Details of estuary
-32.63	28.44	Ncizele	B	TOC				Limited intertidal area. Unlikely to support more than a few trees.
-32.63	28.43	Qelora	B	TOC				Suitable intertidal area for mangrove forest. Some developments near mouth of estuary.
-32.65	28.42	Ngogwane	B	TOC				Suitable intertidal area for limited mangrove forest. Suitable intertidal area for limited mangrove forest.
-32.67	28.4	Gxara	B	TOC				No developments were present in 2005.
-32.68	28.39	Great Kei	C	POE				Suitable intertidal area for limited mangrove forest. Limited intertidal area. Mangrove establishment unlikely. Some development around the mouth, with a bridge over estuary.
-32.69	28.37	Cwili	B	TOC				Coastal development present along the length of estuary. Possible mangrove habitat exists 1 km from the mouth.
-32.71	28.35	Morgan	C	TOC				Suitable intertidal area for mangrove forest.
-32.73	28.31	Quko	A	TOC				No suitable area. Very small estuary.
-32.74	28.29	Mtendwe	B	TOC				Suitable intertidal area for mangrove forest. Limited coastal development at present.
-32.76	28.25	Haga-haga	B	TOC				Suitable intertidal area for mangrove forest. Some developments exist near the mouth.
-32.78	28.18	Nyara	A	TOC				Suitable intertidal area for mangrove forest.
-32.8	28.15	Kwenxura	B	TOC				Suitable intertidal area for mangrove forest.
-32.81	28.14	Cefane	B	TOC				Suitable intertidal area for mangrove forest.
-32.83	28.12	Cintsa	C	TOC				Suitable intertidal area for mangrove forest. Coastal developments exist near the mouth.
-32.86	28.11	Cunge	A	TOC				No suitable area. Very small estuary.
-32.89	28.09	Bulura	B	TOC				Limited suitable intertidal area for fringe mangrove forest.
-32.91	28.08	Kwelera	B	POE				Suitable intertidal area for mangrove forest.
-32.93	28.03	Gqunube	B	POE				Suitable intertidal area for mangrove forest.
-32.97	27.97	Qinira	B	TOC				Suitable intertidal area for mangrove forest.
-32.99	27.95	Naboon	C	POE				Mangroves have been planted here and are flourishing.
-32.99	27.95	Hlaze	C	TOC				No suitable area. Very small estuary. Road bridge runs over the estuary
-33.01	27.93	Blind	C	TOC				No suitable area. Very small estuary. Major road infrastructure over and near the estuary.
-33.03	27.92	Buffalo	D	POE				Highly industrialised and transformed harbour area. Establishment unlikely.
-33.07	27.84	Hickman's	B	TOC				Limited intertidal area. Developments are present around estuary.
-33.09	27.81	Hlozi	B	TOC				Limited intertidal area. Unlikely to support more than a few trees.
-33.1	27.78	Goda	B	TOC				Suitable intertidal area for limited mangrove forest.
-33.12	27.73	Gxulu	B	TOC				Limited intertidal area. Unlikely to support more than a few trees.
-33.15	27.7	Mcantsi	C	TOC				Limited intertidal area. Unlikely to support more than a few trees.
-33.16	27.68	Mlele	B	TOC				Limited intertidal area. Unlikely to support more than a few trees.
-33.17	27.67	Ncera	B	TOC				Suitable intertidal area for mangrove forest.
-33.18	27.66	Ross' Creek	B	TOC				No suitable area. Very small estuary.
-33.19	27.64	Lilyvale	B	TOC				No suitable area. Very small estuary.
-33.21	27.62	Shelbertsroom	C	TOC				No suitable area. Very small estuary.

This ensemble of majority of model projections did not predict climatically suitable estuaries beyond the current latitudinal limit in 2050 for the species *Rhizophora mucronata*. Hence, this species cannot be included in this summary table. Species acronyms follow Table 1. Suitability of intertidal area in estuaries is based on images of Google Earth

TOC temporarily open/closed estuary, POE permanently open estuary

estuaries and (ii) there should be suitable intertidal areas for mangroves to establish. Today, half of the climatically suitable estuaries have suitable intertidal areas for mangrove forest with a good health status (Table 4). The maximum latitudinal distance between two

of these consecutive estuaries is 12 km. Since these three mangrove species have reached remote islands (Spalding et al. 2010), colonization by propagule dispersal to these estuaries is possible if all requirements for establishment are then fulfilled. Unfortunately, only three of these estuaries currently have permanently open river mouths (Table 4). Hence, after establishment in estuaries with a temporarily open river mouth, seedlings and trees can die due to high water level and flooding depending on the duration of closed river mouth period. Climate change will also directly affect the sea level and then indirectly intertidal areas and river mouth conditions. In addition, increase in rainfall and flood events have been predicted along the east coast of South Africa (Hewitson et al. 2005; Schulze et al. 2005; Hewitson and Crane 2006; Lumsden et al. 2009) which will result in an increase in open mouth conditions. At the same time, an increase in storms on the sea could deposit sand in the mouths of these estuaries, resulting in an increase in mouth closure.

Conclusion and future research directions

Climate change will create climatically suitable sites for the mangrove forest and the species *A. marina* and *B. gymnorhiza* south of the current limits, but model outcomes did not agree on the future potential distribution of *R. mucronata*. Within the range of the mangrove forest, the fragmented distribution pattern of the mangroves in South Africa cannot be explained by climate variables alone. The geomorphic and human-driven perturbation factors we used did not or only slightly improve the model predictions of this pattern. Therefore a first direction for further research would be to better understand the effect of the duration of the temporary closed river mouths on the mangrove distribution and how the human impact on mangroves is related to species occurrence and abundance, apart from mangrove logging which has been already studied by Rajkaran and Adams (2010). Second, it would be useful to validate our results by testing the transferability of SDMs at other high latitudinal regions of the same mangrove species. Daily in situ records of temperature and relative humidity along the north–south distribution of mangroves in South Africa would also provide insights on how species occurrence and abundance, vegetation structure and climax vegetation of the different mangrove forests are related to proximal climate measurements. Beside this, assessing the connectivity between mangrove forests and the minimum requirements for mangrove species to disperse towards estuaries without mangroves would help future conservation planning.

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