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ORIGINAL PAPER

Spatiotemporal dynamics of the spread of African tilapias (Pisces: *Oreochromis* spp.) into rivers of northeastern Mesoamerica

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Abstract African tilapias (*Oreochromis* spp.) occur in more than 100 countries outside of their native ranges and research on their invasions is largely lacking. We investigated spatiotemporal patterns of tilapia spread into 29 drainage basins in Belize and parts of Guatemala and Mexico, drawing on field data and interviews with fishermen. Habitat-suitability models for tilapias were created from geospatial and species occurrence data, and fishermen interviews were used to reconstruct the chronology of tilapia spread into predicted suitable habitats. Tilapia (predominantly Nile tilapia, *O. niloticus*) presence was confirmed at 78 sites in 9 of 29 drainage basins. Our habitat-suitability model predicted that 7,510 linear km of river habitat in the study area were vulnerable to colonization by tilapias, predominately in mid- to low elevation main stem rivers, from sea level to 277 m above sea level. The reconstructed spatial chronology of spread showed that the invasion started in 1990 and progressed slowly (2 km yr^{-1}) through an establishment phase before rapid expansion ($\sim$30 km yr^{-1}) between 1996 and 2002, after which new detections slowed. Human movement of fish for aquaculture was identified as a primary cause of dispersal that interacted with flooding as an important secondary cause. The shortest paths across low elevation drainage divides between major basins revealed several potential corridors for future tilapia spread during flooding. Research into tilapia spatial metapopulation structure and economic fisheries status, more stringent regulation of aquaculture activities, pro-active fisheries management, and development of policies to screen potentially invasive species before importation are recommended to avoid additional releases of tilapia and further spread in the region.

Keywords Species distribution modeling · Cost surface analysis · Dispersal · Rivers · Management

Introduction

Tropical freshwater ecosystems, though poorly known, exhibit high levels of endemism and species richness (Benstead et al. 2003; Dudgeon 1999, 2000; Leveque et al. 2008; Strayer et al. 2004). More than 70 % of the 13,000 fish species that occur in

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freshwaters live in the tropics (Leveque et al. 2008), and each year about 40 new species are described from neotropical waters (Vari and Malabarba 1998). However, extinction rates for freshwater animals are high, estimated at 4 % per decade in North America (Ricciardi and Rasmussen 1999), with similar rates expected in the tropics (Dudgeon et al. 2006). Biological invasions by aquatic non-indigenous species are thought to be particularly important drivers of biodiversity loss in freshwater ecosystems (Sala et al. 2000). Yet research on non-indigenous species invasions into tropical freshwaters is scarce, with a few well-publicized exceptions (e.g., Nile perch in Lake Victoria; Balirwa et al. 2003). For instance, tilapias in the genus *Oreochromis* have a nearly pan-tropical distribution (Froese and Pauly 2008; Welcomme 1988) in more than 100 countries outside of their native ranges in Africa, but research on their invasions is largely lacking. Tilapias can cause declines of native species (Goudswaard et al. 2002; Twongo 1995), predation on eggs and young of other fishes (Arthington and Bluhdorn 1994), altered nutrient dynamics and eutrophication (Starling et al. 2002), de-vegetation of extensive areas of lake bottom, introduction of non-indigenous parasites (McCrary et al. 2001), and food web alterations (Taylor et al. 1984). Tilapias colonize a wide array of habitats in subtropical and tropical rivers, lakes and wetlands, brackish coastal lagoons, and estuaries (Phillippart and Ruwet 1982). Their ability to colonize a broad range of habitats can be attributed to their broad physiological tolerances, and leads to high rates of successful establishment in ecosystems outside their native range (Courtenay 1997). High colonization success mixed with the potential to cause ecosystem damage makes control of tilapia spread a high management priority for aquatic ecosystem protection at every scale.

Few studies have documented the process of tilapia dispersal, rates of spread, and habitat suitability. Such information can be extremely useful to the development of management interventions to protect native ecosystem integrity (Everett 2000; Floerl and Inglis 2005; Sharov and Liebhold 1998). For non-air breathing fishes, the water's edge creates a hard barrier to species movement, thus confining natural dispersal to the permanent or intermittent interconnecting streams and wetlands between water bodies (Lodge et al. 1998). Many studies have examined the influence of dispersal and colonization dynamics on the survival and distribution of fish species in lakes and rivers (e.g., Barbour and Brown 1974; Dunham and Rieman 1999; Schlosser 1991; Tonn et al. 1990). These studies show that fish spread to and successful colonization of new habitats are dependent on the dispersal abilities of the species, the configuration and connectivity of suitable habitats patches, and the local conditions present (Havel et al. 2002; Moyle and Light 1996; With 2002). Past studies of tilapias in wet tropical environments suggest that human translocation is the primary cause of dispersal, with flooding as an important secondary dispersal mechanism that flushes tilapias from aquaculture ponds into natural water bodies and across swampy drainage divides (Arthington and Bluhdorn 1994; Schmitter-Soto and Caro 1997).

Tropical countries being invaded by tilapias are often faced with limited availability of baseline data, insufficient human technical capacity and technology, and low investment in research and monitoring (Pringle et al. 2000). The end result is that critical information for management is often unavailable. This is the case with the Mesoamerican country of Belize, where tilapias have been expanding their range since the early 1990s (Esselman and Boles 2001). With limited economic development options, Belize is evaluating the expansion of tilapia aquaculture as a way of generating foreign income. Given that tilapias have yet to colonize the whole country, landscape-scale information about occupied habitats, unoccupied suitable habitats, spread rates, and dispersal routes and drivers are particularly useful for Belizean decision makers.

In this study, landscape-scale habitat and tilapia occurrence data were used to create habitat suitability models, and investigate the spatiotemporal patterns of spread into suitable habitats. The specific goals were to:

1. Train and validate a species distribution model to predict habitat vulnerability to tilapias in rivers.
2. Reconstruct the chronology of tilapia invasion into aquatic habitats, and make initial observations about drivers and rates of spread.
3. Identify possible natural dispersal routes.
4. Synthesize the above information into a set of management recommendations to inform tilapia control strategies in Belize and other places around the world.

We met these goals in the absence of historical fish census data, which were last collected in Belize in the 1970s. Instead, we relied on the information sources that were available: geospatial and remote sensing data about possible abiotic determinants of species distributions, species occurrence data collected in recent field sampling, and interview and catch data from artisanal fishermen.

Methods

Study area

The assessment was carried out in the domestic and international waters that drain to the coast of Belize, including portions of southern Mexico and northeastern Guatemala. This 45,750 km^2 area comprises 29 drainage basins including 16 major basins and 13 small coastal tidal creeks (Fig. 1). These basins vary in size and drain a variety of geologic, soil, and terrestrial land cover types (Esselman and Boles 2001). Twelve of the 16 major rivers originate in the Maya Mountains (Fig. 1) as high-gradient streams within granite and metamorphic geologies, after which they traverse limestone-dominated landscapes, build up alluvial plains and wetlands, and discharge into the shelf lagoon that separates the coast from the Mesoamerican Barrier Reef. The two northernmost rivers in the area (Rio Hondo and New River; Fig. 1) originate in karst hills, drain the low relief limestone platform of the Yucatan Peninsula, and discharge into Chetumal Bay, which then connects to the shelf lagoon. The headwaters of the rivers in the three southernmost basins (S to N; Sarstoon, Temash, and Moho Rivers) begin in Guatemala and flow eastward to the Gulf of Honduras. The Sarstoon River (demarcating the southern border of Belize) originates in Guatemala, within the mountain range of the Sierra de Santa Cruz. In addition to flowing waters, the study area has an abundance of fresh and brackish water lagoons and wetlands that include swamp forests, herbaceous marshes, and open water areas, often in association with riverine habitats (Esselman and Boles 2001).

Daily mean temperatures are warm throughout the year, ranging from a low of 16 °C in the winter months to a high of 33 °C in summer (Hartshorn et al. 1984). A strong north-to-south precipitation gradient exists with the northern portion of the study area receiving approximately 1,000 mm of rain annually and the southern portion receiving up to 4,000 mm annually (Wilson 1980). The timing of precipitation is strongly seasonal, with a dry season lasting from January to May, and a wet season from June to November, during which intense floods can occur. The area is highly prone to hurricanes in the late summer and early fall (Wilson 1980).

Northern Mesoamerica has been called a "strong center of evolution" for fishes, because of its many endemic genera and species (Miller 1966). The Caribbean slope drainages of Belize, Guatemala, and Honduras share a common biogeographic history and contain a high diversity of poeciliids (34 species, 15 genera) and cichlids (44 species, 5 genera) (Bussing 1976; Miller 1966). At least 130 species of freshwater fishes in 34 genera and 10 families inhabit this area (Bussing 1976), a number that rises to over 200 when predominantly marine species that inhabit freshwaters are included (Miller 1966). One hundred and twenty-six of these species have been reported in the study area, including at least 22 native species in the family Cichlidae, not counting tilapias (Esselman et al. 2006; Greenfield and Thomerson 1997; Schmitter-Soto 1998, 2007; Schmitter-Soto and Gamboa-Perez 1996). Five fishes are endemic to Belize or a small area shared by Guatemala and Belize (Esselman and Allan 2010; Greenfield and Thomerson 1997), but the conservation status (threatened or endangered) of these and other aquatic species remains unknown (IUCN 2012).

Overview of approach

Our analysis consisted of three parts. We used recently collected species occurrence data together with geospatial data about landscape-scale habitat factors to create a species distribution model (SDM) to estimate potential habitat suitability for tilapias. SDMs generalize the empirical relationships between species collection localities and underlying habitat conditions to predict the probability of species occurrence in a landscape area. SDMs have the potential to use incomplete information, such as historical point occurrence data from only a part of a species' range, to generate spatial predictions of the realized niche of a species relative to the environmental variables in the model (Guisan and Zimmermann 2000). We used SDMs trained from data collected inside the invaded

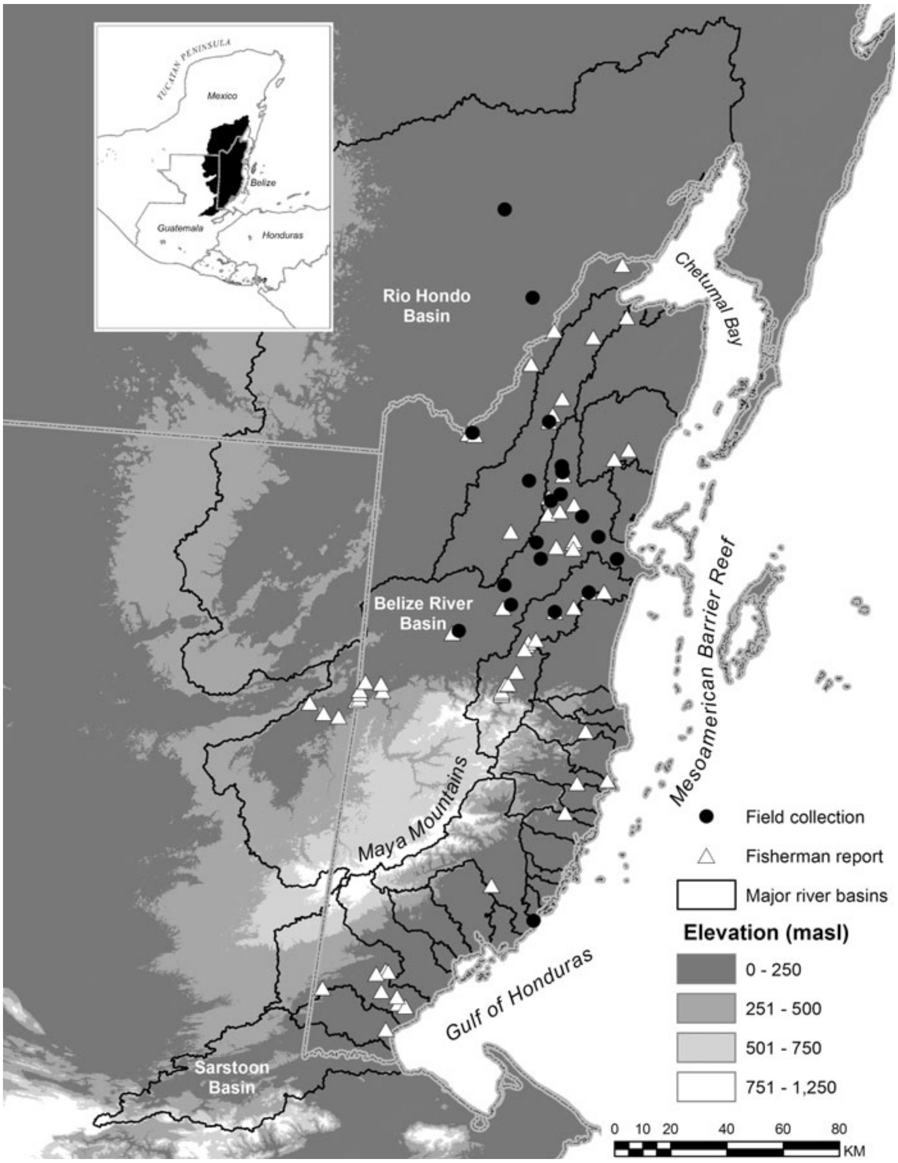

Fig. 1 Study area showing elevation, major drainage basins, important geographic features and the locations of sampling sites used for habitat suitability modeling with Maxent (both field collections and fisherman reports used)

range of tilapias to predict habitat suitability for tilapias in the entire study area. Second, we used interview data about the locations and years that fishermen first detected tilapia in their catches to infer the spread of tilapia from 1990 through 2007. This spatial chronology of spread was used to make a first estimate of the rates of tilapia expansion in individual drainage basins. Fishermen observations on possible dispersal mechanisms were considered in conjunction with our spread chronology to infer probable dispersal mechanisms and routes between basins. Finally, we used hydrographic and topographic data to infer natural colonization routes using a GIS-based approach known as cost surface analysis. All of the above were synthesized to make management recommendations for tilapia management.

Data sources

Three primary data sources were used in this study: (1) geospatial data representing large scale habitat factors that were used as independent variables in SDMs; (2)

tilapia occurrence data collected through field sampling and surveys with fishermen, and (3) fisherman interview data.

The geospatial database consisted of 33 variables prepared as individual raster layers for possible inclusion in SDM development (Table 1). The database consisted of variables representing landscape position, geology, climate, hydrology, soils, watershed characteristics, and human influence on the landscape. The cumulative upstream influence of different variables was represented using the weighted flow accumulation tool in the spatial analyst extension

Table 1 Environmental variables prepared for entry into Maxent models of tilapia habitat suitability

Variable (units)	Min	Max	Mean	PC 1	PC 2	PC 3	PC 4	PC 5
Average annual air temp in catchment (degrees C)	**21.86**	**26.00**	**23.87**	**−0.18**	**0.08**	**0.14**	**0.14**	**0.40**
Average annual rainfall in catchment (mm)	1,259.56	3,317.92	1,969.14	−0.04	−0.41	−0.11	−0.04	0.11
Average catchment elevation (masl)	1.50	591.44	222.84	0.36	−0.03	0.06	0.10	−0.03
Average catchment slope (degrees)	**0.00**	**18.00**	**7.09**	**0.33**	**−0.12**	**0.05**	**0.16**	**−0.06**
Average local annual air temperature (° C)	21.98	26.00	24.79	−0.13	0.12	0.15	0.22	0.36
Average local annual rainfall (mm)	1,258.00	3,867.00	2,029.64	−0.04	−0.25	0.14	0.32	0.09
Local elevation (masl)	**0.00**	**157.00**	**33.33**	**0.32**	**0.02**	**−0.02**	**−0.21**	**0.17**
Local slope (degrees)	0.00	32.00	3.13	0.19	−0.01	0.07	−0.09	0.14
Flow accumulation (10^3 pixels)	**0.01**	**10,892.7**	**2,042.57**	**0.06**	**0.32**	**0.08**	**0.17**	**−0.24**
Horizontal land distance to next perennial lake (km)	0.07	93.14	21.91	0.31	0.10	−0.08	−0.16	0.17
Surface area of nearest lake (km^2)	0.52	40.12	5.23	−0.21	−0.01	0.03	−0.14	0.04
Distance downstream to sea (km)	**1.49**	**348.60**	**102.24**	**0.24**	**0.18**	**0.07**	**−0.23**	**0.24**
Upstream distance to furthest basin divide (km)	0.17	497.69	130.84	0.10	0.30	0.09	0.20	−0.22
Catchment geology proportions								
Quaternary alluvium	**0.00**	**1.00**	**0.23**	**−0.23**	**−0.03**	**0.05**	**−0.36**	**−0.12**
Cretaceous limestone	0.00	1.00	0.47	−0.02	0.25	−0.14	0.19	0.17
Lavas-pyroclastics-volcanic sediments	0.00	1.00	0.22	0.27	−0.19	0.21	0.08	−0.07
Tertiary sedimentary	0.00	0.89	0.05	−0.06	0.03	0.04	0.04	0.00
Toledo formation	0.00	1.00	0.03	−0.01	−0.10	−0.36	0.15	0.07
Catchment soil proportions								
Cambisol–Leptosol–Vertisol	**0.00**	**0.93**	**0.08**	**0.02**	**−0.12**	**−0.42**	**0.21**	**0.07**
Fluvisol–Cambisol–Vertisol	0.00	0.26	0.01	0.05	−0.12	0.09	0.09	−0.23
Gleysols	0.00	0.35	0.02	−0.05	0.12	0.07	0.09	−0.05
Gleysols–Fluvisols	0.00	0.44	0.07	−0.14	0.02	0.05	−0.07	0.24
Gleysols–Vertisols	0.00	0.99	0.02	−0.02	0.08	−0.11	−0.17	−0.21
Gleysols–Vertisols–Fluvisol	0.00	1.00	0.13	−0.21	−0.17	0.08	−0.26	−0.11
Leptosol	0.00	0.22	0.01	0.05	−0.08	−0.30	0.11	0.09
Leptosol–Cambisol	0.00	1.00	0.22	0.24	−0.25	0.18	0.13	−0.08
Leptosols–vertisols	0.00	0.92	0.42	0.01	0.39	0.07	−0.02	0.05
Litosol–Cambisol	0.00	0.15	0.00	0.04	−0.10	0.08	0.08	−0.23
Catchment landuse proportions of:								
Agriculture	0.00	1.00	0.21	0.08	0.09	−0.37	−0.08	−0.22
Urban	0.00	0.05	0.00	−0.01	0.06	−0.16	−0.13	−0.21
Linear distance to nearest human settlement (km)	0.27	8.80	2.82	−0.10	−0.21	0.10	0.05	0.04
Proportion of pixels in catchment with roads present	0.00	0.06	0.01	−0.05	0.01	−0.40	0.14	0.05
Mean upstream risk intensity	**0.00**	**135.00**	**19.88**	**0.00**	**0.06**	**−0.33**	**0.13**	**−0.25**

Variables in bold represent those that were selected for entry into the model after using PCA to summarize data set. The first five PCA axes explained a total of 62 % of the variance in the predictor dataset of ArcGIS 9.2® (ESRI Corp., Redlands, CA, USA). Weighted flow accumulation performs a downstream summation of pixel numeric values within a grid of equally sized cells, drawing on a flow direction grid to infer downstream directionality. This is in contrast to raw flow accumulation—the count of all pixels upstream of a given pixel in a map grid. To calculate proportion variables (e.g., upstream proportion of igneous geology), binary grids showing the presence or absence of each geological or soils class were created, used as the weight grid in the weighted flow accumulation process, and then divided by raw flow accumulation to yield a representation of the proportion of the upstream catchment in a given feature class. Mean upstream values of continuous variables were calculated by the same process, except that we used continuous (e.g., mean annual temperature) instead of binary values in the weight grid. All layers consisted of a uniform extent and cell size (30 × 30 m) and were masked after processing to constrain the datasets to only those pixels underlying a river segment.

To represent risk of environmental degradation at specific locations along the river network, we created an environmental risk surface (ERS). An ERS is a modeled composite raster surface that is created in GIS to combine information about the locations and relative intensities of perceived environmental risks to aquatic ecosystems (see Esselman and Allan 2011 for a detailed description). To create the ERS, mapped vector risk elements (polygons, points, lines) are attributed with numeric intensity scores (from 0 to 100; low to high) and a distance of influence representing the maximum distance over which the feature has a negative impact on biodiversity. Based on available data we selected current agriculture and urban land cover (polygons), roads (lines), and the locations of villages (points) as risk elements. The assignment of intensity and distance values (Fig. 2) was a logical process informed by the literature, and by professional judgment. The mapped locations of each risk element was converted to a raster grid and assigned with intensity values where they were present. A linear decay function was used to reduce the intensity value outward from each feature's edge to a value of zero at the distance of influence. The risk values were then summed across all grids. To make the resultant surface relevant to riverine ecosystems, the cumulative ERS was used as the weight grid in weighted flow accumulation to estimate cumulative downstream risk along the flow path. Finally, the weighted flow accumulation grid was divided by raw flow accumulation to calculate the "relative upstream risk intensity" scaled by contributing area.

Georeferenced data on tilapia occurrences were collected using backpack electrofishing, boat electrofishing, and surveys with fishermen. Electrofishing sites were defined systematically each 20 km along the river channel from a random starting point in the first 5,000 river meters. The reach length of a backpack electrofishing site was 39 times the mean stream width, within which a single electrofishing pass was performed with a Smith-Root® 12 battery-powered electrofisher. Boat electrofishing reaches were all 1,300 m long, within which a single pass was made along a single bank using a Smith-Root® GPP 5.0 generator-powered electrofisher deployed with booms from the front of a 4.25-m aluminum boat.

Interviews and catch surveys were conducted with 40 fishermen in villages on the main stems of all major rivers (except Rio Sarstoon) about the presence of tilapias in their fishing grounds. All interviews used a standardized approach and were conducted by the same three individuals. Interviewers located fishermen in each village through referrals from local residents, administered a standard questionnaire, and, when possible, collected voucher specimens from catches to confirm tilapia presence and species identity. When voucher specimens were not available, fishermen were asked to identify tilapia from an unlabeled laminated card with pictures of all of Belize's native cichlids plus adult *Oreochromis niloticus* and *Oreochromis mossambicus* to confirm that they were reporting on tilapias. All fishermen were asked to mark the river reaches where they captured tilapias on photocopied 1:50,000 color topographic maps. They were also asked to share: (1) the locations and years of tilapia first detection in their catches; (2) hypotheses about initial sources of introduced individuals; (3) observations about dispersal; and (4) general patterns of tilapia abundance through time. A GIS shapefile was created with the tilapia presence localities from all methods combined.

Species distribution model development and validation

Because we combined data from different methods and could not reliably estimate species absences, a

Table 2 Initial introduction sources reported by fishermen, and possible dispersal mechanisms and/or routes for initial spread into each drainage basin in Belize

Map ID	Drainage basin	Status	Hypothesized introduction source(s)	Possible natural dispersal route(s)
1	Rio Hondo	P	Tilapia cage culture in river Aquaculture ponds on floodplain or tributaries	
2	New River	P	Dispersal from adjacent basin	Belize River Progresso Lagoon Chetumal Bay
3	Progresso and Shipstern Lagoons	P	Aquaculture near Progresso Lagoon Dispersal from adjacent basin	New River Chetumal Bay
4	Northern River	P	Dispersal from adjacent basin	Belize River Freshwater Creek
5	Belize River	P	Aquaculture ponds on floodplain or tributaries	
6	Sibun River	P	Dispersal from Belize River Aquaculture ponds on floodplain	Burdon Canal
7	Manatee River	AN	Dispersal from adjacent basin	Burdon Canal
8	Mullins River	AN	Dispersal from adjacent basin	Southern Lagoon
9	North Stann Creek	P	Aquaculture ponds on floodplain or tributaries	
12	Big Creek	?		
13	Sennis River	?	Aquaculture ponds on floodplain	
14	Pine Ridge Creek	?		
15	Monkey River	P	Dispersal from adjacent basins Tilapia stocking in lagoon near tributary	Sennis River
19	Moho River	P	Aquaculture ponds on tributary in Guatemala	
21	Sarstoon River	AN		

Map ID numbers identify basins in Fig. 4. Status codes are: P = tilapia present; AN = Anecdotal reports of tilapia; ? = unknown

modeling approach was selected that required presence-only data on species occurrences. Maximum entropy, or Maxent, is a mathematical approach to predicting an unknown probability distribution that estimates the most uniform distribution (e.g., the one with maximum entropy) across a defined area subject to the constraints imposed by environmental conditions (Phillips et al. 2006). The software used (Maxent software for species habitat modeling, version 3.3.3 k; http://www.cs.princeton.edu/~schapire/maxent/) iteratively adjusts weights associated with each environmental variable to maximize the likelihood under the species presence locations. The output of a Maxent model is a continuous surface of occurrence probability values between 0 and 1, with higher values indicating a higher suitability for tilapias. Several studies have shown Maxent to consistently outperform other presence-only techniques (Elith et al. 2006; Hernandez et al. 2006; Phillips et al. 2004, 2006).

Principal components analysis (PCA) was used to aid the reduction of the predictor dataset by identifying composite axes that explained the most variation and interpreting variable loadings onto these axes. PCA was run for all environmental variables (using PC-ORD, version 4.10, MjM Software Design, Gleneden Beach, Oregon) at the tilapia presence localities and variable loadings were interpreted on five principal components axes that had eigenvalues greater than expected under the broken stick distribution (McGarigal et al. 2000). Eight variables were selected that loaded heavily (> 0.30) on the retained axes and that were landscape proxies of habitat parameters known to be limiting to fishes (Table 1). The eight selected variables were used to train models of tilapia habitat suitability, which were then projected to all river habitats.

Three models of tilapia occurrence probabilities were trained for different purposes. Two models were

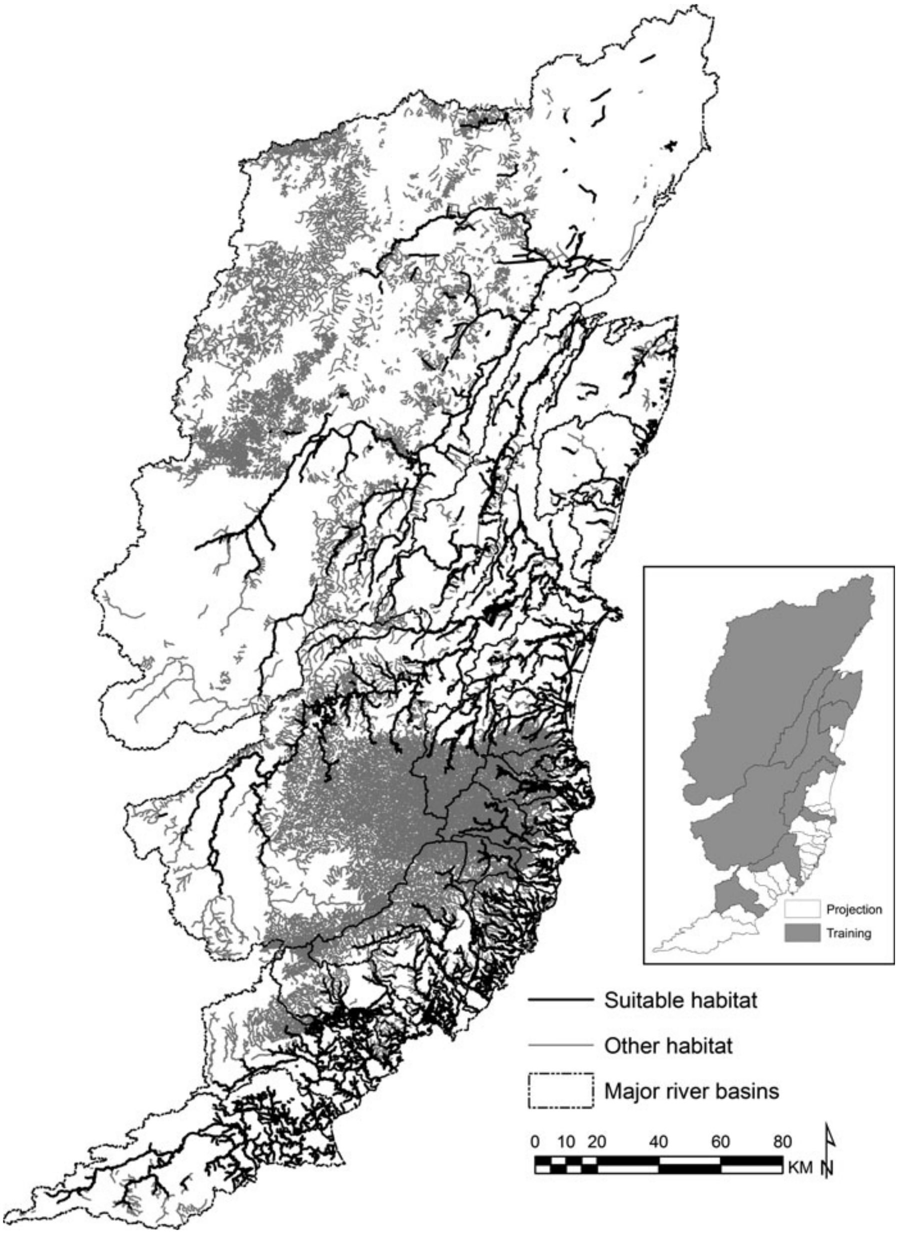

Fig. 2 River habitats predicted to be suitable (*black lines*) and not suitable (*gray lines*) to tilapias. Models were trained from data collected in basins with confirmed tilapia presence (*inset*, *shaded*), and predicted to basins with no recorded presence (*inset*, *unshaded*)

trained using approximately half the dataset to assess model accuracy in the absence of spatial autocorrelation, due to sample sites being closer together than would be expected if site locations were completely random. Though our electrofishing samples were collected under a random sample design, the interview data used tended to report tilapia presence in a spatially biased way (i.e., close to villages where fishermen lived). Spatial autocorrelation among sample localities has the potential to lead to inflated assessment of model accuracy when training and test data are drawn from a common dataset (Veloz 2009). Thus we separated samples gathered in the Belize River basin (N = 34) from those gathered in other watersheds (N = 44; Fig. 1), and then used each subset of data to train a model and the other spatially independent set to assess model accuracy. Model accuracy was assessed using the area under the curve (AUC) of a receiver operator characteristic (ROC) plot. An ROC plot displays the relationship between model sensitivity (the true positive fraction) and 1-specificity (the false positive fraction) across all presence-absence thresholds, and the area under the ROC function provides a single threshold-independent measure of overall accuracy (Fielding and Bell 1997). Thus, we used the two parts of our dataset to calculate and report two AUC measures. We then trained a model using all presence localities ($N = 78$) to make the final prediction of tilapia habitat suitability and generate maps. All models were trained with the Maxent default parameters (regularization multiplier = 1; maximum iterations = 500, convergence threshold = 0.00001), which have been shown to perform well for a wide range of presence-only datasets (Phillips and Dudik 2008). A decision threshold was applied to the all-localities result to convert the continuous probability of occurrence to a binary classification of habitats predicted as 'suitable' or 'not suitable'. The minimum probability value under a known presence locality (e.g., the minimum known suitable condition) was used as a threshold. It was assumed that the AUC values of the two subset models represented a spatially unbiased estimate of the accuracy of the final model.

Chronology of spread

The chronology of spread was mapped in annual time increments based on the dates and locations of first detection in fishermen's catches. Cumulative new detections were plotted against time for a graphical representation of progress. Initial estimates of rates of spread were made within each drainage basin by calculating the distance between the reach where tilapia was first detected and the reach where detections were made in subsequent years. This distance was divided by the number of years separating the detection events to yield an estimate of km yr^{-1}. An implicit assumption in this rate calculation is that fishermen detected tilapias near the furthest extent of their spread in any given year, and that they attributed the year accurately. Because of these potential sources of error, we used this number as a rough first approximation to establish a range of possible rates, rather than a precise estimate.

Identification of possible natural dispersal routes

Fishes have the ability to move between connected water bodies even if these connections are temporary. The intermittent heavy flooding common to the study area has the potential to disperse fish within drainage basins, and across drainage divides with low elevational relief. To identify possible inter-basin crossing points for natural dispersal, we used ArcMap 9.2 to run cost surface analysis (CSA) to identify least cost paths between riverine habitats in adjacent drainages. CSA is a spatially-explicit method for estimating the permeability of complex landscapes for organism movement (Gonzales and Gergel 2007). Inputs to the analysis include a raster representation of permanent river features and a digital elevation surface representing the impedance to movement of a fish across a landscape, leading to definition of paths between basins that overcome the shortest distance and the least cumulative elevational change. The outputs are an accumulative cost surface with pixels representing the sum of costs to move from one basin to the next, and a line representing the least cost path.

The ArcMap 9.2 Cost Distance algorithm determines the shortest weighted distance from a start point and an end point defined in the central location of each basin. The first iteration assigns weighted distance values—calculated as the sum of elevations of the source pixel and the adjacent pixel divided by the distance between the centers of each pixel—to all pixels that are adjacent to the starting and ending points. In the next iteration the costs for pixels adjacent to the least cost pixel from the previous iteration are calculated and summed with the lowest cost pixel from the previous iteration. As new pixels are added, pixels that were previously assigned accumulative costs are updated if a newly added adjacent pixel leads to a lower accumulative cost. This process proceeds until all cells in a grid connecting a start point and an end point have been assigned weighted cost values. We conditioned our elevation cost surface to impose zero cost to organisms traveling through mapped water bodies (rivers, canals, lakes, ponds, or lagoons), so costs accrued only in pixels where no river line or water body was located. The path between the start and end points with the least accumulative weighted cost is then defined as the least cost path. After least cost path lines were determined, the final accumulative cost of each line, and the elevational range underlying each line were summarized to aid with interpretation.

We used publicly available 90-m resolution shuttle radar topography mission (SRTM) elevation data to define least cost paths. SRTM data measure the elevation of the highest surface that was sensed first by the radar device on the space shuttle (e.g., forest canopy, buildings). Thus, in areas with high forest canopies, cost values may accumulate more rapidly potentially biasing results. In the case where individual pixels along a low drainage divide have a high elevation (e.g., a karstic hill is present or a tall tree sensed by the SRTM device), the least cost path would tend to circumvent that pixel in favor of lower elevation adjacent pixels.

Results

At 61 of the 78 localities where tilapias were recorded present, whole fish vouchers or photographic vouchers were collected and the identities of the fish species were assessed using Carpenter (2001). Of the 61 vouchers taken in Belize, all but three of the fish were identified as Nile tilapia [*Oreochromis niloticus* (Linnaeus 1758)] based on external morphological characteristics. Two individuals were pink hybrid tilapias with likely direct origins as aquaculture stock, or within several generations of reproduction in the wild (Majumdar et al. 1997). The third individual, collected from a rice irrigation ditch on the Rio Hondo floodplain, was identified as Blue tilapia [*Oreochromis aureus* (Steindachner 1864)] with greater than 20 gill rakers on the lower limb of the first gill arch, but a lack of caudal banding. The Mexican specimens were also identified as Nile tilapia, although they approach Mozambique tilapia [*Oreochromis mossambicus* (Peters 1852)] in that they sometimes had 18 or fewer gill rakers on the lower limb of the first arch. Given the long history of mixing and manipulation of aquaculture stocks and tilapias' propensity to hybridize (Costa-Pierce 2003), fish identified as Nile tilapia may still be hybrids.

Habitat vulnerability to tilapia colonization

The model of tilapia habitat suitability predicted that 7,510 linear km of river habitat in the study area were vulnerable to colonization by tilapia (Fig. 2). This represents approximately 24 % of all river length (31,257 river km) in the study area. Suitable habitats were present in mid- to low elevation (0–277 m above sea level) main stem rivers (mean upstream watershed area = 566 km^2), extending from the river mouth into mountain valleys (0–446 km from sea). These results are consistent with expectations that tilapias would be widely distributed within the study area.

The two subset models performed well according to the test AUC statistic calculated by applying the model to the spatially independent subset of locality data. The test AUC of the Belize River basin model was 0.88, while that of the other basins model was 0.89. These results suggest that the models could correctly order randomly selected presence and background locations a high percentage of the time.

Chronology of spread and potential drivers

According to fishermen, the tilapia invasion in Belize began in 1990 in Crooked Tree Lagoon in the Belize River system (Fig. 3). Rio Hondo was the next river system where tilapias were detected in 1995 in three locations in the middle reaches, followed by Belize River habitats nearest to Crooked Tree Lagoon in 1996. By 1998, tilapias had spread to several more reaches within the Belize River, and were first detected in the Sibun River, and in the Monkey River in southern Belize. The following year, tilapias were detected in Moho River, and in two lagoon systems on the northeastern coastal plain (Progresso Lagoon and Shipstern Lagoon). By 2000, tilapias reportedly reached a small coastal drainage east of Crooked Tree Lagoon, and were well-dispersed within the Belize River system. In 2002, tilapias were first detected in the New River, and in 2004, in the North Stann Creek (Fig. 3). Anecdotal reports suggested that three other basins (Manatee River, Mullins River, and Sarstoon River) may also have tilapias in them, though we were unable to confirm these reports despite multiple sampling attempts (Fig. 4).

Interview results confirmed the importance of flooding as a dispersal mechanism. The initial spread of tilapia into Belize waterways in 1990 corresponds with a very large flood event that year (Fig. 3). Furthermore, the largest single-year jumps in new tilapia detections in Belize occurred in 1998 and 2000 when Hurricanes Mitch and Keith caused high flood pulses in the Belize River valley and throughout the

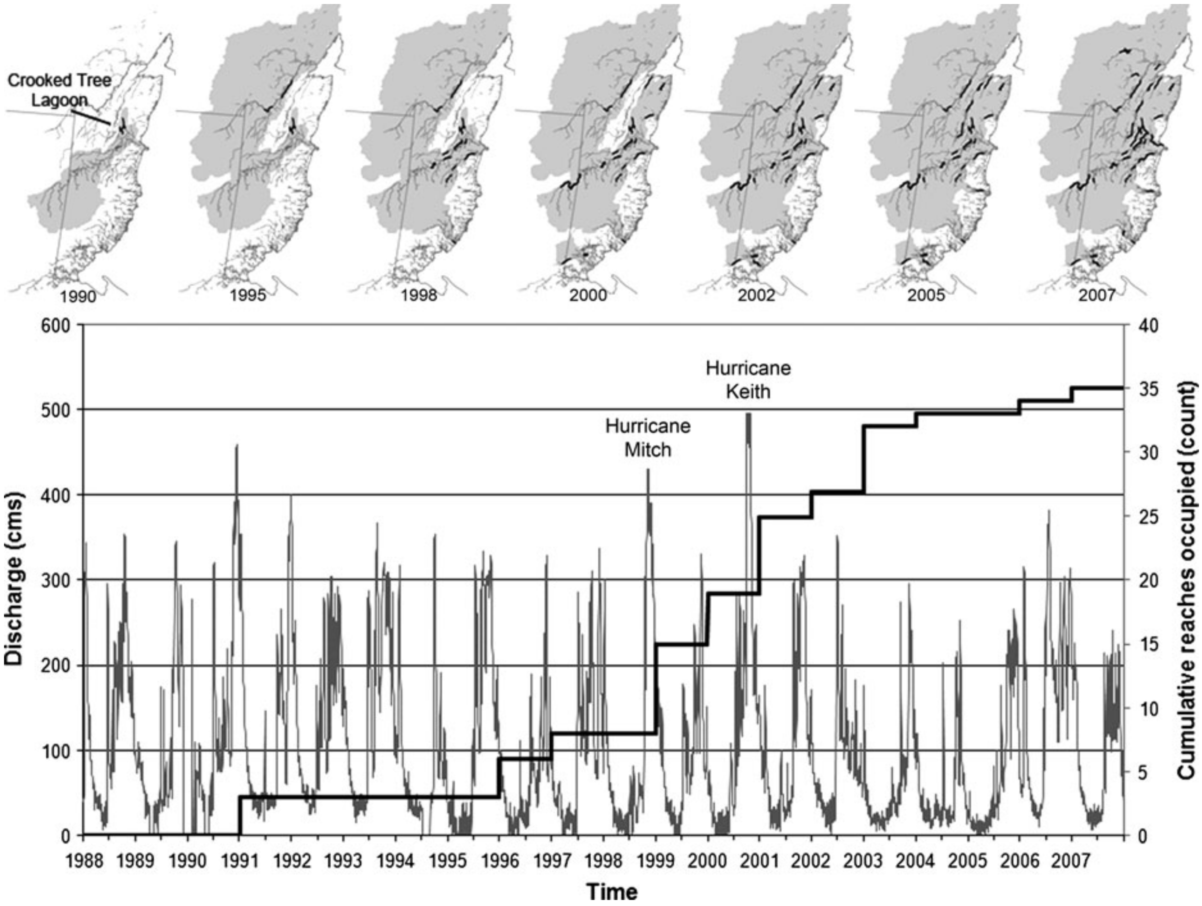

Fig. 3 The chronology of spread of tilapias in Belize based on fishermen's responses. *Bottom graph* shows detections of tilapia in new river reaches through time (*right axis*), and river discharge (*left axis*) at a station on the lower Belize River near Crooked Tree. Discharge values are in cubic meters per second (cms), and the years of Hurricanes Mitch and Keith are labeled. The initial introduction of tilapia and the two largest jumps in detections all followed large flood events (>400 cms). The small maps across the top of the figure show a time series of colonized reaches (*dark black lines*) starting with the colonization of Crooked Tree Lagoon. *Shaded gray areas* show presence of tilapia within drainage basins, signifying that tilapia founders were able to cross a drainage divide through natural or human-aided dispersal

country (Fig. 3). Acknowledging the potential for a delay in fishermen detection after the initial arrival of a propagule, it is also possible that the tilapias first reported in Moho River, Progresso Lagoon, and Shipstern Lagoon in 1999 may have dispersed with Hurricane Mitch floods in 1998, and the spread of tilapias to New River may be associated with Hurricane Keith.

The primary cause of tilapia presence in the rivers of the study area was reported as pond aquaculture conducted in flood prone areas (Table 2; Fig. 4). Based on interview data, we hypothesize that initial propagules originated from flooded aquaculture ponds in six of the nine major basins where tilapias were confirmed to be present (Table 2). There is no evidence of direct stocking of natural waterways in the Belize portion of the study area, however on the Mexican side of Rio Hondo it is not uncommon for stocking to occur in sinkholes and wetlands (Schmitter-Soto and Caro 1997). We hypothesize that the initial propagules arrived in the other three systems through natural dispersal, particularly during large flood events. Possible dispersal pathways include (a) intermittently inundated low gradient drainage divides; (b) interconnected wetland complexes that join during floods; (c) a man-made canal that connects

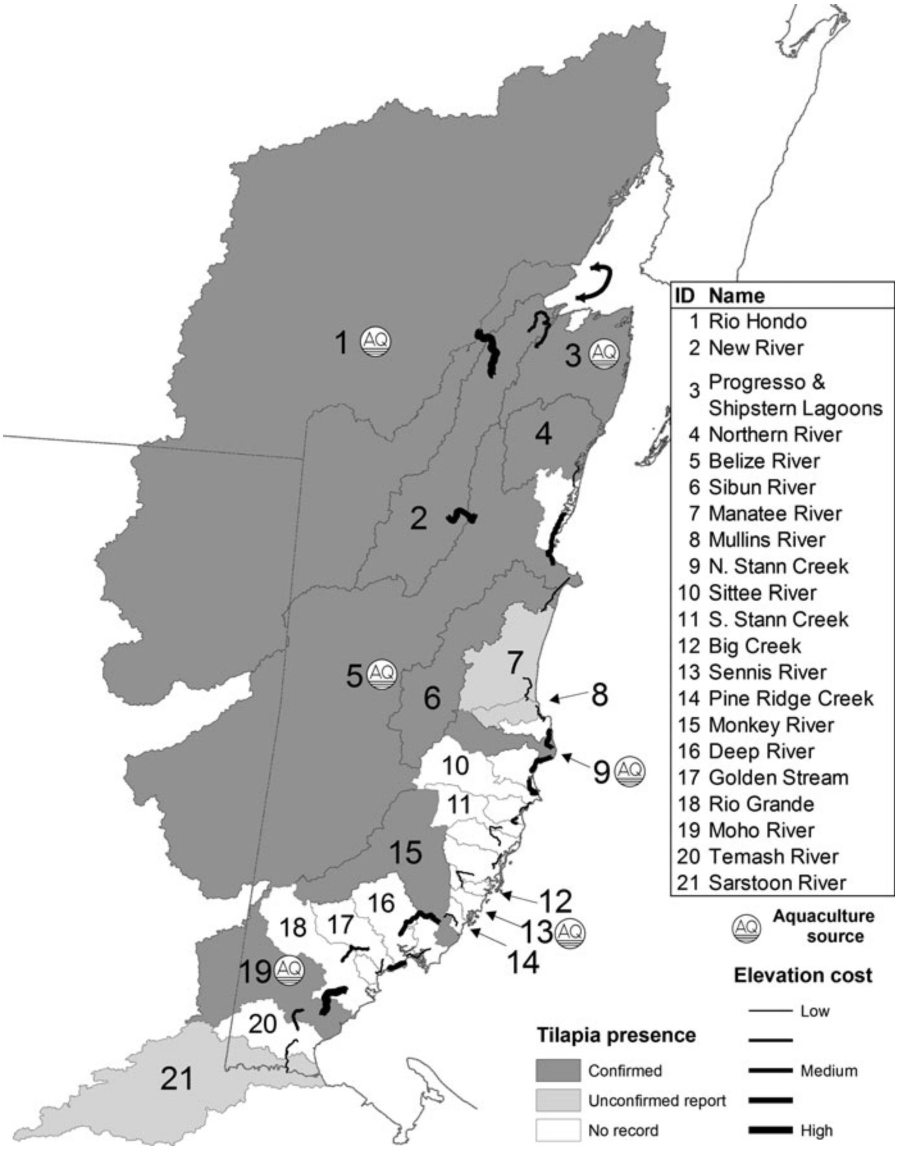

Fig. 4 Map of drainage basins, their tilapia presence, relative cost for inter-basin crossings (*black lines*), and whether aquaculture was present in the basin at any time before or during the study (AQ symbol). Unconfirmed reports represent places where interviewees indicated presence, but where physical vouchers could not be established. Summary statistics for each crossing are contained in Table 4

the Belize River system to the Sibun River and the Northern and Southern Lagoons; and (d) dispersal at sea. It has yet to be proven that the Nile tilapia disperses through sea water, but as a euryhaline species it has been shown in laboratory conditions to survive in salinities up to 30 ppt (Phillippart and Ruwet 1982). The closely related Mozambique tilapia (*O. mossambicus*), whose genes may be present in hybrids, has been captured in full sea water (Lobel 1980). After Hurricane Keith, two fishermen reported that they captured tilapias in their fish traps in the brackish waters of Chetumal Bay (Fig. 1). They believed that the fish were pushed out of the mouth of Rio Hondo by flooding and dispersed into river and creek mouths along the margin of the Bay.

Our initial calculations of dispersal rates led to five estimates in different years in the Belize River, and one estimate each from three other rivers. Dispersal rates ranged from 2.48 to 37.37 km yr^{-1}, with a mean of 16.37 km yr^{-1} (Table 3). It is impossible to assess the degree to which our estimates were influenced by human-aided dispersal, without knowledge of all potential propagule sources. Based on our interviews and chronology, we speculate that all dispersal rate

Table 3 Estimated dispersal rates calculated for the river systems for which multiple years of observation were recorded

Dispersal route	Distance (km)	Years	Rate (km yr^{-1})
Crooked Tree to Mussel Creek	14.90	6	2.48
Crooked Tree to Belize River main stem (lower)	79.95	6	13.33
Crooked Tree to Belize River main stem (upper)	178.83	8	22.35
Crooked Tree to Mopan Branch	333.78	10	33.38
Crooked Tree to Macal Branch	250.62	12	20.89
Sibun River (lower to upper)	74.74	2	37.37
Monkey River (lower to upper)	35.15	8	4.39
Moho River (upper to lower)	69.93	2	34.96
		Mean	16.37

Distances tilapia moved along the river channel were calculated between the first reported establishment site and reaches that were reported to be established later in time. This value was divided by the number of years separating the two observations

calculations with the exceptions of Crooked Tree to Mopan and Macal Branches reflect natural dispersal due to the absence of known commercial or subsistence aquaculture operations close to the more recently colonized habitats in each case.

Least cost paths between drainage basins

Paths of least elevational resistance were identified between all drainage basins (Fig. 4; Table 4). These data show that at least 11 potential low-elevational crossing points exist between basins where flood waters may disperse tilapias. Importantly, several low-cost linkages exist between currently invaded basins and adjacent uninvaded systems. These are potential routes for future spread. Additionally, several of the crossings represent man-made linkages between basins via canals and agricultural ditches with potential to serve as movement corridors (Fig. 4).

Discussion

Tilapias have an extraordinary ability to establish populations in non-native settings across many different aquatic community contexts (Costa-Pierce 2003; Courtenay 1997). If native community resistance to tilapias is not effective, then two factors will limit further tilapia range expansion: (1) unsuitable environmental conditions within newly accessed ecosystems, and (2) limitations on dispersal (human and natural). For these reasons it is important to understand habitat suitability to tilapias and the chronology and spatial patterns of spread.

Table 4 Summary table of crossings between drainage basins (Fig. 4), and the associated elevational ranges, distances between river networks, and accumulative cost measure from cost surface analysis

Crossing	Elev. range (m)	Length (km)	Accum. cost
1–2	6	24.08	32,225
2–3	15	1.49	8,760
2–5	26	18.60	21,573
4–5	8	34.52	19,274
5–6	0	18.35	0
6–7	0	2.43	0
7–8	3	1.30	1,596
8–9	9	17.95	14,265
9–10	11	6.76	16,936
10–11	7	0.65	7,058
14–15	11	0.24	3,960
15–16	7	0.52	13,469
16–17	7	15.13	18,589
17–18	3	0.29	9,594
18–19	20	1.14	30,475
19–20	4	0.40	12,575
20–21	13	1.09	2,153

Crossings with 0 elevational range are connected by the Burdon Canal which runs parallel and several kilometers in from the coast

Habitat vulnerability to colonization

Prediction of non-indigenous species distributions and spread through time is important for development of management interventions (Sharov and Liebhold 1998; Tobin et al. 2007). SDMs have been used often to infer potential future distributions of invasive species as they spread through a landscape (e.g., Drake and Bossenbroek 2004; Loo et al. 2007; Vander Zanden et al. 2004). Models implemented for this purpose use information about hypothesized niche parameters to predict the spatial limits of the realized niche (Peterson 2003). Such models do not predict spread explicitly, but attempt to define the spatial limits of habitat where a species' spread will stop.

Our prediction of potential distributions of tilapias in Belize drew on coarse-scale indicators of landscape position, climate, geologic substrates, and human influence to predict tilapia habitat suitability. As observed by Rondinini et al. (2006), the predictions yielded by habitat suitability models are likely to fall somewhere between the true limits of a species' potential range (i.e., its extent of occupancy; EOO), and the locations within a species' range where it may actually occur (its area of occupancy; AOO). Given the coarse nature of the input data, it is likely that our model more closely approximates potential EOO, and that tilapias may be patchily distributed within the habitats predicted to be suitable to them. The relatively high accuracy of our model indicated by the spatially-independent estimates of AUC suggests that the predictors used did a good job identifying the limits of tilapia habitat suitability. The strongest predictors in our models were proxies of longitudinal position along the continuum from mountains to sea. Measures of longitudinal position (e.g., distance from sea, elevation, slope, watershed size) correlate strongly to habitat availability, habitat structure, flow, trophic status, and fish faunal changes (reviewed by Matthews 1998), and have been previously shown to structure both local habitats and fish assemblages in Belize (Esselman and Allan 2010). Our results suggest a strong correlation of longitudinal position to the limits of tilapia habitat suitability as well.

Our models reflect the training data that were available—namely, localities collected on main stem rivers and tributaries, with a bias toward collection sites in Belize. The Mexican portion of the study area may have been underrepresented, which may have led to an underestimation of tilapia EOO in the Rio Hondo basin. Two specimens were found in the Rio Hondo basin out of 30 sites sampled with electrofishing. A more extensive presence dataset would likely expand the predicted EOO, rather than diminish it. For this reason, the predictions represent a conservative estimate of habitat vulnerability to tilapia colonization. Future efforts should move towards better predictions of EOO, AOO, and abundance through expansion of the variety of habitats represented in the presence dataset, inclusion of measured or modeled local habitat parameters, and biological sampling focused on catch per unit effort or yield statistics.

Spread of tilapia

The invasion process has been characterized as being composed of three sequential phases: (1) an initial establishment phase with low rate of spread; (2) an expansion phase where rates of spread increase; and (3) a saturation phase where spread rates plateau (Shigesada and Kawasaki 1997). A lag period is often observed in the establishment phase, which has been variously attributed to slow initial population growth, rapid evolution among rare or newly created genotypes, Allee effect, or the pressures that environmental or demographic stochasticity can place on a small colonizing population (Mack et al. 2000; Taylor and Hastings 2005). In the saturation phase of an invasion, spread rates may slow or halt as a population nears the geographic limits of available suitable habitats (Shigesada and Kawasaki 1997).

Our data seem to exhibit several of these invasion stages. The plot of first detections through time (Fig. 3) exhibits a pattern consistent with those predicted for the three invasion stages, with a slow initial rise in detections (establishment) followed by rapid increase (expansion), and leveling (saturation). An initial lag phase is clearly suggested by the data, which seems to transition between the establishment and expansion phases around 1996. A transition from the lag phase to the expansion phase may occur when a small initial population increases in size until emigration occurs as a result of high population density or stochastic natural environmental forces (Shigesada and Kawasaki 1997). Interviews with fishermen in Crooked Tree Lagoon support the idea that tilapia populations increased dramatically in this wetland system prior to their presumed emigration and first detection outside of the lagoon in 1996. Crooked Tree fishermen reported catching only a few tilapias in 1990, half of a 50-lb rice sack in 1991, and "many sacks" in 1994. An establishment-to-expansion transition is also suggested by the increasingly rapid spread rates for the Belize River system, with estimates of 2 and 13 km yr^{-1} for the two river reaches where tilapias were detected in 1996, and much higher rates of 20–33 km yr^{-1} in 1998 to 2002 (Table 3). The expansion phase of tilapias in Belize was clearly assisted by human- and flood-aided dispersal, and the subsequent establishment and spread from peripheral populations may have created multiple foci of invasion (Fig. 3).

It is difficult to conclude if the leveling of detections through time represents a true saturation of available habitats. The evidence suggests that tilapias have colonized much of the habitat available in the New, Belize, Sibun, and Moho River systems (Fig. 3, top right), lending support to the idea that these systems are nearing saturation. However, many basins—particularly the small river systems draining east from the Maya Mountains—have no reported incidence of tilapias despite the presence of suitable habitats. Thus, if tilapias are close to a saturation phase it is because they have yet to reach un-colonized basins, where the spread would continue.

Spread into un-colonized basins could occur through human assisted or natural dispersal. Cost surface analysis suggests the existence of low-elevation, short-distance connections between some colonized and un-colonized basins (Fig. 4). Inundation of low lying drainage divides in inland locations will depend on flood magnitudes and on sheet flow associated with intense rainfalls that are often associated with hurricanes and tropical depressions. In rivers along the foothills of the Maya Mountains flood waters can rise more than 8 m during intense flooding, and closer to the coast large rivers may rise 4 m or more. Intense rains can inundate coastal savannas with sheet flow that exceeds two meters depth in low lying areas (PCE, personal observation). Along the coast, storm surges associated with hurricanes can reach 5 m above high tide as was observed in the vicinity of Monkey River during Hurricane Iris in 2001 (Avila 2001). From these observations, we expect that elevational divides $\leq$ 4 m are sufficiently low to allow periodic natural dispersal during floods. Further research is needed to confirm this expectation and to investigate whether connections are made across higher divides.

Human aided dispersal occurred in the past, and promises to occur again in the future. The first commercial stocks of *O. niloticus* were brought to the Sennis River basin in 1995, but the farm was abandoned by 1997. *O. niloticus* hybrids (cross uncertain) were then imported from Taiwan for experimentation at an operation in the Belize River basin in 2000. The only commercial-scale tilapia farm in Belize is Fresh Catch Belize Ltd., which was established in 2002 near the Sibun River with 121 ha of ponds and a production of 1,900 metric tons of tilapia filets and whole fish in 2009 (Phillips et al. 2011). Fresh Catch Ltd. has used *O. niloticus* × *O. aureus* hybrids and pure strains of *O. niloticus* during the course of its operation (FAO 2012). The Belize Fisheries Department has promoted small-scale fish farming since the early 1990s in the form of backyard pond culture operations focused on locally occurring cichlid species and *O. niloticus*. In 2009, there were a total of 55 farmers engaged in small-scale tilapia farming with an aggregate pond area of 6 ha (CRFM 2001). The department maintains a hatchery facility and distributed over 100,000 all-male tilapia fingerlings to rural farmers in 2010 (CRFM 2001). The locations of the 55 rural tilapia farms are unknown, but these represent an important potential source of continued introductions via accidental or intentional release.

Local knowledge gathered in interviews with fishermen was a key source of information on tilapia spread in the study area. Knowledge from local fishermen has been shown in past studies to complement quantitative science by providing concordant and additional information about fish population and community patterns (Aswani and Hamilton 2004; Fraser et al. 2006; Garcia-Quijano 2007; Johannes 1978, 1981; Neis et al. 1999), and an abundance of research has reinforced the scientific accuracy of local and traditional fact-based claims. Previous works comparing local knowledge to mensurative scientific studies have shown that fishermen can recognize taxa, have accurate knowledge on fish behavioral traits and spatiotemporal changes in fish assemblage composition (Poizat and Baran 1997), and can accurately attribute causation to complex limnological occurrences (Calheiros et al. 2000). Yet, a substantial body of research also identifies the limitations of humans to accurately translate their experiences into explicit information, because of human tendencies toward judgmental biases, difficulties at understanding complex probabilities, and limited abilities to learn about complex systems (Fazey et al. 2006). Several sources of bias may have affected our results. First, fishermen may have had difficulty attributing accurate dates to the year of first occurrence. Second, the accuracy of claims about the origins of propagules may be based on hearsay rather than direct observation by the respondent. Finally, it is possible that fishermen may have misrepresented the locations where they capture tilapias, because of poor map reading skills, exaggeration, or other factors. To the extent possible, the vouchers, catch data, and electrofishing data collected in this study verified (1) fishermen's' abilities to identify tilapia correctly, and (2) many of the presence localities claimed by fishermen. Despite these weaknesses, local ecological knowledge was useful for assembling a general picture of invasion progress, and forming hypotheses about tilapia spread in an information-poor context.

Tilapia management

We have established that the colonization of suitable habitats by tilapias is well underway in the study area. A large percentage of available habitats were predicted to be suitable for tilapias, and when given access to these habitats in the past, tilapias have colonized successfully. Once tilapias have gained access to a basin, they were estimated to disperse an average of 16 km yr^{-1}. Nonetheless, we estimate that 17 of 29 basins had yet to be colonized by tilapias as of 2008 (Fig. 4). Human-aided dispersal—including aquaculture and, potentially, intentional release—was identified as a primary cause of dispersal, and flooding as an important secondary cause. Several drainage divides have sufficiently low elevational relief as to be likely dispersal conduits during flooding. Where tilapias are present, they are targeted in a multi-species artisanal fishery, and fishermen tend to have a positive opinion of them as a food fish due to their large size and productivity. Tilapia species diversity was low, suggesting that genetic diversity may also be quite limited. We did not establish whether tilapias have negative consequences for ecosystems or socio-economic well-being in the study area. Studies in southeast Asia and the Pacific have concluded that tilapias had positive effects on capture fisheries, and little to no measurable impact on biodiversity and ecosystems (Arthur et al. 2010; DeSilva et al. 2004, 2006). Competition intensity is often thought to be most severe between taxonomically related fishes that require similar resources (Ross 1986), but the fishes of southeast Asia and the Pacific are neither taxonomically related nor have much niche overlap with tilapias (Arthur et al. 2010). By contrast one might hypothesize that introduced tilapias will have the strongest interspecific competition in confamilial assemblages rich in other cichlids such as Central America, with 125 species of cichlids inhabiting many habitat types (Conkel 1997). Tilapias' potential to disrupt ecosystems and important ecosystem services has been established in new world tropical ecosystems (Canonico et al. 2005), thus we support a precautionary approach to management.

Our management recommendations are grouped into three general categories: research, control, and policy. Research must play a central part in efforts to manage tilapias and aquatic ecosystems more generally. The most critical research question that must be answered is do tilapias have negative impacts on ecosystems and/or human well-being? If so, what are these impacts? Studies that test hypotheses about direct and indirect effects of tilapias on native competitor species are needed, with a special emphasis on adult competition for space, which is particularly important for nesting cichlids, and on competition for food among juveniles when resource bottlenecks are known to occur (Piet 1996). Research should also focus on food web structure and nutrient cycling, changes to which have been documented in other locations in the Americas (Starling et al. 2002). Characterizing tilapia spatial metapopulation structure could yield a landscape perspective on management options. Large, well-connected metapopulations with a high proportion of occupied patches are less prone to extinction, in part because they are likely to be less variable (Hanski 1998). There is a rich literature exploring the application of metapopulation concepts and models to determination of optimal invasive species control strategies (e.g., Bogich and Shea 2008; Whittle et al. 2007). Investigation of tilapia dispersal during flooding should be done to help establish organism exchange rates between suitable habitat patches, and define thresholds in flood magnitudes that lead to inter-basin transfers of organisms. Routine monitoring should be conducted at select locations along the expanding front of the invasion. Such monitoring should take the form of annual checks in uninvaded waters after the wet season, with particular emphasis on waters along low-lying drainage divides (Fig. 4).

Social science research is needed to document the tilapia fishery and help establish what constitutes acceptable risk associated with continued introductions and expansion of tilapias (Pullin 1994; Schrader-Frechette 1995). It is important to understand tilapias as an economic fishery to contextualize its importance to society and to support fisheries-based control. Research into fisheries landings and local markets are warranted. Risk: benefit analysis should be focused in basins that have yet to be colonized by tilapias

(Manatee River, northern and Southern Lagoon areas; Sittee River to Pine Ridge Creek; Deep River to Rio Grande; and Temash River; Fig. 4). Risks and benefits must be evaluated in relation to local priorities and national interest. When tilapias first arrived in Belize there was an active dialogue in national newspapers about possible risks and benefits associated with their presence, which has since dissipated. For this dialogue to be rekindled, it will be necessary to educate the populous about lessons learned from tilapias in other locations with similar fish faunas to Belize (e.g., McCrary et al. 2007).

Several authors have observed that tilapia eradication is an ambitious and highly unlikely management goal, particularly after an invasion is well-advanced within a drainage basin (Arthington and Bluhdorn 1994; McCrary et al. 2007; Riedel 1965). Though complete eradication may be untenable or even undesirable given the potential benefits of the tilapia fishery to local populations, tilapia control may be warranted under certain situations, and will be critical should tilapias be found to cause undesirable environmental or social impacts. Long-term persistence of healthy native species communities may require habitats that are free of tilapias. Esselman and Allan (2011) recommended a network of fish conservation focal areas that could maximize the protection of native fauna in the minimum possible area. Selective control of tilapias where they occur in native fish reserves is a wise precautionary measure until more information is available about tilapia effects on ecosystems.

Fisheries activities can and should be used to manage tilapias to the benefit of native species and local human populations. Reduction of tilapia source-populations can be accomplished through intensive harvest in habitats known to be dominated by tilapias. Because tilapias co-occur with native cichlid fisheries species, an evaluation of gear types that target tilapia size classes that exceed maximum sizes of native cichlid fishes could lead to targeted tilapia fisheries. The minimum allowable mesh size for gill nets (7.6 cm), seine nets (3.8 cm), and cast nets (no limit) (Government of Belize 2003) are likely to catch native and tilapia species alike. Tilapias outgrow many other fishes, so mesh sizes could be adjusted to target tilapias and avoid native by-catch (Pet et al. 1995) in areas with high tilapia abundances. In the development of fisheries management, it is important to consider that tilapias are prone to stunting when they are overfished. Stunted fish have characteristics that make them less desirable food fish including small maximum size, attainment of reproductive maturity at small sizes (9 cm has been observed) and young ages (3–4 mo.), increased brood frequency, increased fecundity, high juvenile mortality, and a decrease in egg size (Lorenzen 2000). In addition to fishing for tilapias directly, protection and/or augmentation of stocks of large piscivores (e.g., tarpon, snook, barracuda, Goliath grouper) may reduce tilapia abundances in coastal freshwater and brackish habitats. Several fishermen interviewed for this study reported that tilapias are preyed on by native piscivores in rivers and lagoons. A secondary advantage of enhanced piscivore abundances is that all of these species are highly desired food fishes that could themselves lead to enhance local fisheries as well as increased sport fishing opportunities.

Policies are needed to protect Belize's waters from future introductions of new stocks of tilapias and other unwanted non-indigenous species. Aquaculture, as one of the main causes for tilapia presence and spread throughout Belize, should be regulated more carefully in the future. We echo recommendations of McCrary et al. (2007) in promoting: (1) the use of totally closed aquaculture systems and avoidance of cage aquaculture; (2) siting restrictions for pond culture away from flood prone areas; (3) a strict ban on tilapia cultivation and transportation in watersheds where they have not yet colonized and promotion of native species with aquaculture potential (e.g., *Cichlasoma urophthalmus*) instead; and (4) limitation of the genetic stocks used in aquaculture to those varieties already introduced into the natural waters of the country. We acknowledge that bans are difficult to carry out in developing countries with little enforcement capacity. Nonetheless, bans can serve as a strong disincentive if accompanied by fines or other penalties. Colonization of a river network by tilapia does not mean that aquaculturalists should be released from responsibility for controlling further unintended releases. Subsequent releases into already colonized areas may exacerbate the severity of the invasion by augmenting populations and/or increasing genetic diversity (Roman and Darling 2007).

Policies should be established in anticipation of future requests to import non-indigenous aquatic species for aquaculture, aquarium trade, pest control, or other purposes. Codes of practice governing the use of non-indigenous species are used by many nations and are an important precaution against adverse effects of exotic species (ICES 1995). Codes of practice tend to require a detailed proposal about the use, location, and source of an exotic species; an independent review focused on potential diseases, ecological interactions, hybridization potential, socio-economic considerations, and local species that may be impacted; a decision making process to approve or deny an application; and follow up activities (e.g., quarantine, confinement) that ensure safe release of organisms into managed or natural ecosystems (Bartley and Minchin 1996). Such a priori policies force importers to submit a proposal to use an introduced species and force managers to assess risks associated with a potential introduction. Until the risks for ecosystem change or impairment have been shown to be acceptably low to Belizean society, we encourage the development and application of codes of conduct to introductions of new genetic stocks of tilapias and to non-indigenous species in general.

Our study has the potential to inform investigations of tilapias in other locations, and particularly in other developing countries. Aquatic management in developing countries is impeded by a limited understanding of how freshwater ecosystems function, a paucity of baseline research, limited human technical capacity and technology, and limited investment in research and monitoring (Pringle et al. 2000; Wishart et al. 2000). These conditions pose challenges to assembling the basic information needed for ecosystem planning and management. Yet GIS data and basic data about species occurrences are increasingly available in developing countries, and local ecological knowledge is an abundant and potentially robust information source. Here we leverage the available data to demonstrate how diverse types of data, landscape analysis and novel modeling techniques can produce useful predictions about potential future spread of tilapias, and thereby support practical and achievable management interventions. Our methods could be easily transferred to other species or new locales. Past introductions have caused real and lasting ecological and economic damage to ecosystems, making the status quo undesirable. Careful management of non-indigenous species introductions and spread can help Belize and other countries avoid the costly and catastrophic invasions that have occurred elsewhere.

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