Comparative distribution and invasion risk of snakehead (Channidae) and Asian carp (Cyprinidae) species in North America

Leif-Matthias Herborg, Nicholas E. Mandrak, Becky C. Cudmore, and Hugh J. MacIsaac

Abstract: As nonindigenous species are a major threat to global biodiversity, cost-effective management requires identification of areas at high risk of establishment. Here we predict suitable environments of 14 high-profile species of nonindigenous snakehead (Channidae) and Asian carp (Cyprinidae) species in North America based upon ecological niche modelling and compare the driving environmental variables for the two fish groups. Snakeheads distributions were correlated with thermal factors, whereas those of Asian carps were related mainly to precipitation. Predicted suitable ranges for these nonindigenous species can be divided into three main areas: Mexico and the southern United States (five species); Mexico and the United States up to ~35 °N (three species); and most of Mexico, continuous United States, and southern Canada (six species). For the province of Ontario, we combined the number and location of aquarium stores and live fish markets with predicted areas of suitable environments to identify areas at risk of introduction and establishment. We identified several watersheds draining into northwestern Lake Ontario as having the highest risk, highlighting the increased predictive value of this approach.

Résumé : Comme les poissons non indigènes représentent une menace importante à la biodiversité globale, une gestion efficace du point de vue des coûts requiert l'identification des zones où le risque d'établissement est élevé. Nous prédisons ici les milieux adéquats pour l'établissement de 14 espèces non indigènes bien connues de poissons-serpents (Channidae) et de carpes asiatiques (Cyprinidae) en Amérique du Nord d'après la modélisation écologique des niches et nous comparons les variables du milieu qui régissent l'établissement des deux groupes de poissons. Les répartitions des poissons-serpents sont en corrélation avec les facteurs thermiques, alors que celles des carpes asiatiques sont reliées surtout aux précipitations. Les aires adéquates de répartition prédites pour ces les poissons non indigènes se retrouvent dans trois régions principales: le Mexique et le sud des États-Unis (cinq espèces), le Mexique et les États-Unis jusqu'à ~35°N (trois espèces) et le Mexique presque dans son entier, les États-Unis continentaux et le sud du Canada (six espèces). Pour l'Ontario, la combinaison du nombre et de l'emplacement des boutiques d'aquariophilie et des marchés de poissons vivants, d'une part, et des régions prédites à habitats convenables, d'autre part, permet d'identifier les zones à risque pour les introductions et les établissements. Nous identifions plusieurs bassins versants qui se jettent dans le nord-ouest du lac Ontario comme étant à risque très élevé; ces résultats soulignent la valeur prédictive de notre méthodologie.

[Traduit par la Rédaction]

Introduction

Identifying high-risk areas for the establishment of nonindigenous species (NIS) using quantitative techniques is an important tool for the design and implementation of preventative management strategies (Leung et al. 2002; Simberloff 2005). Many risk assessment techniques are based on the NIS's invasive history elsewhere (e.g., Reichard and Hamilton 1997; Chen et al. 2007) or on basic environmental suitability (e.g., Goodwin et al. 1999; Ruesink 2005). A few studies have used environmental niche models to predict suitable areas for establishment (e.g., Drake and Bossenbroek 2004; Iguchi et al. 2004; Roura-Pascual et al. 2004). In recent years, the increased availability of environmental, georeferenced data sets and low-cost, high-speed computers has resulted in the development of a variety of ecological niche modelling techniques (see Guisan and Thuiller 2005). These techniques determine suitable habitat based upon the species' presence in an area and its associated environmental conditions.

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L.-M. Herborg[1,2] and H.J. MacIsaac. Great Lakes Institute for Environmental Research, University of Windsor, Windsor, ON N9B 3P4, Canada.
N.E. Mandrak and B.C. Cudmore. Great Lakes Laboratory for Fisheries and Aquatic Sciences, Fisheries and Oceans Canada, Burlington, ON L7R 4A6, Canada.

[1]Present address: Pacific Biological Station, Fisheries and Oceans Canada, Nanaimo, BC V9T 6N7, Canada.
[2]Corresponding author (e-mail: HerborgL@pac.dfo-mpo.gc.ca)

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One of these approaches, the genetic algorithm for rule-set prediction (GARP; Stockwell and Peters 1999), has been used to predict the potential distribution of NIS of molluscs, crustaceans, fishes, and ants according to their environmental habitat preferences (e.g., Drake and Bossenbroek 2004; Iguchi et al. 2004; Herborg et al. 2007). GARP has been widely used and tested in biogeography, usually but not always with successful outcomes (Elith 2000; Peterson and Vieglais 2001; Stockwell and Peterson 2002; but see Elith et al. 2006).

The key stages for the successful establishment of a NIS in a new habitat include introduction potential (i.e., presence of a pathway, number of introduction events, and number of propagules introduced per event), physiochemical requirements (i.e., environmental suitability), and biological community interactions (Colautti and MacIsaac 2004). Ecological niche modelling is able to discriminate areas where an introduced species can survive from those where it cannot. By combining ecological niche modelling with estimates of introduction potential, managers can identify areas at greatest risk of successful establishment by a NIS (e.g., Herborg et al. 2007).

This study focuses on two groups of fishes — the snakeheads (Channidae) and the Asian carps (Cyprinidae) — that have extensive histories of invasions and subsequent negative impacts on native biodiversity (Courtenay and Williams 2004; Kolar et al. 2005; Nico et al. 2005) and whose threat of establishment and spread in North America has garnered tremendous attention in the popular press. Snakeheads are freshwater fishes native to Asia, Malaysia, Indonesia, and tropical Africa. All species of snakeheads are piscivorous, although they also consume crustaceans and small vertebrates (Guseva 1990; Dutta 1994; Dasgupta 2000). In their native ranges, some snakeheads are highly valued as food fishes, particularly northern snakehead (*Channa argus*), blotched snakehead (*Channa maculata*), Chinese snakehead (*Channa asiatica*), bullseye snakehead (*Channa marulius*), and chevron snakehead (*Channa striata*). These species are either caught in the wild or raised in aquaculture facilities (Courtenay and Williams 2004). All snakeheads are either obligate or facultative air-breathers (Liem 1987), which allows these species to survive in moist conditions outside water over long periods (Courtenay and Williams 2004). The main pathway of introduction for snakeheads into the USA and Canada is sale at live fish markets (Courtenay and Williams 2004). Even after implementation of laws prohibiting public possession of live snakeheads in 26 American states and the Canadian province of Ontario, as well as a ban on import and interstate transport among all American states (in 2003), illegal shipments still occur. Some of these illegal shipments of live snakeheads into the USA originated from British Columbia (Courtenay and Williams 2004). The aquarium trade and subsequent indirect release of unwanted fish into local rivers seems to be of less importance for the introduction of snakeheads (Courtenay and Williams 2004). Owing to their predatory nature, high price, rapid growth of some species, and the high cost of live food, snakeheads are only a minor part of the aquarium trade. Nevertheless, several species were periodically available to hobbyists in the USA and Canada (Klee 1963; Courtenay and Williams 2004). Currently, three species of snakeheads are established and spreading: the bullseye snakehead in Florida; the northern snakehead in Maryland, Pennsylvania, and Virginia; and the blotched snakehead in Hawaii (Courtenay et al. 2004; Orrell and Weigt 2005).

The four species of Asian carps examined in this study were the grass carp (*Ctenopharyngodonn idella*), silver carp (*Hypophthalmichthys molitrix*), bighead carp (*Hypophthalmichthys nobilis*), and black carp (*Mylopharyngodon piceus*). The grass carp is a herbivorous fish introduced for macrophyte control (Crossman and Cudmore 1999*a*), although it also has negative impacts on phytoplankton, invertebrate communities, and native fishes (Chilton and Muoneke 1992). The silver and bighead carps were intentionally introduced into the southern USA and the Canadian province of Alberta to control eutrophication in lakes and ponds (Crossman and Cudmore 1999*a*, 1999*b*; Mandrak and Cudmore 2004). These species feed on phytoplankton and small zooplankton and may compete with juveniles of many native fishes (Dong and Li 1994; Fuller et al. 1999). Black carp are molluscivorous and pose a threat to endangered molluscs (Ferber 2001); they may also compete with native molluscivorous fishes. The main pathway of black carp introduction is associated with their use by fish farmers in the southern USA to control parasite-carrying molluscs (Ferber 2001; Nico et al. 2005). Repeated occurrences of black carp in the southern Mississippi River (Nico et al. 2005) suggest that an established population is present.

The aim of this study is to predict the potential distribution of Asian carp and snakehead species in North America and to provide a more refined assessment of invasion likelihood estimate for the province of Ontario such that management efforts can be focused on areas at greatest risk.

Materials and methods

Species studied

In our study, we included northern snakehead, Chinese snakehead, rainbow snakehead (*Channa bleheri*), bullseye snakehead, giant snakehead (*Channa micropeltes*), spotted snakehead (*Channa punctata*), golden snakehead (*Channa stewartii*), chevron snakehead, blotched snakehead, and Niger snakehead (*Parachanna africana*) (common names according to Courtenay and Williams 2004). Ecological niche models were developed for each of these species based on their native distribution as reported in a recent review (Courtenay and Williams 2004). Models were also developed for the black, bighead, grass, and silver carps. Predictions of suitable habitat were based on reported native ranges for the grass carp (Opuszynski and Shireman 1995) and the silver, bighead, and black carps (Mandrak and Cudmore 2004, Kolar et al. 2005).

Environmental niche model development

The development of the rule set in GARP requires the definition of an analysis mask used in developing the model. All major watersheds within the native range plus each watershed adjacent to an inhabited drainage basin defined the masks for each species. Previous studies have typically used museum records to represent the native range of the species. There are several potential drawbacks of using only museum records: too few records may be available to generate a robust model, and the available records may not fully represent the extent of the species' ecological niche in its native range. To overcome these potential drawbacks, random points within native range polygons were extracted using Hawth's tool extension (available from www.spatialecology.com/htools/tooldesc.php) within Arcmap 9.1 (ESRI, Redlands, California) to convert the range outline into point occurrence data, as required by GARP. Two hundred occurrence points were generated for each species, except for two species (rainbow and Niger snakeheads) with a restricted native distribution for which only 100 points were created. The development of ecological niche predictions was based on three steps: (*i*) determining environmental coverages that contributed significantly to model accuracy; (*ii*) predicting suitable environments based on this subset of environmental layers; and (*iii*) assessment of the contribution of each retained environmental variable to the final model.

The global climatic and geographic coverages tested for each species' model included frost frequency (days of frost per year), slope, compound topographic index (wetness index based on flow accumulation and slope), mean daily precipitation, river discharge, wet day index (days of precipitation per year), and minimum, mean, and maximum annual air temperatures (see Table 1 for more details). A GARP simulation using all possible combinations of environmental coverages allowed us to determine the effect of each coverage on model accuracy using multiple linear regression analysis. We used the tolerance value to test for multicollinearity among environmental variables (Minitab 12, Minitab Inc., State College, Pennsylvania; Quinn and Keugh 2002). Model accuracy was determined by the number of presence points (omission errors and false negatives) and pseudo-absence points (pseudo-commission and false positives) correctly predicted by GARP for all permutations of the environmental coverages. Variables positively correlated to omission errors (i.e., increased the number false positives) were rejected. In case the relationship between omission errors and an environmental variable was not significant, it was only included in the prediction if it was positively correlated with pseudo-commission (Anderson et al. 2003; Drake and Bossenbroek 2004).

Once suitable environmental coverages for each species were determined, models were generated using a maximum of 1500 iterations and a 0.001 convergence limit following the best subset method (Anderson et al. 2003). This approach uses a <5% limit on the ratio of test data points outside the predicted range (false negatives, omission errors) and a <50% limit for ratio of predicted suitable environment without test data points (false positives, commission errors) (Anderson et al. 2003). Once 100 models fulfilling these criteria were generated, they were converted into a map of percent environmental suitability (Arcmap 9.1, ESRI, Redlands, California; Drake and Bossenbroek 2004). One drawback of using GARP for ecological niche modelling is the lack of information on the contribution of different environmental variables and their suitable range on the final prediction of a species' range.

To improve transparency of the results, we applied two additional analytical techniques to the prediction. We tested the overall effect of environmental coverages on predictive accuracy of the final models using hierarchical partitioning (Peterson and Cohoon 1999). This approach measures the relative contribution of each environmental layer using all possible combinations of environmental variables included in the final GARP prediction as well as its associated accuracy. We also used the evaluation strip method to determine the actual range of environmental conditions deemed suitable by the model (Elith et al. 2005). This approach is based on the insertion of columns containing the full range of values for each environmental parameter into the environmental coverages. The number of models predicting each particular value of each environmental variable as suitable can then be used to identify the suitable ranges for each variable (for more detail, see Elith et al. 2005)

Table 1. Environmental coverages tested for their contribution to predictive accuracy in the environmental models predicting the potential range of snakeheads and Asian carps in North America.

Variable	Grid size
Climatic*	
Ground frost frequency (days·year^{-1})	0.5° × 0.5°
Maximum air temperature (°C)	0.5° × 0.5°
Mean air temperature (°C)	0.5° × 0.5°
Minimum air temperature (°C)	0.5° × 0.5°
Wet day index (days precipitation·year^{-1})	0.5° × 0.5°
Mean daily precipitation (mm)	0.5° × 0.5°
Topographic†	
Topographic index (wetness index based on flow accumulation and slope)	1 km × 1 km
Slope (maximum change in elevation between cells)	1 km × 1 km
River discharge (km^3·year^{-1})‡	0.5° × 0.5°

*From the Climate Research Unit global climate data set, available from www.ipcc-data.org/obs/get_30yr_means.html.
†From the US Geological Survey Hydro1k Elevation Derived Database, available from edc.usgs.gov/products/elevation/gtopo30/hydro/index.html.
‡From Xenopoulos et al. 2005.

Validation of ecological niche models

As an independent measure of model performance, we calculated the area under the receiver operating characteristic curve (AUC), a widely used measure of the ability of the model to discriminate between sites where a species is present and where a species is absent (see Hanley and McNeil 1982; Wiley et al. 2003; Elith et al. 2006). The AUC measures predictive accuracy on a scale between 0 and 1, with 1 representing perfect prediction for both presence and absence points, and a value of 0.5 indicating a no-better-than-random predictive ability. The AUC was based on occurrence points generated for the GARP prediction and an equal number of randomly selected absence points obtained from the area within each species' analysis mask (all major watersheds of the native range plus each adjacent watershed) but outside the species' native range polygons. The mean GARP score from the 100 best subsets used in the final prediction were extracted for each of these points. We calculated the AUC using the "verification" package within the R 2.3.0 software (www.r-project.org/).

We used georeferenced collection data for introduced carps and snakeheads occurrences in the USA as an independent test of the predictive ability of our ecological niche models. Data were obtained from the USGS Nonindigenous Aquatic

Table 2. Assessment of model performance for each species' range prediction.

Species	AUC*
Snakehead	
Bullseye	0.7657
Blotched	0.8785
Chevron	0.9409
Chinese	0.7372
Giant	0.8359
Golden	0.9267
Niger	0.8165
Northern	0.9097
Rainbow	0.9212
Spotted	0.8723
Carp	
Black	0.9707
Bighead	0.9506
Grass	0.9366
Silver	0.8844

*The area under the reporter operator receiver curve (AUC) is an estimate of model performance, with 1 indicating a perfect prediction and 0.5 a purely random model. Level of significamce was $p < 0.0001$ for all species.

Species database (nas.er.usgs.gov/) and includes the location of established populations, or single specimens, within an eight-digit hydrologic unit code watershed as defined by the Water Resources Council of the USA (Seaber et al. 1987). Using the Spatial Analyst extension (Arcmap 9.1, ESRI, Redlands, California), we extracted the mean environmental suitability prediction for each hydrologic unit code where each NIS was established.

Estimate of introduction potential

We combined environmental suitability models with estimates of introduction potential to develop a spatially explicit relative risk measure. We estimated introduction potential for two major, human-aided transport pathways: the live fish market and aquarium fish trades. Limitations in data availability for these pathways restricted our geographic coverage to Ontario. We used the number of live fish markets found in each watershed in Ontario (Cudmore and Mandrak 2005) as a basic estimate of introduction potential for fish species in our study. Fishes reported by the Ontario Ministry of Natural Resources (Goodchild 1999) for sale in live fish markets included the silver, bighead, black, and grass carps as well as the blotched, bullseye Chinese, chevron, spotted, and northern snakeheads. All 96 live fish market locations were georeferenced, incorporated into GIS (Arcmap 9.1, ESRI, Redlands, California), and overlaid with Water Survey of Canada drainage area boundaries at the tertiary watershed level in Ontario. The number of live fish markets per watershed was used as a basic estimate of introduction potential. We assumed that the number of live fish markets in an area was positively correlated to the risk of accidental or intentional introduction of nonindigenous fishes into the local watershed. The risk associated with aquarium releases was estimated based on the location of aquarium and pet shops in Ontario (Cudmore and Mandrak 2005). A total of 208 retailers were georeferenced based on their postal code, and their cumulative number per watershed (see previous paragraph for details) were determined. Our approach is based on the assumption that the number of aquarium retailers per watershed is proportional to the introduction potential for this area.

Table 3. Summary of the number of eight-digit hydrologic unit codes with established populations of snakeheads or Asian carps in the USA according to the USGS Nonindigenous Aquatic Invasive Species database.

Species	No. watersheds established	Mean environmental suitability±SE*
Snakehead		
Northern	3	100±0
Blotched	1	100†
Bullseye	1	100†
Carp		
Grass	45	97±13
Silver	37	100±0.6
Bighead	51	100±2
Total	138	98±8

*The mean environmental suitability is calculated per watershed with an established population.
†No standard error (SE) calculated, as only one observation.

Results

Validation

Development of environmental niche models was successful for each of the species under study. The AUC statistic was significant for all models and the overall scores were high (>0.737; Table 2). AUC values of <0.800 were obtained for two species of snakeheads, although these values were >0.900 for seven species, including three of the carp species (Table 2). Independent tests for our models were provided by a comparison of predicted environmental suitability values for the watersheds with actual presence of established populations for five species (northern and blotched snakeheads; bighead, grass, and silver carps). Watersheds with established populations (n = 138) for all five species had a very high percentage of environmental suitability (98.8% ± 7.6%). In addition, only two established populations of grass carp were recorded in areas with an environmental suitability of <85% (22.9% in the Upper Columbia River, Washington, and 55.9% for Middle Gila, Arizona; Table 3). Thus, GARP models based upon each species' native distribution successfully predicted the habitats in which they are presently established in North America.

Effect of environmental variables on predictions

The number of environmental variables that contributed significantly ($p < 0.05$) to prediction accuracy varied from nine for the bighead and silver carps to three for the chevron snakehead (Table 4). Independent of the number of layers used in the final prediction, hierarchical partitioning analysis determined that only between one and three layers contributed more than 20% to prediction accuracy in all cases (Table 4). Critical multicollinearity ($t < 0.1$) of environmental coverages in the multiple regression analysis during coverage selection process was detected in only five out of 252

Table 4. Environmental variables used for predicting potential ranges for 14 species of nonindigenous freshwater fish in North America and their relative contribution (%) to prediction accuracy determined by hierarchical partitioning.

						Air temperature			
Species	Frost frequency	Slope	CTI	Precipitation	Annual river discharge	Min.	Mean	Max.	Wet day index
Snakehead									
Blotched	—	0.3	1.8	—	0.8	25.6	22.1	**45.1**	4.4
Bullseye	4.3	—	3.1	—	—	33.4	**36.2**	23.1	—
Chevron	—	—		—	—	1.5	27.2	**71.3**	—
Chinese	19.1	—	1.1	17.1	2.4	**52.5**	—	—	7.7
Giant	36.2	—		0.8	1.8	—	—	**61.1**	0.1
Golden	—	—		25.0	2.4	3.3	27.7	8.9	**32.8**
Niger	16.4	0.2	0.6	9.9	—	—	**72.9**	—	—
Northern	25.2	—	4.6	—	0.2	11.1	19.7	**39.1**	—
Rainbow	0.4	0.2	0.5	—	0.1	6.2	19.0	**73.5**	—
Spotted	10.1	—	2.4	—	0.4	22.4	30.1	**30.9**	3.7
Carp									
Black	7.7	—	1.5	**58.8**	0.8	10.8	7.9	5.6	6.9
Bighead	3.9	1.1	1.5	**60.5**	3.1	11.2	6.5	5.2	7.0
Grass	16.1	—		**39.8**	—	24.4	14.2	5.5	—
Silver	5.7	<0.1	0.6	**34.7**	1.4	10.8	6.7	6.2	34.0

Note: The variable with the highest effect for each species is bolded. CTI is the compound topographic index (see Table 1 for more details). Common names provided for snakeheads here are based on Courtenay and Williams (2004).

cases, which did not validate the exclusion of environmental variables.

Carp and snakehead species distributions were correlated with different features of the environment. For example, precipitation was important to all four Asian carps distribution models, while frost day frequency, wet day index, and air temperature attributes contributed less to the accuracy of these models (Table 4). Areas with a mean daily precipitation of >5–15 mm and <50–60 mm were most suitable to Asian carp species. The second most important predictor of silver carp was the number of wet days, where 58–185 days of precipitation per year was ideal. For black, bighead, and grass carps, the second most important environmental variable was minimum air temperature. The most suitable habitat for this variable was in areas with a minimum temperature of –11 to 4 °C for grass carp (Fig. 1*e*) and –4 to 20 °C for black carp (Fig. 1*h*), but there were no clear limits for bighead carp (Figs. 1*c*, 1*g*). The Asian carps were predicted to find a suitable environment in most of Mexico, the USA, and southern Canada (Fig. 2).

Snakehead species distributions were correlated with a wider array of environmental variables than was observed for carp species. Maximum air temperature was the most important variable for six species (northern, rainbow, blotched, giant, spotted, and chevron snakeheads). Northern snakeheads have the most northern native distribution and an optimum maximum air temperature range (5–16 °C; Fig. 1*i*) lower than that (25–32 °C) for species from more southern locales (Fig. 1). Mean air temperature was the key variable for bullseye snakehead (medium suitability over 22 °C; Fig. 1*m*) and Niger snakehead (low suitability 26–27 °C; Fig. 1*w*). Minimum air temperature was the most important variable for Chinese snakehead, which had the highest predicted suitability between 9 and 23 °C minimum temperature (Fig. 1*j*). Wet day index was the strongest predictor for golden snakehead (Fig. 1*u*), although the output of the evaluation strip was inconclusive.

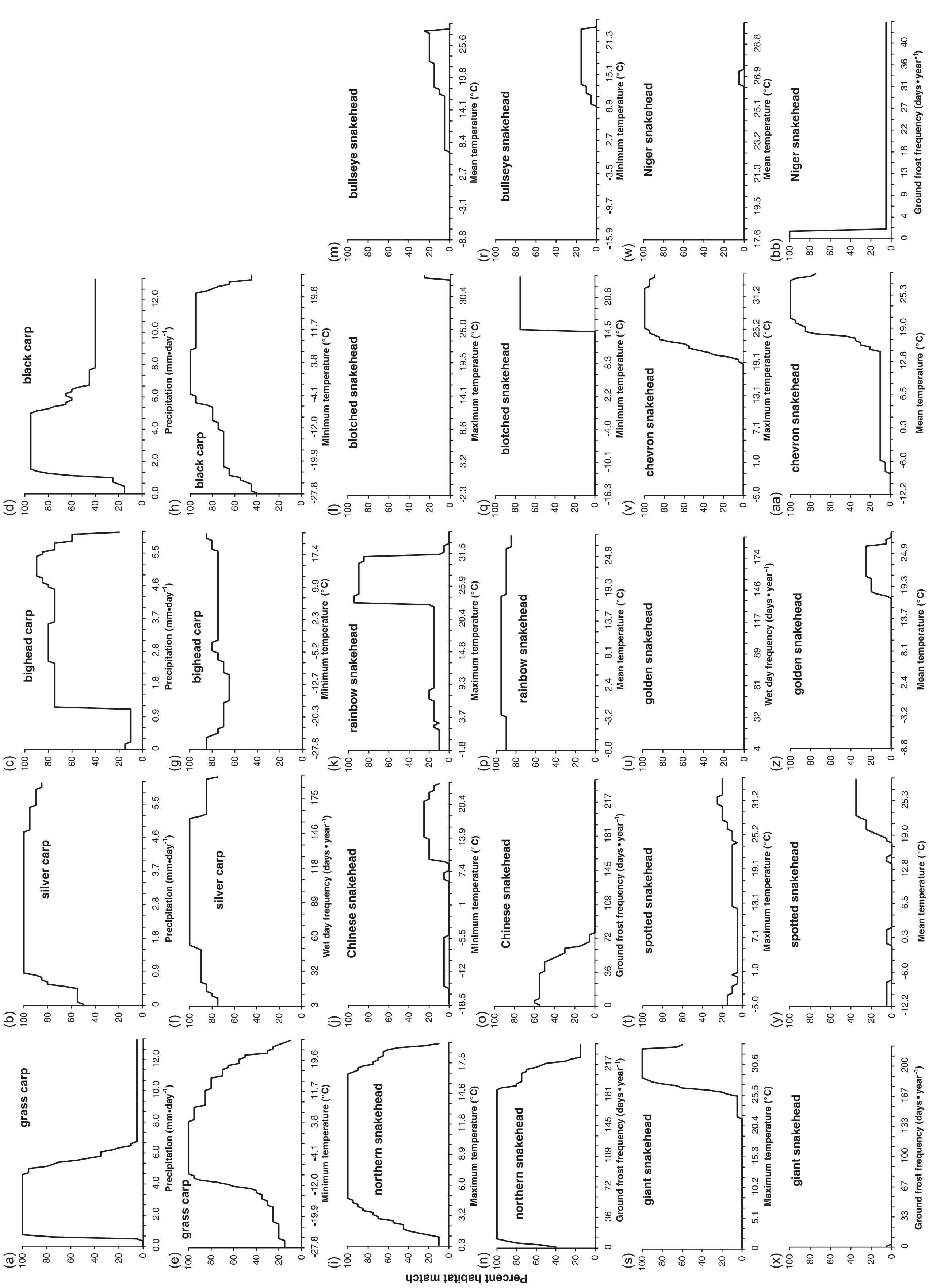
Predicted ranges in North America

The distribution of predicted suitable habitat for snakeheads can be separated into three broad categories. The most southern distribution limit includes coastal areas of Mexico and USA states bordering the Gulf of Mexico, particularly in coastal Texas and Florida. Species that fall into this category include Chinese, blotched, giant, spotted, and golden snakeheads. Species with a mid-USA distribution limit were predicted to have suitable habitat in most of Mexico and the USA, up to ~35°N, including bullseye, chevron, and Niger snakeheads. Two species of snakeheads (northern and rainbow) were predicted to have suitable habitat throughout most of Mexico and the USA, as well as the southern half of Canada (Fig. 3). Northern snakeheads are predicted to have high environmental suitability in the northern USA and southern Canada, whereas, for rainbow snakehead, these regions would have medium to low environmental suitability.

Spatially explicit introduction risk for Ontario

We estimated introduction potential by combining environmental suitability and pathway strength for the six carp and snakehead species whose predicted suitable environments extended into Ontario. Five of these species (i.e., northern snakehead and bighead, grass, silver, and black carps) are associated with live fish markets, and one (i.e., rainbow snakehead) is available to aquarium hobbyists. The highest risk of introduction of nonindigenous fish via live fish markets in Ontario occurs within five watersheds within the Great Lakes basin. The highest numbers of live fish markets are concentrated in two watersheds (78 and 10 stores) in the area around Toronto on the northern shore of Lake Ontario. A further three watersheds along the northwestern tip

Fig. 1. Predicted environmental sustainability for the two environmental variables with the highest contribution to prediction accuracy (see Table 4) for each species. The range of each environmental parameter is based on the minimum and maximum value within the masked area of the native range.



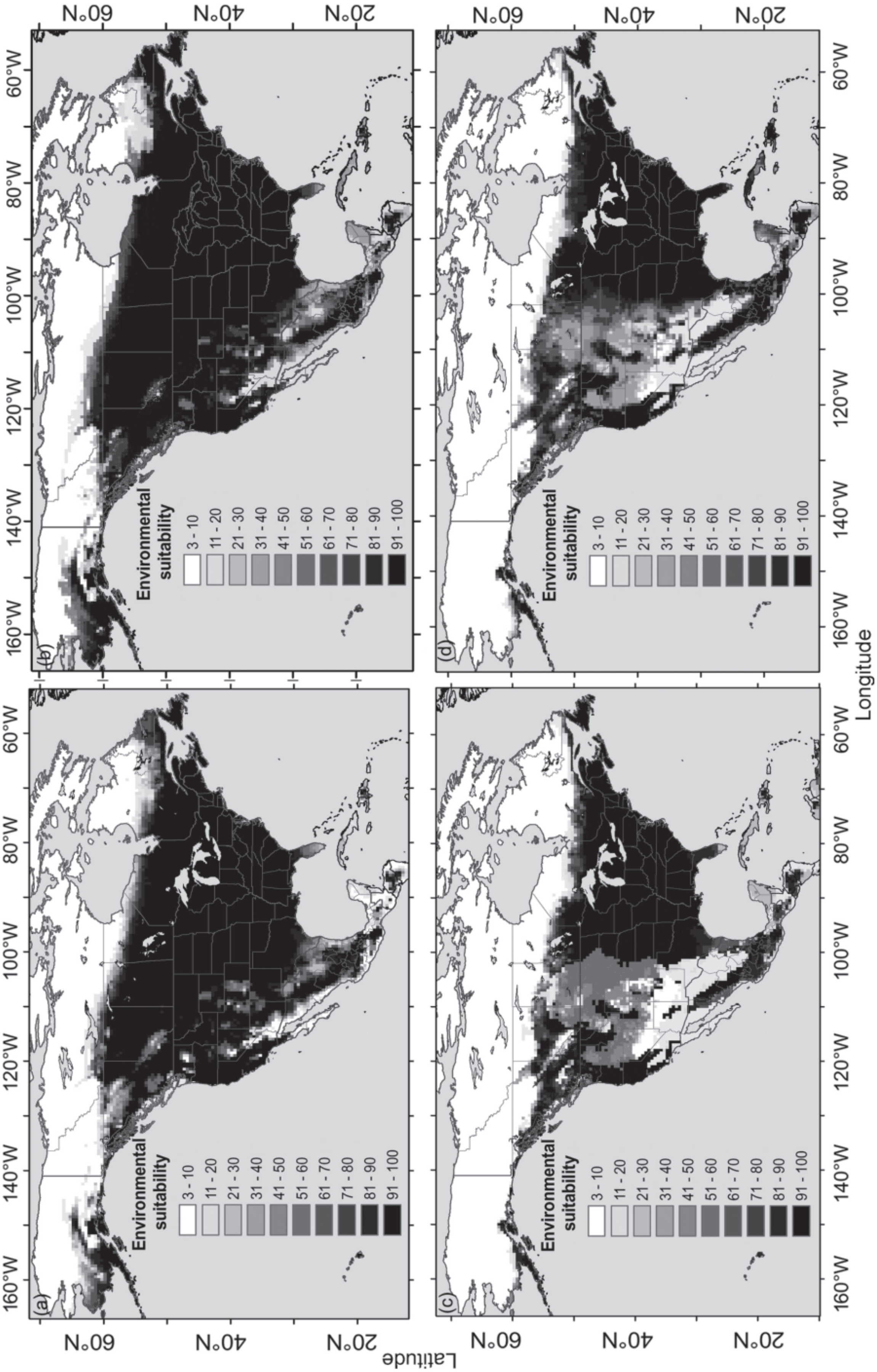


Fig. 2. Predicted suitable environment for four species of Asian carp (Cyprinidae) in North America. Environmental suitability is represented as the number (out of a maximum of 100) of models that predicted a particular location as suitable. (*a*) Grass carp, (*b*) silver carp, (*c*) bighead carp, (*d*) black carp.

Fig. 3. Predicted suitable environment of 10 species of nonindigenous snakehead (Channidae) in North America based on ecological niche models. Environmental suitability is represented as the number (out of a maximum of 100) of models that predicted a particular location as suitable.

of Lake Erie, the northwestern tip of Lake Ontario, or north of Lake Ontario have one, two, and five live fish markets, respectively. Since the environmental suitability for all five species for central and southern Ontario is very high (>90), the highest risk of introduction and establishment for these species is focused in the area around Toronto, followed by the watersheds with comparatively very few live fish markets (Fig. 4*a*).

Introduction risk based on the distribution of aquarium shops is more widespread in Ontario, including locations in the Great Lakes and Hudson Bay watersheds. A total of 44 watersheds in Ontario contain at least one aquarium store, with the highest densities (50, 18, 16, 14) occurring in four watersheds along the northwestern shore of Lake Ontario (Fig. 4*b*). The rainbow snakehead is the only species known to be sold through the aquarium trade that our model indicates has some level of environmental suitability in Ontario (Fig. 3*c*). The introduction risk for the rainbow snakehead associated with aquarium trade is highest for the Toronto area, although other watersheds across Ontario are also at risk. However, predicted environmental suitability (7–16) is very low for these areas, thus overall risk is also very low.

Discussion

Ecological niche models in invasion biology

Substantial resources have been devoted to prevent spread of Asian carps and snakeheads and to eradicate some established populations (Rasmussen 2002; Courtenay and Williams 2004). Ecological niche modelling can identify suitable habitats susceptible to future invasions, thereby providing an important preventative management tool (Peterson 2003; Drake and Bossenbroek 2004; Roura-Pascual et al. 2004). We identified that the four species of Asian carp and the northern snakehead pose the most widespread risk of establishment and spread across North America in that all of them have a very broad, predicted suitable range and all have, or may have, established populations in the USA. Bighead, grass, and silver carps are established in portions of the Mississippi River watershed. Based upon our species-specific model projections, these species pose major threats to adjacent watersheds (including the Great Lakes), where suitable habitats occur. Thus, current efforts devoted to vector control — including prohibition of interstate movements of live fishes and the construction and implementation of an electrical barrier to prevent the spread to the Great Lakes via the Chicago Ship and Sanitation Canal (Rasmussen 2002) — seem prudent.

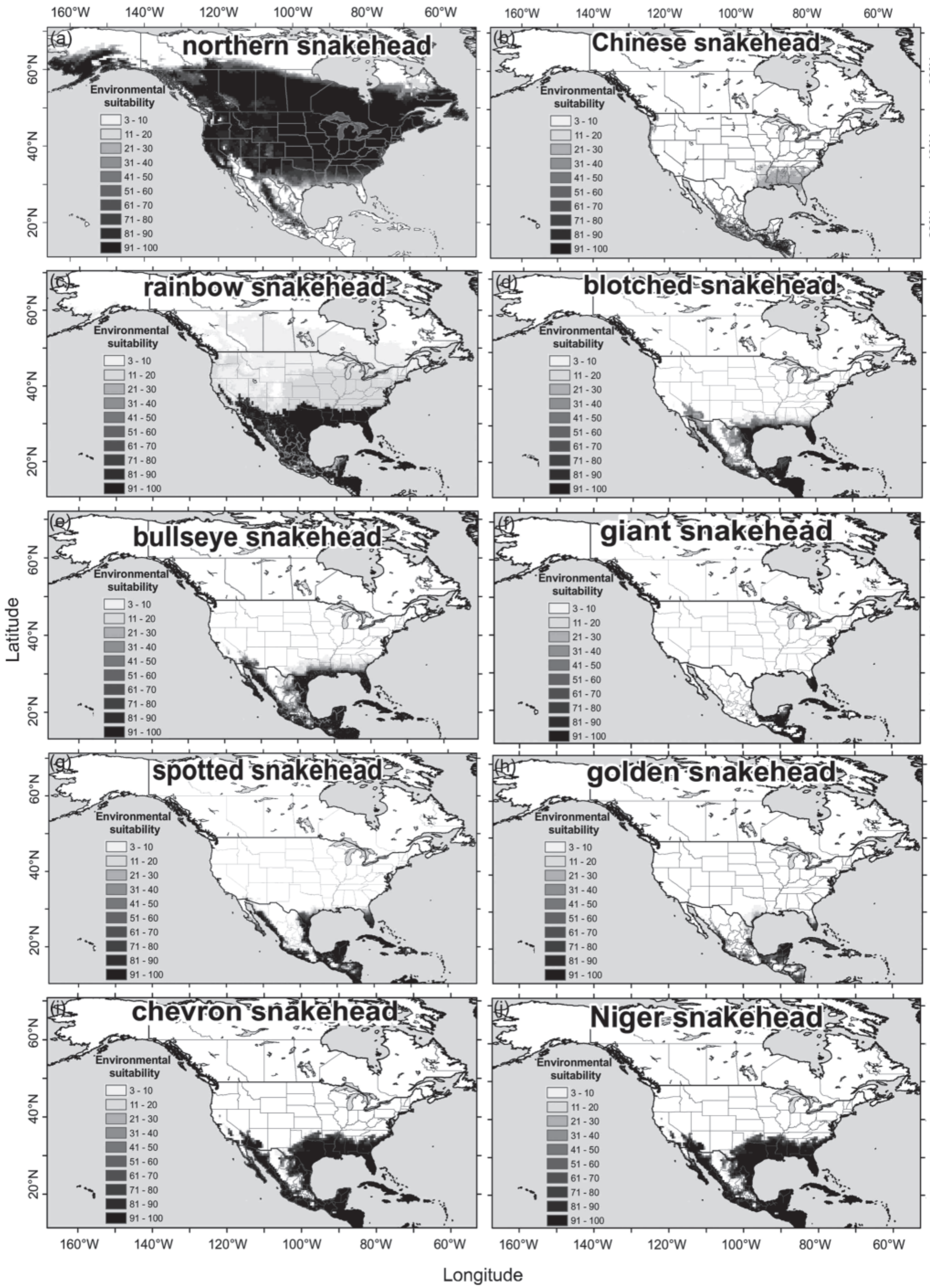
Comparison of environmental predictors for Asian carps and snakeheads

Our study identified marked differences in the environmental variables correlated with environmental suitability for carp and snakehead species. The key environmental parameter influencing the prediction for all snakeheads, except golden snakehead, was minimum (Chinese snakehead), mean (bullseye and Niger snakeheads), or maximum air temperature (northern, rainbow, blotched, giant, spotted, and chevron snakeheads). Most preferences indicated a thermal requirement over a threshold value, consistent with these species' native subtropical range. The one exception was the northern snakehead, which was tolerant of lower maximum air temperatures and has a correspondingly more northern native range. In contrast, precipitation was the key environmental variable for all four species of carp. A maximum precipitation threshold appears to apply for at least two species (black and grass carps). The different variables driving the predictions for snakeheads and carps could be related to several factors. All four species of carps have widespread distributions in eastern China, stretching from 22°N to 52°N (Mandrak and Cudmore 2004), indicating their ability to thrive across a wide range of temperatures and accounting for the relatively low importance of temperature as a determinant of distribution. The importance of precipitation for Asian carps could be related to their preference for large rivers for spawning (Abdusamadov 1986; Schrank et al. 2001). The inclusion of other hydrological parameters such as flow, water temperature, and water chemistry could potentially improve the predictions of suitable environments and the variables that drive carp models; however, these parameters were not available for our study areas.

Our predictions of environmentally suitable areas for silver carp in the USA are similar to those of Chen et al. (2007), who also used environmental niche modelling. However, the predicted range for bighead carp by Chen et al. (2007) excluded the northern USA as well as the Great Lakes region, areas with established bighead carp populations that our model forecasted as suitable. The differences in the results of the two models may be due to different definitions of species' native ranges (i.e., museum records versus random points from range maps) or different selection processes for environmental variables. It should be noted that Kolar and Lodge (2002) predicted that neither black carp nor silver carp would successfully establish in the Great Lakes. Differences between these models may be explained by the factors each considered. While our study compared climatic, topographic, and hydrological variables between the native and potential introduced range, Kolar and Lodge (2002) assessed life history differences between successful and unsuccessful invaders of the Laurentian Great Lakes.

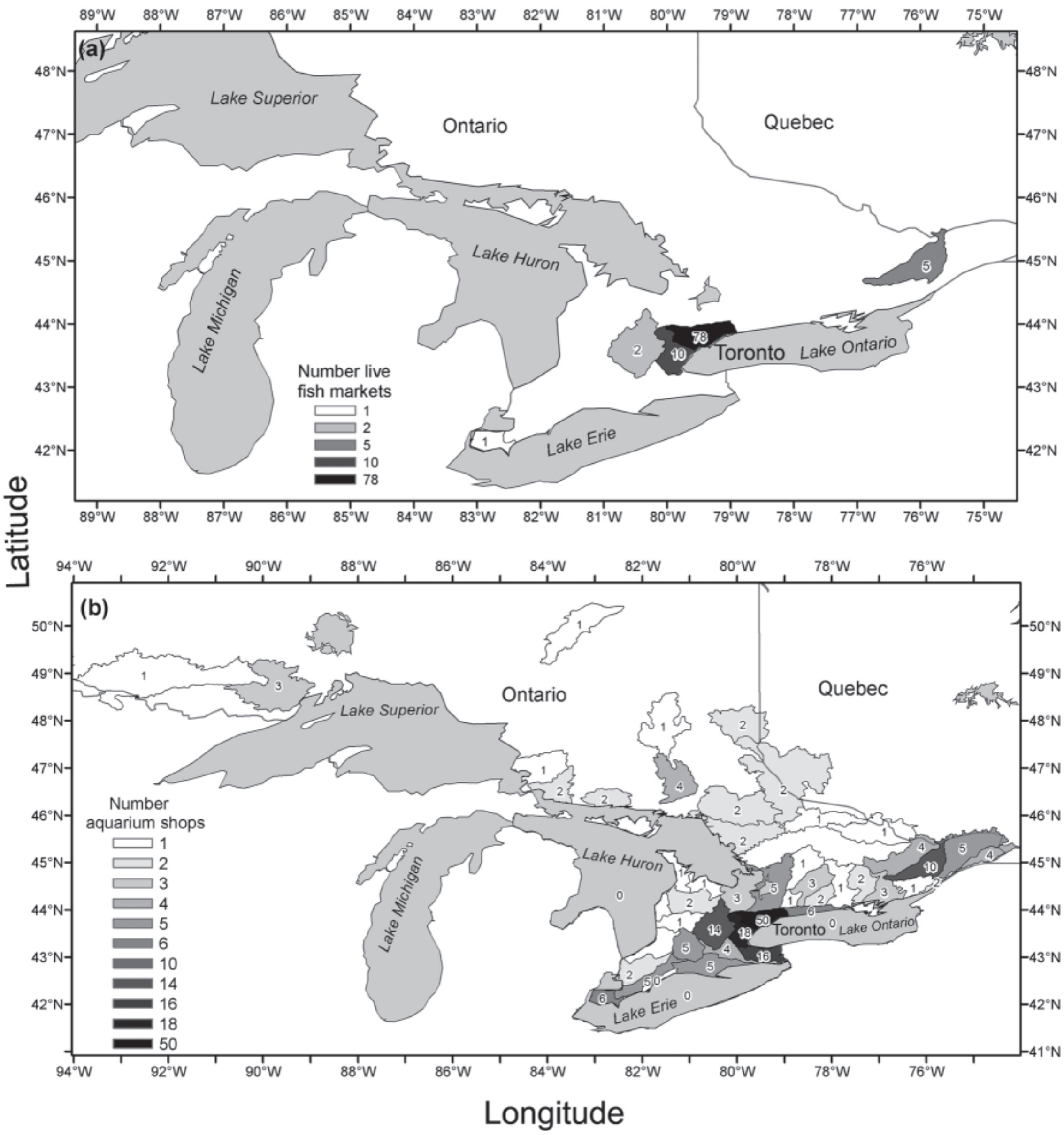
Introduction risk for Asian carps and snakeheads in North America

In Ontario, live fish markets are a potentially important vector for bighead, grass, and silver carps, in addition to the threat posed by secondary dispersal from invaded areas in the region (Crossman and Cudmore 1999*a*; Rixon et al. 2005). Recent legislative changes prohibit possession of live Asian carp and snakehead fishes in Ontario. However, there has been at least one conviction for the possession of grass carp (B. Cudmore, personal observation). Therefore, the illegal live trade of these species exists and leaves open the pos-



(a) northern snakehead
(b) Chinese snakehead
(c) rainbow snakehead
(d) blotched snakehead
(e) bullseye snakehead
(f) giant snakehead
(g) spotted snakehead
(h) golden snakehead
(i) chevron snakehead
(j) Niger snakehead
Environmental suitability
3 - 10
11 - 20
21 - 30
31 - 40
41 - 50
51 - 60
61 - 70
71 - 80
81 - 90
91 - 100
160°W 140°W 120°W 100°W 80°W 60°W
20°N 40°N 60°N
Latitude
Longitude

Fig. 4. Density of live fish markets (*a*) and aquarium or pet shops (*b*) per watershed across the province of Ontario (Canada). Values within each watershed represent the numbers of retailers per watershed.



sibility of accidental releases via accidents during transfer to stores or sales of live fishes to customers. Fishes may then be released by customers into the wild accidentally or deliberately for animal rights, biocontrol, religious, or sport reasons (see Severinghaus and Chi 1999). The isolated records of bighead and grass carps in the Great Lakes are thought to have originated through this vector (Mandrak and Cudmore 2004).

The northern snakehead has been established and spreading in the Potomac River since at least 2004 (Orrell and Weigt 2005), most likely as a result of secondary release from the live fish trade, where it is the most important snakehead species (Courtenay and Williams 2004). This species has a wide native range in rivers of China and Siberia, prefers relatively low maximum air temperatures (5–18 °C), and tolerates up to 193 annual frost days. The highest risk area — based upon the density of live fish shops (i.e., introduction potential) and areas of suitable habitat — are the two watersheds in the Toronto area along the western shores of Lake Ontario. Other locations in Ontario with potential vector activity include the Rideau River watershed (five live fish markets) and the Cedar Creek watershed (one live fish market) between Lake Erie and Lake St. Clair.

The rainbow snakehead has a wide range of predicted suitable habitats in North America. Environmental suitability for this species was highest in the southern USA and Mexico and lower in the northern USA and southern Canada. The distribution of aquarium retailers in Ontario, the main human dispersal vector for this species (Courtenay and Williams 2004), indicates the highest introduction risk occurs in, and west of, Toronto, but because of low environmental suitability the species would probably not survive.

The bullseye snakehead is the only snakehead other than the northern snakehead that is presently established in the conterminous USA. A reproducing population of this species was discovered in 2000 in Tamarac, Florida (Courtenay and Williams 2004). Our results indicate that Florida and other American states along the Gulf of Mexico, as well as large parts of Mexico, provide suitable environments for establishment of this species. Northern spread seems unlikely because of the absence of suitable environments associated with warm maximum (>22 °C) and mean (>6 °C) air temperatures. While current control measures prohibit the possession and transport of live snakeheads in most states within this area, no measures have been implemented to curtail secondary dispersal of bullseye snakehead into nearby Everglades National Park (Courtenay and Williams 2004).

Other species with a similar predicted range to the bullseye snakehead include the chevron snakehead and the Niger snakehead. The chevron snakehead is an important aquaculture species in Asia and is cultured and sold in live fish markets in Hawaii (Courtenay et al. 2004). Its predicted range in North America is limited mainly by maximum (>19 °C) and mean (>14 °C) air temperature, consistent with its native range in Southeast Asia and India. The Niger snakehead has been available to aquarium hobbyists in the USA and Canada in the past (Courtenay and Williams 2004), although no records of introduction exist in either country.

The Chinese snakehead is predicted to have medium to low environmental suitability as far north as ~37°N in the eastern USA and southern British Columbia along the west coast and as far south as southern Mexico, indicating a low probability of establishment. Nevertheless, Cudmore and Mandrak (2005) found that at least 1.3 tonnes of live fish were imported into British Columbia over a 1-year period, indicating a high introduction potential.

Four species of snakeheads (blotched, giant, spotted, and golden) have the most limited potential range in North America, restricted to the Florida panhandle and narrow coastal regions along the Gulf of Mexico and western Mexico. The blotched snakehead is an important food fish in the USA (Courtenay and Williams 2004) and is commonly imported into Canada (3.8 tonnes) (Cudmore and Mandrak 2005). Despite this high introduction potential, the risk of establishment is limited to areas much farther south. The giant snakehead is another species with a limited potential range and is mainly sold to aquarium hobbyists. Release of large aquarium fishes is the most likely vector of introduction for the six occurrences of this species in the USA and one occurrence in Mexico (Zambrano and Marcias-Garcia 1999). The spotted snakehead and the golden snakehead are both associated with either the food or aquarium fish trade. There are no reports of either species in the wild in the USA or of importation into Canada, suggesting that introduction potential is nil.

We used two separate methods to determine the range and effect of environmental variables on the prediction of suitable environmental suitability. The measure of the influence of each environmental variable on model predictions identified variables most important for different species groups (Peterson and Cohoon 1999). In combination with the evaluation strip method, which identified the suitable range for each environmental variable, our models identified the environmental variable and its suitable range most important for the prediction (Elith et al. 2005). This method provides greater transparency to the modeling process. Without these additional analytical steps, GARP only provides a suitable environmental area without any output indicating the driving parameters. Nevertheless, the results of the evaluation strip are somewhat inconclusive for some species (i.e., bullseye, golden, Niger, and spotted snakeheads). One potential cause for unclear results could be associated with the evaluation strip method. While this method inserts the whole range of a particular environmental parameter in a column of the data layer, it inserts the mean value for all other environmental parameters in the column of the respective data layers to identify the effect of this particular variable on predicted environmental suitability. In cases where the mean value of one or several environmental layers is predicted unsuitable, the results will be inconclusive. The mean value of an environmental parameter could be unsuitable because of several possibilities: a wide environmental range of a particular variable, a small native range vs. large study area, or separated native range polygons divided by unsuitable environments.

Combining environmental niche modelling with estimates of introduction potential

The combination of ecological niche modeling and estimates of introduction potential allow a spatially explicit assessment of establishment risk for Ontario. Clearly, the same approach would be desirable for all North American jurisdictions, although data limitations precluded this in our study. Many studies have focused on either introduction potential (Leung et al. 2002; Drake and Lodge 2004; MacIsaac et al. 2004) or environmental niche modelling (Ganeshaiah et al. 2003; Iguchi et al. 2004; Roura-Pascual et al. 2004) to assess the invasion risk, although combinations of these approaches has been used only recently (Herborg et al. 2007).

The comparison of the spatial distribution of introduction potential for the two introduction vectors considered here exhibit interesting patterns. While both vectors (aquarium fish releases, live fish market releases) have their hot spots in the most populated areas of Ontario, the localized distribution and relatively low number of live food fish stores is easier to monitor. Aquarium stores are more numerous and widely distributed, rendering monitoring more difficult. The aquarium trade and the aquaculture industry (including live fish markets) are believed to be the primary source of 41 and 49 established nonindigenous fish species in North America, respectively (Crossman and Cudmore 1999*a*, 1999*b*). A study comparing the aquarium trade with live fish markets before the ban on the sale of live Asian carps in April 2004 found that the number of fish species available in aquarium stores (308 species in 20 stores) was much higher than in live fish markets (14 species in 6 markets) (Rixon et al. 2005). Nevertheless, the same survey found live bighead and grass carps for sale in live fish markets. Cudmore and Mandrak (2005) found that based on a subset of importers, 121 tonnes of bighead carp and 19 tonnes grass carp were brought into Ontario from the USA over 1 year prior to the ban of possession of live Asian carps. These findings highlight the possible introduction of carp species via accidents or live fish markets in Ontario. Considering the large areas of suitable habitat across North America, public education efforts are needed to prevent unlawful introductions of these species into the wild.

Preventative measures

Ecological niche modeling identified the American Gulf states and western Mexico as the areas most suitable for establishment of all species, except giant snakehead. Policy makers have addressed the growing concern of snakehead species introduction across the USA by prohibiting their live interstate transport (Courtenay and Williams 2004). Another 26 states (Courtenay and Williams 2004) as well as Ontario prohibit possession of live snakeheads. The ban on the possession of live snakeheads applies to the states with the most suitable habitat along the Gulf of Mexico coast, with the exception of Louisiana. Coastal areas in this state are predicted to have suitable environment for 13 of the 14 species in this study. While some regulations exist regarding the import and release of Asian carps in Alabama, Missouri, Florida, Texas, and Mississippi (Nico et al. 2005), an attempt to create a national ban on release of black carp into the wild failed (Simberloff et al. 2005). Thus, while policymakers have made some progress with respect to regulations precluding transport of these fishes, some of the species we profiled remain unregulated (Courtenay and Williams 2004). The greatest protection against the undesirable effects associated with these NIS is afforded by prohibiting live transfer to or through at-risk areas to which they are not established.

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