Invasive potential of common carp (*Cyprinus carpio*) and Nile tilapia (*Oreochromis niloticus*) in American freshwater systems

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Abstract: Nonnative fish introductions disrupt ecosystem processes and can drive native species to local extinction. Two of the most widespread, introduced species are the common carp (*Cyprinus carpio*) from Eurasia and the Nile tilapia (*Oreochromis niloticus*) from Africa. In North and South America, these introductions stem from aquaculture facilities, as well as historical introductions for recreational angling. An emergent field of ecological niche modeling provides robust predictions of the geographic potential of alien species to better understand their capacity to become established at broad scales. We used this modeling approach to produce spatially explicit predictions of the invasive potential of common carp and Nile tilapia in the Americas. Model predictions were tested using occurrence data for established populations in their native area and in the Americas. Results indicated that predictive power of niche models was high. Distributional potential of common carp in the Americas covers most temperate regions and high mountain tropical aquatic systems, whereas that of Nile tilapia is focused in the tropics and coast areas. The consequences of the potential establishment of these exotic species can be profound on native aquatic faunas, particularly on highly diverse regions such as the Amazon Basin and central Mexico.

Résumé : Les introductions de poissons non indigènes perturbent les processus écosystémiques et peuvent causer l'extinction locale d'espèces indigènes. Deux des espèces les plus généralement introduites sont la carpe commune (*Cyprinus carpio*) d'Eurasie et le tilapia du Nil (*Oreochromis niloticus*) d'Afrique. En Amérique du Nord et du Sud, ces introductions proviennent des établissements d'aquaculture, ainsi que des empoissonnements passés pour la pêche sportive. Un domaine en émergence de la modélisation des niches écologiques permet de faire des prédictions robustes sur le potentiel géographique d'espèces exotiques et ainsi de comprendre leur capacité à s'établir sur de larges espaces géographiques. Cette approche de modélisation nous a permis de faire des prédictions explicites du point de vue spatial concernant le potentiel d'invasion de la carpe commune et du tilapia du Nil dans les Amériques. Nous avons testé les prédictions du modèle à l'aide de données de présence de populations établies dans leur aire d'origine et dans les Amériques. Les résultats montrent que le pouvoir prédictif des modèles de niches sont élevés. Le potentiel de répartition géographique de la carpe commune dans les Amériques englobe la plupart des régions tempérées et les écosystèmes aquatiques tropicaux de haute montagne; en revanche, le tilapia du Nil se concentre surtout dans les tropiques et les régions côtières. L'établissement potentiel des ces espèces exotiques peut avoir de graves conséquences sur les faunes aquatiques indigènes, particulièrement dans les régions de forte diversité, telles que le bassin de l'Amazone et le centre du Mexique.

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Introduction

Introductions of non-indigenous fishes can reduce diversity and modify local community dynamics in freshwater systems (Minns and Cooley 2000). Introductions can be intentional, such as in extensive aquaculture or with introductions of top predators for recreational fishing, or incidental, such as escape from aquaculture facilities or via shipping ballast water. Consequences of introductions can be profound; species diversity of native fish assemblages can be greatly reduced (Rahel 2000; Jackson 2002), and food web function can be disrupted (Vander Zanden et al. 1999). Population viability can be lowered because of predator–prey interactions, as in the case of sea lamprey (*Petromyzon*

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marinus) introductions to the Laurentian Great Lakes of North America (Mills et al. 2003).

Most research on fish introductions has focused on site-specific processes (e.g., loss of species, food web disruptions). A clear focus has been on top-down predator effects stemming from species introductions, such as the role of Nile perch (*Lates niloticus*) in the destruction of the native cichlid fauna of Lake Victoria (Barel et al. 1985). A broader perspective is necessary to better assess areas vulnerable to fish introductions, for example to set up policies for preventing or mitigating negative effects of introductions.

Common carp (*Cyprinus carpio*) and Nile tilapia (*Oreochromis niloticus*) introductions in North and South America have been extensive, but may not yet represent the full distributional potential of both species. This point becomes relevant because these species have important effects in aquatic ecosystems (Tapia and Zambrano 2003). Common carp increase suspended solids in the water column (Zambrano et al. 2001), reduce water transparency (Pinto et al. 2005) and macrophyte coverage (Zambrano and Hinojosa 1999), and decrease habitat heterogeneity for native species (Perrow et al. 1999). Nile tilapia alter trophic web structure by competing with other fish and preying on juveniles of other fish (Morgan et al. 2004) and amphibians (L. Zambrano, unpublished data).

The emerging field of ecological niche modeling has proved useful in developing robust predictions of the distributional potential of alien species (Peterson 2003). This approach focuses on modeling the geographic manifestation of species' ecological niches (i.e., the conjunction of ecological conditions within which a species is able to maintain populations without immigration) (Grinnell 1917; Hutchinson 1957). Software applications that relate georeferenced occurrence points to geographic information systems' (GIS) layers, representing environmental conditions of the landscape, have been developed to characterize the ecological niches of species and produce predictive distribution maps (Stockwell and Noble 1992; Stockwell and Peters 1999). With recent evidence that niches are highly conserved over evolutionary time periods (Peterson et al. 1999; Martínez-Meyer et al. 2004) and several successful applications (Peterson 2003), it is now clear that this approach offers excellent predictivity regarding species' geographic potential on landscapes beyond their native ones (Peterson and Robins 2003; Iguchi et al. 2004; Peterson et al. 2004).

Herein, we present an analysis of the invasive potential of carp and tilapia in the New World, based on ecological niche models from their native ranges. Detailed evaluations of the capacity of particular fish species for establishing and extending populations in new environments would help decision-makers evaluate risks and benefits of particular introductions. Indeed, under some circumstances, potential benefits of aquaculture could be overshadowed by costs of control or eradication of alien species causing ecological damage.

Materials and methods

Ecological niche models were based on georeferenced occurrence points drawn from diverse sources, including museum specimen records, the World Wide Web, a fish pro-

duction atlas (Carta Nacional Pesquera 2004) and literature (see Acknowledgements). In all, 54 points were available for common carp and 76 for Nile tilapia on their native ranges, and 747 and 43 points in the Americas, respectively. All occurrences were georeferenced with Internet-based electronic gazetteers (http://www.fallingrain.com/world/index.html) to the nearest 0.01° of latitude and longitude.

Ecological niches were modeled using the Genetic Algorithm for Rule-set Prediction (GARP) (Stockwell and Peters 1999). This algorithm relates ecological characteristics of known occurrence points to those of points randomly sampled from the rest of the study region, seeking — in an evolutionary-computing environment — to develop decision rules that best summarize factors associated with the species' presence. Previous tests of GARP's ability to predict geographic distributions accurately have been successful (Peterson 2001; Peterson and Vieglais 2001; Peterson 2003), including previous applications to predicting fish distributions (Wiley et al. 2003; Iguchi et al. 2004; McNyset 2005).

In GARP, occurrence points are divided twice evenly into training and test data sets — that is, an initial 50% of the data points are set aside for a completely independent test of model quality (extrinsic testing data); of the remaining points, half are used for developing models (training data) and half are used for tests of model quality internal to GARP processing (intrinsic testing data). GARP works in an iterative process of rule selection, evaluation, testing, and incorporation or rejection; a method is chosen from a set of possibilities (e.g., logistic regression, bioclimatic rules), applied to the training data, and a rule is developed or evolved. Predictive accuracy is then evaluated based on 1250 points resampled (with replacement) from the interface testing data and on 1250 points sampled randomly from the study region as a whole. Rules may evolve by a number of means that mimic DNA evolution: point mutations, deletions, crossing over, etc. Changes in predictive accuracy from one iteration to the next are used to evaluate whether particular rules should be incorporated into the model, and the algorithm runs either 1000 iterations or until convergence.

All modeling in this study was carried out on a desktop implementation of GARP available for public download (http://www.lifemapper.org/desktopgarp). This program offers excellent flexibility in choice of predictive environmental–ecological GIS data coverages. In this case, initially, we used 15 data layers summarizing elevation, slope, aspect, flow accumulation, flow direction, and topographic index at a native pixel size of 1 arc-second (~1 km^2, obtained from the US Geological Survey's Hydro-1K data set; http://edcdaac.usgs.gov/gtopo30/hydro). We also used aspects of climate, including 1961–1990 annual means representing diurnal temperature range; freeze days; mean annual precipitation; solar radiation; maximum, minimum, and mean annual temperatures; vapor pressure; and wet days (all at 0.5° native resolution — ~2500 km^2), obtained from the Intergovernmental Panel on Climate Change (http://www.ipcc.ch). All environmental coverages were resampled to an intermediate resolution of 0.1° (10 km^2) prior to analysis. This set of environmental variables has been seen to be appropriate and adequate for modeling distributions in several studies (Peterson and Vieglais 2001; Peterson 2003).

Fig. 1. Common carp (*Cyprinus carpio*) native distribution across Eastern Europe and Asia. Circles represent collection localities, and potential distribution is represented by shaded areas; light gray indicates low agreement (1–5), dark gray indicates medium agreement (6–8), and black indicates high agreement (9–10) among the 10 best-subset models.
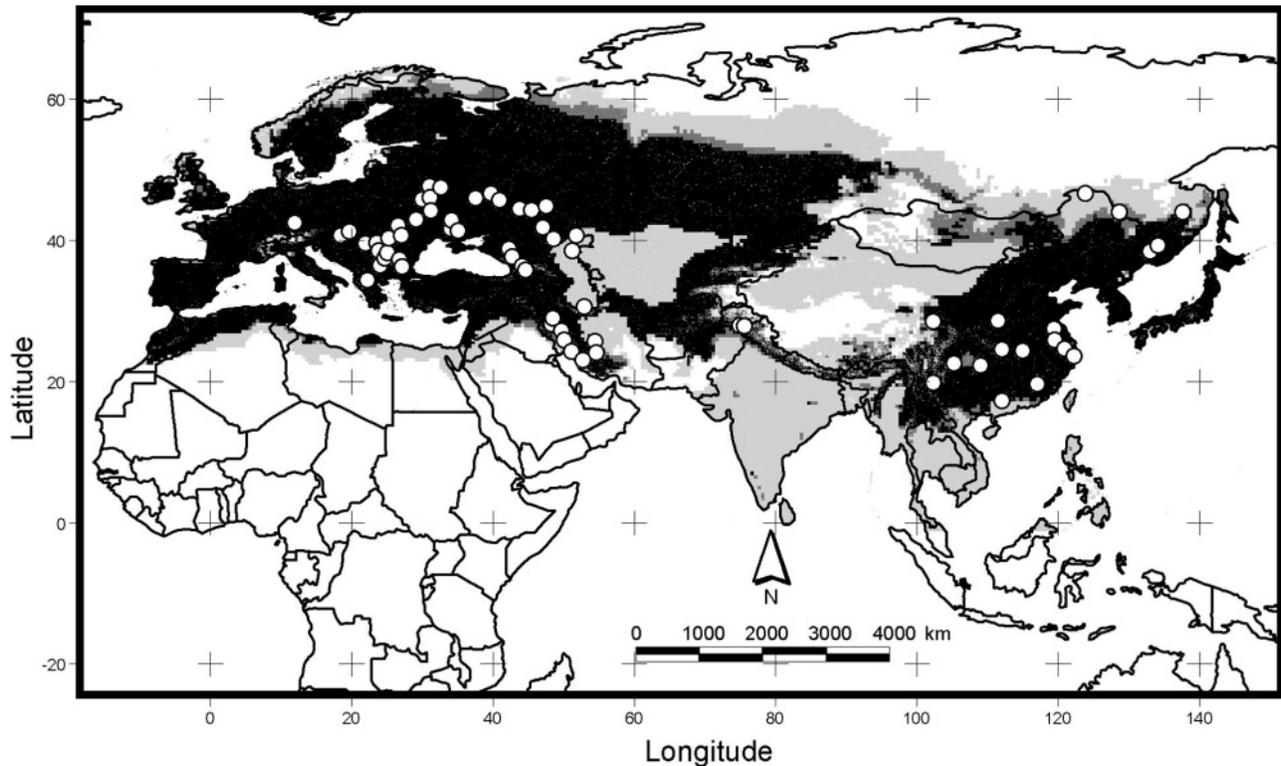
To reduce environmental coverage sets to just those coverages that provide highest predictive accuracy, we used a series of jackknife manipulations (Peterson and Cohoon 1999). In general, we ran multiple iterations (1–20) of models omitting each coverage or each suite of coverages systematically. We then examined correlations between inclusion or exclusion of each coverage (binary coded) and omission error (percentage of extrinsic test presence data not predicted as present). Correlations on the order of $r > 0.1$ were considered indicative of strong detrimental contribution of a particular coverage to model quality, and such coverages were removed from further analyses. It is important to note that the jackknife manipulations were done solely on the native distribution of each species and so do not detract from the independent nature of the invaded-range predictions and tests presented herein.

To optimize model performance, we developed 100 replicate models of each species' ecological niche based on random 50–50 splits of available occurrence points and followed a modified procedure for extracting a "best subset" of the replicate models for further consideration (Anderson et al. 2003). The procedure is based on the observations that (*i*) models vary in quality, (*ii*) variation among models involves an inverse relationship between errors of omission (leaving out true distributional area) and commission (including areas not actually inhabited), and (*iii*) best models (as judged by experts blind to error statistics) are clustered in a region of minimum omission of independent test points and moderate area predicted (an axis related directly to commission error). The position of the cloud of points relative to the two error axes provides an assessment of the relative ac-

curacy of the models. To choose best subsets of models, we (*i*) selected the 20 models with lowest omission error based on independent test points, (*ii*) calculated the median area predicted present among these low-omission models, and (*iii*) identified the 10 models that were closest to the median overall average area predicted present. A final map was created as the sum of these 10 best models (consensus map).

Model predictions were validated on native distributional areas (i.e., Africa for Nile tilapia, Asia for common carp) via the extrinsic testing data set. A χ^2 test was used to compare observed success in predicting distributions of test points with that expected under random models (the product of proportional area predicted present and number of extrinsic test presence points provides an estimate of occurrence points correctly predicted were the prediction to be random with respect to the distribution of the test points). Positive results in these tests would establish that models developed had sufficient predictive ability to be able to predict distributional phenomena for these species.

Projecting these models to the Americas provided predictions of potential geographic distributions of each species on its invaded range. We validated model predictions via overlaying known occurrence points for non-indigenous populations on the projections of the native-range models to the invaded distributional areas, using the same χ^2 approach as described above. To provide a binary prediction for these tests, we used 90% model agreement as a threshold for prediction of presence. To provide a more conservative test, we evaluated proportional area predicted present within a buffer of 750 km around the area predicted present.

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Fig. 2. Common carp (*Cyprinus carpio*) potential and known distribution in the Americas. Circles represent localities where this fish has been collected, and potential distribution is represented by shaded areas; light gray indicates low agreement (1–5), dark gray indicates medium agreement (6–8), and black indicates high agreement (9–10) among the 10 best-subset models.
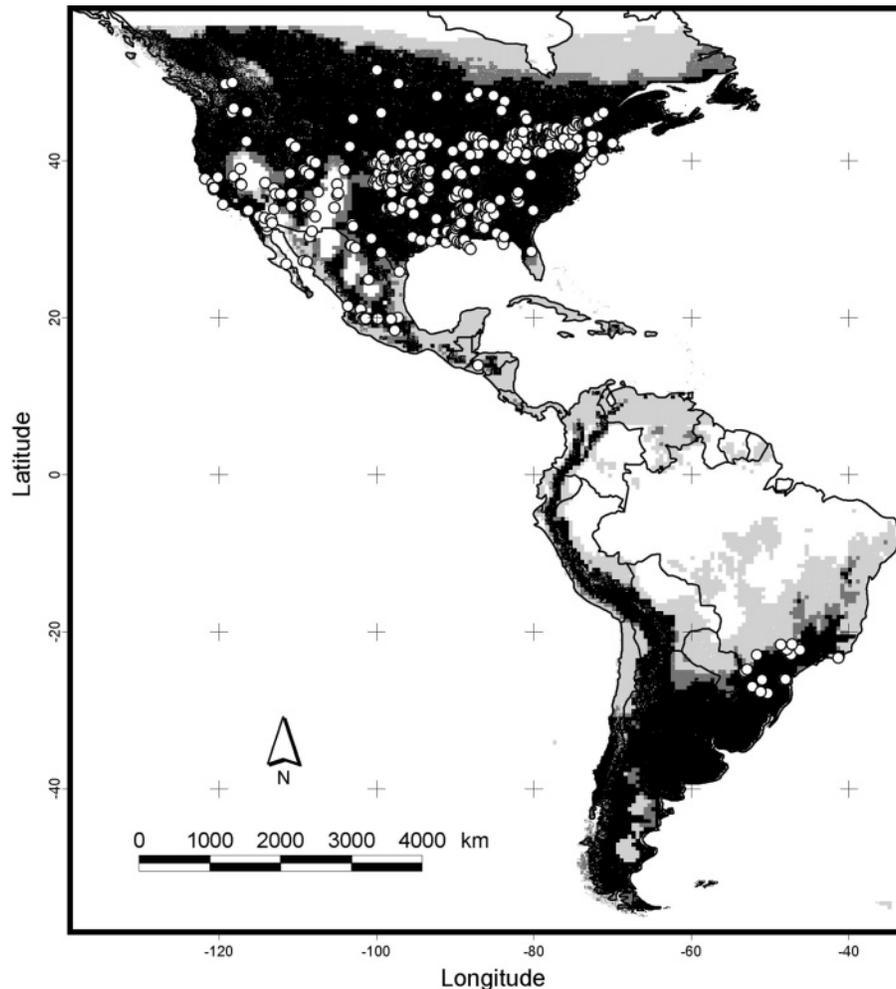
Results

Common carp distribution

The native distribution of common carp covers a large area from Eastern Europe eastward across Russia and China (Fig. 1). In most of this area, temperature in winter is cold enough to freeze lakes, but in summer water reaches 25 °C, which is the temperature needed for carp reproduction (Matiland and Campbell 1992). Our models predicted distributional areas for carp across broad swaths of Asia (Fig. 1). Statistical tests indicate that models had much higher predictivity than random expectations (predictive success = 92.64%, χ^2 = 28.51, df = 1, P < 0.0001).

Projection of native-range ecological niche models for common carp to the Americas shows broad areas with suitable conditions for the species. In North America, the predicted potential range includes most of Canada, the United States, and Mexico. Only the Sonoran Desert appeared inappropriate for carp (Fig. 2). In South America, areas prone to invasion are located principally in the south (Argentina, southern Brazil, and southern Chile; Fig. 2), but areas in the Andes suggest that opportunities exist even in tropical areas. Tests of model predictions for non-indigenous carp
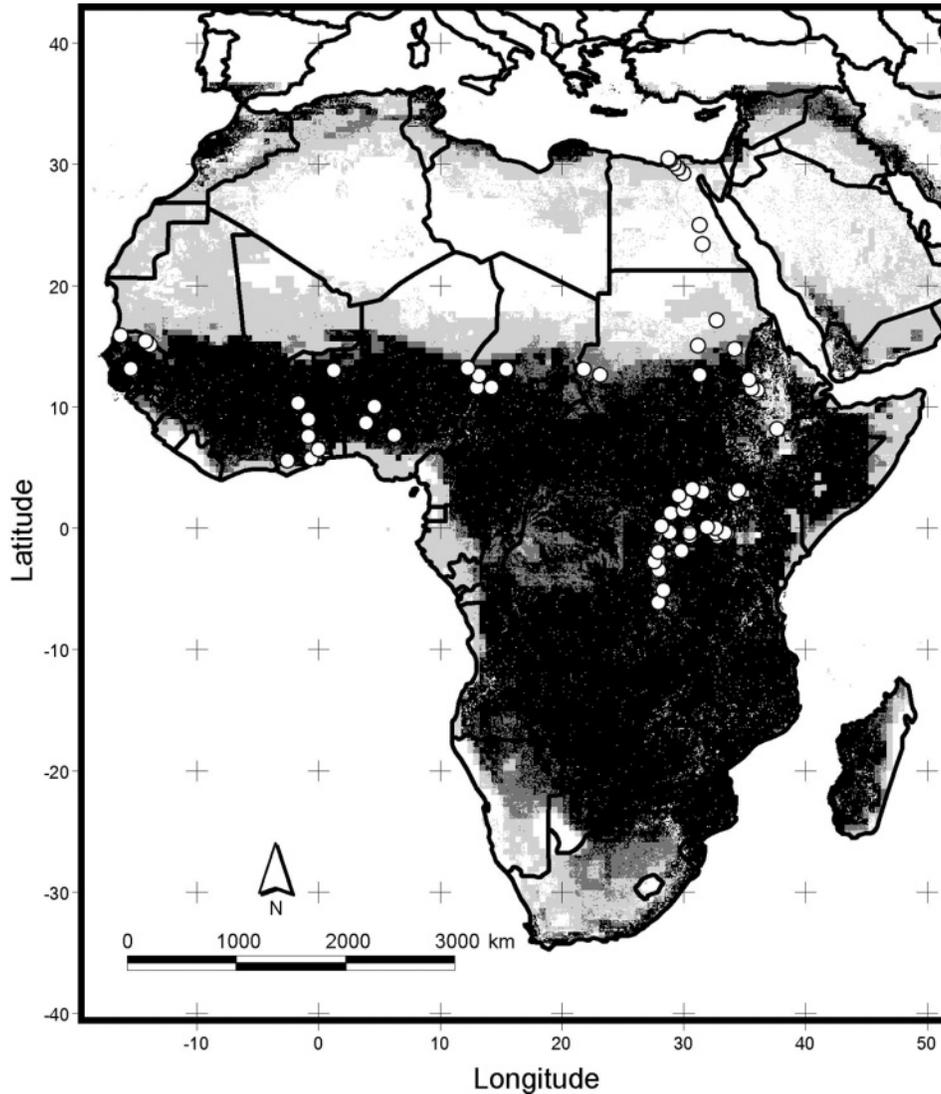
populations were significant both for North American populations (predictive success = 87.43%, χ^2 = 292.25, df = 1, P < 0.0001) and South American populations (predictive success = 53.33%, χ^2 = 9.93, df = 1, P < 0.002).

Nile tilapia distribution

The native distribution of Nile tilapia covers most of central Africa, limited to the north by the Sahara Desert and to the south in northern South Africa, where the limiting factor might be low air and water temperatures (Sifa et al. 2002). Our models predicted potential distributional areas across most of Africa except for the Sahara and the Kalahari deserts, but including the Mediterranean coast (Fig. 3). Model predictivity was high and statistically significant (predictive success = 87.48%, χ^2 = 17.5, df = 1, P < 0.001).

Projection of the best-subset models to the Americas indicates suitable conditions for Nile tilapia establishment from the southeastern United States south along the coastal lowlands of Mexico and Central America (Fig. 4). In South America, however, the species' shows a broader geographic potential: from central Brazil to central Argentina, and from the eastern slopes of the Andes to the Atlantic Ocean, as well as parts of the coast of Venezuela and Guyana (Fig. 4).

Fig. 3. Nile tilapia (*Oreochromis niloticus*) native distribution across the African continent. Circles represent localities where this fish has been collected, and potential distribution is represented by shaded areas; light gray indicates low agreement (1–5), dark gray indicates medium agreement (6–8), and black indicates high agreement (9–10) among the 10 best-subset models.

Tests of model predictions for non-indigenous Nile tilapia populations were significant both in North American populations (predictive success = 59.37%, χ^2 = 33.17, df = 1, $P <$ 0.001) and in South America populations (predictive success = 77.27%, χ^2 = 54.25, df = 1, $P <$ 0.001).

Discussion

The area that common carp or Nile tilapia may potentially inhabit in Asia, Africa, and the Americas indicates broad invasive potential. According to our results, common carp and Nile tilapia have a geographically extensive, invasive potential in the Americas, owing to their broad ecological niches. Common carp has the potential to establish in temperate systems, in both subtropical and temperate regions, and in the highlands within the tropics. Nile tilapia, on the other hand, has the potential to invade almost all tropical regions, particularly in the lowlands; indeed, this species is presently established in virtually every country in the Americas

(Fitzsimmons 2001). Only the Sonoran Desert, northern Chile, and southeastern Argentina are likely to be unsuitable for both species.

The resulting invasive potential of these species in the Americas is a spatial representation of the appropriate environmental conditions (i.e., ecological niches) modeled in their native ranges. Hence, the veracity of the results depends on how well the GARP system was able to represent the niche of species, which in turn depends directly on the quality of the input data. For this study, we did not have available range-wide aquatic environmental data on factors that directly determine the presence of fish species (e.g., water temperature, pH, turbidity, etc.). Instead, we used atmospheric variables as proxies that have some limitations and may bias the results, as can be observed in the Nile tilapia, which was not predicted present in the Sahara. However, populations can be established there when water is available.

Ecological consequences of invasion and establishment of these species in local systems can be serious. Direct impacts

Fig. 4. Nile tilapia (*Oreochromis niloticus*) distribution in the Americas. Circles represent localities where this fish has been collected, and potential distribution is represented by shaded areas; light gray indicates low agreement (1–5), dark gray indicates medium agreement (6–8), and black indicates high agreement (9–10) among the 10 best-subset models.
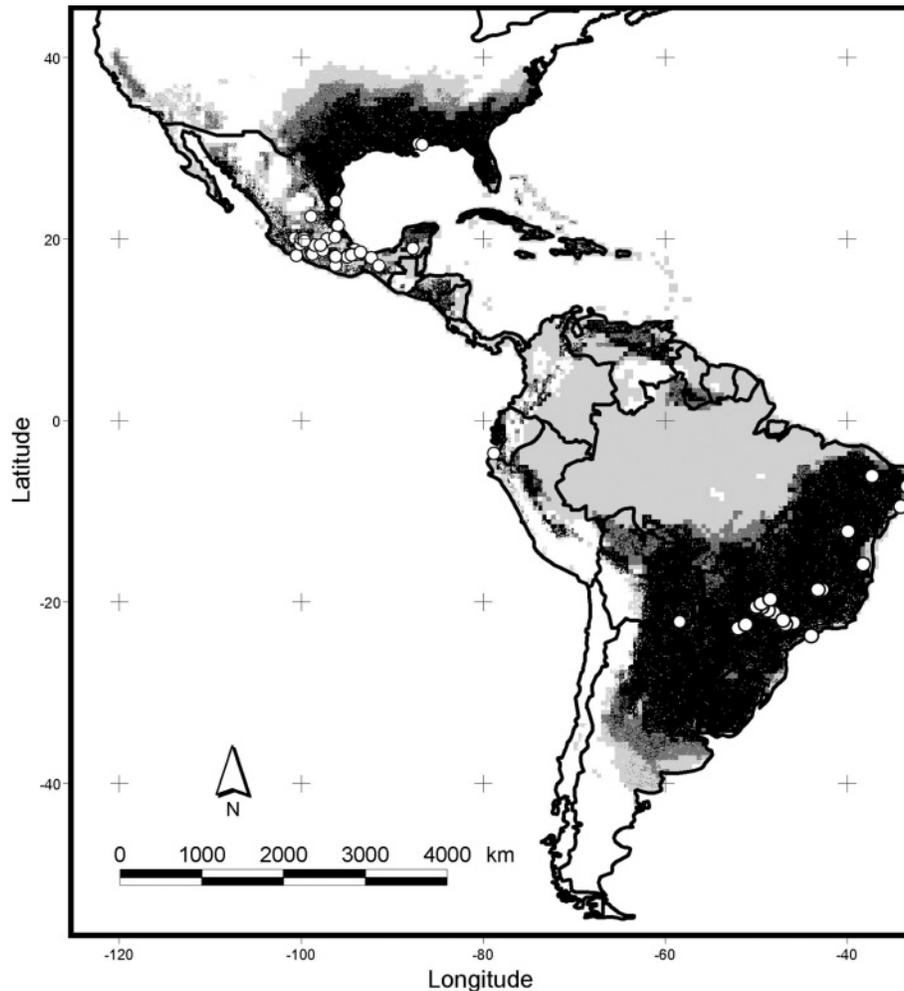
of introduced common carp and Nile tilapia in natural systems include population depletion and even local extinctions of native species (Cahn 1929; Ogutu-Ohwayo 1990; Canonico et al. 2005). Furthermore, these species are known to affect the physical conditions of aquatic systems via increasing turbidity, changing concentrations of nutrients and suspended solids, and reducing spatial heterogeneity, particularly in rooted plants (Zambrano and Hinojosa 1999), altering the whole system structure and dynamics.

The Americas hold an impressive fish diversity, including >5400 freshwater species (Reis et al. 2003). Endemism reaches 30% in the United States, Mexico, and Chile. Together with Brazil, with its immense Amazonian diversity, these countries have seen the highest increases in Nile tilapia production in recent years (Fitzsimmons 2001). Nile tilapia can establish in systems dominated by American fish families such as Poecilidae (216 species), Cichlidae (406 species), and Characidae (952 species), which together include >1574 species (Reis et al. 2003). Similarly, carp invasion may jeopardize even entire endemic American families (e.g., Goodeidae, >40 species).

General considerations for aquaculture

In recent years, common carp and Nile tilapia aquaculture has increased in many American countries as a consequence of a crisis in the fisheries resulting from overfishing and reduction in shrimp culture (Aiken et al. 2002; Alceste et al. 2001). The economic strategy has tended towards a switch from species of high monetary value but high production cost (e.g., shrimp, *Litopenaeus vannamei*) to species of lower economic value but very low production cost (e.g., common carp, *C. carpio* and Nile tilapia *O. niloticus*). Under this scheme, common carp and Nile tilapia production has to be high to generate acceptable profit, increasing risk of negative impacts on the system. In some regions, this production system has been economically and socially successful; however, in many others, ecological consequences were counterproductive (Tapia and Zambrano 2003).

Concern about potential negative effects of introductions of alien fish species is minimal in most countries. Awareness of dangers of introductions and the potential for dire ecological and biodiversity consequences has developed only relatively recently, after decades of promotion of aquaculture as

a solution to fulfill protein needs for human populations. Once these species are established in a system, eradication is extremely expensive and in many cases impossible. Hence, before releasing alien species in a system, it is necessary to estimate the potential success and counterbalance the ecological aftermath. This analysis should be mandatory in regions such as the Amazon Basin and central Mexico, where the potential for major loss of fish diversity is higher than any potential economical benefits.

Acknowledgements

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