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Effects of climate change on the future distributions of the top five freshwater invasive plants in South Africa

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ABSTRACT

A recent study shows that most aquatic alien plants in temperate cold climate are of tropical and subtropical origins and only those that can withstand cold climates become invasive. This suggests that a changing climate that becomes warmer may result in currently non-invasive alien plants becoming invasive in the future. To facilitate pre-emptive actions when controlling invasive aquatic plants in South Africa under climate change, we reconstructed predictive models for the five most damaging aquatic alien plants of freshwater systems in the country. We found evidence of contrasting shifts in species distribution ranges: the ranges of *Myriophyllum aquaticum* and *Pistia stratiotes* will contract, while *Azolla filiculoides*, *Eichhornia crassipes*, and *Salvinia molesta* will increase their future ranges with most suitable habitats found in the Western Cape province and along coastal areas. In addition, the predicted range contraction and expansion would result in some dams currently vulnerable to invasion becoming resilient while others that are currently resilient may become vulnerable due to climate change. These results can be used to develop future monitoring programs for aquatic ecosystems, prioritize control efforts, and raise public awareness on risks posed by these aquatic invasive plants, especially under future climate scenarios.

1. Introduction

Plants are moved around the globe into non-native areas to satisfy human needs. Of these non-native species, those that successfully spread beyond the point of introduction pose negative ecological and economic challenges (Mooney and Hobbs, 2000; Van Wilgen et al., 2001; Pimentel et al., 2005; McGeoch et al., 2010). These challenges are expected to be aggravated in the future as climate change is predicted to facilitate further spread of these species (Coetzee et al., 2009; Willis et al., 2010). Compared to terrestrial plants, aquatic plants are shown to have a higher probability of becoming invasive in new environments (see Andreu and Vilà, 2010) and, therefore, deserve perhaps more urgent attention (Padilla and Williams, 2004; Andreu and Vilà, 2010; Azan et al., 2015). Furthermore, ornamental pond industries and aquarium trade have been singled out as a strong contributing pathway to the introduction and spread of aquatic invasive plants (Kay and Hoyle, 2001; Henderson and Cilliers, 2002; Padilla and Williams, 2004; Madeira et al., 2007; Martin and Coetzee, 2011; Strecker et al., 2011; Azan et al., 2015).

In their recent study, Azan et al. (2015) showed that most plants traded in Canadian aquaria are of tropical and subtropical origins and that only those that can withstand cold climates become invasive. This finding suggests that if the Canadian climate becomes warmer in the future under climate change scenarios, even aquarium plants that are not currently invasive would likely become invasive (Verlinden et al., 2014). In this regard, reconstructing ecological niche models of alien plants under climate change becomes important in the sense that these models may assist in identifying (i) plants that might expand their geographic ranges while tracking favorable climates as well as (ii) areas likely to be invaded due to climate change.

In South Africa's freshwater systems, the top five most damaging alien plants, generally termed the "bad five" (Henderson and Cilliers, 2002), are of South American origin. This top five includes water hyacinth (*Eichhornia crassipes* (Mart.) Solms), water lettuce (*Pistia stratiotes* L.), parrot's feather (*Myriophyllum aquaticum* (Vell.) Verdc.), Kariba weed (*Salvinia molesta* D.S. Mitch.), and red water fern (*Azolla filiculoides* Lam.) (Van Wilgen et al., 2001; Hill, 2003; Richardson and Van Wilgen, 2004). Based on DNA barcoding, Hoveka et al. (2016) revealed that some prohibited aquatic alien plants are already in circulation in South Africa's aquarium trade. There is therefore an urgent need to strictly regulate this trade and design pre-emptive actions that take into account the behavior of alien plants in response to climate change.

In this study, we reconstruct predictive models of species ecological niches to identify how the "bad five" aquatic plants are likely to

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re-adjust their geographic ranges in response to future climate change. We also identify South Africa's dams located in areas climatically favorable for a range expansion of the "bad five" aquatic plants.

2. Materials and methods

2.1. Study species

In total, 21 aquatic weeds have been documented to be present in freshwater systems of South Africa (Henderson and Cilliers, 2002). Our focus in this study is on the five most damaging alien plants of South Africa's freshwater systems referred to as "bad five": *A. filiculoides*, *E. crassipes, M. aquaticum*, *P. stratiotes*, and *S. molesta*.

2.2. Species occurrence data

Distribution data for the "bad five" invaders were sourced from the National Herbarium Pretoria Computerized Information System (PRECIS) and the South African National Biodiversity Institute (SANBI)'s Integrated Biodiversity Information System (SIBIS). After removing duplicate records or doubtful point data, a total of 711 geographic points were obtained for *A. filiculoides*, 649 for *E. crassipes*, 180 for *M. aquaticum*, 129 for *P. stratiotes*, and 166 for *S. molesta*.

2.3. Climate data

Nineteen raster-based bioclimatic parameters for both current and future climate scenarios were used for ecological niche modeling (see supplementary Table S1). Spatially downscaled estimates of future climate for the year 2080 were obtained from the WorldClim database (http://www.worldclim.org/; Hijmans et al., 2005) at a spatial resolution of 2.5 arc minutes using the Commonwealth Scientific and Industrial Research Organization CSIRO-Mk3.0 GCM and the Special Report on Emissions Scenarios SRES A1B carbon emission scenario. Environmental variables were interpolated onto ArcGIS grids to ensure that all spatial data have the same geographic bounds and cell size as the study region.

2.4. Species distribution modeling

We used MaxEnt version 3.3.3 K (Phillips et al., 2006) to generate predictive models for current and future distribution (maps of climate suitability) of the "bad five" aquatic invaders. Although spatial autocorrelation is an issue of concern in most species distribution models, methods on how to correct or test for correlation between climatic variables are still not standardized (Lennon, 2002; Dormann, 2007). Notwithstanding, we tested for spatial autocorrelation in all environmental variables to address the issue of multicollinearity (Pearson correlation coefficient, $r < \pm 0.75$; supplementary Table S2). Variables that showed correlation strength above this range were excluded from the analysis. Additionally, we used jackknife statistics to evaluate the relative contribution of each of the 19 predictor variables to the models using the area under the curve (AUC) score (Pearson et al., 2007) (Figs. S1 and S2). An AUC value of 0.5 indicates that model prediction is not different from random, a value of 0.5–0.7 indicates poor performance, 0.7–0.9 indicates acceptable performance, and AUC >0.9 indicates high performance (Peterson et al., 2011). Based on the AUC score, the best predictor variables were identified. We then re-ran all models using only the best predictor variables, assigning 75% of the occurrence data for model training and the remaining 25% for model testing. To measure the variability in the model performance, 15 subsampling replicates were run for each model, and the default iteration parameter was changed to 5 000, which is sufficiently large to ensure model convergence. We employed the 10th percentile training presence threshold in order to generate prediction probability maps (Phillips and Dudik, 2008). Our model outputs followed a logistic distribution, with values ranging from 0 (indicating areas that are climatically unsuitable) to 1 (indicating areas that are climatically suitable) for species persistence.

2.5. Determination of habitat suitability

Output projections from MaxEnt for both current and predicted future climate parameters were converted from ASCII to Raster float using the ArcGIS software (ESRI ArcGIS version 10). Changes in geographical ranges of each species between current and future climate were calculated using the Spatial Analyst tools in ArcGIS (O'Donnell et al., 2012). Using the Zonal Statistics extension, we calculated the differences in projected shifts in climatic extent (estimated as the number of pixels gained or lost) such that species with an increased probability of occurrence under future climate projections were assigned a positive value (i.e., range expansion), whereas species with a decreased probability of occurrence under future projections were assigned a negative value (i.e., range contraction). The numbers of pixels gained or lost were then converted to surface area (km^2).

2.6. Fresh water system data

We retrieved from the South African Department of Water Affairs database (http://www.dwaf.gov.za) the shape files of all South Africa's dams. These shape files were then imported into ArcGIS and overlaid onto both maps of current and future climate suitability of all five species studied. This allows us to identify the dams that are located in areas climatically favorable for range expansion of these species.

3. Results

The minimum and maximum AUC values from model outputs generated by MaxEnt ranged from 0.832 to 0.916, with an average AUC value of 0.874. These results indicate a relatively high performance of our species distribution model. The current climate suitability maps for the "bad five" invaders are presented in Fig. 1. Areas that are climatically suitable (areas in red in Fig. 1) for the distribution of *A. filiculoides* are found in six of the nine provinces of South Africa, including the North West, Gauteng, Mpumalanga, Free State, Eastern Cape, and Western Cape provinces (Fig. 1a). However, *E. crassipes* has suitable climatic conditions in all nine provinces (Fig. 1b). In addition, areas suitable for the distribution of *M. aquaticum* are found in seven provinces including the Limpopo, North West, Gauteng, Mpumalanga, Eastern Cape, KwaZulu Natal, and Western Cape provinces (Fig. 1c). Lastly, for *P. stratiotes* and *S. molesta*, climatically suitable areas are found in the Limpopo, Mpumalanga, KwaZulu Natal, Eastern Cape, and Western Cape Provinces (Fig. 1d, e).

Of the 612 dams found in South Africa, 234 (38%) occur in areas that are currently climatically suitable for the establishment of at least one of the "bad five" invaders (Table 1). Of these, the highest number of vulnerable dams is located in the Western Cape province and the lowest number in the Northern Cape province (Table 1).

When the current distribution of the "bad five" invaders was projected into the future (year 2080), our model suggests that the distribution of the majority of the "bad five" plants is likely to expand except for two species. In particular, the range of *A. filiculoides* in the future will increase by 249912 km^2 (~1% of the currently suitable area; Table 2). The Limpopo and Northern Cape provinces, which are currently unsuitable (areas in blue) for *A. filiculoides,* will become suitable in the future (Fig. 2a). Similarly, for *E. crassipes*, its geographic range is predicted to expand by 471477.5 km^2 (~1.5% of the current suitable area; Fig. 2b). In contrast to this range expansion, the ranges of *M. aquaticum* and *P. stratiotes* are predicted to contract in the future by 2,113,839 km^2 (~9% of the current ranges) and 199,582.5 km^2 (~10% of the current potential suitable area), respectively (Fig. 2c, d). Although at the country scale, there was an overall range contraction for these two species, their ranges will locally expand mostly towards the

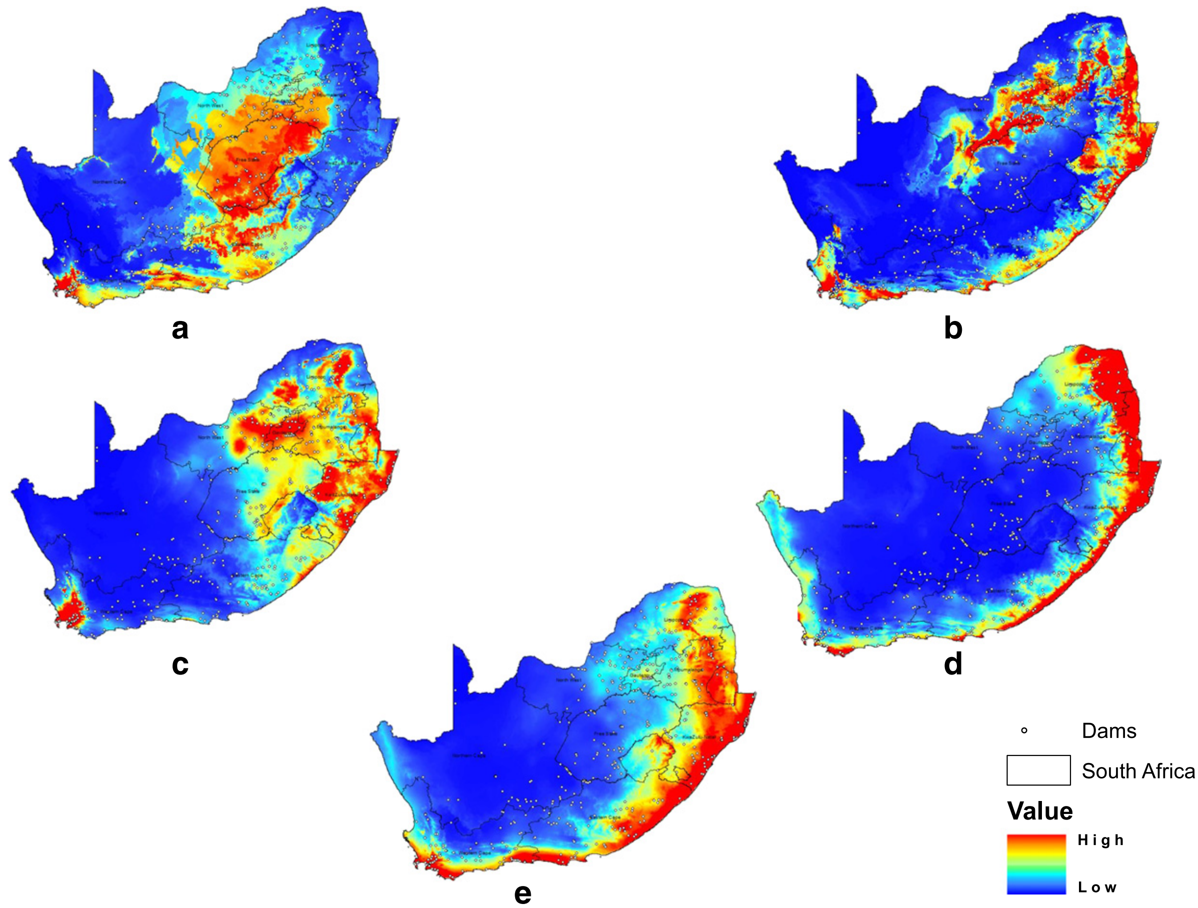

Fig. 1. Ecological niche modeling of species distribution based on current climate. (a) *Azolla filiculoides*, (b) *Eichhornia crassipes*, (c) *Myriophyllum aquaticum*, (d) *Pistia stratiotes*, and (e) *Salvinia molesta*. Areas in red indicate regions that are climatically suitable for species establishment whereas areas in blue indicate region that are less suitable. Dams located in areas that are climatically suitable/less suitable to current climate are indicated by dots. For the names of these dams in each province, see Table 1. On the legend, low = low probability of species occurrence; high = high probability of species occurrence.

coastal areas (Fig. 2c, d). The range of *S. molesta*, however, will expand by 1037250.5 km^2 (~10% of the current suitable area; Fig. 2e).

4. Discussion

We performed ecological niche modeling of the five most damaging plant invaders of South Africa's freshwaters. All the models had AUC values greater than 0.8, which is indicative of the robustness of the predictive models reconstructed. These models reveal that climate change may favor the expansion of *A. filiculoides*, *E. crassipes*, and *S. molesta*, while there may be a reduction in the ranges of *P. stratiotes* and *M. aquaticum*. The Western Cape province and coastal areas of South Africa are identified as the most climatically suitable areas in the future for species range expansion (see also Chytrý et al., 2008). Coastal areas in particular may be more prone to invasion by alien species because of human disturbance and a high nutrient availability (Kowarik, 1995 and Walter et al., 2005).

All five alien species used in this study have sufficient residence time in South Africa to establish non-native distribution ranges in the country, and as such, residence time is not a limiting factor to our ecological niche modeling. For example *A. filiculoides* has been in South Africa for over 65 years, *E. crassipes* for more than 129 years, *M. aquaticum* for 92 years (Henderson, 2006), *P. stratiotes* for 148 years (Cilliers, 1987), and *Salivinia molesta* for >100 years (Hill, 2003). Therefore, given the long residence time of all studied species, they are likely to have reached an equilibrium state with their new environment, although it is an arduous task to say with certainty when non-native species have approached or reached an equilibrium state with their new climate, even after several years of introduction (Jones, 2012; García-Valdés et al., 2013).

The ability of alien species to spread and occupy all climatically suitable habitats is limited by their dispersal ability (Vaclavik and Meentemeyer, 2009). Aquarium trade, however, contributes to introduction and subsequent dispersal of aquatic alien species (Funnell et al., 2009; Strecker et al., 2011; Azan et al., 2015). A continued monitoring and regulation of this trade should be encouraged and environmental education of aquarists should be implemented. This is especially critical for South Africa where some prohibited plant invaders have already been identified through DNA barcoding to be in circulation in some aquaria (Hoveka et al., 2016). Climate change is also acknowledged to further facilitate the spread of alien plants (e.g., Willis et al., 2010). Our results presented here show mixed effects of climate change. In particular, climatically suitable areas for two of the most damaging aquatic invaders in South Africa may contract with projected climate change. Consequently, climate change may contribute to lessen species ability to spread in the future, thus rendering control measures more efficient. However, our ecological niche models also identify some species that might expand their geographic ranges mostly towards the Western Cape province and coastal areas of South Africa as future climate becomes favorable.

One limitation of this study is that water-specific variables (e.g., flow rate, pH, dissolved oxygen, etc.; Joye et al., 2006) were not used as predictors in our species distribution models. However, earlier studies have used environmental variables alone that are not water related to

Table 1
List of dams located in areas climatically suitable to the establishment of at least one of the "bad five" species in each province of South Africa. Names of threatening species and locations of vulnerable dams in each province are shown in Figs. 1 and 2.

Gauteng	Mpumalanga	North West	Northern Cape	Free State	Eastern Cape	KwaZulu NATAL	Western Cape	Limpopo
Alexander	Bethal	Boskop	Kriegerspoort	Allemanskraal	Bonkolo	Albert Falls	Arieskraal	Albasini
Bon Accord	Blyderivierspoort	Bospoort	Nooitgedacht13	Armenia	Bridle Drift	Amanzimnyama	Berg River	Black Heron
Bronkhorstspruit	Da Gama	Buffelspoort	Vaalharts	Bellary825	Buffelsvlei120	Amcor	Bot River Vlei	Buffelspruit443KR
Cinderella	Doringpoort	Elandskuil	Vanderkloof	Bethulie	Cata	Bloemveld	Brandvlei	Cramer
Cowles	Driekoppies	Houwater		Bloemhoek	Dudley Pringle	Driel Barrage	Buffeljags	Donkerpoort
Cullinan	Evander	Klerksdorp		Damplaats190	EJ Smith	Dudley Pringle	Ceres	Dr Neethling
Jan Smuts	Grootdraai	Klerkskraal		Fouriespruit	Gariep	EJ Smith	De Bos	Ebenezer
Leeupan, Tamboville	Grootvlei	Klipdrif		Groothoek	Gcuwa	Gilbert Eyles	De Hoop Vlei	Fundudzi
Peter Wright	Inyaka	Klipvoor		Kalkfontein	Grassridge	Goedertrou	Duiwenhoks	Hans Merensky
Rietvlei	Klipkopjes	Koster		Klipfontein010	Gubu	Hazelmere	Elandskloof	Inyaka
Roodeplaat	Kwena	Kromellenboog		Knellpoort	Hazelmere	Hluhluwe	Fortuin083	Jasi
Rosherville	Leeupan532IR	Lindleys Poort		Koppies	Howisons Poort	Inanda	Garden Route	Kanniedood
Vanryn	Longmere	Little Marico Poort		Krugersdrift	Impofu	Klipfontein	Groenvlei	Klaserie
	Loskop	Manana026IP		Leeukuil	Inanda	Kosi Estuary	Klein River Vlei	Lola Montes
	Mapochs	Marico-Bosveld		Masels Poort	Indwe	KuHlange	Kleinplaas	Lornadawn
	Middelburg	Modder		Menin	Kelly-Patterson	KuShengeza	Klipheuwel	Magoebaskloof
	Nooitgedacht	Olifantsnek		Montague547	Klipperif112	KuZilonde	Knysna Lagoon	Middle Letaba
	Ohrigstad	Potchefstroom		Newbury	Kouga	Lake Cubhu	Korinte-Vet	Mutshedzi
	Primkop	Schweitzer Reneke		Potsdam645	Krom River	Lake Msingazi	Lower Langvlei	Nsami
	Roodepoort B	Sout Pan		Rolandseck068	Laing	Lake Sibayi	Noordhoek lagoon	Nwanedi
	Rooikraal	Swartruggens		Roodepoort468	Loerie	Lake St Lucia	Noordhoek Soutpan	Nzhelele
	Shiyalongubo	Taaibosspruit		Rustfontein	Magwa	Mgobezeleni	Nuweberg	Palabora
	Tonteldoos	Vaalkop		Saulspoort	Milner	Mhlatuze Lagoon	Paardevlei	Phalaborwa Barrage
	Trichardsfontein	Witpoort394IP		Sterkwater189	Mlanga	Mzinto	Skuifraam	Piet Gouws
	Vlugkraal			Strydpoort	Nagle	Nagle	Soetendalsvlei	Roodepoort467KR
	Vygeboom			Tierpoort	Nahoon	Nhlabane	Steenbras (Lower)	Rooibosrand
	Westoe			Tweespruit 90	Toleni	Nsezi	Steenbras (Upper)	Turfloop
	Witklip			Vaal	Van Stadens – Upper	Ntshingwayo	Stettynskloof	Tzaneen
				Vaal Barrage	Waterdown	Phobane Lake	Stompdrift	Vondo
				Welbedacht	Xilinxa	Pongolapoort	Swartvlei	Warmbad
				Weltevrede	Xonxa	Richards Bay	Touws River Estuary	
						Shongweni	Upper Langvlei	
						Spioenkop	Vogelvlei	
						Umgababa	Wemmershoek	
						Woodstock	Zandvlei	
							Zeekoevlei	
							Zwiegelaars	

successfully predict the potential distribution of aquatic species (McNyset, 2005; DeVaney et al., 2009; Williams et al., 2009). Additionally, these data (flow rate, pH, dissolved oxygen, etc.) for South African water bodies are currently not readily available for all watercourses, making it difficult to include them in our models (see also studies by Julien et al., 1995; Welk, 2004; Coetzee et al., 2009; Lehtonen, 2009; Mukherjee et al., 2011). As such, little is known as to how including or omitting these variables will affect species distribution model and this limitation opens new windows for future studies. Also, future studies could also explore how different general circulation models (GCM) and emission scenarios could affect species distribution in the future. Nonetheless, ecological niche models provided in this study are useful for the management of aquatic weeds as they identify regions and water bodies that are at risk of invasion currently and in the future based on climate data. An earlier study showed that 20 of South Africa's dams occur in areas that are climatically suitable to the distribution of the aquatic invasive plant *Hydrilla verticillata* (Coetzee et al., 2009). Our study also shows a similar trend but identifies 234 dams as located in areas that are climatically suitable for the establishment of the "bad five." This calls for a renewed commitment to monitoring the most vulnerable dams with shift in climate regimes.

The mixed impacts of climate change (range contraction and expansion) provide ways of prioritizing species and geographical regions while designing control measures for invasive plants. These measures would not be efficient if potentially invasive species are not quickly detected at port of entry. A DNA barcoding library of alien aquatic plants of South Africa's freshwaters would significantly contribute to achieve rapid species identification.

Table 2
Predicted range changes in aquatic invasive species distribution assuming the Commonwealth Scientific and Industrial Research Organization (CSIRO-Mk3.0) general circulation model.

Species names	Current range occupied (km^2)	Future range occupied (km^2)	Change in range occupied (km^2)	General circulation model
Azolla filiculoides	133,906,552	1341,156,464	249,912	CSIRO-Mk3.0
Eichhornia crassipes	131,699,575	132,171,052	471,478	CSIRO-Mk3.0
Myriophyllum aquaticum	131,969,734	129,855,895	2113,839	CSIRO-Mk3.0
Pistia stratiotes	134,282,577	134,082,995	199,583	CSIRO-Mk3.0
Salvinia molesta	126,288,864	127,326,115	1,037,251	CSIRO-Mk3.0

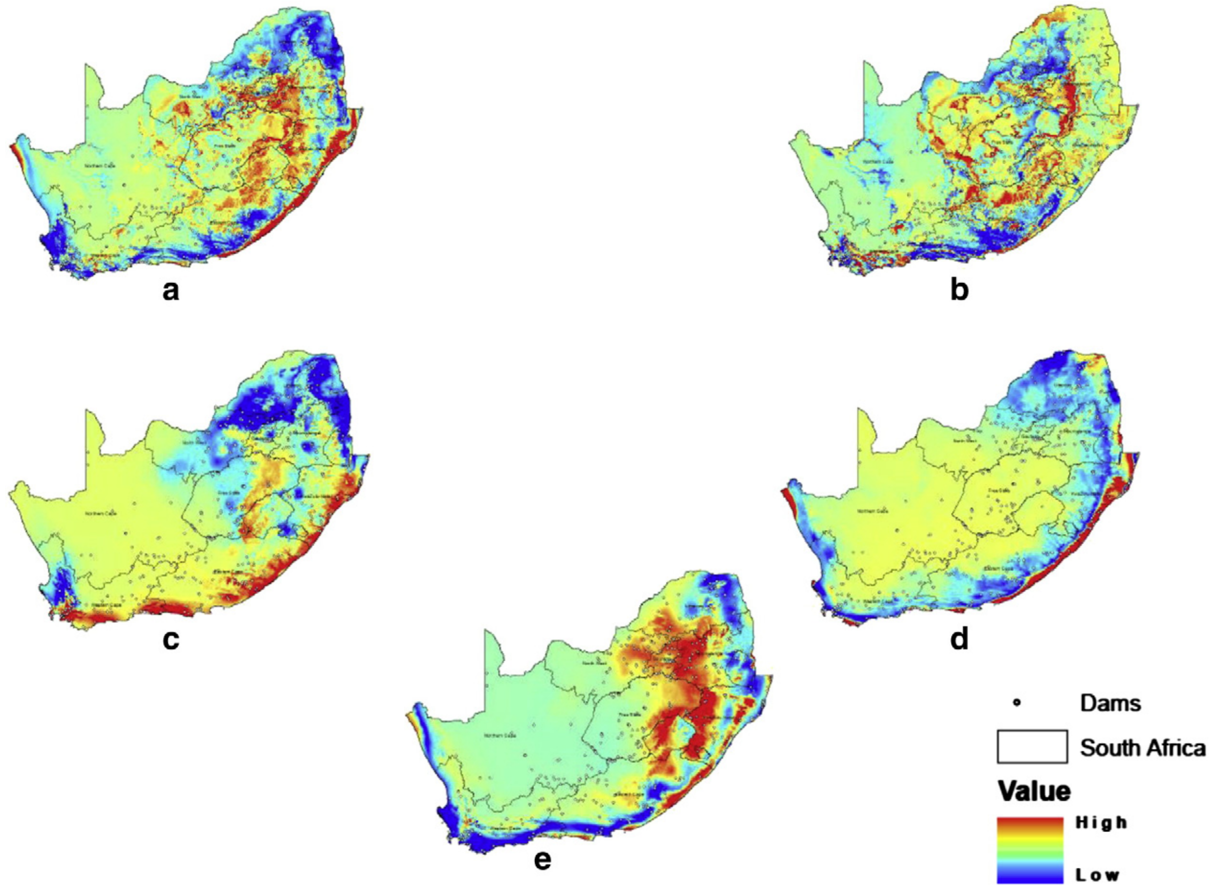

Fig. 2. Ecological niche modeling of species distribution based on predicted climate for 2080. (a) *Azolla filiculoides*, (b) *Eichhornia crassipes*, (c) *Myriophyllum aquaticum*, (d) *Pistia stratiotes*, and (e) *Salvinia molesta*. Areas in red indicate regions that are climatically suitable for species establishment whereas areas in blue indicate region that are less suitable. Dams located in areas that are climatically suitable/less suitable to current climate are indicated by dots. For the names of these dams in each province, see Table 1. On the legend, low = low probability of species occurrence; high = high probability of species occurrence.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.sajb.2015.07.017.

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