



El Colegio de la Frontera Sur

Distribución potencial de peces dulceacuícolas tropicales
bajo escenarios de cambio climático

TESIS

presentada como requisito parcial para optar al grado de
Maestro en Ciencias en Recursos Naturales y Desarrollo Rural
Con orientación en Manejo y Conservación de Recursos Naturales

Por

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2019



El Colegio de la Frontera Sur

Villahermosa, Tabasco, 11 de diciembre de 2019.

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“Distribución potencial de peces dulceacuícolas tropicales bajo escenarios de cambio climático”

para obtener el grado de **Maestro en Ciencias en Recursos Naturales y Desarrollo Rural.**

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Dedicatoria y agradecimientos

Todita la tesis está dedicada a mi familia por su apoyo incondicional en todo momento durante mi vida. Gracias a su esfuerzo del día a día pude alcanzar ciertos privilegios que ellos no tuvieron. Infinitamente agradecidos, jamás echaré por la borda la educación que recibí de ustedes. Gracias MAMÁ y PAPA.

Especial agradecimiento para mis abuelitos Carmen y Tarco que desde el cielo sé que me siguen consintiendo.

Xanny gracias por tu irremplazable compañía y estar conmigo en los momentos difíciles; esos son los que importan. Te acompañaré en tu camino. A mis amigas Julito y Lirisl, por los buenos momentos. Gergi gracias por esas llamadas de amistad. Santos gracias por los ánimos durante momentos relativamente difíciles. A la caxaqueña porque a pesar de todo, creo que es buena persona.

Al comité por su enorme paciencia y permitirme desarrollar mis ideas, así como por sus puntuales cuestionamientos.

A las personas que me acompañaron durante mi estadía en Ecosur y la hicieron más amena y confortable.

AL CONACYT por haber otorgado una beca para estudios de posgrado. Asimismo, recibió la beca PAFM de Ecosur con la que se adquirió parte del equipo de cómputo necesario para el proceso del modelado.

A la heroína Alexandra Asanovna Elbakyan por hacer público el conocimiento científico.

“Miedo, frustración, reflexión, resiliencia y paz”

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Resumen

El cambio climático está modificando las áreas de distribución de peces dulceacuícolas alrededor del mundo. La región sur de México y norte de Centroamérica es considerada un hotspot de vulnerabilidad ante el cambio climático, por lo que es indispensable evaluar los posibles efectos de este fenómeno sobre las áreas de distribución de peces dulceacuícolas. El objetivo del presente estudio es predecir la distribución potencial de los peces dulceacuícolas secundarios *Atractosteus tropicus* y *Petenia splendida* bajo escenarios de cambio climático, mediante el enfoque de modelos de nicho ecológico. La distribución potencial de *A. tropicus* y *P. splendida* se predijeron bajo los modelos de circulación general BCC-CSM1-1, MIROC5 y HadGEM2-ES correspondientes a las trayectorias de concentración representativas (RCP) 4.5 (moderada) y 8.5 (extrema) durante los horizontes 2050 y 2070. El modelado de nicho se desarrolló en el software Maxent automatizado en R 3.6.1. Los resultados mostraron que ambas especies estuvieron asociadas a condiciones cálidas y húmedas-subhúmedas, lo que indica su afinidad hacia ambientes tropicales. Los cambios proyectados a futuro mostraron una tendencia general de ganancia de áreas idóneas en todos los RCP's y horizontes debido al aumento de condiciones cálidas en las cuencas medias de la cordillera centroamérica y zona centro de la Península de Yucatán. En menor cantidad hubo una reducción de áreas idóneas relacionada con la disminución de la precipitación, principalmente, en la cuenca Usumacinta correspondiente a la distribución potencial de *P. splendida*. El escenario 85-2070 mostró la mayor área de extrapolación estricta. Las áreas de pérdida de idoneidad ambiental y de mayor incertidumbre deben evaluarse si coinciden con sitios de procesos de reproducción y/o reclutamiento. Las ganancias y reducciones de áreas idóneas podrían conllevar a la expansión del rango geográfico de muchas especies dulceacuícolas tropicales hacia mayores altitudes, así como a procesos de aclimatación, migración y/o extinción de poblaciones.

Palabras clave: Antropoceno, Biogeografía, Cichlidae, Humedales, Lepisosteidae.

Capítulo 1. Introducción

La revolución industrial en el siglo XVIII y la gran aceleración de actividades socioeconómicas durante la segunda mitad del siglo XX aumentaron considerablemente las emisiones de gases de efecto invernadero (GEI) principalmente de dióxido de carbono, metano y óxido nitroso, entre otros gases (Crutzen 2002; WWF 2016). Las emisiones GEIs han contribuido al aumento de la temperatura media global en 0.85 °C durante el período 1850-2012 (IPCC 2014). Para finales del siglo XXI se espera un aumento de entre 2 a 5°C de la temperatura media global, lo que amenazaría a más del 20% de la biodiversidad global (IPCC 2007; IPCC 2014). Estos aumentos de temperatura promueven variaciones de los regímenes de precipitación a diferentes escalas espaciotemporales (Graham y Harrod 2009).

Las variaciones en los regímenes de temperatura y precipitación repercuten sobre la biodiversidad acuática (IPCC 2013). En el futuro, estos cambios presentarán mucha variación en diferentes latitudes, proyectándose una mayor frecuencia de eventos extremos de sequías o inundaciones (IPCC 2013). Particularmente, en las zonas tropicales es más probable que los eventos de precipitación extrema ocurran con mayor frecuencia e intensidad (IPCC 2014). Estas variaciones de precipitación son importantes de considerar debido a que están directamente relacionadas con el aumento o disminución de los cuerpos de agua dulce, humedad del suelo y almacenamiento de agua subterránea (González-Zeas et al. 2019).

En las últimas décadas, las cuencas hidrográficas han sido fuertemente fragmentadas, sobreexplotadas y contaminadas por el cambio de uso de suelo, represas, crecimiento demográfico, aguas residuales, entre otros estresores (MEA 2005; Kozlowski and Bondallaz 2013). En este contexto, las variaciones de los regímenes de temperatura y precipitación asociados al cambio climático se suman a esta serie de estresores que pueden impactar gravemente a las cuencas

hidrográficas y, en consecuencia, a la distribución de peces dulceacuícolas (Knouft and Anthony 2016; Manjarrés-Hernández et al. 2018; Rolls et al. 2018).

La temperatura y precipitación han sido reconocidas como unas de las variables ambientales que más influyen sobre los aspectos fisiológicos, biológicos y ecológicos de la ictiofauna dulceacuícola (Georgiev y Nazarova 2015). Los efectos de estas variables sobre la distribución de peces han sido evaluados a diferentes escalas espacio-temporales, demostrando que los peces dulceacuícolas en ambientes templados se han desplazado, en escalas biogeográficas, hacia mayores altitudes debido al calentamiento, baja precipitación y salinización de las cuencas bajas (Graham y Harrod 2009; Xiujuan et al. 2013). En cambio, los posibles efectos sobre la distribución de peces dulceacuícolas tropicales permanecen poco claros.

El grado de afectación del cambio climático sobre la distribución de peces dulceacuícolas dependerá de sus límites de tolerancia térmica y salina (Villegas-Hernández et al. 2015). Así, peces euritermos y/o eurihalinos (especies con un amplio rango de tolerancia hacia la temperatura y salinidad, respectivamente) podrían beneficiarse del incremento de temperatura y salinidad asociados al cambio climático a través del aumento de sus abundancias y áreas de distribución; por el contrario, las especies estenotermas y/o estenohalinas (especies con un estrecho rango de tolerancia hacia la temperatura y salinidad, respectivamente) podrían ser desplazadas y posiblemente migren hacia zonas polares latitudinalmente o hacia mayores altitudes restringiendo sus áreas de distribución (Comte et al. 2013).

Modelos de nicho ecológico

Los modelos de nicho ecológico (MNE) son una herramienta utilizada para aproximar las condiciones ambientales idóneas (A) de una especie en un espacio multidimensional (E) para luego proyectar estas condiciones a espacios

geográficos (G) mediante mapas que representan la distribución potencial de las especies (Soberón et al. 2017). La región de calibración debe limitarse a partir de la accesibilidad, reproducción y mantenimiento de poblaciones viables a través de un período de tiempo representativo (M), mientras la región de proyección puede variar dependiendo del objetivo del estudio (Barve et al. 2011; Peterson et al. 2011). Con esta información los MNE aproximan el nicho fundamental existente (NF_E) de las especies, el cual representa un subconjunto de condiciones ambientales del nicho fundamental (NF). Esto debido a la limitada información ambiental asociada al número de registros georreferenciados con los que se cuenta. Por su parte, los modelos de distribución de especies aproximan el nicho realizado (NR) al incluir las interacciones bióticas (B) (Peterson y Soberón 2012), En conjunto, las condiciones ambientales (A), el área accesible (M) e interacciones bióticas (B) predicen el área ocupada (Go) exclusiva de los modelos de distribución, mientras los modelos de nicho predicen áreas potenciales de distribución (Peterson et al. 2011).

Una de las principales ventajas de los MNE es que permiten predecir la distribución potencial de las especies a partir de relativamente pocos registros georreferenciados, sin necesidad de muestrear todos los sitios de distribución, lo que reduce esfuerzo, dinero y tiempo. Aunque cabe señalar que su precisión dependerá de la información ambiental contenida en estos registros para no subestimar el nicho ecológico y, por ende, las áreas de distribución potenciales (Warren et al. 2008; Peterson et al. 2011).

Los MNE han tomado importancia en la última década debido a sus múltiples aplicaciones con diferentes enfoques (Cuervo-Robayo et al. 2017). Los MNE han sido ampliamente utilizados para predecir la distribución potencial de especies invasoras (Pech-May et al. 2016), la distribución potencial de especies en tiempos geológicos pasados considerando los refugios pleistocénicos (Carvalho y Del Lama 2015), identificar áreas prioritarias de conservación (Cooper-Bohannon et al. 2016), y la distribución potencial de las especies bajo escenarios de cambio

climático (Lamsal et al. 2018), entre otros. Este último tipo de aplicación, también conocido como transferencias temporales, están íntimamente ligadas a una caracterización adecuada del nicho ecológico en el presente, por tanto, es primordial seleccionar las variables ambientales adecuadas, así como tener la mayor variabilidad ambiental posible (Araújo et al. 2005). Otros puntos importantes al realizar transferencias al pasado o futuro, es que estas presentan un mayor grado de incertidumbre a medida que aparecen condiciones ambientales nuevas (Mainali et al. 2015), asimismo los nichos de las especies se consideran estáticos, es decir, no cambian con el tiempo (Peterson et al. 2011).

A pesar de la utilidad de estos modelos, los estudios en peces dulceacuícolas aún son escasos y sesgados hacia familias que se distribuyen en el hemisferio norte, por ejemplo, las familias Cyprinidae y Salmonidae (Comte et al. 2013), mientras que los efectos del cambio climático sobre la distribución de peces dulceacuícolas tropicales aún no son claros. La aplicación sobre los peces dulceacuícolas se ha centrado en predecir la distribución potencial de peces invasores en Norteamérica (Zambrano et al. 2006; Chen et al. 2007; Walsworth y Budy 2015) y en Gran Bretaña (Elliott et al. 2015). En México, Domínguez-Domínguez et al. (2006) predijeron una reducción de la distribución de peces dulceacuícolas de la región debido a estresores antrópicos y especies invasoras.

En ambientes dulceacuícolas es importante considerar las dificultades y limitaciones del modelado de nicho. En primer lugar, existe una falta de información ambiental propia de estos ambientes, por ejemplo, velocidad de la corriente, temperatura y pH del agua, nutrientes, etcétera debido a la dificultad de medición de variables en todos los cuerpos de agua de una región determinada (Papeş et al. 2016). En segundo lugar, la mayoría de los trabajos utilizan variables climáticas para predecir la distribución potencial a escala regional. Sin embargo, la información hidrológica podría contribuir a mejorar la precisión de los modelos a escalas locales (Chu et al. 2005). En el enfoque de transferencias temporales, incluir variables hidrológicas proyectadas en condiciones futuras o pasadas

actualmente es imposible dado que no se han generado, por lo que incluir exclusivamente variables climáticas son relativamente adecuadas para predecir la distribución potencial bajo escenarios de cambio climático.

Casos de estudio

Los hotspots de biodiversidad son aquellas regiones geográficas con una gran diversidad de especies (Cooper-Bohannon et al. 2016), mientras los hotspots de cambio climático son regiones muy vulnerables al impacto de este fenómeno (Giorgi 2006). La región de la frontera sur de México y norte de Centroamérica se ubica dentro de un hotspot de cambio climático. De acuerdo con las diferentes proyecciones del IPCC, en dicha región se predicen grandes cambios ecológicos en los sistemas naturales debido al cambio climático (IPCC 2014). Uno de los sistemas naturales más vulnerables ante este fenómeno son las cuencas hidrográficas, las cuales albergan una amplia diversidad de especies acuáticas, entre las que se encuentran los peces (Carabias et al. 2015).

Para este estudio se seleccionó al pejelagarto (*Atractosteus tropicus*) y la tenguayaca (*Petenia splendida*) como modelos para evaluar el impacto del cambio climático sobre el hábitat de la región del sur de México y norte de Centroamérica. Las áreas de distribución de ambas especies se restringen a cuencas hidrográficas ubicadas dentro del hotspot de Mesoamérica (Miller 2009). Asimismo, ambas especies son de importancia cultural y económica para la región, siendo depredadores topos (Mendoza-Alfaro et al. 2008; Méndez-Marin et al. 2016). Modelar la distribución potencial de estas especies bajo escenarios de cambio climático podría vislumbrar los potenciales efectos del cambio climático sobre la distribución de peces dulceacuícolas de esta región y, con ello, contribuir a desarrollar medidas de conservación y adaptación ante este fenómeno.

El pejelagarto (*Atractosteus tropicus* Gill, 1863) pertenece a la Familia Lepisosteidae, caracterizados por ser fósiles vivientes. El pejelagarto habita

ecosistemas de agua dulce cálidos de aproximadamente 25 °C a 32 °C y poco profundos, de aguas estancadas y pantanosas con abundante vegetación acuática. Esta especie tiene una distribución disyunta, en la Vertiente Atlántica desde Coatzacoalcos hasta el Usumacinta (México y Guatemala). En la Vertiente Pacífica desde el sur de Chiapas hasta el río Negro en Nicaragua y más al sur en el Lago Nicaragua y el río San Juan y sus tributarios en Costa Rica (Nelson et al. 2016; Froese y Pauly 2018). Las poblaciones silvestres han disminuido en las últimas décadas debido a la sobrepesca, así como a la pérdida, fragmentación y contaminación de su hábitat (Arias-Rodríguez et al. 2009). Previamente, la distribución potencial de *A. tropicus* fue modelada en condiciones actuales con áreas de calibración y proyección limitadas exclusivamente para el Estado de Tabasco, México (Castillo-Torres et al. 2017). Por ende, los registros georreferenciados utilizados estuvieron asociadas a rangos estrechos de variables topográficas y climáticas pudiendo generar predicciones sesgadas en dichas áreas. Predecir la distribución potencial de ambas especies podría ayudar a identificar y establecer zonas prioritarias de conservación, donde se espere que este fenómeno impacte con una mayor intensidad.

Respecto a la tenguayaca (*Petenia splendida* Günther, 1862), esta especie pertenece a la Familia Cichlidae. La distribución de la tenguayaca está restringida a las cuencas hidrográficas Grijalva, Usumacinta y Este-Oeste de la Península de Yucatán (Miller 2009). Dicha especie habita ríos, lagos y lagunas con aguas tranquilas, cálidas entre aproximadamente 24.9 y 30.5 °C y bajas salinidades. Los organismos juveniles se asocian a sitios con abundante vegetación acuática, mientras los adultos prefieren sitios con fondos lodosos o pedregosos sin vegetación acuática. La calidad de su carne y precio accesible ha generado sobreexplotación y reducción de las poblaciones (Méndez et al. 2011).

Pregunta de investigación

¿Los cambios de temperatura y precipitación asociados al cambio climático modificarán las áreas idóneas de distribución de *Atractosteus tropicus* y *Petenia splendida*?

Hipótesis

Las condiciones ambientales favorables en las áreas de distribución de *Atractosteus tropicus* y *Petenia splendida* se reducirán debido al efecto de los cambios de temperatura y precipitación asociados al cambio climático.

Objetivo general

Predecir la distribución potencial de *Atractosteus tropicus* y *Petenia splendida* bajo escenarios de cambio climático mediante el enfoque de los modelos de nicho ecológico.

Objetivos específicos

- Predecir la distribución potencial en condiciones actuales de los peces dulceacuícolas tropicales *A. tropicus* y *P. splendida*.
- Proyectar la distribución potencial actual en los escenarios de trayectorias de concentración representativas (RCP) 4.5 (moderado) y 8.5 (extremo) durante los horizontes 2050 y 2070.
- Estimar e identificar áreas idóneas ganadas, perdidas o que permanecerán estables en las áreas de distribución de *A. tropicus* y *P. splendida* debido al cambio climático.

Capítulo 2. Artículo enviado a la revista Aquatic Conservation: marine and freshwater ecosystems

Modelling the potential distribution of tropical freshwater fishes under climate change scenarios

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ABSTRACT

1. Climate change is producing and will produce changes in distribution patterns of freshwater fish at various spatial-temporal scales. Especially in tropical regions that are highly vulnerable to this phenomenon. Therefore, there is an increasing need to predict these changes to determine conservation and adaptation strategies that help face climate change.
2. Ecological niche models offer a relatively simple and reliable way to predict the potential effects of climate change on species distribution. In this context, we determined the existing fundamental climatic niche of the secondary freshwater fish *Atractosteus tropicus* and *Petenia splendida* to predict potential distribution changes under climate change scenarios using the ecological niche model approach.
3. The potential distribution *A. tropicus* and *P. splendida* were predicted under three general circulation models corresponding to the representative concentration trajectories 4.5 (moderate) and 8.5 (extreme) during the horizons 2050 and 2070 using the maximum entropy software (Maxent).
4. The potential distribution of both species was associated with warm and humid-sub-humid conditions. Seasonality and variability of temperature and precipitation were coupled with breeding seasons. Future projections showed a trend of gain of suitable areas for both species due to the increase of warmer conditions in middle and upper basins of the Central American mountain range, as well as in the centre of the Yucatan peninsula. Losses of suitable areas mainly for *P. splendida* were located in the Grijalva-Usumacinta basins due to the decrease in precipitation.
5. Increasing warm conditions would cause the geographic range of many tropical freshwater species to expand to higher altitudes, while greater aridity would lead to a decrease in available habitats. The gains and losses of suitable areas could generate processes of acclimatization, migration, and/or local extinctions in medium- and long-term.

Keywords: Anthropocene, biogeography, Cichlidae, ecological niche modeling, freshwater ecosystems, Lepisosteidae, suitability, wetlands

INTRODUCTION

According to the IPCC (2018) during the decade of 2006-2015 the global average temperature increased 0.87 °C in comparison with the pre-industrial levels in the second half of the 19th century and by almost half of the 2 °C considered as the threshold for not producing strong changes in natural and human systems by the end of the 21st century (IPCC 2014; IPCC 2018). One of the immediate effects of this increase are changes in precipitation regimes at different spatial-temporal scales, which would impact various freshwater ecosystems (i.e., wetlands, rivers, lakes) due to their close relationship with climatic variables (Graham and Harrod 2009). These impacts are intensified by floods and/or droughts, where drought leads to evaporation of water bodies (MEA 2005).

Climate variables such as ambient temperature and precipitation influence the abundance, distribution, and dispersal of freshwater fish at regional and biogeographic scales (Knouft and Anthony 2016; Manjarrés-Hernández et al. 2018; Rolls et al. 2018). The effect of climate change on freshwater fish depends, among other factors, on the limits of tolerance towards different environmental and climatic variables such as temperature and precipitation. For example, eurythermal and euryhaline species tolerate a wider range of temperature increase and salinization compared with stenothermal and stenohaline species (Lejeusne et al. 2010). Previous observations show that freshwater fish from temperate environments migrated to upper basins due to warming and salinization of lower basins (Comte et al. 2013). However, the possible effects on the distribution of tropical freshwater fish remain unclear.

One way to predict the impact of climate change on species ranges is through ecological niche models (ENM). These models correlate presence and absence/pseudoabsence data of species as a function of environmental variables to approximate the existing fundamental niche (EFN), i.e., to approximate the environmental suitability associated with the available presences. Among other requirements, it is a priority to have basic biological and ecological information of

the species to be modelled (Peterson et al. 2011). ENM is underused for modelling tropical freshwater fish, with only few studies of the family Goodeidae in Mexico under current conditions (Domínguez-Domínguez et al. 2006), as well as an evaluation of the invasive potential of *Pterygoplichthys ambrosettii* in Brazil (Frederico et al. 2019). In the face of climate change, there are still no studies aimed at estimating potential impacts on tropical freshwater fish compared to those on temperate freshwater fish (e.g., Bond, Thomson, Reich, & Stein, 2011; Yu et al., 2012).

In a context where tropical environments will experience warmer and more arid conditions in the coming decades (IPCC 2014), it is crucial to estimating the potential effects of climate change on the distribution of tropical freshwater fish to allow developing conservation and adaptation strategies to this phenomenon. The potential effects could be particularly aggravated in regions where big changes in climate variables and sea-level rise are expected (MEA 2005; Reguero et al. 2015). Identifying key freshwater fish and modelling their potential distribution in the face of climate change could provide signs of the possible effects of such a phenomenon on an aquatic community in a given region.

The tropical freshwater fish *Atractosteus tropicus* (Lepisosteiformes: Lepisostidae) and *Petenia splendida* (Perciformes: Cichlidae) are distributed in hydrographic basins within southern Mexico and northern Central America (Rush Miller 2009; Nelson et al. 2016) considered hot spots of vulnerability to climate change and rising sea levels (Giorgi 2006; Reguero et al. 2015), as well as a wide diversity of ecosystems and freshwater fishes (Gómez-González et al. 2015; Matamoros et al. 2015). Both species are of commercial and cultural importance for the region (Arias-Rodríguez et al. 2009; Méndez et al. 2011). They both have diurnal trophic activity and are top predators (Schmitter-Soto 1996; Mora-Jamett et al. 1997). The spawning of *A. tropicus* occurs in the rainiest months of the year between July and October (Mora-Jamett et al. 1997), while *P. splendida* spawns from late dry season to mid rainy season (Ixquiac-Cabrera et al. 2010).

Previously, the potential distribution of *A. tropicus* was modelled under current conditions with limited calibration and projection areas exclusively for the State of Tabasco, Mexico (Castillo-Torres et al. 2017). Therefore, the occurrences used were associated with narrow ranges of topographic and climatic variables and could generate biased predictions in these areas. In this context, the objectives of the present study are: 1) to predict the potential distribution of *A. tropicus* and *P. splendida* under current conditions throughout their geographic range through the approach of ecological niche models, and 2) to project this potential distribution under climate change scenarios with the goal of estimating potential changes in the distribution of these species.

METHODS

Inputs and M

The occurrences of both species were obtained from the GBIF, FishBase, Fish-Net2, VERTNET databases, as well as from the ECOSUR ichthyological collection (ECOSC) and the University of Costa Rica Fish Collection. All the databases composed a single database that was corrected to remove duplicated records, with 0 coordinates, in the sea, and with an accuracy of fewer than three digits (Cobos, Jiménez, Nuñez-Penichet, Romero-Alvarez, & Simões, 2018). Only records from scientific collections and bibliographies were included from this database in order to reduce the uncertainty associated with them. To avoid overfitting, the spatial autocorrelation of the presences was eliminated at 10 km due to the dispersion capacity of both species. The occurrences corresponded to two periods: the first, from 1970-2000 for calibration and the second, from 2001-2015 for validation, thus guaranteeing the independence of the data. Finally, the environmental outliers in the calibration and validation data were eliminated in order to exclude records from populations with negative reproduction and survival rates (Simões and Peterson 2018).

The corrected dataset resulted in 101 records for *A. tropicus* and 175 records for *P. splendida*, which were used for the calibration process of the ENM. Subsequently, these records were divided into 68 for calibration and 33 for evaluation of *A. tropicus*, as well as 124 for calibration and 53 for evaluation of *P. splendida* using the spThin package (Aiello-lammens et al. 2015). The independent records purified and filtered at 10 km used for the final evaluation of the calibrated models amounted to 35 and 65 for *A. tropicus* and *P. splendida*, respectively.

The 19 bioclimatic variables of the current weather were obtained from worldclim at a resolution of 30 arcseconds (~ 1 km) (Hijmans et al. 2005). BIOS 8, 9, 18, and 19 were eliminated a priori as methodological artefacts (Escobar et al. 2014). The remaining 15 BIOS were downloaded into three general circulation models (GCMs) BCC-CSM1-1, MIROC5, and HadGEM2-ES corresponding to two typical Representative Concentration Pathway (RCPs) 4.5 (moderate) and 8.5 (extreme) (Moss et al. 2008) over two horizons 2050 and 2070 in order to project the future potential distribution of both species. These GCMs show a reasonable distance and less interdependence between their results (Sanderson et al. 2015). Environmental data and variables were projected in the World Geodetic System (WGS84).

The range (M) for the two species was delimited by considering the areas accessible to natural dispersal during a representative period (Barve et al. 2011). For this were overlapped the range proposed by Miller et al. (2005), the freshwater ecoregions for Central America and southern Mexico (Abell et al. 2008), wetlands, and rivers (Gumbricht et al. 2017), geographic barriers and geological events in the region (Mastretta-Yanes et al. 2015), as well as the opinion of freshwater fish experts (Fig. 1). From the delimited M, the 15 BIOS representing the current environmental conditions were cut.

Following recent advances in the more robust construction of environmental variables (Cobos, Peterson, Osorio-Olvera, & Jiménez-García, 2019), subsets of

these BIOS were constructed as follows: first, a preliminary model was run with all the BIOS, with which the importance and contribution of information of each of the variables was observed by means of the Jack-knife resampling method. At the same time, the 15 BIOS were subjected to a Pearson correlation analysis to identify strong correlations ($r^2 > 0.8$). Climatic variables that influence the biological and ecological processes of both species were prioritized. Then, from the random combination of non-correlated variables of biological and ecological importance, as well as the gain and contribution of information from each one, 29 sets of variables were constructed for *A. tropicus* and 25 sets for *P. splendida*.

Calibration and evaluation

The parameters Linear (L), Quadratic (Q), Product (P), and their combinations were included to reconstruct the climate EFN. Also, 40 regularization multipliers (RM) were used from 0.1 to 3 in intervals of 0.1, from 3.5 to 7 in intervals of 0.5, as well as 8, 9, and 10 with a background of 10,000. The output used was logistic. The best models of these combinations were selected based on three criteria in the following order of importance: 1) statistical significance of the partial area under the Receiver Operating Characteristic (ROC) curve (≤ 0.05), that is, models with better than random performance (Peterson et al. 2008); 2) omission rate $< 5\%$, calibrated models with yields capable of omitting evaluation presences below the established threshold (Anderson et al. 2003); and 3) Akaike Information Criterion ($\Delta AICc < 2$), simple models that fit the data well (Warren and Seifert 2011; Radosavljevic and Anderson 2014).

Generation and validation of final models

The final models were created with the parameters that met the three previously mentioned evaluation criteria. For each final model, the minimum, maximum, median, and range (maximum minus minimum) environmental suitability was obtained with ten replicas each by Bootstrap resampling. These models were validated with a data set independent of the calibration process. The metrics used

were: 1) statistical significance of the Partial ROC (≤ 0.05) and 2) omission rate < 5%.

Transfers to the future

The configuration of the final *A. tropicus* and *P. splendida* models that met the two-validation metrics were transferred to the future under three GCMs corresponding to RCPs 4.5 and 8.5 during horizons 2050 and 2070. Future models were projected with extrapolation and clamping (EC) considering the fit of the response curves obtained during the calibration process (Peterson et al. 2018). For each combination of GCM, RCP, and horizon, the minimum, maximum, median, and range (maximum minus minimum) environmental suitability were obtained from 10 replicas each through Bootstrap resampling. Current and future models of medians were converted to presence-absence binary maps (1,0) using a cohort threshold of error susceptible presences ($E = 5\%$). The gain, stability or loss of suitable areas in the geographic space was represented by consensus maps between the binary maps of the three GCMs for each combination of RCP and horizon (GCMs + 1 RCP + 1 horizon) (Campbell et al., 2015; Cobos, Osorio-Olvera, & Peterson, 2019).

Analysis of variation and uncertainty

The variation provided by replicas, parameters, GCMs, and RCPs in geographic space under current and future conditions was identified by creating variance maps for each of these sources. Quantitatively, this contribution of variation was obtained through hierarchical participation of variance. In the case of *P. splendida*, it was not necessary to partition the variance because the replicas represented 100 % of the variation as there was only one better ENM (Peterson et al. 2018). These measures of variability were made following the methodology of Cobos, Osorio-Olvera, & Peterson (2019). The identification of non-analogous environmental conditions among the sets of future variables with respect to the current ones was carried out through a Mobility-Oriented Parity (MOP) analysis (Owens et al. 2013). For the commonly used Multivariate Environmental Similarity Surface analysis, the

MOP analysis improves the quantification of environmental similarity between the pixels of two or more sets of variables, where pixels with values of 0 indicate strict extrapolation. Subsequently, a consensual map of extrapolation risk between the three GCMs for each combination of RCP and horizon was made. The entire ENM process was performed with the Kuenm package (Cobos, Peterson, Barve, & Osorio-Olvera, 2019) in software R 3.6.1 (R Core Team 2019).

RESULTS

A total of 4,674 ENM were generated for *P. splendida* and 7,134 for *A. tropicus*, of which 246 corresponded to a set of variables for each species. Table 1 details the parameters of the models selected for both species. The selected sets of climatic variables were 15 and 27 for *A. tropicus* and *P. splendida*, respectively. Set 15 was composed, in order of importance, by the mean temperature of warmest quarter (BIO 10), precipitation of wettest quarter (BIO 16), precipitation seasonality (BIO 15), mean diurnal range (BIO 2), temperature seasonality (BIO 4), while set 27 was made up of the minimum temperature of the coldest month (BIO 6), BIO 2, BIO 4, precipitation of driest month (BIO 14) and BIO 15.

The ENM for *A. tropicus* identified three large potential distribution areas with medium-high environmental suitability (yellow and red zones) located on the coastal plain of the southern Gulf of Mexico from the Papaloapan basin to Lake Izabal north of the Guatemala-Honduras border, the Pacific coastal zone from southern Oaxaca in Mexico to the Guatemala-El Salvador border, and finally an area extending from the Pacific coast between the El Salvador-Honduras border to the Caribbean coast of Costa Rica. These three areas were separated by zones of low and null suitability (blue zones) of the Central American mountain range. These blue areas represented absences by converting the maps to binary using the cohort threshold (Fig. 2).

The potential distribution of *P. splendida* corresponded to a continuous area of medium suitability, connected mainly by the basins of the Grijalva, Usumacinta, and Hondo rivers in the Atlantic that extended into the East and West basins of the Yucatan Peninsula. Through this area, sites of high suitability were observed (zones in red). Areas of low suitability were also identified in the centre of the Yucatan Peninsula, as well as sites of unsuitability in the Chiapas highlands, Mexico southeast of the calibration area (Fig. 3).

Consensus of projected changes according to future conditions for both species quantified a general trend of gain of suitable areas as GCMs, RCPs, and horizons increased (Figs 2 and 3; Fig 4, X values G1, G2, and G3). *A. tropicus* models showed a more pronounced trend. Gain areas (red zones) were located in the surroundings of mountainous areas for the *A. tropicus* calibration area, whereas for *P. splendida*, they were located mostly in the Yucatan peninsula, Mexico, near the northern border of Guatemala. A slight loss of suitable areas under future conditions (blue zones) was mainly quantified for *P. splendida* at 1 and 2 GCMs in areas overlapping the Usumacinta river basin (Figs 2 and 3; Fig 4). The areas unsuitable for both species showed a declining trend of percentages as the RCP and horizon increased, being more pronounced for *A. tropicus*. This trend coincided with the percentages of gain areas.

The hierarchical partition of the variance showed that the replicas provided the highest percentage of variation under current conditions for both species (Fig. 5). Under future conditions, the GCMs provided the greatest variation, followed by the replicas in the *A. tropicus* models. In the case of *P. splendida*, the replicas represented the greatest variation, being slightly higher than the variation represented by the GCMs. RCPs contributed to a low variation for both species, being even below 1 %. These sources of variation represented in the geographic space under current conditions show that the replicas and parameters did not coincide with the suitability areas in the coastal plain of the southern Gulf of Mexico for the *A. tropicus* models (Fig. 6). The areas of highest suitability for *P. splendida*

models also did not coincide with the greatest variation in range or replicas (Fig. 7). These predictions were reliable. Under future conditions, the greater variation of the GCMs and RCPs mostly coincided with the areas of gain in both horizons and species. Also, the GCMs and RCPs coincided with the areas of loss of suitability in both horizons.

The uncertainty analysis (MOP) associated with future conditions identified higher risks of strict extrapolation in overlapping areas with areas of greater suitability under current conditions for *A. tropicus* models under all combinations of RCPs and horizons (Fig. 2). The areas at the highest risk of strict extrapolation were located in the north and northeast region of the *P. splendida* calibration area (Fig. 3). Most of these regions did not coincide with suitable areas under current conditions for this species. In contrast, they did coincide with gain areas in the Yucatan Peninsula under future conditions for all combinations of RCPs and horizons. The greatest extrapolation risks were identified in scenario 8.5-2070 for both species.

DISCUSSION

In order to understand distribution changes in future conditions at different spatiotemporal scales, it is necessary to understand environmental preferences in current conditions and how these, together with other factors such as dispersal events, geographical barriers, generated the distribution patterns of the species. In this context, the selected BIOS indicated that both freshwater species are sensitive to temporal variability of temperature and precipitation throughout the year, particularly during the breeding seasons, possibly due to the greater availability of habitat (Graham and Harrod 2009). Likewise, the strong affinity to warm conditions shows that they are species from tropical environments. Therefore, environmental suitability was low at high altitudes of the Central American mountain range. The location of some individuals of both species at this altitude could be due to the

dispersal capacity that allowed them to travel to these sites, without being able to maintain populations given the unsuitable conditions (Maguire 1973).

The potential distribution of *A. tropicus* under current conditions presented modifications with respect to the three large populations mentioned in the literature (Rush Miller 2009): 1, Atlantic watershed from the Coatzacoalcos river basin, through the Usumacinta to the Hondo river basin (Mexico and Guatemala); 2, Pacific watershed from southern Oaxaca to Lake Nicaragua and Río Negro in Nicaragua; and 3, Atlantic watershed in the Caribbean Sea from the San Juan river basin to the southern Tortuguero lagoon in Costa Rica. Here the potential distribution of the coastal plain of the southern Gulf of Mexico extended a little further north to the Papaloapan Basin. The potential distribution of the Pacific slope was fragmented into two, the first from southern Mexico to the border between Guatemala and El Salvador, while the second from Lake Nicaragua and Río Negro, which together with the area of the Costa Rican Caribbean slope formed an area of low-medium suitability.

The potential disjunct distribution reinforces the idea of null gene flow between the populations in the present time coinciding with the results obtained by Barrientos-Villalobos & Espinosa-De Los Monteros (2008), who found a genetic structuring and divergence between populations of *A. tropicus* due to allopatric isolation generated by the Central American mountain range. This isolation could occur after the dispersion of individuals from the Atlantic slope to the Pacific slope through the Chivela pass. This site of low elevation in the Isthmus of Tehuantepec experienced during Pleistocene interglacial events an increase in temperature (Mastretta-Yanes et al. 2015) that triggered the connection of many isolated freshwater ecosystems with higher precipitation (Barrientos-Villalobos and Espinosa-De Los Monteros 2008). Migrant individuals possibly colonized the freshwater ecosystems of the Pacific slope due to the environmental suitability relatively similar to that existing in the Gulf of Mexico slope. This connection of freshwater ecosystems during periods of abundant rainfall has been described as recurrent pathways of dispersion and

colonization of freshwater fish through the Central American mountain range, as the cases of the families Cichlidae and Poeciliidae (Hulsey and López-Fernández 2001; Smith and Bermingham 2005).

The potential distribution of *P. splendida* under current conditions ranged from the Grijalva-Usumacinta basins to the East-West basins of the Yucatan peninsula, the latter basins not colonized by *A. tropicus*. The Yucatan peninsula has warm sub-humid climates (Kottek et al. 2006) similar to the climatic conditions found in the coastal plain of Chiapas where there are suitable conditions for *A. tropicus*. However, the peninsula is influenced by carbonate compounds that generate freshwater ecosystems with chemical properties and aquatic vegetation different from those existing in the coastal plain of the southern Gulf of Mexico (Tapia-González et al. 2008), which could indicate a greater dispersal and colonization capacity of *P. splendida*.

The projections revealed an increase in suitable areas for *A. tropicus* and *P. splendida* at the foothills of the Central American mountain range and at higher altitudes of the Yucatan Peninsula, respectively, due to an increase in warm conditions (Figs. 2 and 3; appendix 1). Increases in environmental suitability have also been predicted for other tropical taxonomic groups such as mosquitoes (Campbell et al. 2015) and palms (Lopes Vaz and Nabout 2016). Previous studies in freshwater fish from temperate environments (e.g., salmonids) showed displacements towards medium and upper basins generated by warming and salinization of lower basins (Comte et al. 2013), which is consistent with the findings in this study. Future conditions will reduce the suitable areas of temperate fish due to warming and aridity associated with climate change (Chu et al. 2005; Bond et al. 2011; Yu et al. 2012). Gains from suitable tropical freshwater fish areas in middle and upper basins could lead to their expansion in geographic range and, consequently, to a reduction in the geographic range of fish inhabiting upper basins of the Central American mountain range, which may be more vulnerable.

Reductions in suitable areas for *P. splendida* in the Usumacinta river basin were directly related to decreases in precipitation (Soares & García, 2017; appendix 1). The populations that inhabit these areas could not tolerate warmer and drier climatic conditions that will undoubtedly lead to changes in their local distributions and/or extinctions. Therefore, it is essential to identify, from field studies, whether these areas coincide with sites of biological processes critical to the maintenance of local populations (e.g., reproduction or recruitment).

Boyd et al. (2016) mentioned that species could cope with adverse environmental conditions through migration and acclimatization processes in a short evolutionary time. Both *A. tropicus* and *P. splendida* can migrate along or between basins as long as there are no geographical or anthropogenic barriers that prevent the movement of individuals, such as the four dams of the reservoirs in the Grijalva river basin. Besides, overexploitation of freshwater ecosystems (Gómez-González et al. 2015), as well as overexploitation of both species at a local scale (Arias-Rodríguez et al. 2009; Méndez et al. 2011) and predators could reduce populations and prevent such movements.

As for acclimatization, the species *A. tropicus* is known to be a living fossil, conserving its morphological traits relatively stable since the Cretaceous, being the species with the most plesiomorphic characters of the genus *Atractosteus* (Wiley 1976). Therefore, they could be species with very low mutation and gene fixation rates before environmental changes in short evolutionary times although this must be evaluated. On the other hand, the species of the family Cichlidae, as is the case of *P. splendida*, are characterized by high mutation rates in short evolutionary times. Perhaps the most emblematic case is the rapid diversification by various factors of Lake Victoria cichlids at short space-time scales (Goldschmidt and Witte 1992). However, the time between the calibration data (1970-2000) for the 2050 and 2070 horizons is not very distant for genes to be fixed in populations, where genetic plasticity would have a more preponderant role if temperature and precipitation changes occur gradually (Mascaró et al. 2019).

Areas of high uncertainty risk for models of both species indicated warmer and arid conditions under future conditions (Giorgi, 2006; Appendix 1) outside the range of values known during calibration. In the first instance, it should not be concluded about the projected changes in these areas, given the strict extrapolations made (Owens et al. 2013). However, there must be caution in the environmental conditions of these areas because freshwater fish could experience sharp changes not only in their distribution patterns but also in biological processes.

On the other hand, although we did not consider salt intrusion in these models, it deserves special mention due to its potential to modify the chemical properties of freshwater ecosystems (Ketabchi et al. 2016) and, therefore, to modify the distribution of purely freshwater species. Coastal areas, peninsulas, and especially areas below mean sea level identified as highly vulnerable to this phenomenon (Reguero et al. 2015). The areas where environmental suitability shown in this study would be lost could be larger, especially near coastal areas due to the interaction of climatic variables with increased salinity. However, both species are secondary freshwater (Smith and Bermingham 2005), suggesting some tolerance to salinity. Figure 8 presents a conceptual summary of the possible previously developed responses of freshwater fish to environmental and geographic changes due to the interaction of climate change with other variables, from which changes could be generated at different levels of organization and space-time scales.

The ENM showed good results in describing the potential distribution of both species based on the metrics obtained. The likely increase in suitable areas for both species due to the increase in warm watershed conditions at medium and high altitudes, as well as the reduction in others due to greater aridity showed that the impact of climate change could expand the geographical range of tropical freshwater species towards higher altitudes, as well as reduce habitats within their geographical range. This adjustment of environmental suitability and, possibly, distribution ranges also was observed and predicted for other tropical species. It is

crucial to consider synergy with other variables not included in these models, as they could impact freshwater fish distribution areas. Although the ENM exhibited potential changes in distribution areas, given specific characteristics of the data, procedure, and algorithm used, these must be complemented with demographic, physiological and genetic studies at the population level of both species to integrate a more precise view of the probable impacts of climate change on freshwater fish.

ACKNOWLEDGMENTS

Special thanks to Doctors Josué Rodolfo García Pérez (Universidad de San Carlos), Maurizio Protti Quesada (Universidad de Costa Rica), Arturo Brenes Angulo (Universidad de Costa Rica), Francisco Javier Barrientos Villalobos (ECOSUR) and Rocío Rodiles-Hernández (ECOSUR) for providing georeferenced data on both species, as well as to the reviewers for improving the quality of the article through their timely comments. First author received a scholarship from CONACYT for postgraduate studies (885466). He also received the PATM scholarship from ECOSUR from which part of the computer equipment necessary for the modelling process was acquired.

REFERENCES

- Abell, R., Thieme, M., Revenga, C., Bryer, M., Kottlat, M., Bogutskaya, N., ... Petry, P. (2008). Freshwater ecoregions of the world: A new map of biogeographic units for freshwater biodiversity conservation. *BioScience*, 58(5), 403–414.
- Aiello-lammens, M. E., Boria, R. A., Radosavljevic, A., Vilela, B., & Anderson, R. P. (2015). spThin: A R package for spatial thinning of species occurrence records for use in ecological niche models. *Ecography*, 38, 541–545.
- Anderson, R. P., Lew, D., & Peterson, A. T. (2003). Evaluating predictive models of species' distributions: Criteria for selecting optimal models. *Ecological*

- Modelling*, 162(3), 211–232.
- Arias-Rodríguez, L., Páramo-Delgadillo, S., Contreras-Sánchez, W. M., & Álvarez-González, C. A. (2009). Cariotipo del pejelagarto tropical *Atractosteus tropicus* (Lepisosteiformes: Lepisosteidae) y variación cromosómica en sus larvas y adultos. *Revista de Biología Tropical*, 57(3), 529–539.
- Barrientos-Villalobos, J., & Espinosa-De Los Monteros, A. (2008). Genetic variation and recent population history of the tropical gar *Atractosteus tropicus* Gill (Pisces: Lepisosteidae). *Journal of Fish Biology*, 73(8), 1919–1936.
- Barve, N., Barve, V., Jiménez-Valverde, A., Lira-Noriega, A., Maher, S. P., Peterson, A. T., ... Villalobos, F. (2011). The crucial role of the accessible area in ecological niche modeling and species distribution modeling. *Ecological Modelling*, 222(11), 1810–1819.
- Bond, N., Thomson, J., Reich, P., & Stein, J. (2011). Using species distribution models to infer potential climate change-induced range shifts of freshwater fish in south-eastern Australia. *Marine and Freshwater Research*, 62(9), 1043–1061.
- Boyd, P., Cornwall, C., Davison, A., Doney, S., Fourquez, M., Hurd, C., ... Mcminn, A. (2016). Biological responses to environmental heterogeneity under future ocean conditions. *Global Change Biology*, 22, 2633–2650.
- Campbell, L. P., Luther, C., Moo-Llanes, D., Ramsey, J. M., Danis-Lozano, R., & Peterson, A. T. (2015). Climate change influences on global distributions of dengue and chikungunya virus vectors. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 370(1665), 1–9.
- Castillo-Torres, P. A., Martínez-Meyer, E., Córdova-Tapia, F., & Zambrano, L. (2017). Potential distribution of native freshwater fishes in Tabasco, Mexico. *Revista Mexicana de Biodiversidad*, 88(2), 415–424.
- Chu, C., Mandrak, N. E., & Minns, C. K. (2005). Potential impacts of climate change on the distributions of several common and rare freshwater fishes in Canada. *Diversity and Distributions*, 11(4), 299–310.
- Cobos, M. E., Jiménez, L., Nuñez-Penichet, C., Romero-Alvarez, D., & Simões, M. (2018). Sample data and training modules for cleaning biodiversity

- information. *Biodiversity Informatics*, 14, 49–50.
- Cobos, M. E., Osorio-Olvera, L., & Peterson, A. T. (2019). Assessment and representation of variability in ecological niche model predictions. <https://doi.org/10.1101/603100>
- Cobos, M. E., Peterson, A. T., Barve, N., & Osorio-Olvera, L. (2019). kuenm: An R package for detailed development of ecological niche models using Maxent. *PeerJ*, 7. <https://doi.org/10.7717/peerj.6281>
- Cobos, M., Peterson, A. T., Osorio-Olvera, L., & Jiménez-García, D. (2019). An exhaustive analysis of heuristic methods for variable selection in ecological niche modeling and species distribution modeling. *Ecological Informatics*, 53. <https://doi.org/10.1016/j.ecoinf.2019.100983>
- Comte, L., Buisson, L., Daufresne, M., & Grenouillet, G. (2013). Climate-induced changes in the distribution of freshwater fish: Observed and predicted trends. *Freshwater Biology*, 58(4), 625–639.
- Domínguez-Domínguez, O., Martínez-Meyer, E., Zambrano, L., & Pérez-Ponce De León, G. (2006). Using ecological-niche modeling as a conservation tool for freshwater species: Live-bearing fishes in central Mexico. *Conservation Biology*, 20(6), 1730–1739.
- Escobar, L. E., Lira-Noriega, A., Medina-Vogel, G., & Peterson, A. T. (2014). Potential for spread of the white-nose fungus (*Pseudogymnoascus destructans*) in the Americas: Use of Maxent and NicheA to assure strict model transference. *Geospatial Health*, 9(1), 221–229.
- Frederico, R. G., Salvador, G. N., Andrade, A., Rosa, G. R., & Torquato, G. V. (2019). Freshwater ecosystem vulnerability: Is native climatic niche good enough to predict invasion events? *Aquatic Conservation: Marine and Freshwater Ecosystems*, 1–7.
- Giorgi, F. (2006). Climate change hot-spots. *Geophysical Research Letters*, 33(8), 1–4.
- Goldschmidt, T., & Witte, F. (1992). Explosive speciation and adaptive radiation of haplochromine cichlids from Lake Victoria: An illustration of the scientific value of a lost species flock. *Internationale Vereinigung Für Theoretische Und*

- Angewandte Limnologie: Mitteilungen*, 23(1), 101–107.
- Gómez-González, A. E., Velázquez-Velázquez, E., Anzueto Calvo, M. D. J., & Maza-Cruz, M. F. (2015). Fishes of the Grijalva river basin of Mexico and Guatemala. *Check List*, 11(5), 1–11.
- Graham, C. T., & Harrod, C. (2009). Implications of climate change for the fishes of the British Isles. *Journal of Fish Biology*, 74(6), 1143–1205.
- Gumbricht, T., Roman-Cuesta, R. M., Verchot, L., Herold, M., Wittmann, F., Householder, E., ... Murdiyarsa, D. (2017). An expert system model for mapping tropical wetlands and peatlands reveals South America as the largest contributor. *Global Change Biology*, 23, 3581–3599.
- Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global and areas. *International Journal of Climatology*, 25, 1965–1978.
- Hulsey, C., & López-Fernández, H. (2001). Nuclear Central America. In J. Albert & R. Reis (Eds.), *Historical Biogeography of Neotropical Freshwater Fishes* (pp. 279–292). California, U.S.A.: University of California Press.
- IPCC. (2014). Cambio climático 2014: Informe de síntesis. Contribución de los grupos de trabajo I, II y III al quinto informe de evaluación del Grupo Intergubernamental de Expertos sobre el Cambio Climático. [Pachauri, R. K. & L. A. Meyer (Eds.)]. Ginebra, Suiza: Organización Mundial de Meteorología, Programa de las Naciones Unidas para el Medio Ambiente.
- IPCC. (2018). Global warming of 1.5 °C. An IPCC special report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change. [Masson-Delmotte, V., P. Zhai, H.-O. Pörtner, D. Roberts, J. Skea, P.R. Shukla, A. Pirani, W. Moufouma-Okia, C. Péan, R. Pidcock, S. Connors, J.B.R. Matthews, Y. Chen, X. Zhou, M.I. Gomis, E. Lonnoy, T. Maycock, M. Tignor, & Waterfield, T. (Eds.)].
- Ixquiac-Cabrera, M., Guzmán, S., Méndez, A., & Morales, J. Crecimiento del pez blanco (*Petenia splendida*) en tres hábitats: cultivo, lago (Petén Itzá) y en río San Pedro por medio de marcaje y recaptura (2010). Guatemala.

- Ketabchi, H., Mahmoodzadeh, D., Ataie-Ashtiani, B., & Simmons, C. T. (2016). Sea-level rise impacts on seawater intrusion in coastal aquifers: Review and integration. *Journal of Hydrology*, *535*(1), 235–255.
- Knouft, J. H., & Anthony, M. M. (2016). Climate and local abundance in freshwater fishes. *Royal Society Open Science*, *3*, 160093.
<https://doi.org/10.1098/rsos.160093>
- Kottek, M., Grieser, J., Beck, C., Rudolf, B., & Rubel, F. (2006). World Map of the Köppen-Geiger climate classification updated. *Meteorologische Zeitschrift*, *15*(3), 259–263.
- Lejeusne, C., Chevaldonné, P., Pergent-Martini, C., Boudouresque, C. F., & Pérez, T. (2010). Climate change effects on a miniature ocean: The highly diverse, highly impacted Mediterranean Sea. *Trends in Ecology and Evolution*, *25*(4), 250–260.
- Lopes Vaz, Ú., & Nabout, J. C. (2016). Using ecological niche models to predict the impact of global climate change on the geographical distribution and productivity of *Euterpe oleracea* Mart. (Arecaceae) in the Amazon. *Acta Botanica Brasilica*, *30*(2), 290–295.
- Maguire, B. (1973). Niche response structure and the analytical potentials of its relationship to the habitat. *The American Naturalist*, *107*(954), 213–246.
- Manjarrés-Hernández, A. M., Guisande, C., García-Rosello, E., Pelayo-Villamil, P., González-Dacosta, J., Heine, J., ... Lobo, J. M. (2018). A procedure to assess the spatial variability in the importance of abiotic factors affecting distributions: the case of world freshwater fishes. *Current Zoology*, *64*(5), 549–557.
- Mascaró, M., Horta, J. L., Diaz, F., Paschke, K., Rosas, C., & Simões, N. (2019). Effect of a gradually increasing temperature on the behavioural and physiological response of juvenile *Hippocampus erectus*: Thermal preference, tolerance, energy balance and growth. *Journal of Thermal Biology*, *85*, 102406. <https://doi.org/10.1016/j.jtherbio.2019.102406>
- Mastretta-Yanes, A., Moreno-Letelier, A., Piñero, D., Jorgensen, T. H., & Emerson, B. C. (2015). Biodiversity in the Mexican highlands and the interaction of geology, geography and climate within the Trans-Mexican Volcanic Belt.

- Journal of Biogeography*, 42(9), 1586–1600.
- Matamoros, W. A., McMahan, C. D., Chakrabarty, P., Albert, J. S., & Schaefer, J. F. (2015). Derivation of the freshwater fish fauna of Central America revisited: Myers's hypothesis in the twenty-first century. *Cladistics*, 31(2), 177–188.
- MEA. (2005). *Ecosystems and human well-being: Wetlands and water*. Washington D.C.: World Resources Institute.
- Méndez, A., García, M. E., & Lozano, L. (2011). Sistemática del pez *Petenia splendida* (Perciformes: Cichlidae) en el lago Petén Itzá, Guatemala. *Revista de Biología Tropical*, 59(3), 1205–1216.
- Mora-Jamett, M., Cabrera-Peña, J., & Galeano, G. (1997). Reproducción y alimentación del gaspar *Atractosteus tropicus* (Pisces : Lepisosteidae) en el Refugio Nacional de Vida Silvestre Caño Negro, Costa Rica. *Revista de Biología Tropical*, 45(2), 861–866.
- Moss, R., Babiker, M., Brinkman, S., Calvo, E., Carter, T., Edmonds, J., ... Zurek, M. (2008). *Towards new scenarios for analysis of emissions, climate change, impacts and response strategies*. Geneva.
- Nelson, S. J., Grande, T. C., & Wilson, M. V. H. (2016). *Fishes of the World* (5th ed.). U.S.A.: John Wiley & Sons.
- Owens, H. L., Campbell, L. P., Dornak, L. L., Saupe, E. E., Barve, N., Soberón, J., ... Peterson, A. T. (2013). Constraints on interpretation of ecological niche models by limited environmental ranges on calibration areas. *Ecological Modelling*, 263, 10–18.
- Peterson, A. T., Cobos, M. E., & Jiménez-García, D. (2018). Major challenges for correlational ecological niche model projections to future climate conditions. *Annals of the New York Academy of Sciences*, 1429(1), 66–77.
- Peterson, A. T., Papeş, M., & Soberón, J. (2008). Rethinking receiver operating characteristic analysis applications in ecological niche modeling. *Ecological Modelling*, 213(1), 63–72.
- Peterson, A. T., Soberón, J., Pearson, R. G., Anderson, R., Martínez, E., Nakamura, M., & Araújo, M. (2011). *Ecological niches and geographic distributions*. New Jersey, U.S.A.: Princeton University Press.

- R Core Team. (2019). R: A language and environment for computing. R Foundation for Statistical Computing. Vienna, Austria. <https://www.r-project.org/>
- Radosavljevic, A., & Anderson, R. P. (2014). Making better Maxent models of species distributions: Complexity, overfitting and evaluation. *Journal of Biogeography*, *41*(4), 629–643.
- Reguero, B. G., Losada, I. J., Díaz-Simal, P., Méndez, F. J., & Beck, M. (2015). Effects of climate change on exposure to coastal flooding in Latin America and the Caribbean. *PLoS ONE*, *10*(7), 1–19.
- Rolls, R. J., Heino, J., Ryder, D. S., Chessman, B. C., Growns, I. O., Thompson, R. M., & Gido, K. B. (2018). Scaling biodiversity responses to hydrological regimes. *Biological Reviews*, *93*(2), 971–995.
- Rush Miller, R. R. (2009). *Peces dulceacuícolas de México* (1st ed.). México, D. F.: Comisión Nacional para el Conocimiento y Uso de la Biodiversidad; Sociedad Ictiológica Mexicana A. C.; El colegio de la Frontera Sur; Consejo de los Peces del Desierto México-Estados Unidos;
- Sanderson, B. M., Knutti, R., & Caldwell, P. (2015). A representative democracy to reduce interdependency in a multimodel ensemble. *Journal of Climate*, *28*, 5171–5194.
- Schmitter-Soto, J. J. (1996). *Catalogo de los peces continentales de Quintana Roo*. Quintana Roo: El Colegio de la Frontera Sur.
- Simões, M. V. P., & Peterson, A. T. (2018). Utility and limitations of climate-matching approaches in detecting different types of spatial errors in biodiversity data. *Insect Conservation and Diversity*, *11*(5), 407–414.
- Smith, S. A., & Bermingham, E. (2005). The biogeography of lower Mesoamerican freshwater fishes. *Journal of Biogeography*, *32*(10), 1835–1854.
- Soares, D., & García, A. (2017). *La cuenca del Río Usumacinta desde la perspectiva del cambio climático*. Mexico: Instituto Mexicano de Tecnología del Agua.
- Tapia-González, F. U., Herrera-Silveira, J. A., & Aguirre-Macedo, M. L. (2008). Water quality variability and eutrophic trends in karstic tropical coastal lagoons

of the Yucatán Peninsula. *Estuarine, Coastal and Shelf Science*, 76(2), 418–430.

Warren, D., & Seifert, S. (2011). Ecological niche modeling in Maxent: The importance of model complexity and the performance of model selection criteria. *Ecological Applications*, 21(2), 335–342.

Wiley, E. O. (1976). *The phylogeny and biogeography of fossil and recent gars (Actinopterygii: Lepisosteidae)*. Lawrence, Kansas: University of Kansas.

Yu, D., Chen, M., Zhou, Z., Eric, R., Tang, Q., & Liu, H. (2012). Global climate change will severely decrease potential distribution of the East Asian coldwater fish *Rhynchocypris oxycephalus* (Actinopterygii, Cyprinidae). *Hydrobiologia*, 700(1), 23–32.

TABLES

Table 1. Configurations of parsimonious ecological niche models of *Atractosteus tropicus* and *Petenia splendida* that met the evaluation criteria of statistical significance and omission rate with independent data.

Specie	FC	RM	ROC Parcial	OR	AICc	Par
<i>A. tropicus</i>	lqp	1	1.269963	0.0285	2541.86	8
<i>A. tropicus</i>	lqp	1.6	1.273376	0.0285	2543.56	8
<i>P. splendida</i>	lq	1.4	1.188344	0.0377	4335.57	7

Feature classes (FC), regularization multiplier (RM), omission rate < 5% (OR), Akaike Information Criterion (AICc) and numbers of parameters (Par).

FIGURES

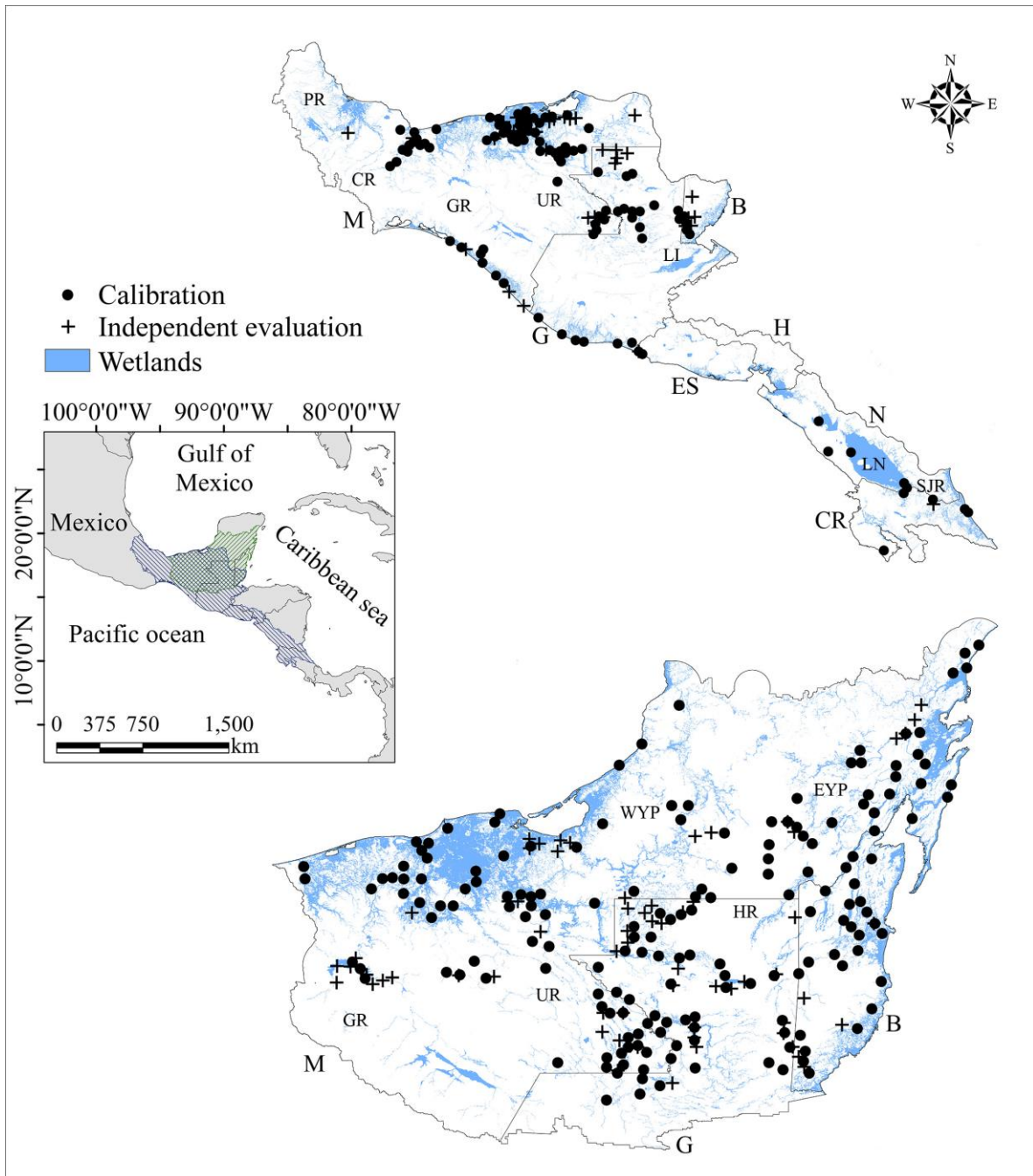


Figure 1. Calibration and projection area for *Atractosteus tropicus* (top) and *Petenia splendida* (bottom). The presences for calibration (points) and final evaluation (crosses) of the models are shown, as well as the wetlands (blue)

existing in both areas. Country names were abbreviated and placed outside the map: M = Mexico, G = Guatemala, B = Belize, ES = El Salvador, H = Honduras, N = Nicaragua and CR = Costa Rica. The names of the basins were abbreviated and placed within the map: PR = Papaloapan River, CR = Coatzacoalcos River, GR = Grijalva River, UR = Usumacinta River, WYP = Western Yucatan Peninsula, EYP = East Yucatan Peninsula, HR = Hondo River, LI = Lake Izabal, LN = Lake Nicaragua and SJR = San Juan River. The blue and green polygons represent calibration and projection area for *A. tropicus* and *P. splendida*, respectively.

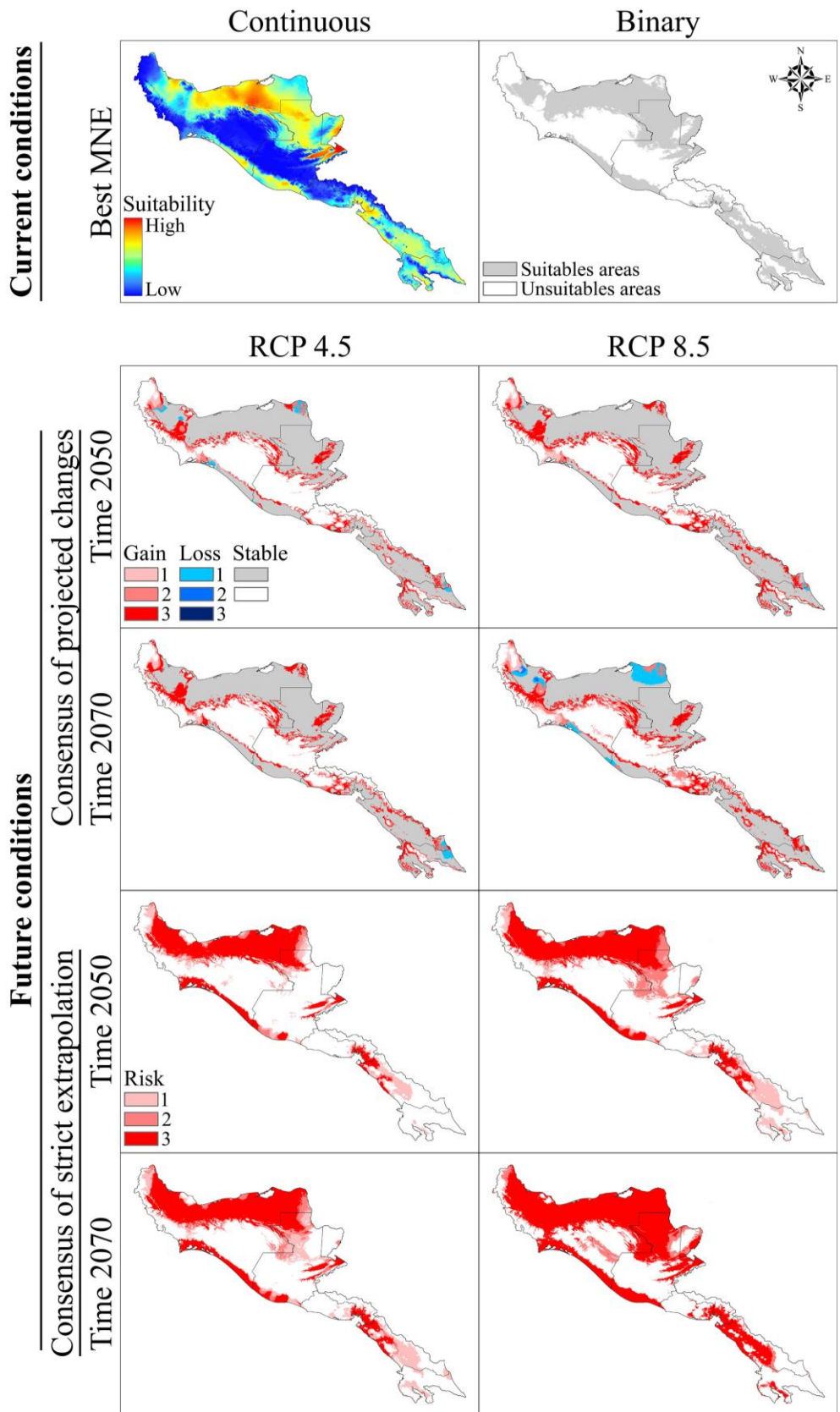


Figure 2. Prediction of suitable regions under current and future conditions with associated uncertainty for *Atractosteus tropicus*. Left panel shows the labels in hierarchical order: 1) current or future conditions, 2) consensus of projected changes or strict extrapolation (MOP), 3) best niche model or horizons (rows), and; above model type or RCPs (columns). Consensus symbology of projected changes: 1, 2 and 3 = gain (red) or loss (blue) of suitable areas in 1, 2 and 3 GCMs, respectively. Grey and white pixels represent stability of suitable and unsuitable areas, respectively, under future conditions. Strict extrapolation consensus symbology: 1, 2 and 3 = strict extrapolation in 1, 2 and 3 GCMs.

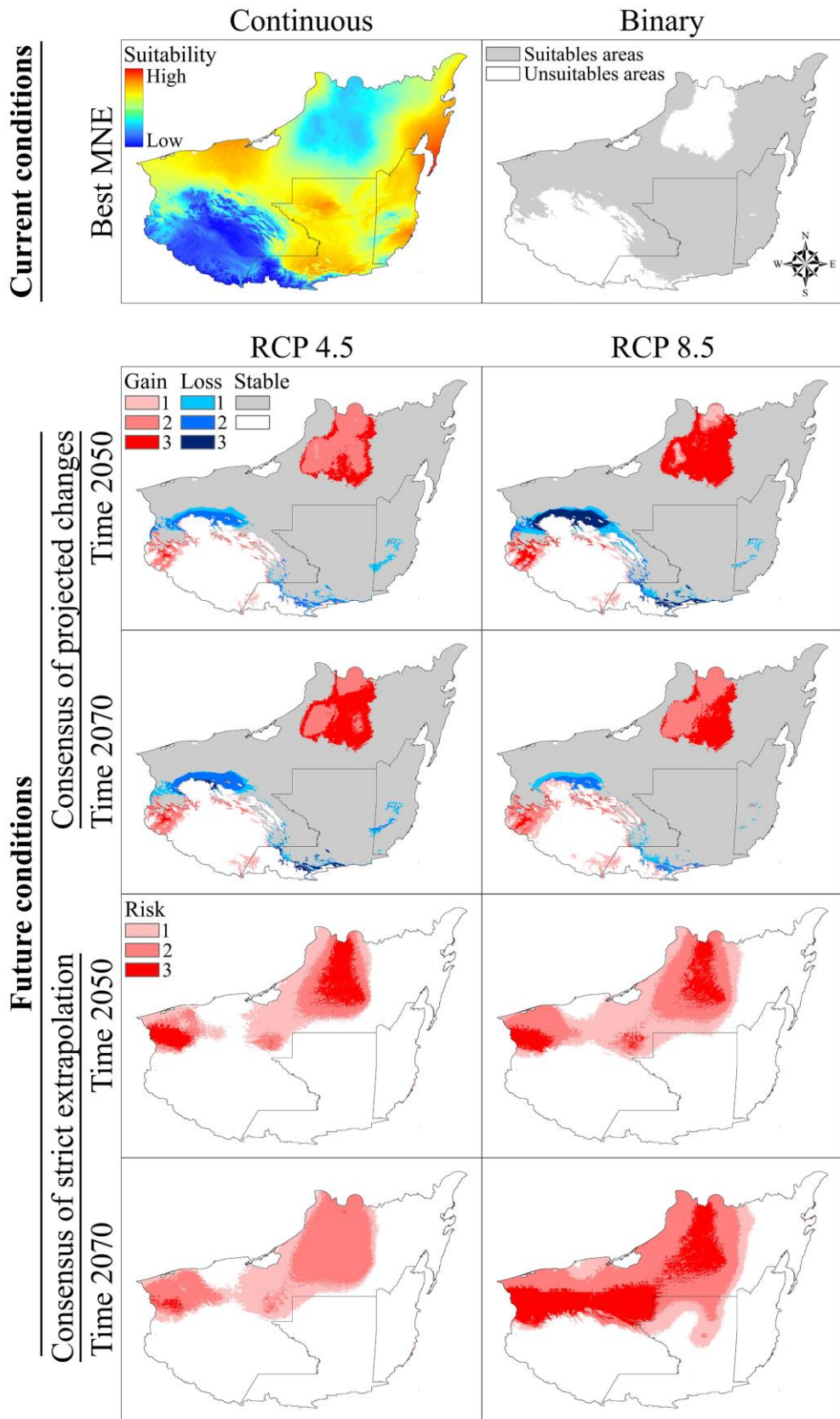


Figure 3. Prediction of suitable regions under current and future conditions with associated uncertainty, for *Petenia splendida*. Figure in left shows the labels in hierarchical order: 1) current or future conditions, 2) consensus of projected changes or strict extrapolation (MOP), 3) best niche model or horizons (rows), and; above model type or RCPs (columns). Consensus symbology of projected changes: 1, 2 and 3 = gain (red) or loss (blue) of suitable areas in 1, 2 and 3 GCMs, respectively. Grey and white pixels represent stability of suitable and unsuitable areas, respectively, under future conditions. Strict extrapolation consensus symbology: 1, 2 and 3 = strict extrapolation in 1, 2 and 3 GCMs.

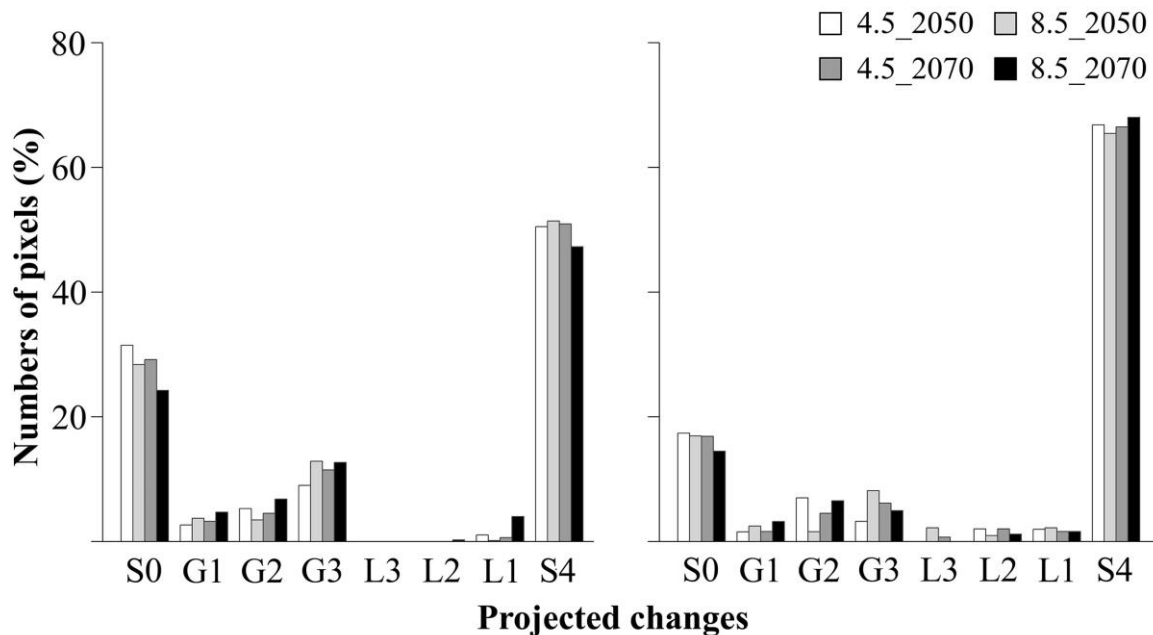


Figure 4. Percentage of projected changes for *Atractosteus tropicus* (left) and *Petenia splendida* (right). Meaning of X-axis: S, G, and L = stability, gain, and loss of suitable areas, respectively. 0 and 4 = unsuitable and suitable areas under current and future conditions, respectively. 1, 2 and 3 = gain or loss of suitable areas in 1, 2 and 3 GCMs, respectively.

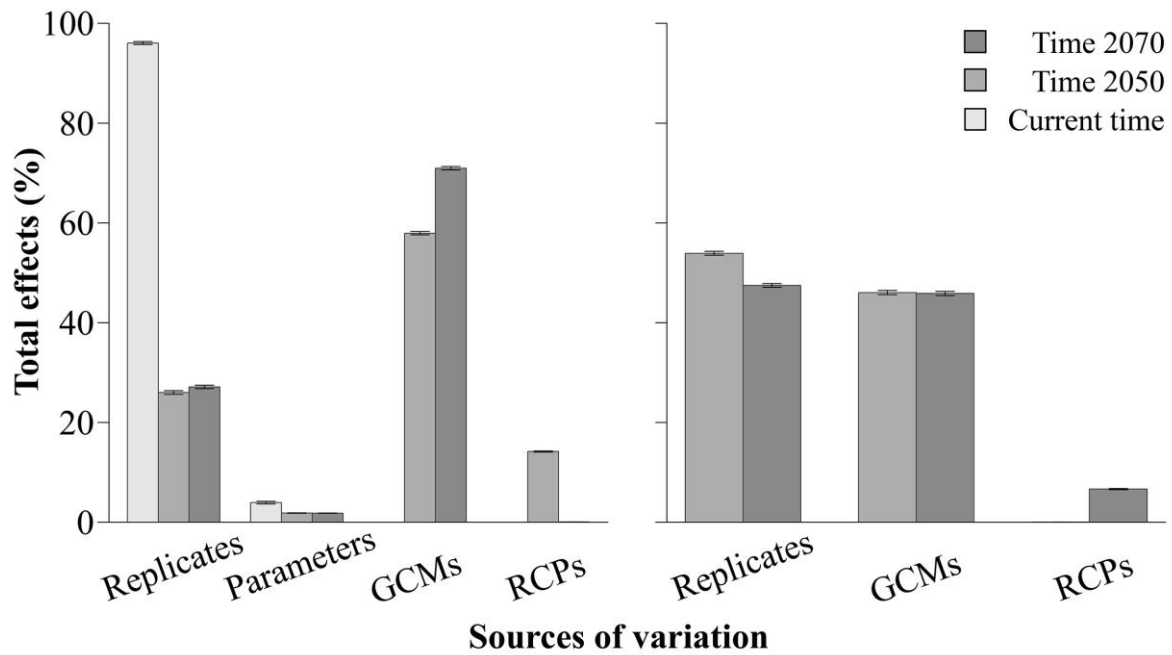


Figure 5. Hierarchical partition of the variance between the different sources of variation for *Atractosteus tropicus* (left) and *Petenia splendida* (right). Note that in the niche models of the *P. splendida*, only one model was the best to explain since it was not necessary to partition the variance under current conditions.

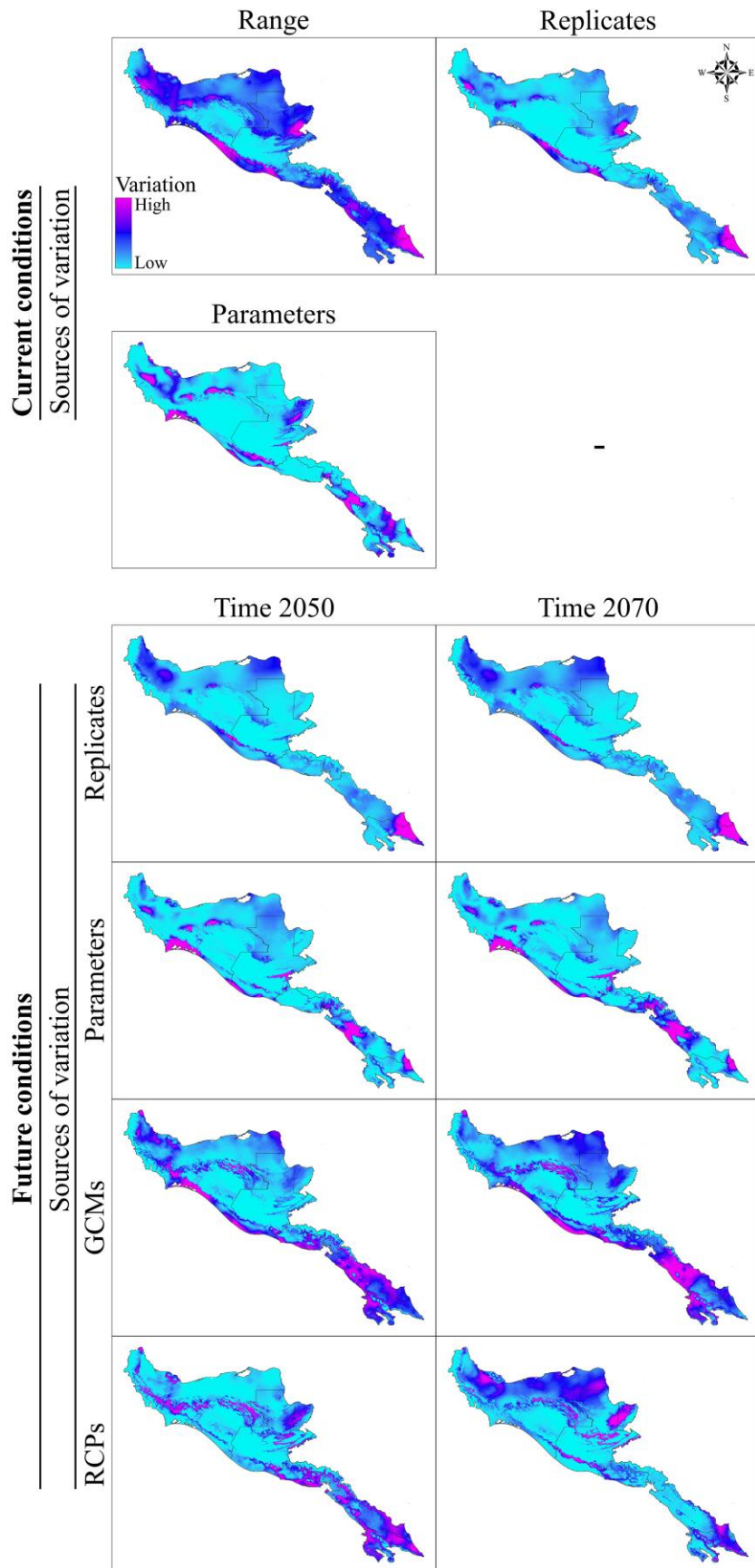


Figure 6. Sources of variation represented in geography under present (top) and future (bottom) conditions for *Atractosteus tropicus*. The range does not represent a source of variation in itself but rather represent a measure of data dispersion in the current time.

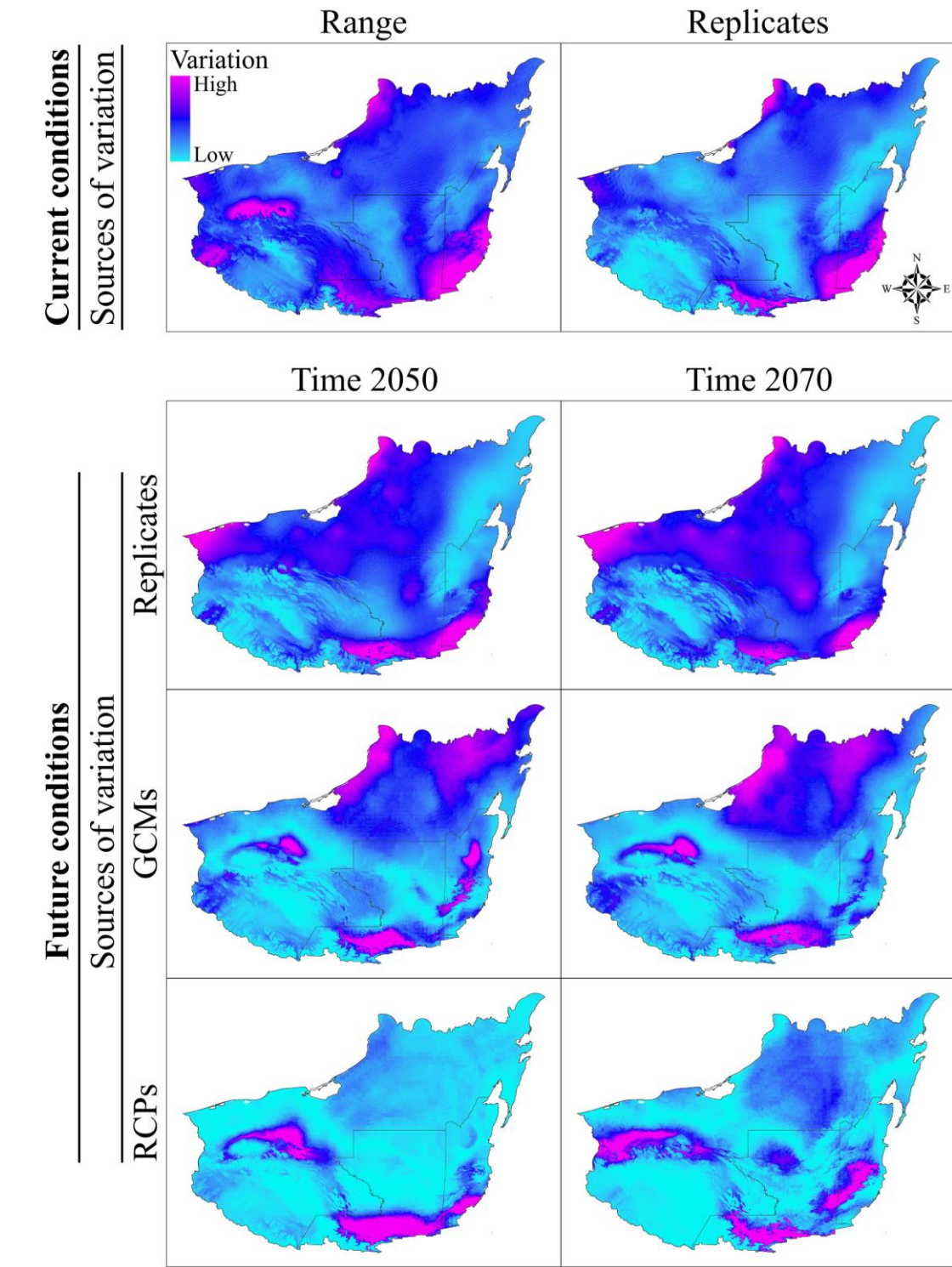


Figure 7. Sources of variation represented in geography under present (top) and future (bottom) conditions for *Petenia splendida*. The range does not represent a

source of variation in itself but rather represents a measure of data dispersion in the current time.

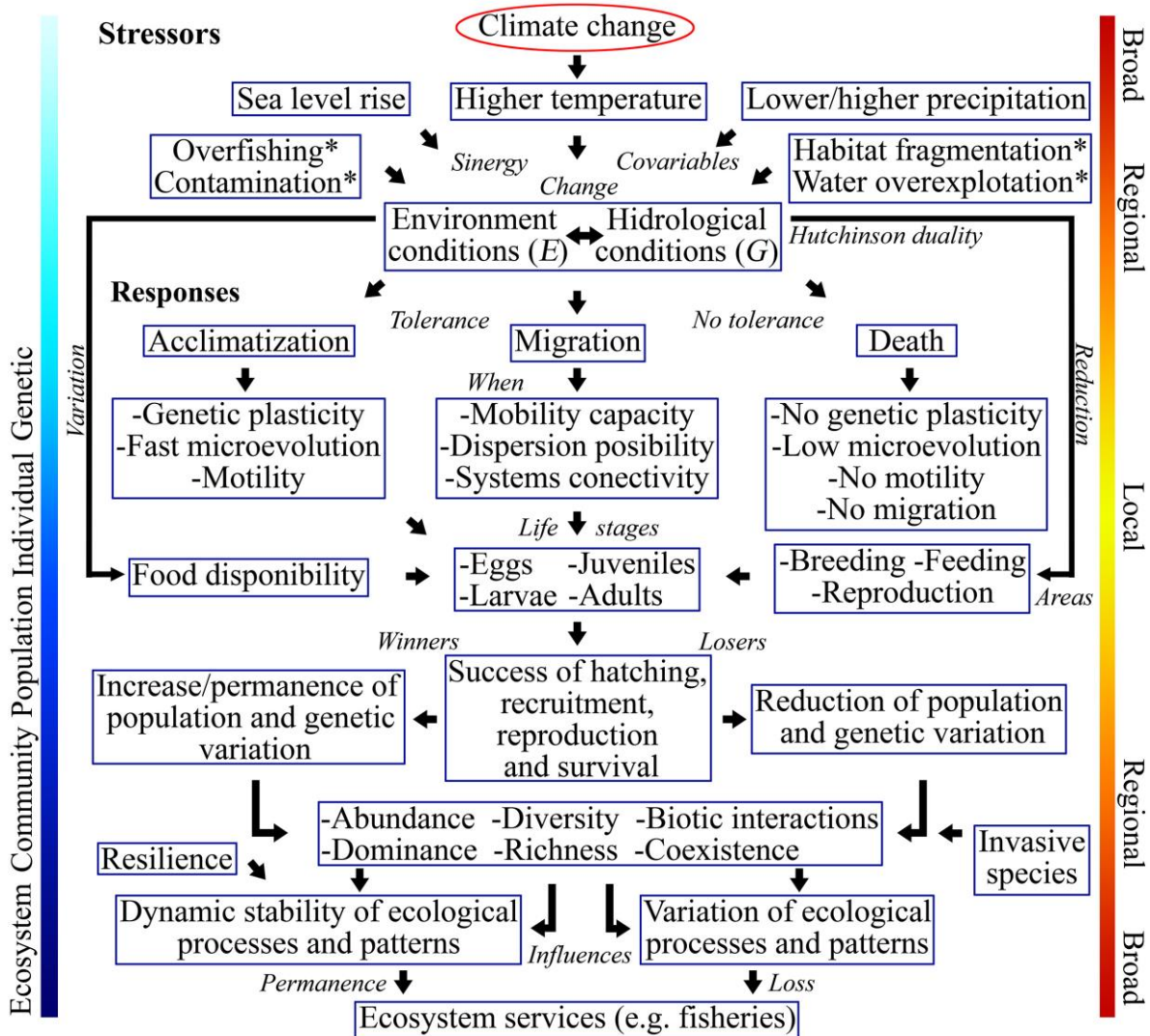


Figure 8. Conceptual map of possible responses of freshwater species to the impacts of climate change and other variables. Left and Right represent changes at different levels of organisation and space-time scales. Two-way arrows represent influence on both sides.

Capítulo 3. Conclusiones y recomendaciones

Los peces dulceacuícolas secundarios *A. tropicus* y *P. splendida* mostraron una fuerte afinidad hacia ambientes cálidos húmedos-subhúmedos en el tiempo actual. El aumento de condiciones cálidas de las cuencas medias y altas en el futuro debido al cambio climático beneficiaría a ambas especies al existir condiciones ambientales más cálidas en áreas donde antes no había. En consecuencia, las áreas de distribución de estas especies podrían expandirse a mayores altitudes siempre y cuando exista hábitats disponibles (e.g. humedales) no fragmentados que permitan el desplazamiento de individuos. En las áreas donde se perdería idoneidad ambiental, los peces dulceacuícolas podrían aclimatarse a las nuevas condiciones ambientales o migrar hacia otras áreas donde permanezcan condiciones idóneas, mientras existan hábitats conectados en cuencas medias y altas. Si esto no ocurre, podrían suceder extinciones de poblaciones locales. Por otra parte, las especies dulceacuícolas que habitan cuencas altas podrían reducir su rango geográfico y, por ende, ser más vulnerables a extinciones locales ante el aumento de la temperatura en la región. Así, los efectos potenciales del cambio climático sobre las áreas distribución de los peces dulceacuícolas tropicales estarían marcados por mosaicos de ganancias, pérdidas y estabilidad de condiciones idóneas a diferentes escalas espaciotemporales.

Es fundamental seguir realizando evaluaciones de los efectos potenciales del cambio climático sobre otras especies dulceacuícolas tropicales con importancia económica y/o claves en la cadena trófica de esta región, así como extender las evaluaciones hacia especies con distribución restringida a cuencas altas. Esto con la finalidad de identificar potenciales patrones de distribución de peces dulceacuícolas bajo condiciones climáticas futuras y cambiantes. Asimismo, se requiere evaluar la tolerancia fisiológica de diferentes estadios de las especies hacia la temperatura a través de la variabilidad genética y plasticidad fenotípica. En el mismo sentido, se requieren evaluaciones sobre la tolerancia fisiológica de ambas especies a la salinidad ya que las áreas de distribución cercanas a las

zonas costeras son altamente vulnerables a la intrusión salina provocada por el aumento del nivel medio del mar.

Los resultados obtenidos en el presente estudio pueden ser útiles para generar estrategias de mitigación, conservación y/o adaptación ante el cambio climático a diferentes escalas espaciales. Los efectos del cambio climático sobre la distribución potencial de ambas especies podrían ser mitigados a través de la evaluación de la tolerancia fisiológica respecto al aumento de la temperatura, disminución de la precipitación y su covariación mediante estudios de variabilidad genética y plasticidad fenotípica, principalmente, en aquellas poblaciones de peces establecidas en áreas identificadas con pérdida de idoneidad ambiental en condiciones futuras. Si las poblaciones no toleran estas nuevas condiciones climáticas, se podrían desarrollar proyectos de acuicultura con los genes provenientes de las mismas poblaciones, de manera que se conserven la variabilidad genética mientras se disminuye la vulnerabilidad alimenticia y económica de las comunidades en México y Guatemala que las capturan como especie objetivo. Aunado a lo anterior, se requiere avanzar en estudios que identifiquen si estas áreas de pérdida de idoneidad ambiental coinciden con sitios de procesos biológicos y ecológicos críticos para las especies, por ejemplo, de reproducción o el reclutamiento que pudieran aumentar la vulnerabilidad de estas especies ante el cambio climático.

Literatura citada

- Araújo M, Pearson R, Thuillers W, Erhard M. 2005. Validation of species-climate impact models under climate change. *Glob Chang Biol* 11:1–10.
- Arias-Rodríguez L, Páramo-Delgadillo S, Contreras-Sánchez WM, Álvarez-González CA. 2009. Cariotipo del pejelagarto tropical *Atractosteus tropicus* (Lepisosteiformes: Lepisosteidae) y variación cromosómica en sus larvas y adultos. *Rev Biol Trop* 57:529–539.
- Barve N, Barve V, Jiménez-Valverde A, Lira-Noriega A, Maher SP, Peterson AT, Soberón J, Villalobos F. 2011. The crucial role of the accessible area in ecological niche modeling and species distribution modeling. *Ecol Modell* 222:1810–1819.
- Carabias J, Zorrilla M, Escobedo AH, Gallardo A, Rodríguez Y, Fernández, A. I. Charruau P, Martínez M, Rodríguez A. 2015. Diagnóstico integral de la cuenca baja del río Usumacinta en Tabasco. Informe técnico. Proyecto TAB-2012-C28-194316. Retos para la sustentabilidad en la cuenca baja del río Usumacinta en Tabasco: ecosistemas, cambio climático y respuesta social. Tabasco.
- Carvalho AF, Del Lama MA. 2015. Predicting priority areas for conservation from historical climate modelling: stingless bees from Atlantic Forest hotspot as a case study. *J Insect Conserv* 19:581–587.
- Castillo-Torres PA, Martínez-Meyer E, Córdova-Tapia F, Zambrano L. 2017. Potential distribution of native freshwater fishes in Tabasco, Mexico. *Rev Mex Biodivers* 88:415–424.
- Chen P, Wiley EO, Mcnyset KM. 2007. Ecological niche modeling as a predictive tool: Silver and bighead carps in North America. *Biol Invasions* 9:43–51.
- Chu, CM, Mandrak Nicholas E. Minns, CK. Potential impacts of climate change on the distributions of several common and rare freshwater fishes in Canada. *Diversity Distrib* 11: 299-310.
- Comte L, Buisson L, Daufresne M, Grenouillet G. 2013. Climate-induced changes in the distribution of freshwater fish: Observed and predicted trends. *Freshw Biol* 58:625–639.

- Cooper-Bohannon R, Rebelo H, Jones G, Cotterill F, Monadiem A, Schoeman MC, Taylor P, Park K. 2016. Predicting bat distributions and diversity hotspots in southern Africa. *Hystrix Ital J Mammal* 27.
- Crutzen PJ. 2002. Geology of mankind. *Nature* 415:2002.
- Cuervo-Robayo A, Escobar LE, Osorio-Olivera L, Nori J, Varela S, Martínez-Meyer E, Velásquez-Tibatá J, Rodríguez-Soto C, Munguía M, Castañeda-Álvarez NP, et al. 2017. Introducción a los análisis espaciales con énfasis en modelos de nicho ecológico. *Biodivers Informatics* 12:45–57.
- Domínguez-Domínguez O, Martínez-Meyer E, Zambrano L, Pérez-Ponce De León G. 2006. Using ecological-niche modeling as a conservation tool for freshwater species: Live-bearing fishes in central Mexico. *Conserv Biol* 20:1730–1739.
- Elliott JA, Henrys P, Tanguy M, Cooper J, Maberly SC. 2015. Predicting the habitat expansion of the invasive roach *Rutilus rutilus* (Actinopterygii, Cyprinidae), in Great Britain. *Hydrobiologia* 751:127–134.
- Froese R, Pauly D. 2018. FishBase. World Wide Web electronic publication. [accessed 2018 Apr 20]. www.fishbase.org.
- Georgiev A, Nazarova L. 2015. Transformation of ichthyofauna in freshwater ecosystems of Karelia under conditions of climate change. *Russ J Ecol* 46:345–352.
- Giorgi F. 2006. Climate change hot-spots. *Geophys. Res Lett* 33:1–4.
- González-Zeas D, Erazo B, Lloret P, De Bièvre B, Steinschneider S, Dangles O. 2019. Linking global climate change to local water availability: Limitations and prospects for a tropical mountain watershed. *Sci Total Environ* 650:2577–2586.
- Graham CT, Harrod C. 2009. Implications of climate change for the fishes of the British Isles. *J. Fish Biol.* 74:1143–1205.
- IPCC. 2007. Cambio climático 2007: Informe de síntesis. Contribución de los grupos de trabajo I, II y III al cuarto informe de evaluación del grupo intergubernamental de expertos sobre el cambio climático. Pachauri RK, Reisinger A, Bernstein L, Bosch P, Canziani O, Chen Z, Christ R, Davidson O, Hare W, Huq S, et al., editors. Ginebra, Suiza: Organización Mundial de Meteorología, Programa de las Naciones Unidas para el Medio Ambiente.

- IPCC. 2013. *Climate Change 2013: The physical science basis. Working group I contribution to the fifth assessment report of the intergovernmental panel on climate change.* Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM, editors. Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press.
- IPCC. 2014. *Cambio climático 2014: Informe de síntesis. Contribución de los grupos de trabajo I, II y III al quinto informe de evaluación del Grupo Intergubernamental de Expertos sobre el Cambio Climático.* Pachauri RK, Meyer LA, editors. Ginebra, Suiza: Organización Mundial de Meteorología, Programa de las Naciones Unidas para el Medio Ambiente.
- Knouft JH, Anthony MM. 2016. Climate and local abundance in freshwater fishes. *R Soc Open Sci* 3:160093.
- Kozłowski G, Bondallaz L. 2013. Urban aquatic ecosystems: Habitat loss and depletion of native macrophyte diversity during the 20th century in four Swiss cities. *Urban Ecosyst* 16:543–551.
- Lamsal P, Kumar L, Aryal A, Atreya K. 2018. Invasive alien plant species dynamics in the Himalayan region under climate change. *Ambio* 47:697–710.
- Mainali KP, Warren DL, Dhileepan K, McConnachie A, Strathie L, Hassan G, Karki D, Shrestha BB, Parmesan C. 2015. Projecting future expansion of invasive species: comparing and improving methodologies for species distribution modeling. *Glob Chang Biol* 21:4464–4480.
- Manjarrés-Hernández AM, Guisande C, García-Rosello E, Pelayo-Villamil P, González-Dacosta J, Heine J, González-Vilas L, Granado-Lorencio C, Duque SR, Lobo JM. 2018. A procedure to assess the spatial variability in the importance of abiotic factors affecting distributions: the case of world freshwater fishes. *Curr Zool* 64:549–557.
- MEA. 2005. *Ecosystems and human well-being: Wetlands and water.* Washington D.C.: World Resources Institute.
- Méndez-Marin O, Hernández-Franyutti AA, Álvarez-González CA, Uribe MC, Contreras-Sánchez WM. 2016. Permanent germinal epithelium and reproductive

- cycle of *Atractosteus tropicus* (Lepisosteiformes: Lepisosteidae) males, Tabasco, Mexico. *Rev Biol Trop* 64:1597–1509.
- Méndez A, García ME, Lozano L. 2011. Sistemática del pez *Petenia splendida* (Perciformes: Cichlidae) en el lago Petén Itzá, Guatemala. *Rev Biol Trop* 59:1205–1216.
- Mendoza-Alfaro R, González-Aguilera C, Ferrara AM. 2008. Gar biology and culture: Status and prospects. *Aquac Res* 39:748–763.
- Nelson SJ, Grande TC, Wilson MVH. 2016. *Fishes of the World*. 5th ed. U.S.A.: John Wiley & Sons.
- Papeş M, Havel JE, Vander MJ. 2016. Using maximum entropy to predict the potential distribution of an invasive freshwater snail. *Fresh Biol* 61(4):457-471.
- Pech-May A, Moo-Llanes DA, Puerto-Avila MB, Casas M, Danis-Lozano R, Ponce G, Tun-Ku E, Pinto-Castillo JF, Villegas A, Ibáñez-Piñon CR, et al. 2016. Population genetics and ecological niche of invasive *Aedes albopictus* in Mexico. *Acta Trop* 157:30–41.
- Peterson AT, Soberón J, Pearson RG, Anderson R, Martínez E, Nakamura M, Araújo M. 2011. *Ecological niches and geographic distributions*. New Jersey, U.S.A.: Princeton University Press.
- Peterson, AT, Soberón, J. 2012. Species distribution modeling and ecological niche modeling: Getting the concepts right. *Natureza & Conservacao* 10(2), 102–107.
- Rolls RJ, Heino J, Ryder DS, Chessman BC, Growns IO, Thompson RM, Gido KB. 2018. Scaling biodiversity responses to hydrological regimes. *Biol Rev* 93:971–995.
- Rush Miller RR. 2009. *Peces dulceacuícolas de México*. 1st ed. México, D. F.: Comisión Nacional para el Conocimiento y Uso de la Biodiversidad; Sociedad Ictiológica Mexicana A. C.; El colegio de la Frontera Sur; Consejo de los Peces del Desierto México-Estados Unidos.
- Soberón, J, Osorio-olvera L, Peterson A. 2017. Diferencias conceptuales entre modelación de nichos y modelación de áreas de distribución Conceptual

- differences between ecological niche modeling and species distribution modeling. *Rev Mex Biodiv* 88(2): 437–441.
- Villegas-Hernández H, Lloret J, Muñoz M. 2015. Reproduction, condition and abundance of the Mediterranean bluefish (*Pomatomus saltatrix*) in the context of sea warming. *Fish Oceanogr* 24:42–56.
- Walsworth TE, Budy P. 2015. Integrating nonnative species in niche models to prioritize native fish restoration activity locations along a desert river corridor. *Trans Am Fish Soc* 144:667–681.
- Warren DL, Glor RE, Turelli M. 2008. Environmental niche equivalency versus conservatism: Quantitative approaches to niche evolution. *Evolution* (N. Y). 62:2868–2883.
- WWF. 2016. Informe planeta vivo 2016. Riesgo y resiliencia en el antropoceno. Young L, Guerraoui M, Zwaal N, Klinge D, editors. Gland, Suiza: WWF Internacional.
- Xiujian S, Pengfei S, Xianshi J, Xiansen L, Fangqun D. 2013. Long-term changes in fish assemblage structure in the Yellow river estuary ecosystem, China. *Mar. Coast Fish* 5:65–78.
- Zambrano L, Martínez-Meyer E, Menezes N, Peterson AT. 2006. Invasive potential of common carp (*Cyprinus carpio*) and Nile tilapia (*Oreochromis niloticus*) in American freshwater systems. *Can J Fish Aquat Sci* 63:1903–1910.