

Article

# Broad Niche Overlap between Invasive Nile Tilapia *Oreochromis niloticus* and Indigenous Congenerics in Southern Africa: Should We be Concerned?

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**Abstract:** This study developed niche models for the native ranges of *Oreochromis andersonii*, *O. mortimeri*, and *O. mossambicus*, and assessed how much of their range is climatically suitable for the establishment of *O. niloticus*, and then reviewed the conservation implications for indigenous congenerics as a result of overlap with *O. niloticus* based on documented congeneric interactions. The predicted potential geographical range of *O. niloticus* reveals a broad climatic suitability over most of southern Africa and overlaps with all the endemic congenerics. This is of major conservation concern because six of the eight river systems predicted to be suitable for *O. niloticus* have already been invaded and now support established populations. *Oreochromis niloticus* has been implicated in reducing the abundance of indigenous species through competitive exclusion and hybridisation. Despite these well-documented adverse ecological effects, *O. niloticus* remains one of the most widely cultured and propagated fish species in aquaculture and stock enhancements in the southern Africa sub-region. Aquaculture is perceived as a means of protein security, poverty alleviation, and economic development and, as such, any future decisions on its introduction will be based on the trade-off between

socio-economic benefits and potential adverse ecological effects.

**Keywords:** ecological niche modelling; invasion; indigenous fishes; Nile tilapia; conservation; southern Africa

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## 1. Introduction

Nile tilapia, *Oreochromis niloticus* (Linnaeus 1758), is an endemic African freshwater cichlid that is native to the Nile River basin, southwestern Middle East, and the Niger, Benue, Volta, and Senegal rivers, as well as lakes Chad, Tanganyika, Albert, Edward, and Kivu [1,2]. Owing to its hardy nature, and its wide range of trophic and ecological adaptations, *O. niloticus* has been widely introduced worldwide for aquaculture, augmentation of capture fisheries, and sport fishing [1,3]. It is currently among the most widely distributed invasive fish worldwide and has established feral populations in most tropical and sub-tropical environments to which it has gained access [3–5].

Within sub-Saharan Africa, *O. niloticus* was initially introduced into Lake Victoria in the 1950s and its distribution has since expanded to include most river systems in eastern and southern Africa [6]. It was imported into Zambia in 1982 for aquaculture purposes and appeared in the Kafue River in the mid-1990s after escaping from nearby fish farms [7]. Subsequent aquaculture introductions occurred in Lake Kariba. It is now widely distributed and common in most sub-catchments of the Middle Zambezi, Nata (Makgadikgadi/Okavango), Runde-Save, Buzi, and Limpopo river systems [8–12]. The advent of *O. niloticus* into novel river systems is a cause for concern for the conservation of indigenous congeners that are at an extirpation risk through hybridization and competition arising from habitat and trophic overlaps. Despite its widespread distribution within sub-Saharan Africa, several river systems are still free of *O. niloticus* but remain vulnerable. These areas currently act as refuges for the conservation of indigenous congeners and it is important to identify such areas to prevent further *O. niloticus* introductions. These areas include the Cunene, Okavango, and the Upper Zambezi rivers where threespot tilapia (*O. andersonii*) and greenhead tilapia (*O. macrochir*) are endemic [1,6]. The localised distribution of endemic tilapiines within southern Africa predisposes them to invasion as the introduction of *O. niloticus* into a given catchment is likely to have a significant impact on species with limited natural ranges. Examples include: (1) Kariba tilapia (*O. mortimeri*) that is naturally confined to the middle Zambezi and Luangwa river systems; (2) black tilapia (*O. placidus*) that is confined to the east coastal plains from the Lower Zambezi to the Mkuze rivers in KwaZulu-Natal Province, South Africa; and (3) Mozambique tilapia (*O. mossambicus*) that occurs from the lower Zambezi River system to the Bushman's River system of Eastern Cape Province, South Africa, spreading far inland within the Limpopo River Basin, but south of the Phongolo River system, and is confined to the closed estuaries and coastal reaches of rivers [6].

This study is an extension of a recent study that applied ecological niche models to predict the potential invasive range of *O. niloticus* and revealed broad invasive potential over most river systems in southern Africa [13]. The present study attempts to explicitly quantify the niche overlap between *O. niloticus* with indigenous congeners in southern Africa and highlights conservation concerns in areas where there is broad niche overlap. This was achieved by developing niche models for the native

range of indigenous *Oreochromis* species in southern Africa and assessing how much of their range is climatically suitable for the establishment of *O. niloticus*. We specifically addressed the following two research goals: (1) what is the degree of niche overlap between the projected invasive range of *O. niloticus* and the natural ranges of endemic congeners in river systems in southern Africa? and (2) we investigated the degree of niche overlap between the projected invasive range of *O. niloticus* and the natural ranges of endemic congeners in river systems in southern Africa, and then reviewed the conservation implications for indigenous congeners as a result of overlap with *O. niloticus* based on documented congeneric interactions.

## 2. Methods

### 2.1. Environmental Data Sources

The environmental variables dataset was composed of bioclimatic variables that have been widely used in ecological niche modelling of species [14]. 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). Variable selection for model training followed [13] and only used six out of 19 bioclimatic variables that represented the availability of water and energy. This allowed for comparative analysis of niche models between the two studies and the six variables have been shown to produce better a model performance than any other variable combinations [13].

### 2.2. Specimen Data Sources

Georeferenced occurrence data for four *Oreochromis* species (*O. andersonii*, *O. mortimeri*, *O. mossambicus*, and *O. niloticus*) that are known to occur in southern Africa were obtained from various sources, including museum specimen records and biodiversity databases such as FishBase [15], Global Biodiversity Information Facility [16], and the published literature and fish survey data from various fisheries departments in southern African countries that included Botswana, Mozambique, Zambia, and Zimbabwe.

### 2.3. Model Building

Modelling was based on the maximum entropy algorithm that was implemented in the Maxent modelling package (Maxent Version 3.3.3k) that utilizes associations between environmental variables and known species' occurrence localities to predict potential areas where a given species is likely to establish [17]. The Maxent method has been shown to perform better than other correlative methods that use presence and background data [18]. For all models, the algorithm's parameters were set to a maximum number of 500 iterations, a regularization multiplier of 1, convergence threshold of 0.00001, test percentage = 0, and only hinge features selected. Hinge features allow for simpler and more concise approximations of the true species response to the environment variables [19,20], thus preventing over-fitting of the model without significantly increasing the complexity of the models and, hence, improving model performance [17]. In addition, clamping was selected to minimize predictions

to regions of environmental space outside the limits encountered during training because extrapolation may overinflate the degree to which species niches are estimated to overlap [21–23]. The logistic output format was used to indicate the probability of a species presence at a default prevalence of 0.5 [20,24]. Values range from 0, indicating low probability, to 1.0, indicating greatest probability of a species presence in a given area.

Maxent makes use of presence and background localities to project potential species distribution models. The extent of the background is known to influence model performance, where a broad background can cause overestimates and a constrained background can cause underestimates [25,26]. In this study, the extent of the native range for each of the three *Oreochromis* species endemic to southern Africa was limited to hydrological basins where each species was known to occur as defined by previous studies [1,6]. This was achieved by overlaying the hydrological basins layer over known occurrence records for each species. A given hydrological zone was included as part of the background if it contained an occurrence point using ArcGIS® v10. (2011; ESRI, Redlands, CA, USA). The native range model for each of species was then calibrated with 10,000 pseudo-absence points drawn at random from the defined native range. Ten niche models were then constructed for each species within its native range and, in each model, all native occurrence records were partitioned using the statistical software package R (R Development Core Team 2008) into a calibration set (training set = 70% of all records) and a testing set (validation set = 30%) using *k*-fold partitioning [17]. 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 predicted distribution of the *O. niloticus* across African river systems was obtained from niche models constructed in a previous study [13]. These models were constructed using both native and introduced range occurrence records while the background selection was delimited using the buffering methods from a previous study [25]. 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.

#### 2.4. Niche Overlap and Similarity

Niche similarity between niche models of *O. niloticus* and its southern African congeners was estimated using ordination techniques [27] in the *ecospat* package in R (R Development Core Team 2008). Ordination techniques for quantifying niche overlap are recommended as a better alternative to other methods that use geographical projections derived from species distribution models, e.g., see [28], because the former allows for random points for similarity tests to be selected in environmental space instead of geographical space, thereby allowing for correction of bias associated with geographical dimension [27]. Niche overlap was measured using the Schoener's index of niche breadth (*D*) [28]. Indices may range from 0 (indicating that niche models are completely different) to 1 (indicating that niche models are identical). The significance of the *D* values was then evaluated using null models of niche similarity. *Ecospat* quantifies niche similarity using several ordination techniques (27), but in this study we only used the principal component analysis (PCA-env) that was shown to consistently out-perform other ordination metrics of niche overlap [27]. For niche similarity, we tested the

hypothesis that ecological niche models drawn from a partially or entirely non-overlapping distribution of *O. niloticus* and that of *Oreochromis* congenics in river systems in southern African are more different from one another than expected by random chance. This test was conducted by calibrating the PCA-env with introduced records of *O. niloticus* but trained on a background randomly drawn from both the known introduction range of *O. niloticus* within southern Africa and the native range of each of its southern African congenics (see model building section for native range delimitation). The same process was repeated by running a PCA-env based on known occurrence records for each of the southern African congenics and trained on a randomly drawn background from its native range and from the hydrobasins with known occurrence records of *O. niloticus* within southern Africa. This process was repeated in either direction (native ↔ introduced) to generate 100 pseudo-replicate datasets for each species comparison with *O. niloticus*. The observed measures of niche similarity ( $D$ ) from the two original populations (*O. niloticus* and each of its southern African congenics) were then compared with percentiles of these null distributions. The hypothesis that niche similarity (or divergence) is different from that expected by chance between *O. niloticus* in its introduced range and that of each southern African congeneric 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.

### 2.5. Model Evaluation

The performance niche models of each *Oreochromis* species were evaluated using the Maximum test area under the curve (AUC) [29] and the Boyce index [30,31]. AUC defines the discrimination ability (between presence and background) of the models where values range from 0 (indicating random distribution) to 1.0 (indicating perfect prediction), with values > 0.5 being considered to indicate that the model discriminates better than random [29]. All AUC model performance measures were calculated in Maxent and predictions with an AUC value greater than 0.8 were considered to be acceptable [32,33]. Although AUC has been widely used as measure of model performance, it is not necessarily an appropriate measure for presence-only model evaluation [34]. Therefore, we used the Boyce index to further evaluate our model outputs. The Boyce index validation method involved partitioning the habitat suitability scores from each model output into 10 classes of equal intervals. For each class, we calculated the predicted and expected frequencies of pixels. Predicted frequency is the number of occurrence points predicted by the model to fall into habitat suitability class  $i$  divided by the total number of occurrence points used to build the model. The expected frequency is the number of grid cells belonging to habitat suitability class  $i$  divided by the overall number of cells in the whole study area. The predicted-to-expected (P/E) ratio was then calculated for each class and Spearman rank correlation was used to test if the P/E ratio increased with habitat suitability. The predicted-to-expected (P/E) ratio values may range from −1 to 1, where negative values indicate incorrect models that predict unsuitable habitats where presences are more frequent, values closer to zero indicate random predictions, and positive values indicate model predictions that are consistent with presence distribution in the evaluation dataset [30,31].

### 3. Results

#### 3.1. Native Range Predictions

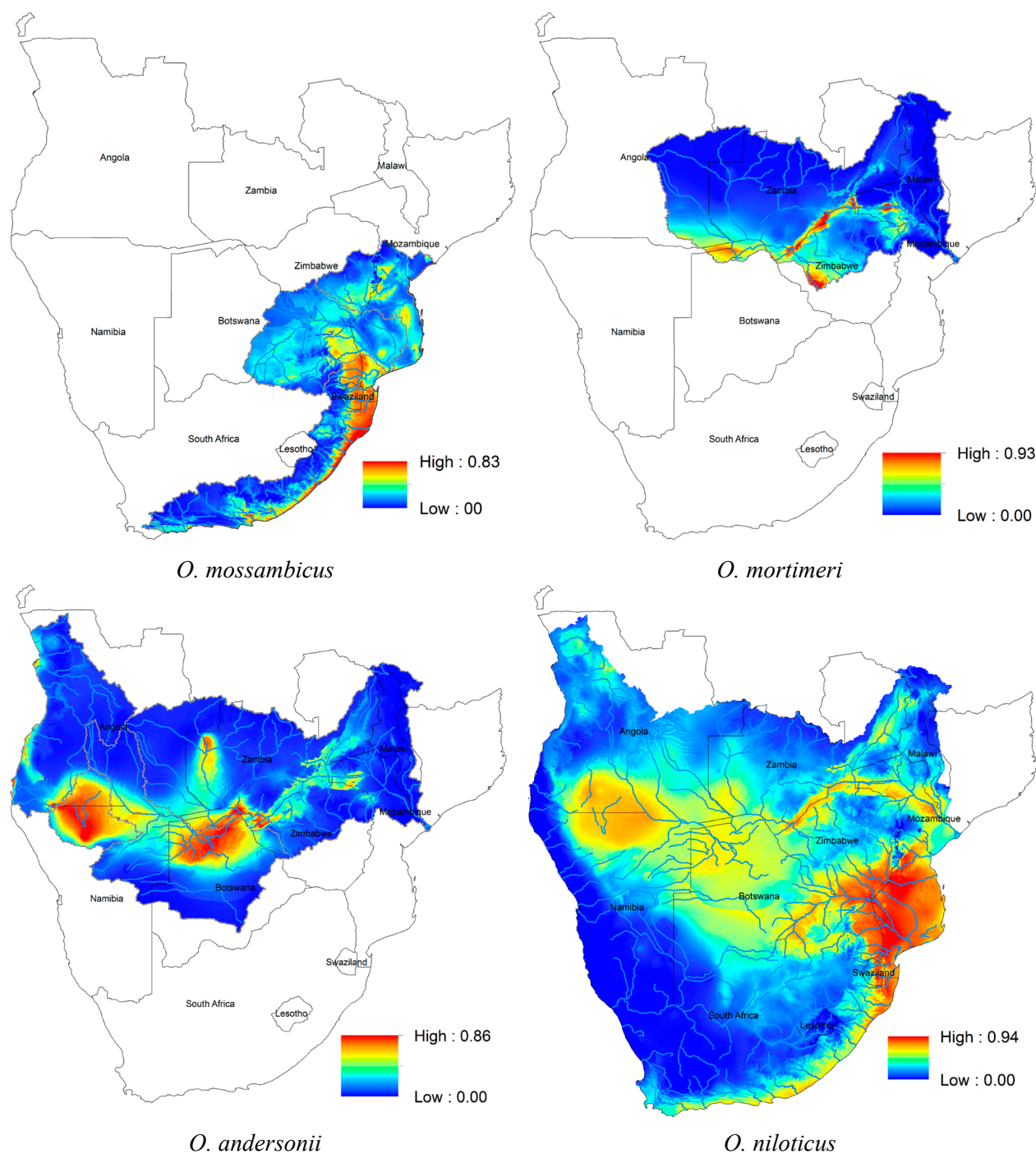
The native ranges of all three tilapia species (*O. andersonii*, *O. mortimeri*, and *O. mossambicus*) that are endemic to southern Africa were correctly predicted with good model performance (AUC > 0.83, Boyce index  $p < 0.001$ ) for all four species (Table 1, Figure 1). There was a wide variation in the relative contribution of each variable to model performance for each respective tilapiine species (Table 2). The most important predictive factor for *O. andersonii* was maximum temperature in the warmest month, while for *O. mortimeri* it was annual precipitation. For *O. mossambicus*, it was annual mean temperature.

**Table 1.** Average model performance evaluated using the maximum test AUC and Boyce index for *O. andersonii*, *O. mortimeri*, and *O. mossambicus* within their native ranges, and *O. niloticus* within its potential invasive range in river systems in southern Africa.

Species	Test AUC	pValue Boyce index (Spearman's $\rho$ )
<i>O. andersonii</i>	$0.89 \pm 0.035$	$< 0.001$
<i>O. mortimeri</i>	$0.93 \pm 0.005$	$< 0.001$
<i>O. mossambicus</i>	$0.83 \pm 0.016$	$< 0.001$
<i>O. niloticus</i>	$0.91 \pm 0.021$	$< 0.001$

**Table 2.** Environmental variables and their relative contribution (%) to build ecological niche models for *O. andersonii*, *O. mortimeri*, and *O. mossambicus* within their native ranges, and *O. niloticus* within its potential invasive range in river systems in southern Africa.

Bioclimatic variable	<i>O. andersonii</i>	<i>O. mortimeri</i>	<i>O. mossambicus</i>	<i>O. niloticus</i>
BIO1 = Annual mean temperature	17.8	0.1	40.7	23.0
BIO5 = Maximum temperature warmest month	37.5	21.5	1.1	0.9
BIO6 = Minimum temperature coldest month	9.1	0.4	29.1	21.8
BIO12 = Annual Precipitation	10.6	69.6	1.1	43.7
BIO13 = Precipitation of Wettest Month	12.5	3.2	8.4	6.7
BIO14 = Precipitation of Driest Month	12.5	5.2	19.6	4.0



**Figure 1.** The projected distributional range for *O. mossambicus*, *O. mortimeri*, and *O. andersonii* within their native ranges, and *O. niloticus* within its potential invasive range in river systems in southern Africa. Each map represents an average of 10 replicates for each species 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.

### 3.2. Introduced Range

The predicted potential geographical range of the *O. niloticus* reveals a broad climatic suitability over most of central 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 models, however, predicted low suitability for most of the Orange River basins and west-flowing rivers in the south Atlantic coast of Africa. There was no significant differences ( $P > 0.05$ ) between training (0.92, SD = 0.002) and test datasets (0.91, SD = 0.021), and the most important predictor variables in the model performance were annual precipitation, annual mean temperature, and minimum temperature of the coldest month (Table 2).

### 3.3. Niche Overlap and Similarity

The predicted potential geographical range of *O. niloticus* within southern Africa shows significant pairwise niche overlaps with the native ranges of all three endemic congeners. Niche overlap was most pronounced between *O. niloticus* and *O. mossambicus* ( $D = 0.59$ ), followed by *O. niloticus* and *O. andersonii* ( $D = 0.55$ ), and *O. niloticus* and *O. mortimeri* ( $D = 0.12$ ). The observed overlap values between *O. niloticus* in its introduced range and that of each southern African congeneric's native range was greater than 99% of the simulated values, indicating that for each species comparison, the species occupy environments that are more similar to each other than expected by chance (Table 3).

**Table 3.** Niche overlap (Schoener's index of niche breadth,  $D$ ) and niche similarity tests for *O. andersonii*, *O. mortimeri*, and *O. mossambicus* within their native ranges and with the potential invasive range of *O. niloticus* in river systems in southern Africa.

	Overlap	<i>O. niloticus</i> compared to	
		Similarity	
		invasive→native	native→invasive
<i>O. andersonii</i>	0.55	>0.01	>0.01
<i>O. mortimeri</i>	0.12	>0.01	>0.01
<i>O. mossambicus</i>	0.59	>0.01	>0.01

## 4. Discussion

The predicted potential range of *O. niloticus* reveals a broad climatic suitability over most of southern Africa. Eight out of 11 of the river basins in the sub-region are predicted as being climatically suitable for *O. niloticus* and it has already been confirmed to be present in six of them. This is a concern as 55% of the river basins in the region already have established *O. niloticus* populations and there is potential for further invasion. In addition, the predicted geographical range of *O. niloticus* overlaps with the complete native ranges of endemic congeners in the sub-region. From previous evidence, these indigenous congeners are likely to become extirpated from the river systems through either competitive exclusion and/or hybridisation [5]. Of additional concern are those areas that have been free of exotic species but are now vulnerable due to the introduction of fish mainly for aquaculture and sport fishing.



#### 4.1. Upper Zambezi and Okavango

The first area of concern is the upper Zambezi and Okavango river systems. The upper Zambezi River is an ecologically diverse “reservoir river” with varied and extensive habitats [35]. As a result, the area has the highest fish diversity within the Zambezian River system [36]. The Upper Zambezi and the Okavango river systems are regarded as pristine areas where minimal fish introductions have occurred, but the ardent promotion of small-scale aquaculture as a means of poverty alleviation and livelihoods has put such river systems at serious invasion risk [37]. In Zambia, aquaculture projects rearing *O. niloticus* have been keenly promoted within the Zambezi River system, and the inevitable fish escaping from such facilities has led to the establishment of feral populations in river systems such as the Kafue River [7]. The distributional range of *O. niloticus* has also spread to include tributaries of the Upper Kapombo River and it is highly likely that it will reach a further spread within the upper Zambezi River, where *O. andersonii* and *O. macrochir* are at risk of being extirpated [37]. In the Kafue River, the *Oreochromis* population may already comprise a hybrid swarm that consists of fish with an admixture of *O. niloticus*, *O. andersonii*, and *O. macrochir* ancestry [38].

It is of concern that beside the introgression of *O. niloticus* alleles into the indigenous *Oreochromis* congeners, the resultant hybrids are non-sterile and are able to backcross with each other and with *O. macrochir* and *O. andersonii*, facilitating gene mixing between the indigenous congeners that do not otherwise frequently hybridise in sympatry. This facilitated hybridisation will likely have a major impact on the conservation of indigenous congeners as they are likely to be extirpated from the river system and replaced by an admixture of introgressed hybrids. Other areas of concern include pristine regions that have experienced little or no fish introductions due to civil strife. These include Angola and the Democratic Republic of Congo (DRC). With the end of these conflicts, it is anticipated that increased development in the form of aquaculture projects may expose novel river systems to a serious risk of invasion [10]. In Angola, potential river catchments for aquaculture development, such as the Cuito, Cubango, and Cunene rivers, were also predicted as potentially suitable systems for the establishment of Nile tilapia.

#### 4.2. Middle Zambezi

Further downstream, within the middle Zambezi River, *O. niloticus* is already established and appears to be displacing the indigenous Kariba tilapia, *O. mortimeri*. In Lake Kariba, *O. niloticus* appeared in the mid-1990s after escaping from *in situ* cage-culture fish farms and has become abundant at the expense of Kariba tilapia that has declined significantly in abundance [39–41]. As a result, Kariba tilapia is now listed as Critically Endangered (CR) on the International Union for Conservation of Nature (IUCN) Red List of threatened species [42]. In Zimbabwe, *O. niloticus* has been extensively propagated by farmers and anglers for recreational and sport fishing. It is now prevalent in most catchments where it has supplanted indigenous tilapiines in most medium- to small-sized dams [43]. For example, in Lake Chivero, a medium-sized reservoir on the Upper Manyame River, a sub-catchment of the middle Zambezi, *O. niloticus* has displaced greenhead tilapia and is now the dominant commercial species harvested [44].

Further south in the Zimbabwean Lowveld, *O. niloticus* is known to attain a body weight of approximately 6 kg in Inyankuni, Mayfair, and other smaller dams. The ability of *O. niloticus* to attain such a large body size could partially explain its success in displacing indigenous congeners, such as *O. mortimeri*, in Lake Kariba [41]. *Oreochromis niloticus* is an aggressive competitor and large males often out-compete other congeners for limited spawning and nursing grounds [45]. Although the hybridisation between *O. niloticus* and indigenous *Oreochromis* congeners has been illustrated in the upper Zambezi, a comparative analysis using the same approach has unfortunately not been done for the Middle Zambezi. Such a study could have, for example, used experimental gill-net data that has been collected at fairly regular intervals by the Lake Kariba Fisheries Research Station for the past 45 years. These data would have likely shown the genetic diversity of indigenous *Oreochromis* species before and after the introduction of *O. niloticus*.

#### 4.3. Lower Zambezi

The third area of concern comprises the Lower Zambezi River and other eastern river systems such as the Buzi, Save-Runde, and the Limpopo River systems, where *O. niloticus* is now established and spreading. It poses a threat to the other indigenous tilapia species such as *O. mossambicus*, which is also listed as Near-Threatened (NT) on the IUCN Red List of threatened species as a result of habitat and trophic overlaps with *O. niloticus* [46,47]. Feral populations of *O. niloticus* are already established in the Runde-Save, Buzi, and Limpopo river systems where adverse ecological impacts such as reduced abundance of indigenous species have already been documented [11]. In addition, similar to the Kafue River, the *Oreochromis* cichlid population in the Limpopo River may already be comprised of a hybrid swarm that consists of fish with an admixture of *O. niloticus*, *O. andersonii*, and *O. mossambicus* [48,49]. The presence of the *O. andersonii* mitochondrial haplotypes in the Limpopo River system indicates another invasion event, also linked to aquaculture. *Oreochromis andersonii* was introduced in the early 1970s into Shashe Dam in Botswana for aquaculture [50] and it appears to have spread further downstream unnoticed because it is morphologically similar to *O. mossambicus* and the two species are difficult to distinguish from each other in sympatry. The impacts of invasive species are most insidious when they affect the genetic integrity of indigenous congeners [51].

Despite the introduction of *O. niloticus* in the Limpopo River basin, several rivers within the system are still free of invasion but remain vulnerable. While *O. niloticus* has established feral populations along the main arm of the Limpopo River and the immediate reaches of its associated tributaries east of the Shashe/Limpopo rivers' confluence, it is yet to establish in most river systems in the upper bushveld sub-catchment [52]. Its spread may have been retarded by limited natural dispersal pathways and physiological limiting environments such as low water temperatures in upstream rivers [52]. Similarly, another comparative study [48] further demonstrated the limited expansion of alien *Oreochromis* species in the lower Limpopo despite multiple introductions in upper sub-catchments, as well as the importance of headwater regions as “refugia” for unintroduced *O. mossambicus* populations that are crucial for conservation and management of the species.

#### 4.4. Lake Malawi

The fourth area of concern is the Lake Malawi system which is comprised of Lake Malawi, its affluents, and the Shire River down to Kapachira Falls. *Oreochromis niloticus* is now present in the Lake Malawi catchment, where it was reported from rivers in Tanzania that drain into Lake Malawi [53]. It was introduced from Morogoro in central Tanzania between 1998 and 2010 as part of initiatives to develop aquaculture. The presence of *O. niloticus* in the Lake Malawi catchment obviously raises concerns about its impact should it reach the lake, which seems likely. Its presence will largely impact the endemic chambo (*O. shiranus*, *O. squamipinnis*, *O. lidole*, and *O. karongae*) and haplochromine complexes in the lake [54]. This has been noted in another Rift Valley lake, Lake Victoria. It is a comparatively similar system to the Lake Malawi system and the introduced *O. niloticus* displaced the indigenous *O. variabilis* and *O. esculentus* [55]. However, the indigenous tilapias in Lake Victoria were severely depleted by overfishing before *O. niloticus* was introduced and the commonly held hypothesis that *O. niloticus* displaced the indigenous species might not be entirely supported. *Oreochromis niloticus* increased slowly in the lake and did not dominate the ichthyofauna until Nile perch *Lates niloticus* was introduced and they more or less eliminated the endemic haplochromines. Much the same happened in Lake Kyoga and it seems that competition with haplochromines might have prevented *O. niloticus* from becoming established [56]. If this is correct, then the impact of *O. niloticus* on Lake Malawi might not be too severe, especially if they can maintain their haplochromine stocks.

#### 5. Conclusions

The major conservation concern is that the predicted potential geographical range of *O. niloticus* within southern Africa overlaps with the complete native ranges of all endemic congeners. In river systems in which *O. niloticus* is already established within the region, it has been implicated in reducing the abundance of indigenous species through competitive exclusion and hybridisation. Despite these well-documented adverse ecological effects, *O. niloticus* remains one of the most widely cultured and propagated fish species in aquaculture and stock enhancements in the sub-region. Aquaculture is perceived as a means of protein security, poverty alleviation, and economic development and, as such, decisions on exotic fish introductions are usually based on the trade-off between socio-economic benefits and potential adverse ecological effects. This is further compounded by the fact that in most invaded systems, the establishment of *O. niloticus* has not led to a decrease in overall yields, but rather a replacement of indigenous species and, in some cases, pronounced fisheries production and poverty alleviation by creating alternative aquaculture and fisheries livelihoods.

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## Author Contributions

All authors conceived the idea, designed the study, analyzed the data, and drafted the manuscript. All authors have read and approved the final manuscript.

## Conflicts of Interest

The authors declare no conflict of interest

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