Predicting the potential distribution of invasive silver carp, *Hypophthalmichthys molitrix* in southern Africa

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Abstract

Predicting the potential geographical distribution and spread of nonnative species is of major concern to ecologists. Silver carp**,** *Hypophthalmichthys molitrix*, was introduced into South Africa in 1975 but the potential spread of this invader has not been addressed, despite recent studies indicating its potential ecological impacts in South Africa. Herein, the potential range of silver carp in southern Africa has been identified based on ecological niche modelling (maximum entropy method). Models were constructed using occurrence records and a defined background and calibrated using a *k*-fold method. The area under the receiver operating characteristics curve (AUC) was used to evaluate model performance. Both the native and introduced range model accurately predicted species occurrences (AUC = 0.98 and 0.94 respectively). Most of the northeastern parts of southern Africa, including the Limpopo River Basin where silver carp are reported, were correctly predicted as climatically suitable for silver carp. Areas with suitable climatic conditions for silver carp were further identified although no occurrence records were available for these areas e.g., Gauteng. Therefore, this study shows that the model demonstrated the potential use of ENM to accurately model species potential range using relatively few occurrence records. The implications of this invasion for South Africa are discussed.

Key words: Asian carp; Correlative approach; Cyprinidae; Ecological niche modelling; MaxEnt; Exotic.

Introduction

Invasive species generally disrupt recipient ecosystems leading to a loss of native biodiversity (Gozlan et al. 2010, Zengeya et al. 2011). Early detection or *a priori* assessment of the invasive potential of non-indigenous species is instrumental in reducing, or even preventing, potential impacts on recipient ecosystems. One method of predicting the potential distribution of species is by means of ecological niche modelling (ENM) (Guisan and Zimmermann 2000, Peterson and Vieglais 2001, Elith and Leathwick 2009). Correlative modelling approaches relate occurrence data to globally available spatial environmental data, summarizing abiotic factors limiting the distribution of species (Peterson and Vieglais 2001, Peterson 2001, 2003). An ENM can be used to identify geographical areas with similar abiotic environmental conditions as the realized niche of the species in its native range (Peterson 2003, Pearson and Dawson 2003).

Silver carp, *Hypophthalmichthys molitrix* (Valenciennes 1844; Cyprinidae), has been widely introduced and its ability to cause changes in ecosystem structure and functioning is well known (Spataru and Gophen 1985, Irons et al. 2007). Its native range extends over eastern Asia, including the major Chinese rivers e.g., Yangtze River, Pearl River, Yellow River, and Heilongjiang River (Zhang et al. 2001, Chen et al. 2007, Kolar et al. 2007, Hong-Xia et al. 2010). Early artificial introductions have extended the range of silver carp in its native range and led to debate about the exact extent of its native range (Chen et al. 2007, Kolar et al. 2007). Silver carp also inhabits ponds and lakes that must be linked to rivers to enable spawning (Kolar et al. 2007). Studies have found that silver carp are capable of establishing in a wide range of environmental conditions (Spataru and Gophen 1985, Opuszynksi et al. 1989, Lu et al. 2002, Kolar et al. 2007, Lübcker et al. (unpublished data), Calkins et al. 2012). This is contrary to the notion that silver carp require specific hydrological conditions to enable its establishment (Linhart et al. 1995, Coulter et al. 2013).

Silver carp is a well-known competitor in invaded ecosystems, owing to life history traits such as high reproductive and fast growth rates that often lead to high population densities (Sass et al. 2010). Silver carp is also known to be a versatile and generalist filter feeder that feeds primarily on phytoplankton and zooplankton, but also consumes other food items such as vegetative detritus (Kolar et al. 2007, Rosemberg et al. 2010). Its ability to fine filter large volumes of water, fast growth rate, high population density and versatile feeding behaviour, can often lead to alteration of community structures such as food webs and nutrient cycles in recipient ecosystems (Milstein et al. 1988, Cooke et al. 2009, Gozlan et al. 2010, Ma et al. 2010, Rosemberg et al. 2010). Such changes to phytoplankton, zooplankton and fish community structure can result in decreased size, growth rate, fitness and abundance of native fishes sharing a similar food niche with silver carp (Ho et al. 1975, Spataru and Gophen 1985, Milstein et al. 1988, Lu et al. 2002, Schuyler et al. 2009). For example, in river systems in North America where silver carp has been introduced, observed dietary overlap between silver carp and indigenous species such as paddlefish (*Polyodon spathula*), gizzard shad (*Dorosoma cepedianum*), and bigmouth buffalo (*Ictiobus cyprinellus*), has been implicated in the decline in condition factor and biomass of these indigenous species (Spatura and Gophlen 1985, Irons et al. 2007, Sampson et al. 2009). Currently, silver carp is ranked as one of the 100 worst invasive species in the world by the Invasive Species Specialist Group (ISSG) (Courtenay 1989) and has been classified as a harmful species under the "Injurious Wildlife Provision" of the Lacey Act; North America (18 U.S.C. § 42, as amended).

Silver carp was the first phytoplanktivorous fish to be introduced to South Africa in 1975 for algae control, which proved unsuccessful (Prinsloo and Schoonbee 1987). In 1992, silver carp was released into Flag Boshielo Dam in Mpumalanga, successfully establishing feral populations that have subsequently spread downstream into the Kruger National Park (Brits 2009). The full extent of the species distribution in southern Africa, however, is unknown. Only a few studies have been undertaken on the invasion biology of silver carp in recipient river systems in South Africa. Firstly, it has been suggested that silver carp could be associated with the mass mortality events of the Nile crocodiles, *Crocodylus niloticus* Laurenti 1786, in the Kruger National Park (Huchzermeyer 2012, Woodborne et al. 2012, Huchzermeyer et al. 2013). Secondly, Lübcker et al. (unpublished data) assessed the trophic ecology of silver carp in the oligotrophic Flag Boshielo Dam on the Olifants River in South Africa, and preliminary evidence indicates the ability of silver carp to establish in novel environments despite potential limiting conditions such as a low food resource base due to low primary productivity in the reservoir. Given the potential negative impacts, it would be useful to determine their potential distribution in river systems in southern Africa.

This study used niche modelling to predict the potential distribution of silver carp in southern Africa, with the aim of increasing our current understanding of the impact of invasive species and the factors that promote their introduction, establishment and spread in novel African river systems. The specific objectives were to: a) develop a niche model for silver carp in its native range and test the accuracy of the model; b) project the niche models onto a novel region (southern Africa) and evaluate the predictive performance of the model; c) identify areas at high risk of an invasion in southern Africa and discuss conservation implications within South Africa. Predicting the potential suitable geographical range of silver carp in southern Africa is necessary to identify river segments that are highly vulnerable to the establishment of the invasive silver carp. Concerted conservation efforts can then be directed in such areas to confirm establishment, direct remediation efforts, and contain further spread.

Methods and Materials:

Occurrence records

Occurrence records were sourced from Global Biodiversity Information Facility (GBIF; http://www.gbif.org; *sourced on 05/04/2011*) and the Nonindigenous Aquatic Species (NAS) information resource from the United States Geological Survey (USGS; http://nas.er.usgs.gov/queries/CollectionInfo.aspx?SpeciesID=549; *sourced on 12/07/2011*). All records obtained were examined for errors, and records with a spatial resolution greater than 0.05°, as well as duplicates, were removed. A total of 248 occurrence records remained for silver carp in North America, the native range (eastern Asia), and southern Africa combined. Of the 248 occurrence records, 12 were obtained for southern Africa and 12 for the native range. The remaining 224 occurrence records represented the silver carp distribution in North America (ranging from 24.59 – 53.79˚ N, 66.14 – 125.02˚ W) (Chen et al. 2007). The larger number of North American records in comparison to the south African and native records resulted in the over representation of North America in the modelling process. North American records were filtered to 1° spatial resolution to remove the bulk of the records by selecting only one occurrence record per 1° grid cell. Since the remaining 88 occurrence records still over represented North America in the modelling dataset, 30 occurrence records were randomly selected using the statistical software package R (R Development Core Team 2008) to obtain a relatively even proportion of North American records to the 24 records (12 native range and 12 southern African) used for modelling.

Bioclimatic variables

A set of 19 globally available, bioclimatic variables were sourced from the climate database, WorldClim (http://www.worldclim.org, Hijmans et al. 2005) and interpolated at a spatial resolution of 0.05° x 0.05. Bioclimatic variables included those representing annual trends (mean annual temperature and precipitation); extreme or limiting environmental factors (mean temperature and precipitation of the driest and wettest quarters); and variables accounting for seasonality (seasonal temperature and precipitation) for climate data recorded from 1950 – 2000. Bioclimatic variables were evaluated using three criteria: correlation analysis; biological relevance to the species; and a jack-knife procedure. Firstly, a correlation analysis was used to identify and group highly correlated variables (Pearson's *r* correlation coefficient > 0.8) (Austin 2002, Mas et al. 2004). Within each group of correlated variables, only the variable(s) with a direct effect on the physiological tolerances of silver carp was used as a predictor in subsequent analysis. Secondly, variables that are known to limit the distribution and survival of silver carp are well documented (Kolar et al. 2007) and therefore, as suggested by Jiménez-Valverde et al. (2011b), response curves obtained from models run using selected variables from the correlation analysis were carefully examined to ensure that they were congruent with the documented physiological tolerances of the silver carp. Lastly, to avoid spurious over-fitting by correlated variables (Phillips et al. 2006), a jack-knife procedure in MaxEnt was used to assess the contribution of each bioclimatic variable to the model performance. Variables contributing little to the initial model performance were omitted. Four direct predictors (out of the initial 19 bioclimatic variables), summarising biologically relevant parameters such as the availability of water and thermal energy, were included in the final model (Table 1). Fishes are ectothermic and rely on external environment to maintain constant body temperature. Changes in water temperature are therefore likely to affect biochemical reactions and influence physiological characteristics such as development and growth rates, as well as ecological and behavioural responses such as the onset of migration and reproduction (Linhart et al. 1995, Chen et al. 2007, Herborg et al. 2007, Buisson et al. 2008, De Vaney et al. 2009). Further, precipitation influences the availability of surface water, habitats, food resources, and overall primary productivity (Galloway and Cowling 1978). A fundamental limitation when using ENM to predict the potential distribution of aquatic species is the lack of aquatic environmental data (e.g., water quality variables). However, atmospheric variables have been used successfully as proxies for aquatic environmental data (Iguchi et al. 2004, Zambrano et al. 2006, Chen et al. 2007,

Table 1: Bioclimatic variables included in modelling the potential distribution of silver carp, *Hypophthalmichthys molitrix*, in southern Africa. Highly correlated variables were removed through a correlation analysis and a Jackknife procedure

Bioclimatic variables
Annual Mean Temperature
Mean Diurnal Temperature Range
Isothermality
Temperature Seasonality
Max Temperature of Warmest Month
Min Temperature of Coldest Month
Temperature annual range
Mean Temperature of Wettest Quarter
Mean Temperature of Driest Quarter
Mean Temperature of Warmest Quarter
Mean Temperature of Coldest Quarter
Annual Precipitation
Precipitation of Wettest Month
Precipitation of Driest Month
Precipitation Seasonality (Coefficient of Variation)
Precipitation of Wettest Quarter
Precipitation of Driest Quarter
Precipitation of Warmest Quarter
Precipitation of Coldest Quarter

- Variables in bold were included in the modeling process

Herborg et al. 2007, DeVaney et al. 2009, Zengeya et al. 2013) due to the strong correlation between water and atmospheric temperatures (Caissie 2001).

Model building

Model building was performed using a maximum entropy method implemented in the MaxEnt modelling package (MaxEnt v3.2.19; Phillips et al. 2006) by combining bioclimatic variables and species occurrence records to construct a model of the niche requirements of the species in the native range (eastern Asia). Maximum entropy has been shown to perform well in comparison to other approaches that use presence and background data (Elith et al. 2006, Peterson et al. 2007, Elith and Graham 2009, Kearney et al. 2010, Wolmarans et al. 2010). User-specified parameters were set to default, as suggested by Liu et al. (2005), with the regularization multiplier = 1; maximum number of iterations = 500; convergence threshold = -10^{-5}; and test percentage = 0, with only hinge features selected (Phillips and

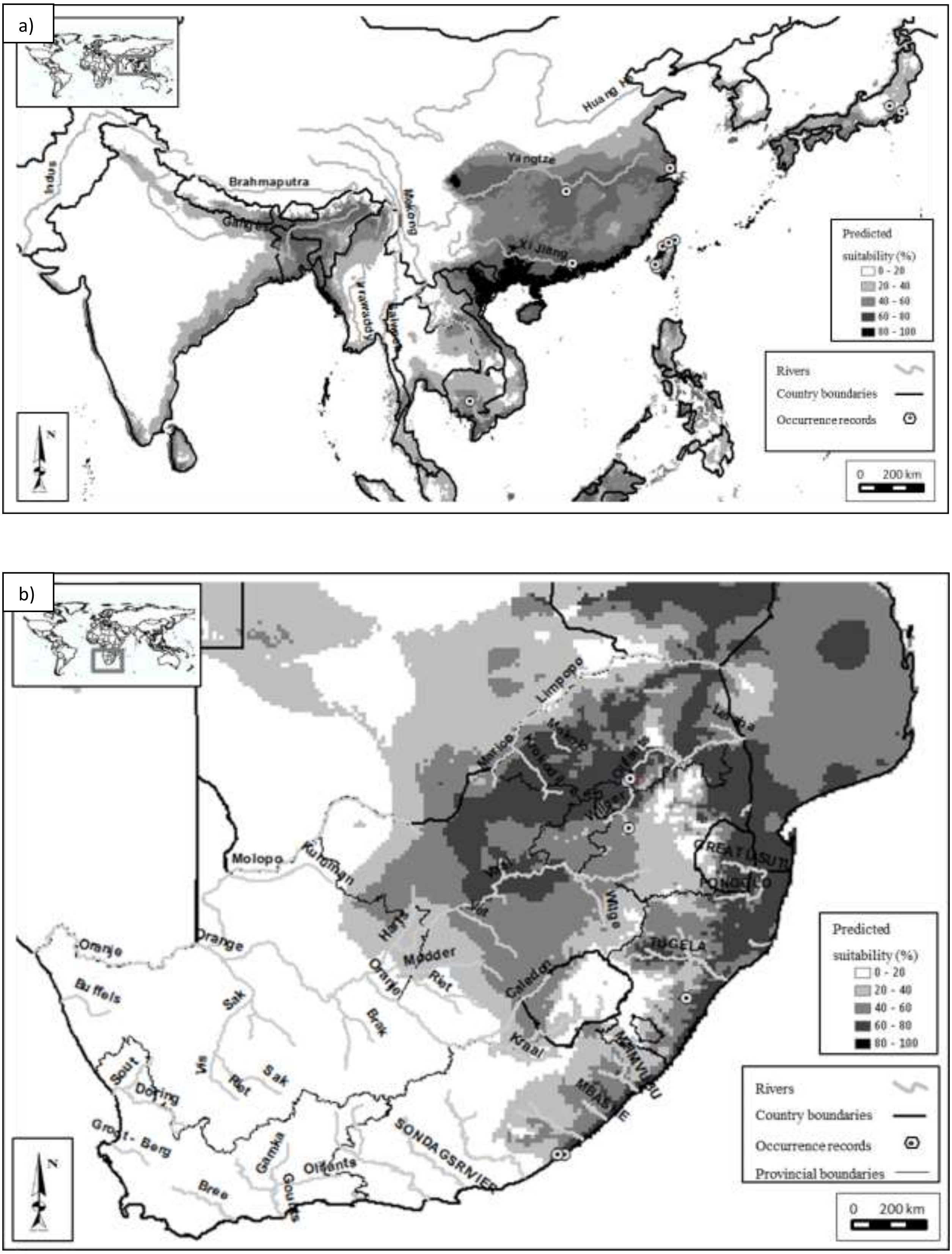

Figure 1 a, b: Spatial explicit predictions of potential climatic suitable areas of silver carp, *Hypophthalmichthys molitrix* a) native range in the south Asian sub-continent and b) southern Africa

Dudik 2008). Hinge features (default setting of MaxEnt) (Phillips and Dudik 2008) are similar to the step function response produced by the "threshold features", but allows a simpler and more concise approximations of the true species response to the environment variables (Elith et al. 2011), thus preventing overfitting of the model without significantly increase the complexity of models and improving the model performance (Phillips et al. 2006). The recommended logistic transformations of the cumulative probabilities (Phillips et al. 2006) were used, rather than the raw formats, to indicate climatic suitability (Elith et al. 2011). This linear logistic probability indicates the climatic suitability of the areas and not the probability of establishment (Pearson et al. 2007), with values ranging from 0-100 % (low to high suitability). The analyses were confined to the study region of the species native range, eastern Asia (Fig. 1a) and its potential range in southern Africa (Fig. 1b).

The maximum entropy method uses occurrence records (representing species presence) and a defined background (representing pseudo absence) to predict the potential distribution of a species. However, the extent of the background area can influence model performance (VanDerWal et al. 2009, Anderson and Raza 2010). A broad background can cause overestimates and a constrained background can cause underestimates. The background extent should typically encompass the geographical native range of the study species. In this study the native range of silver carp was defined as the area where it is known to occur naturally (18.83 – 50.69 ^{0}N; 96.16 – 145.74 ^{0}E), as defined by Chen et al. (2007). We further delimited the background within this region by only using areas that had similar climates to known silver carp occurrence records. This was achieved by overlaying the recent Köppen-Geiger climate classification system (Kottek et al. 2006) with the defined silver carp native range, following Thompson et al. (2011). The Köppen-Geiger polygons identify areas with similar climates (climate zones) and a given climate zone was included as part of the background if it contained an occurrence record within the native range of silver carp, using ArcGIS® v. 10.0 (ESRI 2011) (Fig 1s). By selecting the entire climatic zone, an intermediate background size was obtained, compensating for the few native occurrence records obtained and capturing the expected distribution of the silver carp in their native range (VanDerWal et al. 2009, Jiménez-Valverde et al. 2011b).

The native range model was then calibrated with 10,000 pseudo-absence points drawn at random from the defined native background (Phillips et al. 2009, VanDerWal et al. 2009). 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). This method divides occurrence records into *k* datasets and for each of the iterations, *k*-1 datasets are pooled for model calibration, while the remaining set is used for model evaluation (Phillips et al. 2006). Average 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. The *k*-fold method is the preferred method when using few occurrence records as all the available data are used for model calibration and evaluation (Fielding and Bell 1997, Jiménez-Valverde et al. 2011b).

The introduced range model of silver carp in South Africa was built using known introduction records (southern African and North American) and native range occurrence records in eastern Asia. The introduced range model was then calibrated using the same *k*-fold method as outlined for the native range model (Phillips et al. 2006), while the background selection was restricted to the native range. The combination of the native and introduced occurrence records in model building enhances model performance (Iguchi et al. 2004, Broennimann and Guisan 2008, Beaumont et al. 2009, Liu et al. 2011). This approach provides a better approximation of the invasive species fundamental niche as it includes climatic conditions in disjunct native and introduced ranges that may show variation in environmental variables because of the landscape heterogeneity (Jiménez-Valverde et al. 2011b).

Model evaluation

A receiver operating characteristic curve (ROC) (Swets 1988, Guisan and Zimmermann 2000, Phillips and Dudik 2008) was used to test the performance of the niche models of silver carp from its native and introduced ranges (Iguchi et al. 2004). The ROC curve plots the correctly classified occurrence records (sensitivity) against the incorrectly classified occurrences (1 – specificity) for all possible thresholds, and distinguishes between omission (predicted absent in areas of actual presence) and commission errors (predicted presence in areas of actual absence) (Fielding and Bell 1997). Despite several limitations, such as equal weighting of omission and commission errors (Soberón and Peterson 2005, Jiménez-Valverde 2011a), the ROC is widely used as test of model accuracy (Fielding and Bell 1997, Wiley et al. 2003, Iguchi et al. 2004). The ROC curve, as used in MaxEnt, defines the ability of the model to discriminate between presence records and random background points, and not between presence and absence records since MaxEnt does not make use of absence data (Fielding and Bell 1997, Phillips et al. 2006).

The area under the curve (AUC) of a ROC curve provides a single measure of model performance independent of any particular threshold chosen with the AUC values ranging from 0 to 1 (Phillips et al. 2006). An AUC score of < 0.8 indicates poor model discrimination between presence and random background records, while an AUC score between 0.8 - 0.9 indicates models with fair accuracy; 0.9 - 0.95 indicates a good model; and models with excellent accuracy typically have an AUC score of > 0.95 (Thuiller et al. 2006).

Results

Native range model

A high probability (> 60 %) corresponded to accurate model prediction of occurrence records in the native range (lower and middle reaches of the Yangtze River; Fig. 1a). The AUC value, over replicated runs, was higher (AUC (mean ± SD) = 0.986 ± 0.002) for the calibration dataset than the testing dataset (AUC (mean ± SD) = 0.975 ± 0.028), indicating excellent model performance. . Rainfall (optimal > 1000 mm/year) was highlighted as the most important variable for climate suitability. Precipitation of the warmest quarter contributed 36 % to the model and annual precipitation contributed 27.9 %. Areas with a large mean diurnal range (daily maximum temperature – minimum temperature) were predicted to be less climatically suitable (< 45 %). The mean temperature of the warmest quarter contributed the least to the model (13.9 %).

Introduced range model

The AUC score observed for the testing dataset (AUC (mean ± SD) = 0.944 ± 0.031) and calibration dataset (AUC (mean ± SD) = 0.957 ± 0.002) of the introduced range model, over replicated runs, indicates excellent model performance. The predicted invasive potential of silver carp revealed an extensive area of high climatic suitability (> 70 %; Fig. 1b). The climatically suitable area identified stretches over most of the north-eastern part of southern Africa (Limpopo, Gauteng, and Northwest Provinces); along the KwaZulu-Natal (KZN) coast (Fig. 1b); and extending up into Mozambique and Zimbabwe. The major river systems within this potential distribution include the Limpopo River Basin, Vaal River, and the Tugela River (KZN). The model predicted a low climatic suitability (< 30 %) in the lower Orange River, Western Cape, Northern Cape, and the Vaal River in the western part of the Free State Province. A slightly higher, but still relatively low climatic suitability was predicted in the central part of the Mpumalanga Province (< 40 %). The area of highest climatic suitability was at the convergence of the Gauteng, Limpopo, and North West provincial boundaries (Fig. 1b). The precipitation of the warmest quarter contributed 59.2 % to the model, suggesting high climatic suitability if there is high rainfall during the warmest quarter (optimal > 400 mm). The mean temperature of the warmest quarter contributed 31.7 %, indicating that temperatures < 10 ºC or > 36 ºC are not climatically suitable (as observed from the response curves). The optimum temperature (air temperature) indicating high climatic suitability was 23 ºC - 28 ºC. The annual precipitation contributed 6 % to the model and indicted optimal suitability in high rainfall areas (> 800 mm/year).

Discussion

Native range predictions

The high AUC values indicated excellent model performance (> 0.95) with accurate predictions of known occurrence records. The predicted native range from this study was in agreement with the known native range of silver carp (Chen et al. 2007, Kolar et al. 2007, Hong-Xia et al. 2010, Tan et al. 2010), The predicted native range included the middle and lower reaches of the Yangtze River (Kolar et al. 2007), Yellow River, Lijiang River, Mekong River, and the Pearl River system in eastern Asia. Areas predicted were mostly high rainfall areas (e.g., rainforest) with drier deciduous forest areas being predicted with low probabilities (< 50 %). The presence of silver carp has been recorded in the Brahmaputra River Basin, India, and Bangladesh (Hoque 1995), which was also accurately predicted as being climatically suitable in this study. The predicted native range of silver carp from this study is comparable with previous studies despite the use of different approaches. Previous studies by Chen et al. (2007) and Herborg et al. (2007) predicted the invasive potential of silver carp in North America using Genetic Algorithm for Rule-set Prediction software (GARP) (Stockwell and Peters 1999) and used a larger dataset of native occurrence records (> 100) and more environmental variables than used in this study. This study produced similar native range predictions despite only using 12 native occurrence records and a different modelling approach (maximum entropy). The maximum entropy (MaxEnt) modelling approach has been shown to outperform other modelling approaches (Elith et al. 2006, Poulos et al. 2012) and can be used to accurately predict the realized native distribution range of silver carp in conjunction with a carefully delineated background and limited occurrence records, despite the fact that only a few native occurrence records were available for model building (Fig. 1a).

Introduced range predictions

Large areas of north-eastern southern Africa were predicted as climatically suitable for the establishment of silver carp. Areas where silver carp has already established feral populations in southern Africa had a high predicted climatic suitability e.g., Olifants River, Limpopo (> 0.75 %). Of particular concern are those areas that have been free of silver carp but were predicted to be potentially suitable for its establishment. These include the Steelpoort River and the upper reaches of the Olifants River, which form part of the Limpopo drainage basin where a high climatic suitability (> 80 %) for silver carp establishment was predicted. In addition, the coast of KwaZulu-Natal, especially the Tugela River (> 0.75 %) and parts of the Vaal River were also found to be climatically suitable (Fig. 1b).

Precipitation of the warmest quarter was the most important bioclimatic variable identified. Silver carp require specific spawning habitat requirements, such as large, low gradient, turbid rivers with a flow rate between 0.3 ms^{-1} and 0.7 ms^{-1} (Kolar et al. 2007). Therefore, areas with the highest predicted climatic suitability were generally areas with high annual rainfall, particularly during the warmest quarter of the year. As expected, low rainfall and winter rainfall areas were not predicted, since silver carp require peak river discharge during the warmest quarter of the year for successful reproduction (Linhart et al. 1995, Kolar et al. 2007). Similarly elsewhere in North America, annual precipitation and wet day frequency was identified as the major factors influencing the potential spread of silver carp (Herborg et al. 2007). The suitable temperature range, detected by the response curves obtained from the model in the current study, coincides with the observed species thermal tolerance range of 24 ºC - 34 ºC, which is considered optimal for growth and reproduction (Kolar et al. 2007, Cooke and Hill 2010). The response curves also indicated a sudden decrease in suitability when a temperature exceeded the thermal tolerance level of this species (> 36 ºC). The optimal water temperature range of silver carp was consistent with the subtropical to tropical climate found in the north-eastern part of southern Africa and along the east coast (30 °C – 34 °C in summer and 22 °C – 26 °C in winter (FAO 2004)), which were predicted to be climatically suitable for the establishment of silver carp .

Conservation concerns

The first major conservation concern is that silver carp has already established feral populations in the middle reaches of the Olifants river system. It has further spread downstream and is now common in river systems in the Kruger National Park, a flagship conservation area in South Africa, and Massingir Dam in Mozambique (Brits 2009). Secondly, a large proportion of river systems that are still free of silver carp, were predicted to have a similar climate to the native range of silver carp. This implies that if silver carp was introduced into such river systems, it may be able to establish (other factors not withstanding such e.g. biotic interaction with native species). Thirdly, the realised and potential of range of silver carp in southern Africa encompasses the native range of several indigenous species that are at an extirpation risk because of the silver carp invasion. Silver carp is a well-suited invasive species because it is extremely hardy, has a wide range of trophic and ecological adaptations, and it possesses adaptive life history characteristics such as a fast growth rate and ability to achieve high population densities. The ability of *H. molitrix* to obtain high population densities, their fast growth rate, and versatile feeding behaviour with the capacity to fine filter large volumes of water, can lead to alteration of community structures such as food webs and nutrient cycles in recipient ecosystems (Kolar et al. 2007, Cooke et al. 2009, Ma et al. 2010, Sass et al. 2010). Observed effects in invaded systems include changes in invertebrate and phytoplankton communities, which can lead to a decrease in the abundance of indigenous fish sharing a similar dietary niche (Lu et al. 2002, Irons et al. 2007, Sampson et al. 2009). Furthermore, the fast growth rate and the exponential population increases of silver carp often leads to high population densities in recipient systems that can lead to the spatial exclusion of slower growing and less abundant indigenous species. The impact of silver carp in the Olifants river system is yet to be quantified, though preliminary results from a parallel ongoing study in Flag Boshielo Dam have shown strong niche overlap between silver carp and various indigenous species such as banded tilapia (*Tilapia sparrmanii*); silver robber (*Micralestes acutidens*); redeye labeo (*Labeo cylindricus*); and threespot barb (*Barbus trimaculates*), and rednose labeo (*Labeo rosae*) (Lübcker et al. (unpublished data)). Further, silver carp also exhibited opportunistic and versatile feeding strategies, with the ability to switch between food sources and consume whatever is available. Therefore the observed strong niche overlaps can lead to a decrease in the abundance of indigenous fish sharing a similar dietary niche, and dietary plasticity of silver carp may aid its establishment.

What can be done to control and prevent further spread?

Silver carp is currently listed in category 1b (section 70(1)(a)) under the updated (2013) National Environmental Management: Biodiversity Act, 2004 (Act 10 of 2004)), which means that this species requires control by means of an invasive species monitoring programme. The niche models presented in this study can therefore be used to identify river segments that are highly vulnerable to the establishment of the invasive silver carp. Concerted conservation efforts can then be directed in such areas to confirm establishment, direct remediation efforts, and contain further spread.

1) Confirm establishment:

- There is a need to implement regular monitoring programmes in river system where the silver carp have established feral populations to investigate aspects of its biology and quantify possible impacts that are essential for effective management. In areas that are still free of silver carp, but were predicted to be suitable, regular monitoring will determine if the species is invading and would also assist in identifying introduction pathways.

2) Remediation efforts:

- Invasive fish species are practically impossible to eradicate once established in most systems, hence management protocols that focus on preventing introductions should be encouraged, and are often much easier and significantly less costly to implement. Biological and chemical control measures for invasive fish are often impractical as these methods tend to be none selective and highly destructive and therefore not effective as management options (Gozlan et al. 2010). The only practical management option is often only to predict the species eventual distributional range and adopt measures to either stop or slow down its dispersal across river systems. In the case of the silver carp, this could be done by restricting it to catchments where it has already established and prohibit it in pristine areas that have not been invaded. Fisheries targeting silver carp can also be used as effective management option in systems where silver carp already forms a major component of the local fisheries.

3) Contain further spread:

- Silver carp is established in the middle to lower reaches of the Olifants river systems, but is still absent from the upper catchment. The upstream spread might have been limited by physical barriers imposed by dam and weir systems and the highly seasonal surface water flows that are likely to restrict the natural upstream migration. Such anthropogenic barriers may act as short term management options to prevent upstream migration of invasive fish (Rahel 2013), but their efficacy can be reduced by episodic flood events, which may enable silver carp to move upstream when the water level is high enough to clear low barriers such as weirs. Intentional or accidental fish introductions is another important driver for the potential spread of silver carp into adjacent rivers systems. There is therefore a need to educate people about the possible ecological impacts of invasive fishes in recipient systems and the need to restrict silver carp to catchments where it has already established and prohibit from being introduced to new areas (e.g., Vaal River). The spread of silver carp into adjacent river systems will also be influenced by other conditions in the receiving environment that were not considered our niche models. These include habitat requirements for spawning, food availability, and biotic interactions with native species.

Conclusions:

In this study, model performance demonstrated that invasive species potential distributions can be accurately predicted using few occurrence records, a minimal number of carefully selected bioclimatic variables and a carefully defined background. The model presented in this study can be used for informing management plans and guiding monitoring efforts in preventing the potential further spread of silver carp in southern Africa. The current known extent of the silver carp invasion in South Africa is confined to the Limpopo River Basin (Brits 2009). Eradication of the species from southern Africa may not be feasible, but limiting further spread in southern Africa is crucial for conserving freshwater aquatic systems.

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Supplementary material:

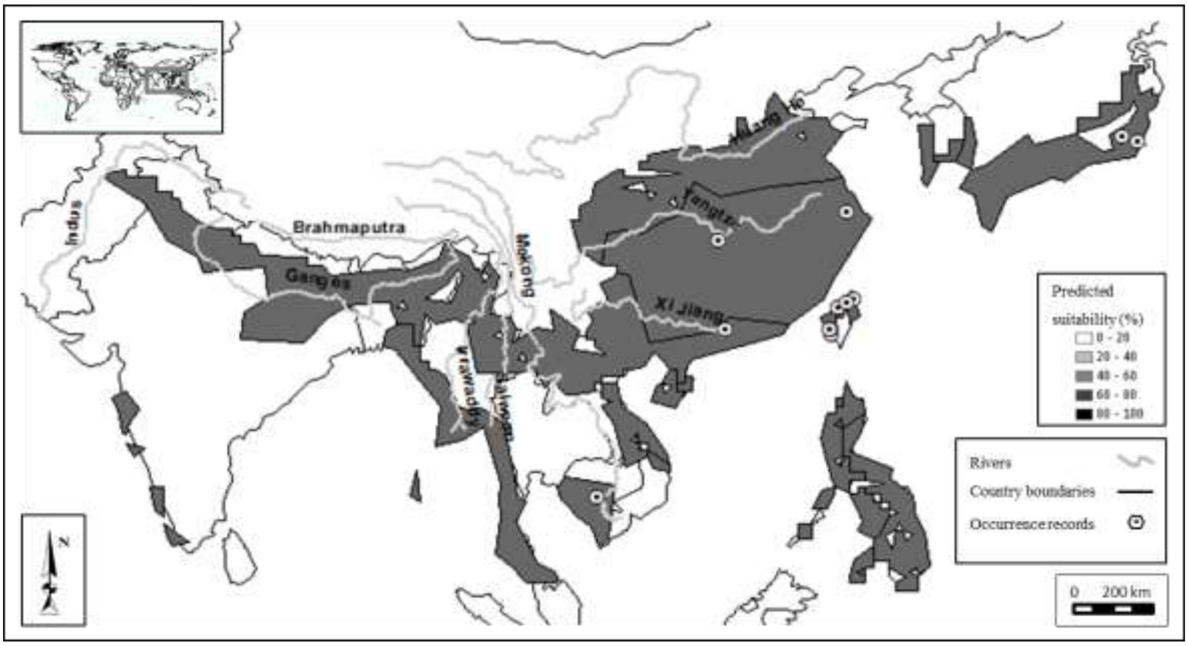

Fig 1s Background extent selected in native range of silver carp, *Hypophthalmichthys molitrix*, used for predicting the potential climatic suitable areas within southern Africa.

The native range (black rectangle) extends from 18.83 – 50.69 ^{0}N; 96.1616 – 145.7416 ^{0}E (Chen et al. 2007). The background for the native range was constrained to areas with similar climates (coloured in grey) (Köppen-Geiger polygons) in the native within range containing an occurrence record in the native range using ArcGIS® v. 10.0 (ESRI 2011). By selecting the entire polygon we increase the background size as based on areas were silver carp are also expected to occur.