Using Ecological-Niche Modeling as a Conservation Tool for Freshwater Species: Live-Bearing Fishes in Central Mexico

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Abstract: *Ecological-niche modeling is an important tool for conservation assessment of terrestrial species; however, its applicability has been poorly explored in the aquatic realm. Goodeines are a monophyletic group of viviparous freshwater fishes that are well known in central Mexico, with 41 species in 19 genera. Given the number of threats to biodiversity in the region, goodeines represent an excellent model with which to test novel conservation approaches. We assessed the conservation status of the goodeines (37 species), based on their potential distributions predicted by ecological-niche models generated with the genetic algorithm for rule-set prediction (GARP). Predictions of species' distributions performed well in six out of eight species for which sufficient information was available to perform estimations of the area under the curve (AUC) in receiver operating characteristic plots. Extensive field surveys conducted in recent years in most cases confirm the models' predictions. Species richness exhibited a nested pattern, in which the number of species increased toward the center of the distribution of the group. At the basin level, the Río Ameca Basin had the highest number of species (11), chiefly because of the high number of microendemic species (6). Human activities within water bodies (e.g., extensive aquaculture) and drainages (e.g., agriculture, ranching, industrial activities) have affected most goodeines severely, given the deleterious effects of pollution and introductions of exotic species, such as carp (*Cyprinus carpio, Ctenopharingodon idella*) and tilapia (*Oreochromis *spp.). Our results paint a pessimistic picture for the long-term survival of many goodeines in their natural environment, and realistic conservation measures are complex and would require immediate protection of specific areas that we have identified. Ecological-niche modeling is a suitable tool for conservation assessment of freshwater species, but availability of environmental information on aquatic systems (e.g., temperature, water speed, pH, oxygen concentration) would improve distributional predictions.*

Keywords: ecological-niche modeling, freshwater fishes, GARP, goodeidae, Mexico

Utilización de Modelos de Nicho Ecológico como Herramienta de Conservación de Especies Dulceacuícolas: Peces Vivíparos en el Centro de México

Resumen: *El modelado del nicho ecológico es una herramienta importante para la evaluación de la conservación de especies terrestres; sin embargo, su aplicabilidad ha sido poco explorada en el medio acuático. Los Goodeinos son un grupo monofilético de peces vivíparos que son bien conocidos en el centro de México, con 41 especies en 19 géneros. Dado el número de amenazas a la biodiversidad en la región, los goodeinos son un modelo excelente para probar estrategias de conservación novedosas. Evaluamos el estatus de conservación de los goodeinos (37 especies) con base en la distribución potencial pronosticada por modelos de nicho ecológico*

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*generados con el algoritmo genético para predicción (GARP por sus siglas en inglés). La predicción de la distribución de especies funcionó bien con seis de ocho especies de las que se contaba con suficiente información para realizar estimaciones del área bajo la curva (AUC por sus siglas en inglés) en parcelas receptoras características. Muestreos de campo extensivos llevados a cabo en años recientes confirman las predicciones de los modelos en la mayoría de los casos. La riqueza de especies mostró un patrón anidado, en el que el número de especies incrementó hacia el centro de la distribución del grupo. A nivel de cuenca, la cuenca del Río Ameca tuvo el mayor número de especies (11), principalmente por el gran número de especies microendémicas (6). Las actividades humanas en los cuerpos de agua (e.g., acuacultura extensiva) y los escurrimientos (e.g., agricultura, ganadería, actividades industriales) han afectado severamente a la mayoría de los goodeinos, dados los efectos deletéreos de la contaminación y la introducción de especies exóticas, como carpa (*Cyprinus carpio, Ctenopharingodon idella*) y tilapia (*Oreochromis *spp.). Nuestros resultados indican un panorama pesimista para la supervivencia a largo plazo de los goodeinos en su medio natural, y las medidas realistas de conservación son complejas y requerirían protección inmediata de áreas específicas que hemos identificado. El modelado de nicho ecológico es una herramienta adecuada para la evaluación de la conservación de especies dulceacuícolas, pero la disponibilidad de información ambiental de sistemas acuáticos (e.g., temperatura, velocidad del agua, pH, concentración de oxígeno) mejorarían las predicción de distribucion.*

Palabras Clave: GARP, goodeidae, México, modelo de nicho ecológico, peces dulceacuícolas

Introduction

Ecological-niche modeling (ENM) is probably the most robust means currently available for estimating actual and potential geographic ranges of species (Guisan & Thuiller 2005). This approach is being used increasingly in conservation planning and decision making (Pearce & Lindenmayer 1998; Ferrier 2002). Despite the proved effectiveness of this set of techniques for reconstructing geographic distributions of terrestrial species, its applicability in the aquatic realm has been poorly explored (Wiley et al. 2003). This is particularly true for freshwater ecosystems, where large-scale, high-quality environmental data are lacking for most parts of the world, and such information is necessary for generating niche models (Iguchi et al. 2004; McNyset 2005). Such is the case for most Mexican freshwater systems. Data are fragmentary and no efforts have been made to produce regional or nationwide geographic databases of the physical and chemical properties of continental waters.

Central Mexico is a region of complex geology and diverse surface configuration that lies in a transitional zone between the Nearctic and Neotropical biogeographical regions. Its major physiographic feature is an uplifted plateau, the Mesa Central, in which the Río Lerma system—a Pacific Ocean drainage—is the major basin (Pérez-Ponce de León 2003). The Lerma system is currently inhabited by a diverse freshwater fish fauna with a strong endemic component that has diversified in the region (Miller & Smith 1986). The World Conservation Monitoring Center identified this region as an area of special importance for freshwater fish biodiversity (Groombridge & Jenkins 1998).

One of the most representative groups of fishes in this area is the family Goodeidae. Mexican members of this group represent the monophyletic subfamily of viviparous fishes Goodeinae, which contains 41 species in 19 genera (Doadrio & Domínguez-Domínguez 2004; Webb et al. 2004). The entire subfamily is endemic to central Mexico, and the major diversification within this group occurs in the Río Lerma-Santiago Basin. Some species of this group (e.g., *Characodon audax*, *Allotoca zacapuensis*, and *Hubbsina turneri*) are restricted to very small geographical areas. Some, such as *Skiffia francesae* and *Zoogoneticus tequila*, are now extinct in the wild.

Unfortunately, aquatic ecosystems in central Mexico rank among the most heavily disturbed by human activities in the country. Water pollution, reductions in groundwater and surface water levels, basin deforestation, habitat modification and fragmentation, introduction of exotic species, and overfishing all have caused severe degradation of water bodies (Zambrano et al. 1999).

In spite of its importance as an endemic and highly diverse group, goodeines have been largely ignored in conservation efforts, likely because of their low fishery value, and until not long ago, no efforts had been made to preserve this important component of freshwater biodiversity. Recently, however, documented extinctions and extirpations have led to some level of legislative protection, and these fishes have caught the attention of aquarists worldwide (de la Vega-Salazar et al. 2003; Domínguez-Domínguez et al. 2005*a*). Goodeines represent an excellent opportunity to use information on a relatively well-known group of fishes to establish conservation strategies for the Mesa Central. Stocks of most species are maintained in captivity at the Universidad Michoacana de San Nicolás de Hidalgo, which makes reintroduction to the wild feasible.

We present a methodological protocol for rangewide assessments of the conservation status of freshwater species, based on their geographic distributions predicted via ecological niche-modeling, land-use, and land-cover data and field survey information. This protocol was implemented with the goodeines with the aim of identifying critical areas for the protection of this group of fishes.

Methods

We used the genetic algorithm for rule-set prediction (GARP) to model ecological niches and predict potential distributions of 37 goodeine species (Stockwell & Noble 1992). In general, GARP identifies nonrandom associations between known occurrences and environmental characteristics across a study region to produce an ecological-niche model (i.e., a set of ecological conditions habitable by a species); then GARP identifies such conditions in the whole study region and produces a presence-absence map. The GARP has been used extensively to estimate potential distributions in terrestrial groups and is fairly accurate (Anderson et al. 2002; Peterson et al. 2002*a*, 2002*b*), and results of the few explorations in which it was used in the aquatic realm suggest promising results (Wiley et al. 2003; Iguchi et al. 2004; McNyset 2005).

A detailed explanation of the technical aspects of GARP is in Stockwell and Noble (1992) and Stockwell and Peters (1999), but the general procedure through which GARP produces the niche models is as follows. First, GARP resamples with replacement the occurrence localities and generates 1250 presence data points and randomly selects from the rest of the study area 1250 points of "pseudoabsences." Then, the algorithm splits the set of 2500 points in half to generate a "training" and a "testing" data set. It uses the training data set to produce a seed-niche model based on four methods: atomic rules, range (BIOCLIM) rules, negated range rules, and logistic regression. The model takes the form of a series of conditional sentences (rules) that describe the niche of the species. The seed model is then validated with the testing data set. Predictive rules are reproduced and altered in a genetic fashion, substituting its ancestor if the new rule fits better, and then the whole model is retested. The process stops after a number of iterations (1000 in our case) or when no significant improvement occurs.

We obtained occurrence records for each goodeine and exotic species through extensive fieldwork and bibliographic reviews and from specimens housed at the University of Michigan Museum of Zoology, Colección de Peces de la Universidad Michoacana (CPUM), and Colección Nacional de Peces, Instituto de Biología, Universidad Nacional Autónoma de México (CNPE). Between June 1999 and November 2004, we conducted 35 field trips and sampled 245 localities, representing either lotic or lentic water bodies. We sampled fish with seine nets, minnow traps, and electrofishing. Some specimens were collected, preserved in 70% ethanol, and deposited in the CNPE and CPUM for further identification. We compiled all field and historical records in a georeferenced database. For exotic species, we considered only field records. All sampled localities were assigned to 1 of 23 basins and subbasins, based on cartographic, hydrologic, and biogeographic information (Fig. 1a; Domínguez-Domínguez et al. 2006).

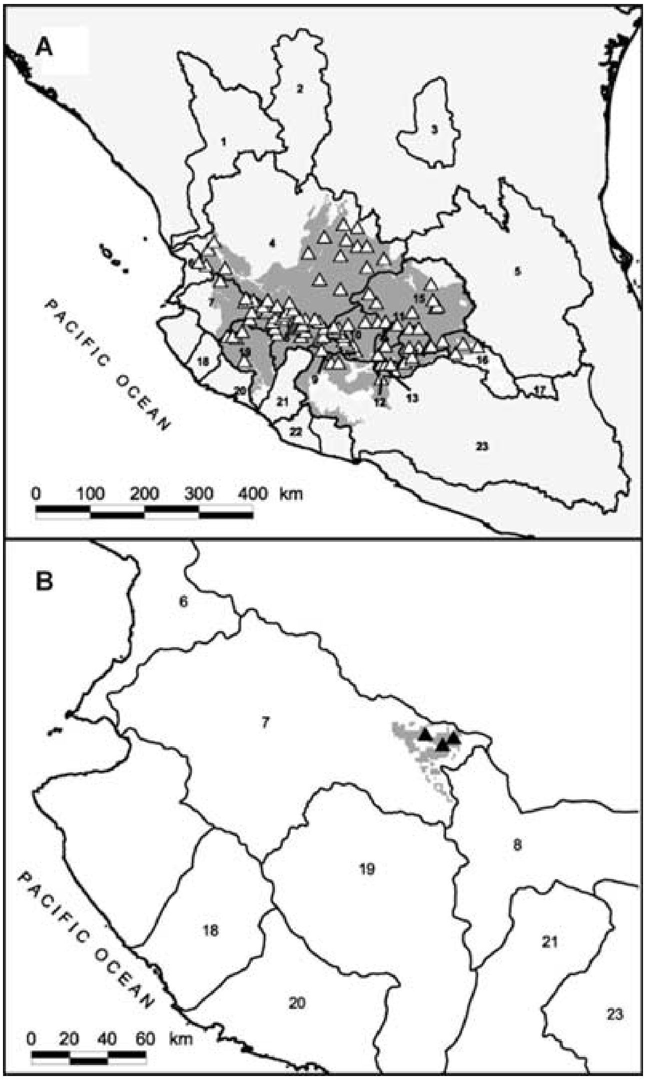

Figure 1. Modeled potential geographic distribution maps of (a) Goodea atripinnis *and (b)* Zoogoneticus tequila*. Triangles represent recorded occurrences. Polygons represent independent biogeographical regions for the goodeines: 1, Mezquital; 2, Nazas-Aguanaval; 3, Moctezuma-Venados; 4, Santiago; 5, Pánuco; 6, Compostela; 7, Ameca; 8, Chapala; 9, Cotija; 10, lower Lerma; 11, Zacapu; 12, Zirahuen; 13, Pátzcuaro; 14, Cuitzeo; 15, Mid-Lerma; 16, High-Lerma; 17, Valle de México; 18, Purificación; 19, Armería-Ayuquila; 20, Marabasco; 21, Coahuayana-Tamazula; 22, Coalcoman; 23, Balsas.*

Fourteen environmental variables in the form of digital maps were used for generating niche models in GARP. Topographic data (elevation, slope, aspect, flow accumulation, flow direction, and topographic index) were obtained from the U.S. Geological Survey Hydro1k facility (http://edcdaac.usgs.gov/gtopo30/hydro/). Climate data consisted of vector maps of annual mean and absolute values for minimum, maximum, and mean temperature and annual precipitation (Comisión Nacional para el Uso y Conocimiento de la Biodiversidad, www.conabio.gob.mx). For the purposes of analysis, we rasterized the climatic maps and resampled all maps to a cell size of 30 arc seconds (approximately 1 km^2).

Stochastic elements within GARP produce models that differ somewhat from one replicate model to the next. Hence, we produced 100 models for each species and selected the 10 best based on Anderson et al. (2003), as follows. All models were plotted in a space of commission index (percentage of area predicted present) in the x-axis and omission error in the y-axis. We selected 20 models with low or null omission error (false absences), and from those, we retained the 10 models closest to the median in the commission index axis (where commission error and overfitting are minimized). The best models were then summed to produce an "agreement" map in which each pixel indicated the number of models that predicted the presence of the target species in that cell.

Given that other elements also determine distributions of species but were not taken into account in the process of modeling ecological niches (e.g., limited dispersal, historical events; Davis et al. 1998; Soberón & Peterson 2005), the maps did not summarize actual distributions of species; rather, they summarized the distribution of their ecological niches. Thus, the maps could be interpreted as the distributional potential of species. Hence, potential distribution maps were "trimmed" with a map representing the subbasin system of central Mexico (Fig. 1a; Domínguez-Domínguez et al. 2006) under the assumptions that (1) subbasins represent dispersal barriers for species and (2) species are fairly well distributed at the subbasin level. Therefore, for each species, we selected the subbasins in which at least one record of that species was found and used those polygons to select the predicted areas in its agreement map, resulting in an estimate of the actual historical distribution for that species.

We validated model predictions in eight species for which we had $\geq$20 unique occurrence localities (*Alloophorus robustus*, *Girardinichthys viviparus*, *Goodea atripinnis*, *Ilyodon whitei*, *Xenotoca eiseni*, *Xenotoca melanosoma*, *Xenotoca variata*, and *Zoogoneticus quitzeoensis*) and calculated the area under the curve (AUC) in a receiver characteristic (ROC) plot (Hanley & McNeil 1982) with the Web implementation developed by Eng (2006). A ROC plot evaluates the agreement between distributional predictions versus independent observed presence and absence data (Fielding & Bell 1997) and is commonly used to evaluate predictive maps (Pearce & Ferrier 2000). To build the ROC plots, occurrence data were randomly split into two equal sets: one to produce models (training data) and the other to validate them (testing data). Absence data were all those sampling points in which a species was not recorded within the subbasins where the species was detected. The AUC may take values from 0.5 (no predictive ability) to 1.0 (perfect prediction). Pearce and Ferrier (2000) suggest that AUC values from 0.5 to 0.7 represent "poor" discrimination capacity, 0.7–0.9 indicate "reasonable" discrimination capacity, and 0.9–1.0 denote "very good" discrimination ability. Pending positive validation results, for production of final distribution maps, we used all occurrence data for each species.

Finally, we overlaid historical distribution maps with maximum consensus for individual species (pixel value 10) to produce a species richness map in which the value of a pixel indicated the number of species predicted to be present in that grid cell. To visualize areas potentially affected by human activities, the most recent national land-use and land-cover assessment (Instituto de Geografía 2000) was used to detect areas in which native vegetation has been transformed into urban areas, croplands, and cultivated and induced grasslands.

Results

For the 37 goodeine species, 551 occurrence points were available (Table 1). Nine species were microendemic to single water bodies (e.g., spring, lake, or tributary). Maps were produced for all 37 species, two of which are illustrated, one with a broad distribution (*G. atripinnis*) and another microendemic (*Z. tequila*) (Fig. 1). Predictive success—the proportion of correctly predicted testing points—for six species (*A. robustus*, *G. viviparus*, *G. atripinnis*, *X. melanosoma*, *X. variata*, and *Z. quitzeoensis*) ranged from 83.0% to 95.8%. For *I. whitei* and *X. eiseni* predictive success was 67.0% and 76.1%, respectively. The ROC analyses indicated that six species (*G. viviparus*, *G. atripinnis*, *I. whitei*, *X. eiseni*, *X. variata*, and *Z. quitzeoensis*) had a reasonable predictive capacity, with AUC values ranging from 0.713 to 0.844, whereas *A. robustus* and *X. melanosoma* had a poor predictive ability, with AUC values of 0.631 and 0.675, respectively.

Richness and Land Use

Species richness increased toward the center of the distribution of the group (Fig 2a). At the basin level the Río Ameca Basin held the highest numbers of species (11), chiefly because of the occurrence of several (6) microendemic species. Three additional areas of high diversity, each with 8 potentially co-occurring species, were

Table 1. Number of occurrence points used to produce distributional models for 37 species of goodeines, percentage of historical localities where species were not found in recent surveys, and the area where each species is predicted to be present.

Species	*No. of occurrence points*	*Extinction in historical localities (%)*	*Predicted area (km^2)*
Allodontichthys hubbsi	7	57.14	476
Allodontichthys polylepis	4	66.67	899
Allodontichthys tamazulae	12	60.00	1,242
Allodontichthys zonistius	8	57.14	6,432
Alloophorus robustus	41	75.61	31,165
Allotoca catarinae	5	20.00	187
Allotoca diazi	4	0.00	767
Allotoca dugesii	33	72.73	26,274
Allotoca goslinae	2	50.00	13
Allotoca maculata	3	33.33	10
Allotoca meeki	2	50.00	2
Allotoca zacapuensis	3	33.33	1
Ameca splendens	5	40.00	52
Ataeniobius toweri	4	50.00	1,401
Chapalichthys encaustus	19	31.58	5,715
Chapalichthys pardalis	2	50.00	210
Characodon audax	7	28.57	316
Characodon lateralis	15	60.00	2,352
Girardinichthys multiradiatus	15	20.00	10,894
Girardinichthys viviparus	9	55.56	21,537
Goodea atripinnis	106	31.96	89,383
Goodea gracilis	8	12.50	7,686
Hubbsina turneri	10	80.00	1,565
Ilyodon furcidens	18	0.00	18,390
Ilyodon whitei	32	50.00	67,466
Neoophorus regalis	3	0.00	211
Neotoca bilineata	11	81.82	5,438
Skiffia francesae	4	100.00	2
Skiffia lermae	13	61.54	3,962
Skiffia multipunctata	18	55.56	3,571
Xenoophorus captivus	9	33.33	6,570
Xenotaenia resolanae	17	33.33	5,792
Xenotoca eiseni	28	67.86	17,376
Xenotoca melanosoma	30	63.33	13,613
Xenotoca variata	36	47.22	52,064
Zoogoneticus quitzeoensis	46	65.22	30,714
Zoogoneticus tequila	3	100.00	35

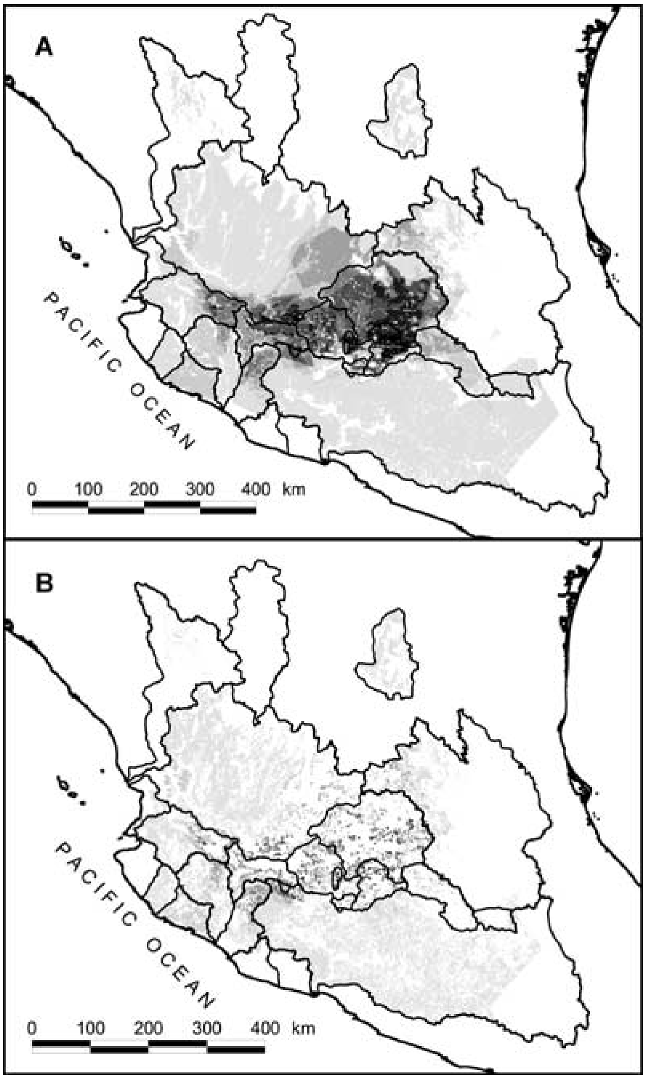

Figure 2. Map of (a) modeled potential goodeine species richness (darker areas represent higher numbers of species; maximum eight) and (b) species richness (shaded areas) and transformed habitat (white areas within the distributional range of Goodeines represent original vegetation types transformed to human-related habitat).

Zacapu Lake, the southeastern portion of the Río Santiago, and several areas in the Cuitzeo Basin (Fig. 2a). Other diverse areas included the lower and middle Río Lerma, each of which potentially holds 7 species. Among all highly diverse subbasins (i.e., Ameca, Zacapu Lake, mid-Río Lerma, and Cuitzeo Basin), goodeine species were concentrated in springs, reservoirs, and tributaries fed by springs. In general, most goodeines were associated with lentic water bodies. Human activities within water bodies (e.g., extensive aquaculture) and drainages (e.g., agriculture, deforestation, cattle raising, industrial activities) have enormous impacts on most goodeines, given the deleterious effects of pollution and introduction of exotic species. The land-use and land-cover assessment showed that 51.4% of the overall distributional area of the group ($\sim$107,866 km^2 out of 211, 502 km^2) has been converted into non-natural environments. Areas with the highest predicted richness ($\geq$7 on the richness map) comprised 1712 km^2, of which 73.4% has been transformed (these figures corresponded to entire subbasins and not properly to the water bodies). Although no information was available on the quality of most water bodies in the region, these estimates provide an idea of the magnitude of the degradation of natural systems and landscapes in the area.

Invasive Species and Local Extinctions

Several exotic species have been introduced in the study area as alternative food sources, including carp (*C. carpio*), tilapia (*Oreochromis* spp.), black bass (*Micropterus salmoides*), and bluegill sunfish (*Lepomis macrochirus*). Other species, including poeciliids (*Xiphophorus* spp., *Poecilia* spp., *Poeciliopsis* spp., *Heterandria* spp., and *Gambusia* spp.), have been translocated from other regions of the country as biological controls for mosquito larvae or as ornamentals.

Of 245 localities surveyed since 1999, *Oreochromis* spp. and *C. carpio* were found at 40%, *M. salmoides* at 13%, *C. idellus* at 12%, *Poecilia* spp. and *Xiphophorus* spp. at 8%, *L. macrochirus* at 3%, *Poeciliopsis* spp. at 3%, and *Heterandria bimaculata* at 2% of the localities. Seven percent of the localities held exotic loricharids, cichlids, and cyprinids.

The historical distribution of most goodeine species has been reduced dramatically; some species are locally extirpated (Table 1, Fig. 3b). Two species (*S. francesae* and *Z. tequila*) are extinct in the wild and survive only in captivity. Only three goodeine species occurred at all their historical localities, two microendemics (*Allotoca diazi* and *Neoophorus regalis*) and one widespread species (*Ilyodon furcidens*). Most local extinctions recorded in the field occurred in areas of predicted high species richness (Fig. 3b).

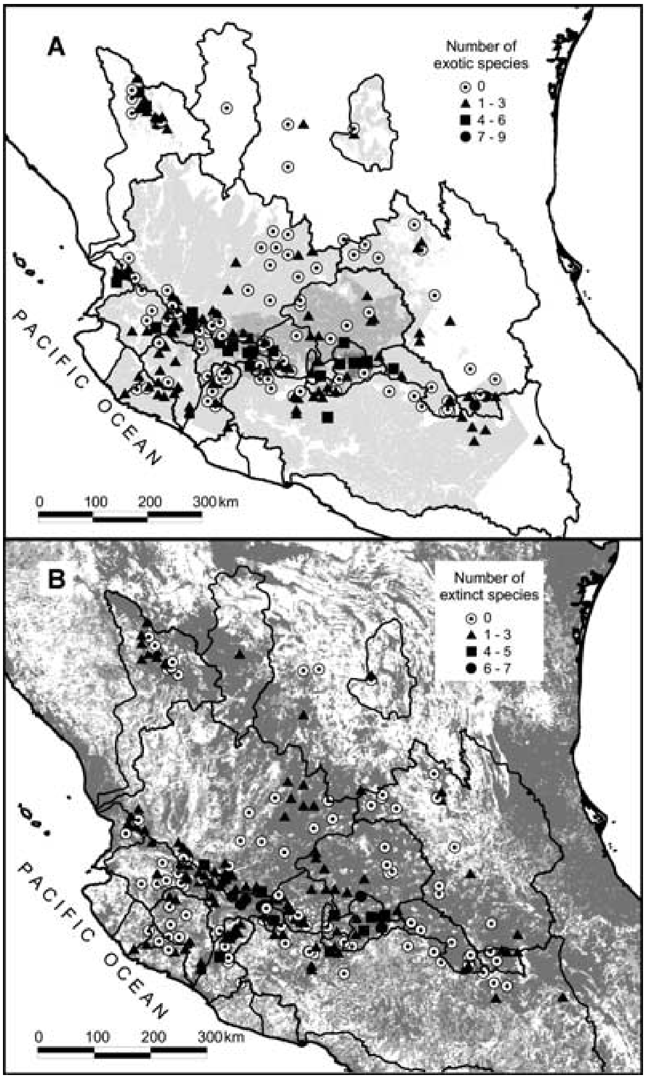

Figure 3. Maps of two disturbance factors for goodeine fishes: (a) incidence of exotic species in goodeine localities (higher goodeine richness represented by darker shades of gray); symbols are numbers of exotic species in each locality and (b) local extinctions of goodeines and three levels of natural vegetation degradation (white, pristine vegetation; light gray, mixture of natural and secondary vegetation; darker gray, completely transformed environments [urban, agriculture, and other deforested areas]; symbols are the number of extinct species in each locality).

Discussion

Ecological-niche modeling (ENM) (along with other spatial analysis tools, especially GIS and remote sensing) is a useful approach for prospective conservation studies in terrestrial systems (Chen & Peterson 2002; Anderson & Martínez-Meyer 2004; Chefaoui et al. 2005). Nevertheless, this approach has been much less explored for aquatic systems (Wiley et al. 2003; McNyset 2005), in large part, because of a lack of environmental information on freshwater systems (Iguchi et al. 2004). Notwithstanding this limitation, prediction of occurrence localities not included in model construction was quite good for species for which enough points were available. The ROC analyses, in turn, were not as good because prediction of absences were relatively low, averaging 44% of the predicted value for the eight species that were validated, ranging from 23% in *A. robustus* to 80% in *G. viviparus*. In other words GARP performed well at predicting presences, but not so well in the case of absences.

Overprediction may have several underlying causes; some are algorithmic and others are conceptual and methodological. (1) Recent intermodel comparison studies show that GARP tends to overpredict (misclassify recorded absences) more than other methods (Elith et al. 2006; Pearson et al. 2006). Nevertheless, these analyses focused on the capacity of algorithms to interpolate (rather than to extrapolate) by testing models built with presence-absence points randomly selected from a larger set. In studies explicitly designed to test the extrapolation capacity (prediction of occurrences in areas where no sampling data have been used to construct models), GARP has performed well (Peterson 2001).

(2) Overprediction is due to the nature of the approach in conjunction with the natural history of the group. The ENM focuses on modeling the environmental conditions where a species could persist (i.e., its ecological niche) and does not include historical and ecological factors that prevent species from occupying in full the spatial extent of their ecological niches (e.g., biogeographic barriers and biotic interactions) (Soberón & Peterson 2005). Therefore, absence of a species from a particular location does not necessarily mean the absence of its ecological niche (Soberón & Peterson 2005). This is particularly important for the goodeines because the high number of endemic and widespread species indicate a highly dynamic history of isolation and reconnection of the water bodies in these basins.

(3) Finally, the lack of environmental information of water bodies represents an important methodological limitation that might be affecting our results. We used macroclimatic and topographic variables as surrogates for causal, water-specific dimensions to model ecological niches of species. Clearly, production and incorporation of environmental information specifically regarding water systems (e.g., deepness, pH, nutrient, and oxygen content) would improve greatly the quality of models.

The number of occurrence records for many of the species modeled here could be an issue for the quality of predictions. Models for 19 species were built with <10 occurrence points, and small sample sizes reduce the accuracy of predictions by increasing the omission error (Reese et al. 2005; Stockwell & Peterson 2002). Results of previous studies show that GARP is one of the algorithms that perform better at small sample sizes, reaching up to 90% of accuracy with only 10 occurrence points (Stockwell & Peterson 2002), and reliable models have been obtained with as few as five data points (Martínez-Meyer et al. 2004). Many of the goodeine species with the fewest occurrence records are microendemic, and models were able to capture this (Fig. 1b). No fatal errors were evident after visual inspection of all models for which we think the observed patterns are valid.

Species Richness

The endemic subfamily Goodeinae is one of the most distinctive elements of freshwater fishes in central Mexico. Several members of this group possess unique biological traits, such as viviparity, internal fertilization, and matrotrophy (the nourishment of viviparous embryos by resources provided between fertilization and parturition). Besides their scientific value (Macías & Ramírez 2005), their high diversity and dominance in freshwater systems of central Mexico indicate an important ecological role for their members. Despite their importance, little has been done to evaluate the conservation status and threats to the persistence of this group; even less has been done at the rangewide, multispecies level.

Our model identified several areas as holding the highest goodeine species richness. Field surveys largely support these findings. In the Río Ameca basin as a whole, 11 species have been recorded (Domínguez-Domínguez et al. 2006). Nevertheless, the richness map indicated that some localities in the upper portion of the basin hold 7 species, but only 6 of those species have been recorded at a single locality in this region. Because it was not always the same species overpredicted at the different localities, the mismatch between the richness model and field surveys may be a result of (1) overprediction in the model, (2) some species being undetected in all surveys, or (3) some species having become locally extinct.

All three situations are possible. As we discussed above, overprediction (i.e., commission error) is common in ecological-niche modeling. On the other hand although field surveys have been extensive and intensive since the late 1970s, they still remain incomplete; hence, several localities may yet produce new species' records. Finally, some species have been extirpated from specific localities in the Ameca Basin: *Z. tequila* and *S. francesae* (de la Vega-Salazar et al. 2003; Domínguez-Domínguez et al., 2005*b*). Thus, a species may have gone extinct in areas of predicted high species richness.

Model predictions and field surveys for the Zacapu and Cuitzeo basins indicate the presence of eight species in each area. Interestingly, Zacapu Basin predictions anticipated the presence of all eight species only in the Zacapu Lake. Other areas within the basin were predicted to hold fewer species. Intensive fieldwork in this basin supports these results. The same situation was observed along the Cuitzeo region.

Richness and Land Use

At least half of goodeines are sensitive to changes in water quality (Lyons et al. 2000; Mercado-Silva et al. 2002). For example, *H. turneri, Xenotaenia resolanae*, and all the *Allotoca* spp. are strongly affected by small changes in the chemical or physical composition of water (Mercado-Silva et al. 2002). Therefore, to maintain goodeine diversity it is important to consider water quality. Nevertheless, areas with the highest species richness, such as Ameca, Cuitzeo, Santiago, and lower Lerma, have suffered much land-cover transformation during the last century, with considerable land transformed for agricultural and grazing activities and to urban and industrial landscapes (Mercado-Silva et al. 2002). These land uses modify water quality directly via pollution, eutrophication (fertilizer input), and soil erosion.

According to our analysis, most regions that had continuous areas of primary habitat were predicted to hold few species of goodeines (Fig. 2b). In contrast, areas predicted to hold high numbers of species were drastically transformed by human activity. In these areas goodeines survived primarily in springs and small tributaries, where rates of water turnover are high and pollution and other perturbation factors are buffered. Land-cover transformation around water bodies has directly and indirectly affected aquatic biota, probably even causing some goodeine extirpations in Cuitzeo, Pátzcuaro, Zirahuén, and Chapala lakes (Chacón-Torres & Rosas-Monge 1998; Soto-Galera et al. 1999; Orbe-Mendoza et al. 2002) and in the Lerma, Santiago, Ameca, and Armería rivers (Soto-Galera et al. 1998; Mercado-Silva et al. 2002).

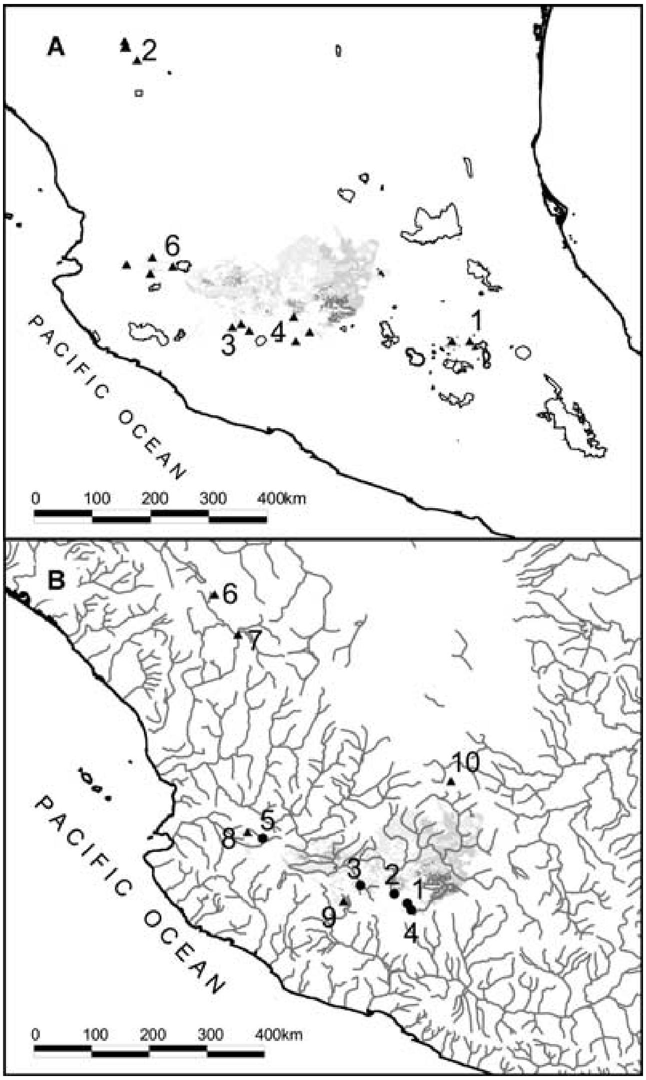

Figure 4. Map of (a) Goodeine richness and protected areas (polygons). Richness is represented by areas with five or more species; darker areas indicate higher species richness. Triangles are localities with microendemic species. Numbers are the total number of microendemic species in a locality. (b) Areas of high priority for conservation action for goodeines (circles, areas of high species richness and endemism; triangles, other important areas for the conservation of endemic species and the genetic diversity of the group): 1, La Mintzita spring in the Cuitzeo Basin; 2, Zacapu Lake in the Zacapu Basin; 3, La Luz and Orandino springs in the lower Lerma Basin; 4, Chapultepec spring in the Pátzcuaro Basin; and 5, Teuchitlán and Los Veneros in the Ameca Basin; 6, Surroundings of Durango City, in the Guadiana Valley; 7, springs around the Rio Mezquital, near Amado Nervo, Los Berros, and Nombre de Dios; 8, water bodies in the Etzatlán-Magdalena Valley; 9, Tocumbo-Cotija Valley, and 10, Jesús María River in the Pánuco Basin.

Invasive Species

Another severe problem in the region is introduction of exotic fishes. This problem is particularly troublesome because 62% of all water bodies in the region contained at least one exotic species. Invasive species affect native faunas in different ways, but they normally reduce fish diversity via effects on the trophic web (Tapia & Zambrano 2003). For instance, largemouth bass (*M. salmoides*) and bluegill have negative effects on native fish communities in artificial ponds, reducing diversity and even driving some species to extinction (Maezono & Miyashita 2003). Additional evidence for damaging effects of alien species comes from numerous other studies (e.g., Lyons et al. 1998; Soto-Galera et al. 1998; Contreras-Balderas et al. 2003).

In general our results show a very pessimistic scenario for the long-term survival of many goodeines in their natural environments. Extensive pollution caused by changes in land cover, industrial and domestic discharges, uncontrolled water extraction, and introduction of exotic species have severely affected local fish fauna. Conservation efforts have focused on captive breeding programs for all goodeine species. Yet, little has been done to promote protection in situ, as reflected in the current national system of protected areas, which covers no areas of high goodeine species richness (Fig. 4a).

Realistic conservation measures for the goodeines are highly complex and require efforts at different spatial and temporal scales. In the short term protection of key areas that maintain high levels of endemicity and richness, and have low levels of human impact is critical. Most species richness is restricted currently to springs and other spring-fed water bodies that provide refugia. To be effective these areas have to be small enough to permit monitoring, education and conservation programs designed in coordination with local people, and coordination with local authorities and the scientific community. We believe that La Mintzita Spring in Cuitzeo Basin, Zacapu Lake, La Luz and Orandino springs in the lower Lerma Basin, Chapultepec Spring in the Pátzcuaro Basin, and Teuchitlán/Los Veneros Spring system in the Ameca Basin deserve special attention (Fig. 4b). Other areas will also be important to maintain high levels of goodeiene species richness and genetic diversity, such as the springs in the Guadiana Valley near Durango City; springs around the Río Mezquital, near Amado Nervo, Los Berros, and Nombre de Dios in Durango, that hold two endemic species (*C. audax* and *C. laterales*); water bodies in the Etzatlán-Magdalena Valley in Jalisco that hold two endemic species; the Tocumbo-Cotija Valley, with three endemic species; and the Río Jesús María in the Pánuco Basin (Fig. 4b).

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