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ORIGINAL PAPER

Ecological niche modeling of the invasive potential of Nile tilapia *Oreochromis niloticus* in African river systems: concerns and implications for the conservation of indigenous congenics

Tsungai A. Zengeya · Mark P. Robertson ·
Anthony J. Booth · Christian T. Chimimba

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Abstract This study applied ecological niche models to determine the potential invasive range of Nile tilapia, *Oreochromis niloticus*, with a particular focus on river systems in southern Africa where it is now established and spreading. Computational tools such as niche models are useful in predicting the potential range of invasive species, but there are limitations to their application. In particular, models trained on native records may fail to predict the full extent of an invasion. This failure is often attributed to changes in either the niche of the invading species or the variables used to develop the models. In this study, we therefore evaluated the differences in the predictive power of models trained with different environmental variables, the effect of species range (native vs. introduced) on model performance and assessed whether or not there is evidence suggestive of a niche shift in Nile tilapia

following its introduction. Niche models were constructed using Maxent and the degree of niche similarity was assessed using Schoener's index. Null models were used to test for significance. Model performance and niche conservatism varied significantly with variable selection and species range. This indicates that the environmental conditions available to Nile tilapia in its native and introduced ranges are not congruent. Nile tilapia exhibited broad invasive potential over most of southern Africa that overlaps the natural range of endemic congenics. Of particular concern are areas which are free of exotic species but are now vulnerable due to the promotion of fish introductions mainly for aquaculture and sport fishing.

Keywords Ecological niche modeling · Invasion · Indigenous congenics · Maximum entropy models (Maxent) · Nile tilapia · Southern Africa

T. A. Zengeya (✉) · M. P. Robertson · C. T. Chimimba
Department of Zoology and Entomology,
DST-NRF Centre for Invasion Biology, University
of Pretoria, Private Bag X20, Hatfield 0028, South Africa
e-mail: tzengeya@zoology.up.ac.za

Present Address:

T. A. Zengeya
Natural Resources and the Environment, Council for
Scientific and Industrial Research (CSIR),
PO Box 395, Pretoria 0001, South Africa

A. J. Booth
Department of Ichthyology and Fisheries Science, Rhodes
University, PO Box 94, Grahamstown 6140, South Africa

Introduction

Invasive aquatic species, once established, are virtually impossible to eradicate (Lockwood et al. 2007). This is of particular concern with highly invasive and wide-ranging species where prevention should be the preferred remediation method (Wise et al. 2007). As is often the case with highly invasive fish species, after their establishment, the only practical management

option is often only to predict the species eventual distributional range and adopt measures to either stop or slow its dispersal across river systems (Chen et al. 2007). Ecological niche modeling is an effective tool to predict species ranges and to direct management efforts to confirm establishment, direct remediation efforts, and contain further spread (Jimenez-Valverde et al. 2011). Ecological niche modeling is a correlative method that utilizes associations between environmental variables and known species' occurrence localities to predict potential areas where a given species is likely to establish (e.g., Guisan and Thuiller 2005; Elith et al. 2006; Elith and Leathwick 2009). It has been successfully applied to an array of ecological disciplines that include ecology and evolutionary biology, impacts of climatic change, invasion biology and conservation biology (see Guisan and Thuiller 2005 for a review on the development and applications of ecological niche models).

Recently, some authors have highlighted the limitations of niche models for forecasting the potential range of invasive species (Elith et al. 2006; Fitzpatrick et al. 2007). In particular, several studies have shown that niche models that were developed using native range occurrences may fail to predict the full extent of an invasion. This failure has often been attributed to lack of niche conservatism by the invading species and/or the choice of environmental variables used to train the models (Peterson and Nakazawa 2008; Rödder et al. 2009; Rödder and Lötters 2009, 2010). Niche conservatism is defined as the retention of niche-related ecological traits by a species over space and time (Wiens et al. 2010). Niche conservatism is a major tenet of ecological niche modeling of invasive species and it is hypothesised that a species will spread primarily into areas whose climatic niche is congruent with that of its native range (Pearman et al. 2008). However, some recent studies have found mismatches between species' native and invasive range climatic niches (Broennimann et al. 2007; Fitzpatrick et al. 2007; Broennimann and Guisan 2008). Such apparent niche shifts during biological invasions violate the basic assumption behind the application of ecological niche models and weaken their reliability (Rödder and Lötters 2010). Evidence for niche shifts is, however, still equivocal, and the entire issue of niche conservatism of invasive species is still under debate (Rödder and Lötters 2009, Peterson 2011). The predictive ability of ecological niche models is also sensitive to

the selection of variables used to build them (Peterson and Nakazawa 2008). Climatic conditions in disjunct native and introduced ranges may show variation in environmental variables because of landscape heterogeneity. As a result, certain environmental variables maybe limiting in the native region but have little or no influence in the introduced range because some other variable may be more limiting (Rödder and Lötters 2009). Therefore, it is likely that the predictive abilities of models will differ if a particular species occupies a different niche space in its native and introduced range (Fitzpatrick et al. 2008).

This study applied ecological niche models to predict the potential geographic distribution of Nile tilapia outside its native range, with a particular focus on river systems in southern Africa where it has become established and is now spreading. Nile tilapia, *Oreochromis niloticus* (Linnaeus 1758), is an endemic African freshwater cichlid that is native to the Nile River basin, south-western Middle East and the Niger, Benue, Volta and Senegal Rivers, lakes Chad, Tanganyika, Albert, Edward, and Kivu (Trewavas 1983; Daget et al. 1991). Owing to its hardy nature, and its wide range of trophic and ecological adaptations, it has been widely introduced for aquaculture, augmentation of capture fisheries, and sport fishing (Trewavas 1983; Welcomme 1988). It is currently one of the most widely distributed invasive fish and has established viable feral populations in most tropical and sub-tropical environments to which it has gained access (Welcomme 1988; Costa-Pierce 2003; Canonico et al. 2005). Within Africa, Nile tilapia was initially introduced into Lake Victoria in the 1950s and its distribution has since expanded to include most of the river systems in eastern and southern Africa (Skelton 1994). The introduction of Nile tilapia into novel river systems is a cause for concern for the conservation of indigenous congenics that are at risk of extirpation through hybridization and competition with Nile tilapia (Chifamba 1998; Canonico et al. 2005; Cambray and Swartz 2007; Zengeya and Marshall 2007; Weyl 2008). Despite its widespread distribution within sub-Saharan Africa, several river systems are still free of Nile tilapia but still remain vulnerable. These areas currently act as reserves for the conservation of indigenous congenics and it is important to identify these areas to direct management efforts to prevent further Nile tilapia introductions.

In this study we evaluated the potential of Nile tilapia to establish and extend feral populations in novel areas outside its natural distributional range. Specifically, we sought to: (1) evaluate the effect of the number and type of environmental variables on the projected native and introduced ranges of Nile tilapia, (2) evaluate the influence of a species' range (native vs. introduced) on model performance, (3) evaluate whether or not there is evidence suggestive of a niche shift in Nile tilapia after introduction, and (4) evaluate the predicted distribution of the Nile tilapia across African river systems and highlight the conservation implications for indigenous congeners as a result of Nile tilapia invasions.

Methods

Environmental data sources

The environmental variables dataset was composed of proxy bioclimatic variables that have been widely used in ecological niche modeling of freshwater systems (Table 1) (Igushi et al. 2004; McNyset 2005; Zambrano et al. 2006; Chen et al. 2007). These variables represent annual trends (mean annual temperature and annual precipitation), seasonality (annual range in temperature and precipitation) and either extreme or limiting environmental factors (temperature of the coldest and warmest months and precipitation of the wet and dry quarters) and were obtained from WorldClim (Hijmans et al. 2005; <http://www.worldclim.org>).

Specimen data sources

Georeferenced occurrence data for Nile tilapia were obtained from various sources including, museum specimen records, biodiversity databases such as FishBase (<http://www.fishbase.org>), Global Biodiversity Information Facility (GBIF; <http://www.gbif.org>), the published literature, and fish survey data from various fisheries departments in southern African countries that included Botswana, Mozambique, Zambia and Zimbabwe. A total of 92 occurrence points were obtained for Nile tilapia in its native range and 81 localities in its introduced range (Fig. 1). We defined its native range as the area where it is known to occur naturally as defined by both Trewavas (1983) and

Daget et al. (1991) (Fig. 1). All occurrence records outside the species' native range were considered to be introductions and as such indicated the current introduced range of the species.

Model building

Maxent uses occurrence records (representing species presence) and a set of background records to predict the potential distribution of a species. This requires the definition of the region from which the background records are drawn that can influence model performance (van der Wal et al. 2009; Anderson and Raza 2010). Preliminary analysis to delimit background size was done using methods of van der Wal et al. (2009) and showed that background size expanded from 10 to 75 km, but beyond that there were only small improvements in model fit. Therefore, background size was set at 75 km.

We used two approaches to build ecological niche models for Nile tilapia in African river systems. We developed niche models to evaluate the effect of: (1) the number and type of environmental variables on the projected native and introduced ranges of Nile tilapia, (2) the influence of species range (native vs. introduced) on model performance, and (3) whether or not there is evidence suggestive of a niche shift in Nile tilapia following introduction. This was done by constructing separate niche models for the native and introduced ranges and training them on four different groups of environmental variables. The Bioclim environmental dataset which consists of 19 variables, was divided into four groups: (1) "comprehensive", which consisted of all 19 variables, (2) "minimum", which consisted of 6 variables that represented the availability of water and energy, (3) "temperature", which consisted of 11 variables that represented temperature parameters, and (4) "precipitation" which consisted of 8 variables that represented precipitation parameters (Table 1). Finally, in each group, variables were evaluated using correlation analysis to exclude those variables that were highly correlated ($r > 0.8$) (Dormann et al. 2012). The spatial resolution of all environmental variables was 30 arc seconds.

We constructed ten niche models for Nile tilapia within its native range and, in each model, all native occurrence records were partitioned into a calibration set (training set) and a testing set (validation set) using k -fold partitioning (Phillips et al. 2006). Average

Table 1 Environmental variable groups and the relative contribution (%) of each variable used to build ecological niche models of Nile tilapia (*Oreochromis niloticus*) in river systems in its native and introduced ranges in Africa

Environmental variables	Native range			Introduced range		
	Comprehensive	Minimum	Temperature	Comprehensive	Minimum	Precipitation
BIO1 = annual mean temperature	0.3	5.7	4.0	1.1	23	24.4
BIO2 = Mean diurnal range	1.5		5.7	4.2		8.9
BIO3 = Isothermality	0		1.9	0.1		0.2
BIO4 = Temperature seasonality	22.2		39.0	29.5		54.2
BIO5 = Maximum temperature of warmest month	0.7	13.1	8.5	0	0.9	11.6
BIO6 = Minimum temperature of coldest month	18.4	51.3	33.6	0	21.8	0.3
BIO7 = Temperature annual range	2.4		7.0	0.2		0.4
BIO8 = Mean temperature of wettest month	5			6.7		
BIO9 = Mean temperature of driest quarter	3.6			7.5		
BIO12 = Annual precipitation	0.8	4.6		2.7	43.7	71.6
BIO13 = Precipitation of wettest month	0.7	20.5		3.2	6.7	14.4
BIO14 = Precipitation of driest month	0.7	4.9		7.8	4.0	6.1
BIO15 = Precipitation seasonality	4.5			19.1	0.0	7.9
BIO18 = Precipitation of warmest quarter	23.1			40.4		
BIO19 = Precipitation of coldest quarter	16.1			3.9		

The variables which explained the most variation in model performance are shown in bold. The Bioclim dataset (19 variables) was divided into four groups: (1) “comprehensive”, which consisted of all 19 variables, (2) “minimum”, which consisted of 6 variables that represented the availability of water and energy, (3) “temperature”, which consisted of 11 variables that represented temperature parameters, and (4) “precipitation”, which consisted of 8 variables that represented precipitation parameters. Only variables that were not correlated in each group ($r > 0.8$) are shown

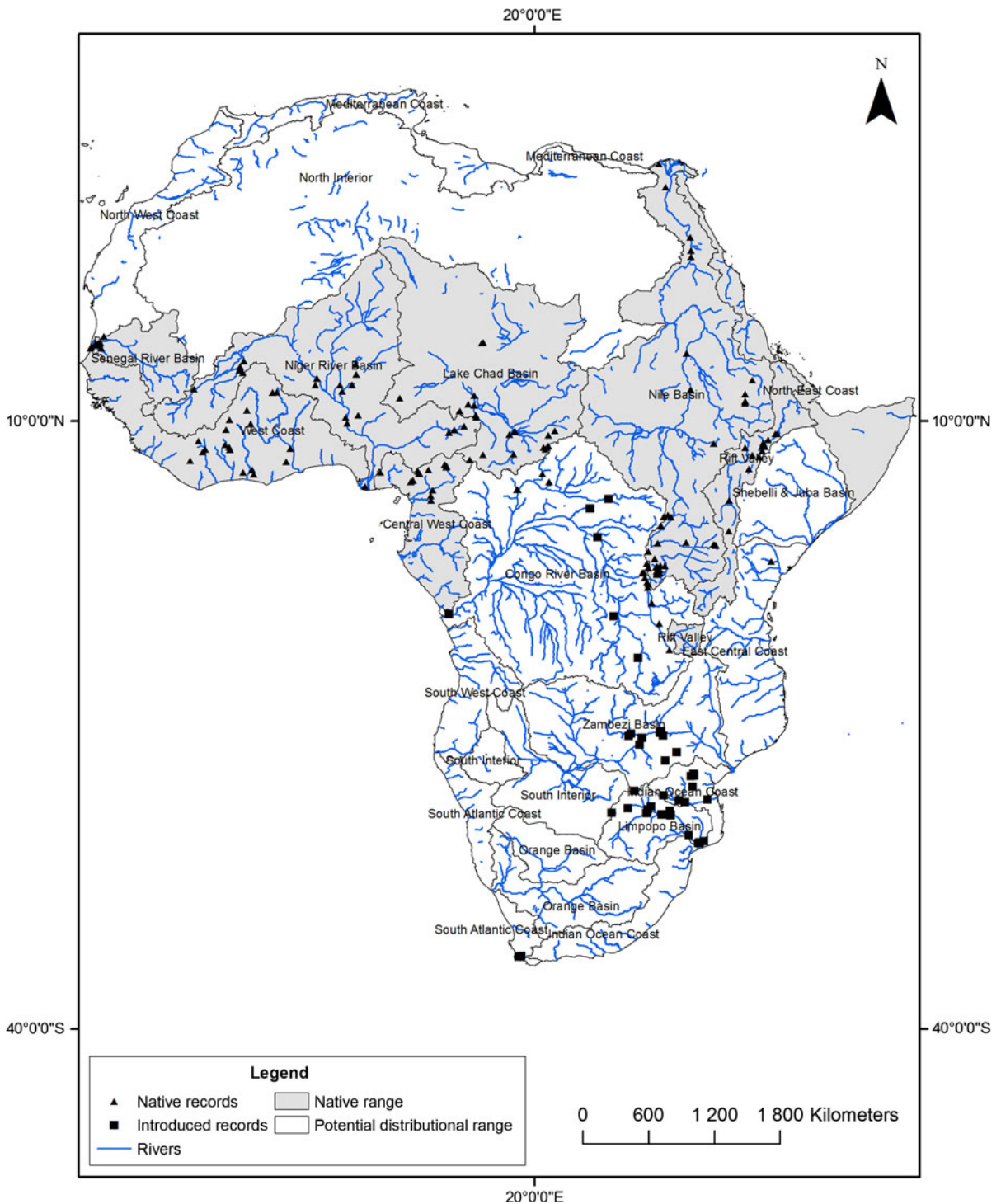


Fig. 1 The major river and lake basins in Africa together with main rivers, georeferenced native occurrence records (*filled triangle*) and known introduction (*filled square*) records of Nile

tilapia (*Oreochromis niloticus*) outside its native range. (Source: African Water Resources Database (AWRD; Jenness et al. 2007; <http://www.fao.org/geonetwork>)

model performance was obtained by repeating the process for 10 iterations. A consensus map was then created as an average of the 10 native range projection maps. We then used known introduction records to project the potential range of Nile tilapia in novel river systems in Africa. Model evaluation was conducted using the same k -fold method as outlined for the native range.

Niche similarity was analysed between ecological niche models of Nile tilapia from its native and introduced ranges using ENMTools (Warren et al. 2010). ENMTools quantifies niche similarity using two measures described by Warren et al. (2008), namely, Schoener's index of niche breadth (D) and Hellinger distance (I). D and I are quantitative measures of differences in habitat suitability between two potential distribution models and values may range from 0 (indicating that niche models are completely different) to 1 (indicating that niche models are identical). In this study, we only used Schoener's index of niche breadth (D) because it has been shown to consistently out-perform other quantitative metrics of niche overlap (Rödder and Engler 2011). The significance of the D values was then evaluated using null models of niche similarity. For niche similarity, we tested the hypothesis that ecological niche models drawn from entirely non-overlapping Nile tilapia populations (native and introduced ranges) are more different from one another than expected by chance given the underlying environmental difference between the two regions. This test was conducted by comparing ecological niche models based on native records of Nile tilapia but trained on a background randomly drawn around known occurrence points in its introduced range (i.e., as opposed to using actual occurrence points). The random samples from the introduced range were drawn from a background whose area was defined as a radius of 75 km from each known occurrence point (see model building section for justification of background selection). The same process was repeated by building ecological niche models based on known introduced records and trained on a randomly drawn background from its native range. This process was repeated in either direction (native \leftrightarrow introduced) to generate 100 pseudo-replicate datasets. The observed measures of niche similarity (D) from the two original populations (native and introduced ranges) were then compared with percentiles of these null distributions. The

hypothesis that niche similarity (or divergence) is different from that expected by chance between Nile tilapia populations in its native and introduced ranges based on the availability of habitats was rejected when the empirically observed values of D were either lower or higher than values obtained from pseudo-replicate datasets, resulting in a Type 1 error of 0.01.

To evaluate the predicted distribution of the Nile tilapia across African river systems, we constructed niche models using both native and introduced range occurrence records. Niche models were trained only with the "minimum" group of biologically important environmental variables (Table 1). Ten predictions were made using the k -fold method and in each model, the calibration set consisted of a subset of occurrence records from the native range and a subset of known introductions elsewhere in Africa. The projected models were then evaluated using a subset of records from the introduced range only. A consensus map was then created to show the average of the 10 introduced range projection maps.

Model evaluation

We used two different methods of model evaluation using those models trained with different environmental predictors to examine the performance of niche models of Nile tilapia from its native and introduced ranges:

- (1) Maximum test AUC: AUC defines the discrimination ability (between presence and background) of the models where values may range from 0 (indicating random distribution) to 1 (indicating perfect prediction), with values >0.5 indicating that the model discriminates better than random (Mantel et al. 2001). AUC values were calculated in Maxent and predictions with an AUC value greater than 0.9 were considered to be acceptable (Swets 1988; Fielding and Bell 1997).
- (2) Minimum difference between training and test data (AUC_{diff}): Overfitted models generally perform better on training data than on test data and by minimising the difference between training and test data, we minimize the risk that our models are over-parameterised in such a way as to be overly specific to the training data (Warren and Seifert 2011).

To further identify over-parameterisation, we evaluated model performance (AUC values) with niche overlap (*D* values) and omission error (known areas of presence that were predicted absent). Models trained with relaxed variables (i.e., variables that show large differences between the native and introduced ranges) are likely to lead to highly conservative models that predict large areas of the background without known occurrence points as either absences or as unsuitable habitat. The AUC statistic is known to be sensitive to the relative ratio of suitable to unsuitable habitat, and tends to increase dramatically when models are projected into an area that contains large areas of unsuitable habitat (Lobo et al. 2007). Highly specific models are therefore likely to have high AUC values (indicating better model performance) but low niche overlap (indicating large differences in habitat suitability between the native and introduced ranges). In contrast, models that are trained with conserved variables (i.e., variables with the least difference between the native and introduced ranges) are likely to be less conservative and produce predictions that show larger areas of the background without known occurrence points as being suitable habitat. Therefore, the AUC statistic is likely to penalise less conservative models for predicting areas as being suitable where there are no occurrence records, leading to low AUC values. On the other hand, omission error is likely to decrease with increasing niche overlap (*D* values) because models become less conservative and predict larger areas of known presence as being suitable.

Model performance (AUC values) was analysed by a two-way ANOVA with environmental variables (four groups) and species range (native and introduced) as fixed factors. Ten replicates were generated for each of the four environmental variable groups in both the native and introduced ranges, giving a total sample size of 80 AUC values. All statistical analyses were conducted using STATISTICA 10 (StatSoft, 2010).

Results

Comparison of bioclimatic variables

The relative contribution of environmental variables varied with environmental variable selection (four groups) and between Nile tilapia’s native and introduced ranges (Table 1). Model performance differed significantly with the environmental variables (four groups) used for model training (ANOVA: $F_{3, 75} = 430.63$; $n = 80$; $P < 0.001$) (Table 2). In general, and irrespective of sampling region (native or introduced), the “comprehensive” group recorded the best model performance (average AUC = 0.96, range = 0.95–0.97) and models developed from the “precipitation” subset recorded the lowest model performance (average AUC = 0.87, range = 0.83–0.90). Overall model performance for all four groups of environmental variables was significantly higher (ANOVA: $F_{3, 72} = 188.66$; $n = 80$; $P < 0.01$) in the introduced range compared to the native range (Table 2).

Table 2 Model performances (AUC), niche overlap (Schoener’s index of niche breadth (*D*)) values and niche similarity tests for Nile tilapia (*O. niloticus*) in its native and introduced ranges in Africa in relation to different environmental variables

Variable set	Model fit (AUC)			D	
	Native	Introduced	Overlap	Background	
				inv → nat	nat → inv
Comprehensive	0.948	0.959	0.242	0.00	0.00
Minimum	0.877	0.924	0.438	0.00	0.00
Temperature	0.876	0.926	0.377	0.26	0.84
Precipitation	0.869	0.893	0.606	0.00	0.00

The Bioclim dataset (19 variables) was divided into four groups: (1) “comprehensive”, which consisted of all 19 variables, (2) “minimum”, which consisted of 6 variables that represented the availability of water and energy, (3) “temperature”, which consisted of 11 variables that represented temperature parameters, and (4) “precipitation”, which consisted of 8 variables that represented precipitation parameters. The final number of variables in each group was further reduced to include only variables that were not correlated ($r > 0.8$)

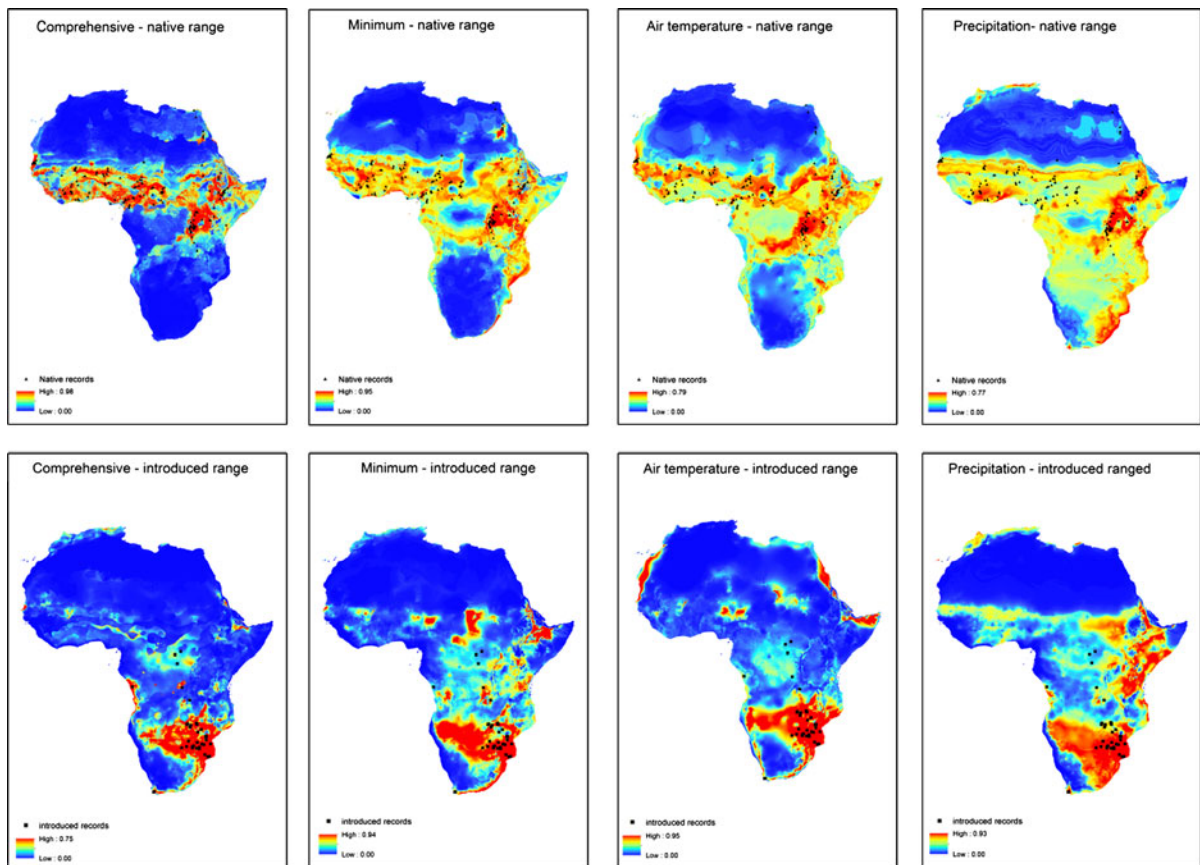


Fig. 2 The projected distribution of Nile tilapia (*Oreochromis niloticus*) in its native and introduced ranges in African river systems. Each map represents an average of 10 replicates for each group of environmental variables and region (native and introduced) created using the k -fold partition method. Potential

distribution is indicated by shaded areas, with red and blue indicating high and low probabilities of suitable conditions, respectively. Triangles (filled triangle) indicate georeferenced native occurrence records and squares (filled square) indicate known introduction records. (Color figure online)

Niche overlap and similarity

The niche overlap and similarity tests varied significantly with environmental variable selection (four groups) and between Nile tilapia's native and introduced ranges (Table 2). The variable group with the highest niche overlap was "precipitation" (average $D = 0.61$, range = 0.58–0.63) followed by "minimum" (average $D = 0.44$, range = 0.42–0.45). The lowest overlap was recorded for "comprehensive" (average $D = 0.24$, range = 0.23–0.26). Niche models trained with "comprehensive", "minimum" and "precipitation" environmental variables had significant differences ($P < 0.01$) in niche similarity between the native and introduced ranges; in contrast models trained with "temperature" variables recorded no significant differences ($P > 0.01$) between the two respective regions (Fig. 2).

A significant relationship was found between niche overlap and model performance, with AUC values decreasing significantly with increasing D values (i.e. increasing overlap, Fig. 3). In contrast, the omission error decreased significantly ($P < 0.01$) with increasing D values (lower omission errors implied that the models were less conservative (i.e. predicted larger areas as being suitable, Fig. 4). For all environmental variable groups, the training AUC was significantly higher than the test AUC in the introduced range while in the native range, the inverse was true (Fig. 5).

Realised and potential distributional range

The actual distribution of the Nile tilapia within its native range covers most of north Africa (Nile River basin, Niger River basin, Lake Chad basin, Central West

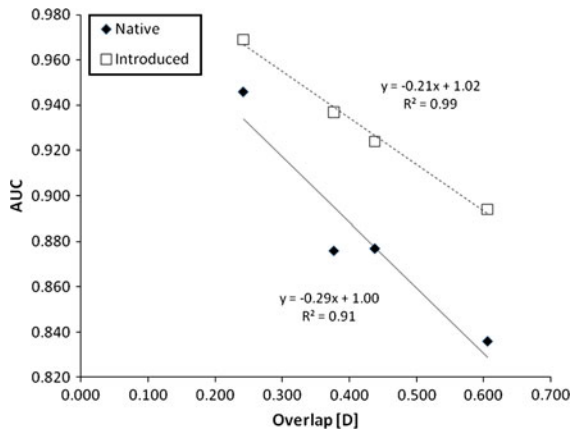


Fig. 3 The relationship between niche overlap and model performance (AUC) for ecological niche models of Nile tilapia (*Oreochromis niloticus*) in its native (filled diamond) and introduced (open square) ranges in Africa. Each data point is an average of 10 replicates that were generated for each of the four groups of environmental variables (“comprehensive”; “minimum”; “temperature”; and “precipitation”) in both the native and introduced ranges

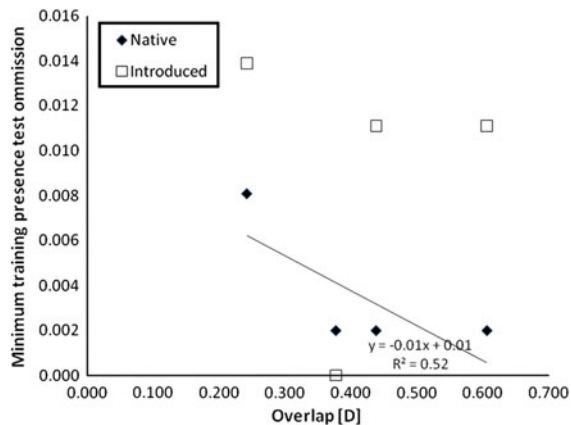


Fig. 4 The relationship between niche overlap and minimum training presence omission error for ecological niche models of Nile tilapia (*Oreochromis niloticus*) in its native (filled diamond) and introduced (open square) ranges in Africa. Each data point is an average of 10 replicates that were generated for each of the four groups of environmental variables (“comprehensive”; “minimum”; “temperature”; and “precipitation”) in both the native and introduced ranges. Only significant regression lines are drawn

Coast basin, West Coast, and Senegal River basin) but is limited to the north by the Sahara desert, and extends south-wards to include most of the great lakes region (Tanganyika, Albert, Edward and Kivu) (Fig. 6). The predicted potential geographical range of the Nile tilapia reveals a broad invasive potential over most of central

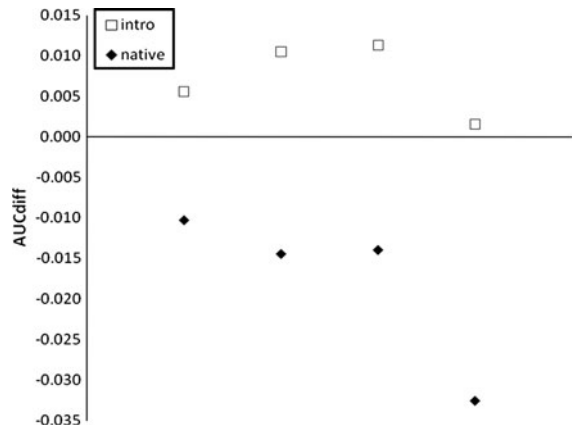


Fig. 5 The minimum difference between training and test (AUC_{diff}) for ecological niche models of Nile Tilapia (*Oreochromis niloticus*) in its native (filled diamond) and introduced (open square) ranges in relation to different environmental variables. Each data point is an average of 10 replicates that were generated for each of the four groups of environmental variables (“comprehensive”; “minimum”; “temperature”; and “precipitation”) in both the native and introduced ranges

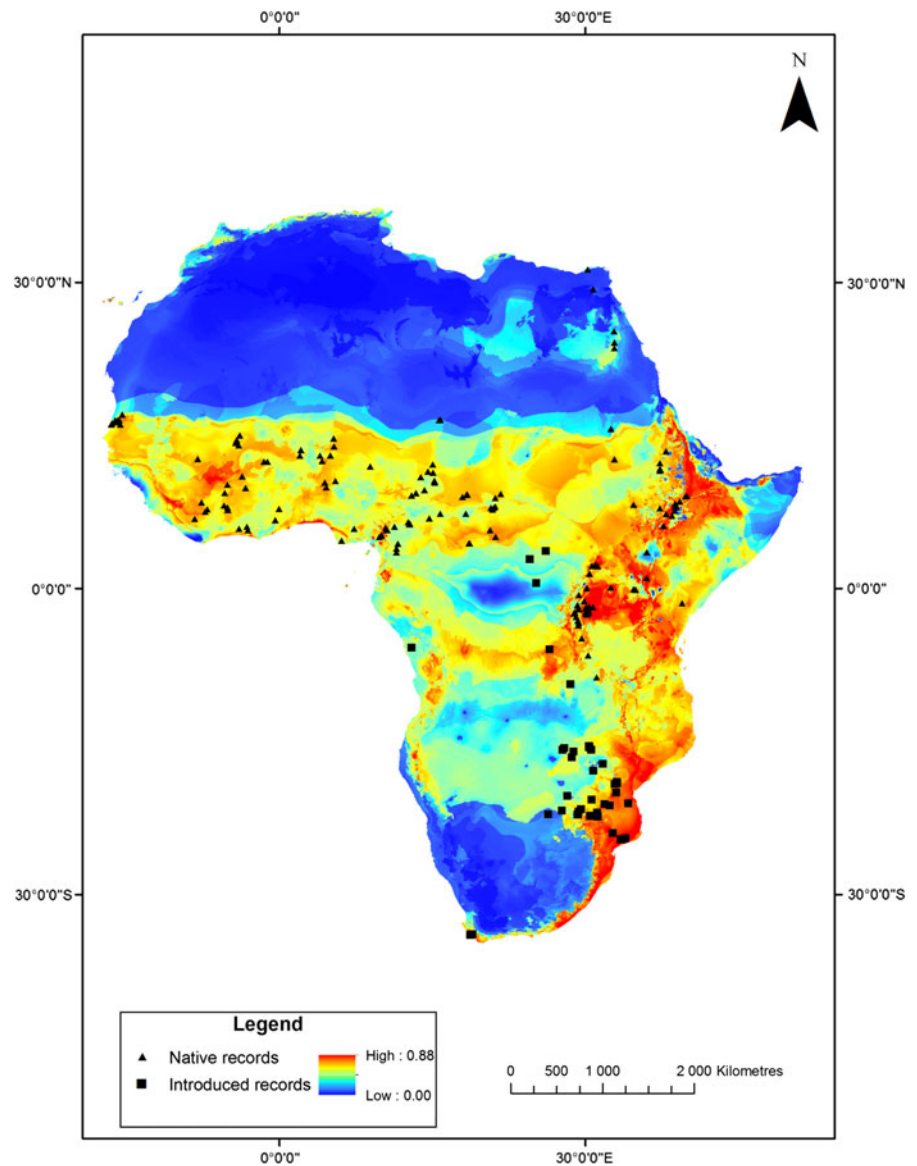
and southern Africa. Its potential distributional range covers the entire basins of the Zambezi and Limpopo rivers and the continent’s coastal rivers along the Indian Ocean. The Nile tilapia is also predicted potentially to occur in the East Central Coast of Africa and the Shebelle and Juba basins (Fig. 6). The models, however, predicted low suitability for most of the Congo and Orange River basins and west-flowing rivers in the south Atlantic coast of Africa.

Discussion

Comparison of bioclimatic variables

Methods used to develop niche models remain variable and unstandardised (Jimenez-Valverde et al. 2011). In agreement with recent studies that have criticised the use of the Area Under the Curve (AUC) statistic to evaluate niche models (Lobo et al. 2007; Jimenez-Valverde 2012), this study also found some major limitations in its application. The AUC statistic was found to be sensitive to the number and type of environmental variable used in model construction and spatial extent of the study area. These caveats of using AUC for model evaluation are especially evident when dealing with invasive species that have disjunct native and introduced ranges that show variation in climatic conditions because of landscape heterogeneity (Peterson 2011). For example,

Fig. 6 The projected distributional range of Nile tilapia (*Oreochromis niloticus*) in Africa based on ecological niche models constructed using both native (filled triangle) and introduced (filled square) occurrence records. Potential distribution is indicated by shaded areas, with red and blue indicating high and low probabilities of suitable conditions, respectively. (Color figure online)



contrary to our findings, other comparable studies evaluating the potential distribution of invasive species, have recorded best model performance with “minimum” variables relative to more “comprehensive” environmental variable groups (Rödger and Lötters 2009, 2010). In our study, models trained with large numbers of variables recorded the highest AUC (indicating better model performance) but low niche overlap (indicating large differences in habitat suitability between the native and introduced ranges). This is likely to be a result of the inclusion of relaxed variables (i.e., those variables that show large differences between the native and introduced ranges) (Rödger and Lötters

2009), which resulted in highly conservative models that predicted large areas of the background without known occurrence points as either absences or as unsuitable habitats. In contrast, “minimum” variable sets consisted of conserved variables (i.e., those variables with the least difference between the native and introduced ranges) that produced predictions that show larger areas of the background as suitable relative to models produced using the comprehensive set. The AUC statistic appeared to have penalised the models trained with minimum and precipitation variables for predicting areas as being suitable where there are no occurrence records, hence the low AUC values (Fig. 2).

Second, we found significantly higher model performance in the introduced range than the native range for all variable sets. The low AUC values in the native range do not necessarily indicate that the models are poor but rather due to a methodological artefact as the training AUC was always higher than the test AUC in the introduced range while in the native range the inverse was true. Such a difference indicates that models in the introduced range are likely to be over-fitting in such a way as to be overly specific to the training data (Warren and Seifert 2011). In our study, the amount of habitat that is predicted to be suitable in the introduced range using known introduced records is less than that the predicted suitable habitats using native range points. It is possible that the observed differences in the distribution of suitable habitats and the occurrence of Nile tilapia populations both in its native and introduced ranges may be a result of differences in sampling effort between the two respective populations.

In southern Africa, Nile tilapia is still spreading and as a result the known occurrence records are unlikely to represent the whole range of environmental conditions that the species can tolerate (a major assumption of ecological niche models). In southern Africa, most occurrence data records are limited to monitoring surveys conducted by various national fisheries departments. These are generally limited in scope and only include major rivers and reservoirs with viable artisanal and commercial fisheries such as the Kafue River and lakes Kariba and Chicamba. Nile tilapia has been extensively propagated by farmers and anglers for recreational and sport fishing and introduced small and medium reservoirs around the sub-region, often circumventing permitting processes. As a consequence, these introductions are seldom documented and monitored. This paucity of information makes it difficult to ascertain exactly those areas where Nile tilapia has been introduced and to predict those areas where it is likely to spread. Although we consulted widely and managed to obtain georeferenced occurrence data for Nile tilapia from museum specimen records, biodiversity databases, the published literature, and fish survey data, only 173 occurrence points were obtained for the species (92 in its native range and 81 points in its introduced range) and we assume that these data represent the most up-to-date compilation of known occurrences of Nile tilapia within the African continent.

Given the limitations of the AUC, which models should be considered to be the most informative models? Although the “comprehensive” variables have the highest AUC, they appear to be overly conservative. It has been suggested that final model selection should be based on biologically meaningful and more conserved variables to avoid over-restriction (Rödder and Lötters 2009; Rödder et al. 2009). Our results are in agreement with these findings and we considered models trained with the “minimum” dataset to be the most informative because they described biologically relevant parameters such as the availability of water and thermal energy. In the “minimum” dataset, the variable which explained the most variation in model performance was minimum water temperature where the probability of Nile tilapia establishment was very low at temperatures below <20 °C but increased exponentially with temperatures up to maximum of ≥ 30 °C. The areas that are highly suitable for the establishment of Nile tilapia were, therefore, mainly associated with a minimum monthly temperature of ≥ 20 °C. Nile tilapia is a eurythermal species that can tolerate a wide range of temperatures (8–42 °C) with a preferred optimal temperature range between 31 and 36 °C (Philippart and Ruwet 1982). However, the natural fitness of Nile tilapia in terms of respiration, feeding, growth and reproduction is reduced at sub-optimal temperatures below 20 °C (Al-Amoundi et al. 1996; Ross 2000; Atwood et al. 2003; Charo-Karisa et al. 2005). Annual precipitation influences the availability of surface water, habitats and food resources for aquatic fauna (Lowe-McConnell 2000) and, indirectly influences the successful establishment of aquatic invasive species. It is therefore not surprising that the actual geographic extent (realised distribution) of Nile tilapia within African river systems is limited by regions of moderate to low rainfall and extreme temperature ranges such as the Sahara desert in the north (native range) and the Kalahari and Namib deserts in the south (introduced range).

A major limitation for the application of ecological niche models in aquatic systems is the lack of environmental data such as physical and chemical water quality variables (McNyset 2005; Zambrano et al. 2006). To circumvent the lack of aquatic environmental data, we used proxy atmospheric variables (air temperature and precipitation) that have been applied in recent studies in freshwater systems

(Igushi et al. 2004; McNyset 2005; Zambrano et al. 2006; Chen et al. 2007; DeVaney et al. 2009). Despite their wide application in ecological niche modeling of aquatic systems, the use of atmospheric variables has its limitations. The main assumption is that air temperature translates to water temperature and precipitation translates to flow; however these variables are not related in a simply linear manner (e.g. see Benyahya et al. 2007). Consequently, air temperature and precipitation are simply surrogates of aquatic data and are likely far from perfect surrogates.

Niche conservation versus niche shift

Consistent with other studies comparing the distribution of invasive species in their native and introduced ranges (see Rödder and Lötters 2009, 2010), we found that the degree of niche conservatism of Nile tilapia between the native and introduced ranges varies with the environmental variables used. Peterson (2011) recently argued that until empirical evidence of niche shifts is robust to alternative means of analysis, biological inferences about species niche conservatism should be made with caution. Nevertheless, in this study, niche similarity tests revealed that the environmental conditions available to Nile tilapia in its native and introduced ranges are not congruent. This is expected because climatic conditions in disjunct areas may show variation in environmental variables because of landscape heterogeneity (Warren et al. 2008). The Nile Tilapia is extremely hardy, with a wide range of trophic and ecological adaptations, and adaptive life history characteristics (Welcomme 1988; Getabu 1994; Balirwa 1998; Njiru et al. 2004). These adaptive life history characteristics of Nile tilapia predispose it to be a highly successful invader, and may partly explain its successful establishment in novel river systems in southern Africa as shown in this study.

Conservation implications

The major conservation implication from this study was that a large proportion of river systems in southern Africa offer suitable habitats/conditions for the establishment of Nile tilapia. Nile tilapia exhibited a broad invasive potential over most of southern Africa that overlaps the natural range of all six endemic congeners. The localised distribution of

these six endemic congeners predisposes them to invasion because the introduction of Nile tilapia into a given catchment is likely to have a significant impact on species that have limited natural ranges. Of particular concern are those areas that have been free of non-native species but were predicted to be potentially suitable for the establishment of Nile tilapia and are now vulnerable due to the ardent promotion of aquaculture and sport fishing. These systems include the Cunene, Upper Zambezi, Okavango, Lower Zambezi, Lake Malawi and associated rivers (Bills and Marshall 2004; Tweddle 2010). These areas currently act as “reserves” for the conservation of indigenous congeners and concerted conservation efforts should be implemented to keep them free of invasive species. The advent of Nile tilapia into these river systems is a cause for concern for the conservation of indigenous congeners that are at risk of extirpation through hybridization and competition with Nile tilapia as observed elsewhere in systems where this species has been introduced (Chifamba 1998; Canonico et al. 2005; Cambray and Swartz 2007; D’Amato et al. 2007; Zengeya and Marshall 2007; Weyl 2008; Zengeya et al. 2012).

Conclusions

Our results provide quantitative evidence that the environmental conditions are not the same in both the native and introduced ranges of Nile tilapia. This indicates the ability of Nile tilapia to survive in conditions incongruent with its native range. It is tempting to ascribe such observations to a change in the species’ fundamental niche. However, it is more likely that the ‘new’ climate envelope (introduced range) represents a better exploitation of its fundamental niche and that the environmental conditions as described by our niche models, do not limit the potential distribution of Nile tilapia to the borders of its native range. A major limitation of correlative methods (e.g. Maxent as used in this study), is that they tend to describe a species’ realised niche rather than its fundamental niche. A mechanistic approach that incorporates a species ecophysiological response to environmental covariates would come closer to describing its fundamental niche (Kearney and Porter 2009; Webber et al. 2011). Further, niche models that are based on native range data and relaxed

environmental variables are likely to misrepresent the potential invasive range of Nile tilapia. Therefore, when modeling the potential spread of this and other invasive species, it is advisable to incorporate data from biologically meaningful conserved environmental variables and occurrence records from both native and introduced ranges because this is likely to give a better approximation of an invasive species' fundamental niche (Mau-Crimmins et al. 2006; Broennimann and Guisan 2008; Beaumont et al. 2009, Rödder and Lötters 2009, Rödder et al. 2009).

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