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Potential range expansion of the invasive Red Shiner, *Cyprinella lutrensis* (Teleostei: Cyprinidae), under future climatic change

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Abstract

We built climate envelope models under contemporary and future climates to explore potential range shifts of the invasive Red Shiner-*Cyprinella lutrensis*. Our objective was to estimate aquatic habitat vulnerability to Red Shiner invasion in North America under future climatic change. We used presence records from within the species' native and invaded distributions, a suite of bioclimatic predictor variables from three climate models (CCCma, CSIRO, and HadCM3), and maximum entropy modeling to generate potential distribution maps for the year 2080. Our model predicted major range expansion by Red Shiner under both low and high carbon emissions scenarios. The models exceeded average area under the receiver operator characteristic curve values of 0.92, indicating good overall model performance. The model predictions fell largely outside of areas of climatic extrapolation (i.e. regions predicted into environments different from training region) indicating good model performance. The results from this study

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Keywords: invasive fishes, Maxent, climate envelope model, climate change, biological invasions, *Cyprinella lutrensis*

Introduction

Human-mediated species introductions are major drivers of global environmental change (Mack et al. 2000; Vitousek et al. 1997). Non-native species are drivers of ecosystem change through the alteration of a variety of processes including primary productivity, hydrology, geomorphology, nutrient cycling, and natural disturbance regimes (Stachowicz et al. 2002; Vitousek et al. 1997). Ongoing shifts in climate will likely exacerbate the effects of invasive species on ecosystem function as native and alien species alike shift their geographical ranges in response to changing environmental conditions (Kelly & Goulden 2008; Parmesan & Yohe 2003). Exotic invaders are well suited to succeed in novel environments because of their tolerance of variable environmental conditions, and global climate change is likely to increase these effects as alien species spread to previously uninhabited locations (Bradley 2009).

While rivers provide an array of key ecosystem services including clean water and biodiversity (Postel & Carpenter 1997), they remain one of the most vulnerable habitats to invasion by exotic species(Cox & Lima 2006). The spread of freshwater invasive species across the globe has stimulated major shifts in riverine community structure through native species displacement and extinction (Gordon 1998; Wilcove et al. 1998) and via the alteration of hydrological cycles (Ricciardi & MacIsaac 2000), nutrient flows (Simon & Townsend 2003; Strayer 2010), and food webs (Baxter et al. 2004; Van Riel et al. 2006). Mounting evidence of the effects of accelerated climatic change on the global biota heightens the urgency of understanding the potential impacts of novel climates on invasive species distributions.

Predicting the potential spread of aquatic species under future climates is critical for developing long-term management guidelines for conservation planning. Climatic envelope modeling (CEM) is a widely-employed method for forecasting the potential distributions of species under climate change (Guisan & Zimmermann 2000; Kriticos et al. 2001) where future species distributions are modeled under the CEM framework by deriving a climatic envelope from contemporary distribution points and projecting this envelope onto future climatic data(Araujo & Guisan 2006; Thomas et al. 2008; Thuiller et al. 2005). While CEM has proven useful for conservation and biodiversity management around the globe, extrapolating species distributions into novel climates must be performed with care because of the difficulties associated with accurately modeling a species' fundamental niche (Araújo & Peterson 2012; Diniz Filho et al. 2010; Rodda et al. 2011; Soberón & Nakamura 2009; Webber et al. 2011). Recent debates on this topic have signaled the need for 1) incorporating biologically meaningful variables into the CEM modeling effort (Elith et al. 2011; Rodda et al. 2011), 2) careful model parameterization (Elith et al. 2010; Rodda et al. 2011; Webber et al. 2011), and 3) thorough evaluation and cautious interpretation of model projections under novel climate scenarios(Webber et al. 2011).

We employed the CEM approach to predict the response of Red Shiner (*Cyprinella lutrensis* (Baird and Girard 1853)) to future climatic change in North America, while attempting to address the short-comings of CEMs through careful model parameterization, model performance assessment, and model interpretation. Although CEM modeling is widespread for terrestrial species, the approach has been little applied to predict the impacts of climate change on invasive fishes living in habitats that are restricted by riparian network structure (Bond et al. 2011; Buisson et al. 2008). This work builds upon prior preliminary research by Poulos et al. (Poulos et al. 2012) who mapped the contemporary potential distribution of Red Shiner across the conterminous United States using topo-climatic predictors by investigating how the distribution of this species may respond to future climatic shifts across North America. Our specific objective in this study was to identify regions with high invasion potential under both low and high future carbon emissions scenarios. We used Maxent (Phillips et al. 2006) to model this species' distribution at the year 2080 under two future climate scenarios (B2 and A1B) representing low and high emissions scenarios, respectively. The B2 scenario predicts CO_2 emissions between 10 and 20 GtC/yr for the year 2080 (Solomon 2007). It represents a balance between environmentalism and life-quality where global population peaks mid-century and increases in resource-efficient technologies develop over time. The A1B scenario predicts predicts CO_2 emissions ranging between 15 and 25 GtC/yr for the year 2080. It represents a more heterogeneous world with continued increases in economic and population growth, and it is considered a realistic, but severe potential outcome.

Materials & Methods

Species biology

Red Shiner's native distribution falls within the Great Plains, American Southwest, and northern Mexico in tributaries of the middle and lower Mississippi River basin, and Gulf drainages westward to the Rio Grande, including several endorheic basins in Mexico (Council) 2010). Bait bucket (Hubbs & Lagler 1964; Jennings & Saiki 1990; Walters et al. 2008) and aquarium releases are the primary vectors of Red Shiner introduction beyond this species' native range (Jenkins & Burkhead 1994; Moore et al. 1976). The fish is an aggressive invader via rapid multiplication, dispersal, and aggressive competition with native minnows (Hubbs & Lagler 1964; Minckley & Deacon 1968). Red Shiner can dilute the gene pools of native *Cyprinella* through the formation of hybrid swarms (Mettee et al. 1996), and it has also displaced native fishes including Spikedace (*Meda fulgida* (Girard 1856)), Woundfin (*Plagopterus argentissimus* (Cope 1874)), and Virgin River Chub (*Gila seminude* (Cope and Yarrow 1875)) (Deacon 1988; Moyle 2002) through larval predation and direct competition for habitat use.

Red Shiners are generalists, but they occur primarily in creeks and small rivers. Like many minnows, Red Shiners are tolerant of harsh environmental conditions and degraded habitats, including low or intermittent flows, excessive turbidity and sedimentation, and natural physiochemical extremes (Baltz & Moyle 1993; Cross 1967; Douglas et al. 1994; Matthews & Hill 1979; Sublette 1975), but they are uncommon or absent from upland, clear water streams with moderate or high species richness (Matthews 1985; Matthews & Hill 1977; Yu & Peters 2002). Red Shiners can tolerate temperatures ranging from -21 to 10° C, as well dissolved oxygen as low as 1.6 ppm (Matthews & Hill 1977), and it has been observed in hot springs with temperatures as high as 39.5° C (Brues 1928).

Occurrence data

We compiled spatial occurrence data from within both the native and invaded ranges of Red Shiner (n = 3446). Native occurrence data were obtained from the global biodiversity information facility (Accessed through the GBIF Data Portal, data.gbif.org, 2013-08-20), and records from within the species' invaded range were compiled from the Nonindigenous Aquatic

Species (NAS) database (http://nas.er.usgs.gov) (Figure 1). We included both native and non-native records because it encompassed the most comprehensive estimation of the species' ecological niches. Ibañez et al. (Ibáñez et al. 2009) highlighted the utility of this approach for modeling the potential distribution of alien invasive plants and Wolmarans et al. (Wolmarans et al. 2010) demonstrated that modeling invasive species distributions using records from a species' native and invaded range did not significantly affect model performance or result in overfitting.

Climatic data

We used 19 current and future bioclimatic variables at a spatial resolution of 1 km that encompassed the native and invaded range of Red Shiner using contemporary climatic data and the IPCC (2007) AR4 assessment data in the WorldClim database (Hijmans et al. 2005) (Table 1). We downloaded interpolations of the 19 bioclimatic variables from three climate models including: 1) CCCma-CGCM2 (Flato & Boer 2001; Flato et al. 2000), 2) CSIRO-MK2 (Gordon and O´Farrell 1997), and 3) UKMO-HadCM3 (Gordon & O'Farrell 1997; Pope et al. 2000). Grids were then clipped to the extent of the HydroSHEDS hydrography dataset for North America (Lehner et al. 2008) to avoid modeling fish distributions outside riparian areas.

The entire dataset of raster predictor variables was reduced prior to model construction through individual variable evaluation and through pairwise evaluation to reduce multicollinearity among the predictors as suggested by Elith et al. (Elith et al. 2010). We used the correlation matrix as a means of identifying highly correlated pairs of habitat predictors ($r > 0.7$). For correlated pairs, we removed the variable that captured less information or seemed the least biologically meaningful for the species. For example, if minimum temperature of the coldest month and mean temperature of the coldest quarter were highly correlated, we kept mean temperature of the coldest quarter since it captured a longer record of winter temperature as a whole.

CEM modeling

We used Maxent 3.3.3k (Phillips et al. 2006) to model the potential habitat of the two invaders under low and high CO_2 emissions scenarios. We chose Maxent after evaluating the area under the receiver operator characteristic (AUC) curve and through visual map inspection after applying the sensitivity plus specificity thresholding of preliminary CEM models of Red Shiner potential distribution maps derived from one-class support vector machines(Chang & Lin 2011), GARP(Stockwell 1999), and DOMAIN(Carpenter et al. 1993). We chose to use MaxEnt in our CEM modeling effort after finding that it was the highest performing individual modeling method for mapping Red Shiner potential distribution and based on results that demonstrated that ensemble modeling methods performed no better than using Maxent alone (Poulos et al. 2012). Maxent uses a deterministic algorithm that finds the optimal probability distribution (potential distribution) of a species across a study area based on a set of environmental constraints. Maxent determines the best potential distribution by selecting the most uniform distribution subject to the constraint that each environmental variable in the modeled distribution matches its empirical average over the known distributional data (i.e. presence data).

We developed maps for each climate model (CCCma, CSIRO, and HadCM3) and emissions scenario (A1B and B2) by randomly dividing our data into training and testing datasets comprising 70% and 30% of each dataset, respectively. We supplied our own background points for the Maxent modeling effort, using a minimum distance of 2 km to minimize issues associated with choosing background points from within the existing range of Red Shiner as suggested by

(Elith et al. 2011). We also experimented with using bias grids. We found that supplying bias grids to Maxent resulted in no improvement in model performance, so we ultimately chose not to include them in the final model outputs. Models calibrated under current climatic conditions were used to generate projections of future potential distributions for the year 2080 for each climate model and emissions scenario. Each analysis comprised ten replicates using a different set of randomly drawn presence points for training and validating the model. The products from each climate-emissions scenario combination were then averaged to generate a low and high emissions map for Red Shiner across North America.

Maxent model performance was evaluated by visual map inspection after thresholding using the sensitivity plus specificity criterion and by calculating an area under the receiver operating characteristic curve (AUC). The AUC is a threshold-independent measure of model performance that ranges from 0 to 1. Values > 0.9 indicate high accuracy, values of 0.7-0.9 indicate good accuracy, and values below 0.7 indicate low accuracy (Swets 1988). Average AUC values for the 10 runs of each independent model were reported. To estimate changes in Red Shiner distribution, we used a threshold to define habitat and non-habitat based on the Maxent model outputs. The threshold indicating maximum training sensitivity plus specificity is considered as a robust approach (Liu et al. 2005), so we used this method to conduct the conversion into habitat distribution.

We also generated multivariate environmental similarity surfaces ('MESS' maps (sensu Elith et al. 2010)) in Maxent by comparing the models' reference climates (or background points) with the projection region under contemporary and future climate scenarios. MESS analysis applies a multidimensional rectangular environmental envelope to characterize the relative position of each grid cell relative to the center of the envelope. In this study, we transformed the MESS map output into a presence/absence map with a cut-off of 0 to identify areas with climatic conditions exceeding those of the training area. These areas describe where at least some degree of extrapolation by Maxent is required to make predictions.

Results

The potential Red Shiner distribution maps reached test AUC values above 0.92 (0.92-0.99 range), indicating good overall model performance (Table 2). All of the independent climate models from the future CCCma, CSIRO, and HadCM3 scenarios predicted increases in Red Shiner distribution under future climatic change (Figure 2). Red Shiner distributions were greater for the high emissions scenario (B2) than the more optimistic, low emissions scenario (A1B). Red Shiner showed a 10.2% (± 4.4) change in distribution under the B2 scenario and a 41.7% (± 7.1) increase in potential distribution under the A1B scenario.

Precipitation and temperature were the major variables influencing Red Shiner potential distribution (Table 3). Precipitation seasonality, maximum temperature of the warmest month, minimum temperature of the coldest month, and annual precipitation were the four most important predictors of Red Shiner distribution. The MESS analysis revealed areas in the model outputs containing non-analogous climatic conditions in the future climate models. Non-analogous climates refer to the extrapolation of models into environments unlike those characterizing the region in which the model was calibrated. The Red Shiner B2 model MESS analysis indicated that the majority of the areas within Red Shiner potential distribution were not highly extrapolated beyond the contemporary climate, although model predictions in limited regions of the Southwest and the Southeastern Coastal Plain differed from contemporary climatic conditions (Figure 2). Areas of the maps for Red Shiner that were outside its contemporary

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climatic envelope included southern California, the midwestern United States, Florida, large areas in Canada in the B2 model, and parts of Mexico and coastal Canada for the A1B model.

Discussion

It is increasingly imperative to understand potential invasive species range shifts in the face of global climatic change (Hellmann et al. 2008; Rahel & Olden 2008). Red Shiner is predicted to exhibit major increases in distribution under both low and high future carbon emissions scenarios. Our results support the contention that warming climates are likely to alter the existing constraints on invasive species distributions, invasion pathways, and river flow regimes (Rahel & Olden 2008). Human transport of alien species due to longer shipping and recreation seasons in temperate regions will increase the movement of non-native propagules around the globe (Hellmann et al. 2008). Increased drought and prolonged low river flows associated with climate change may enhance the establishment success of alien species that are tolerant of warm waters with low dissolved oxygen content like the Red Shiner. Similarly, potential changes in the timing and quantity of stream flow will likely influence invasive fish spread rates through river systems.

Distribution Maps

Potential distribution maps of invasive fishes under climatic change are useful for understanding the impacts of anthropogenic sources of global change on alien species ranges, and for predicting areas that will be susceptible to fish invasion in the future. Areas identified as having high invasion risk can be targeted to reduce human activities that facilitate the spread of

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invasives and as regions for surveillance for early invaders. Our results highlight the widespread increase in potential distribution of Red Shiner under future warmer climates which is consistent with the species' tolerance of warm, turbid, and slow-flowing waters.

This work builds upon Poulos et al. (Poulos et al. 2012) to highlight that much of North America will be vulnerable to invasion by Red Shiner under future climatic change according to our projections. The maps for this species suggest that it could spread well beyond its current distribution in the US and Mexico into the western US and much of Canada, with up to a 42% increase in Red Shiner distributions under future carbon emissions. While Poulos et al. (Poulos et al. 2012) identified similar Red Shiner presence predictors under contemporary topo-climatic conditions (i.e. precipitation and summer temperature) to those of this study, our results highlight that Red Shiner can spread well beyond its potential range under contemporary climatic conditions even under the low emissions climate scenario, although the MESS analysis revealed that portions of Canada may fall outside of the known climate space of our projections. These results also exceed predictions by Mohseni et al. (Mohseni et al. 2003) who predicted a 33% increase in the number of sites in the US that would be suitable for Red Shiner under a doubling of CO_2 concentrations. Although, our model was based on land surface temperatures rather than water temperature, Red Shiner is the most thermotolerant minnow in North America (Brues 1928; Matthews & Hill 1979), and the bioclimatic predictors in this model and prior work by Poulos et al. (Poulos et al. 2012) indicate that this species has the potential to spread to other hot environments in the future.

Our results suggest that Red Shiner's ability to outcompete (Greger & Deacon 1988) and hybridize with natives by creating introgressive hybrid swarms (Blum et al. 2010; Burr & Page 1986; Larimore & Bayley 1996; Ward et al. 2012) may threaten native cyprinid congener that are less thermotolerant in the future. Red Shiner expansion under climate change could also have large-scale impacts on the abundance and distribution of other native fishes because of its negative influences on native larval fish survival (Douglas et al. 1994; Gido et al. 1999; Marsh-Matthews & Matthews 2000; Ruppert et al. 1993) and habitat use (Douglas et al. 1994). Native species that are less equipped to tolerate changes in water conditions from climatic change may ultimately be displaced by aggressive invasive fishes such as the Red Shiner.

Model Uncertainties

Although the CEM results for Red Shiner displayed good overall performance with minimal extrapolation beyond current climatic conditions, both climate change projections and CEMs contain a range of uncertainties (Beaumont et al. 2008; Elith et al. 2010). It is widely acknowledged that CEMs provide simplified representations of the processes underlying species' geographical distributions. Ensemble forecasts that use multiple climate models provide a framework for minimizing the uncertainties associated with CEM modeling. We approached this issue by applying two scenarios of the climate change story line (A1B and B1) (Solomon 2007) and three different climate models (CCCma, CSIRO, and HadCM3). Our use of the mean map outputs from multiple runs of the Maxent algorithm and the MESS map analysis allowed us to measure the amount of variability in the Maxent models and highlight areas of model extrapolation beyond the Red Shiner's contemporary climatic envelope. Even after the implementation of these approaches, the MESS analysis identified some regions of Red Shiner model extrapolation in North America, particularly in parts of Canada well outside its current range and near the edges of its current distribution in the United States and Mexico.

Management Considerations

The future range expansion of the two study species is a key consideration for the adaptive management of Red Shiner because future changes in climate will likely alter the effectiveness of existing control strategies (Rahel & Olden 2008). Changes in water temperature and river flow dynamics due to future hotter and drier conditions could limit the effectiveness of common invasive fish control measures like biological control agents that may not have the same ecological tolerance as the invaders they consume. Rahel et al. (Rahel & Olden 2008) suggest that prioritizing the conservation of native species and maintaining natural flow rates may be a better strategy for dealing with invasive species under future climatic conditions. For example, Tyus and Saunders (Tyus & Saunders 2000) indicate that increases in flow may be effective control measures for non-native cyprinids like Red Shiner that thrive in slow-flowing, turbid waters, and this may also enhance the success of native species adapted to natural flow regimes.

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Table 1: The 19 bioclimatic variables used for modeling the potential distribution of Red Shiner.

BIO1	Annual mean temperature
BIO2	Mean diurnal range ((mean of monthly (max temp – min temp))
BIO3	Isothermaity (BIO2/BIO7)*100
BIO4	Temperature seasonality (standard deviation * 100)
BIO5	Max temperature of the warmest month
BIO6	Min temperature of the coldest month
BIO7	Temperature annual range (BIO5-BIO6)
BIO8	Mean temperature of wettest quarter
BIO9	Mean temperature of driest quarter
BIO10	Mean temperature of warmest quarter
BIO11	Mean temperature of coldest quarter
BIO12	Annual precipitation
BIO13	Precipitation wettest month
BIO14	Precipitation driest month
BIO15	Precipitation seasonality (coefficient of variation)
BIO16	Precipitation of wettest quarter
BIO17	Precipitation driest quarter
BIO18	Precipitation warmest quarter
BIO19	Precipitation coldest quarter

Table 2: The mean area under the curve (AUC) values and projected impacts of climate change for 2080 in terms of percent change in range size for Red Shiner under low (B2) and high (A1B) carbon emissions scenarios. Range size values are means for the three climate models with standard errors reported in brackets.

Species	**Emissions Scenario**	**AUC**	**% change in range size**

Red Shiner	Contemporary	0.92	
	B2	0.94	10.2 (4.4)
	A1B	0.92	41.7 (7.1)

Table 3: Average percent contribution of the top four environmental predictor variables to the Maxent models. Percent Contribution reports the gain of the model by including a particular variable at each step of the Maxent algorithm.

Bioclimatic Variable		Model Contribution (%)	
		B2	A1B
BIO15	precipitation seasonality	41.2	17.1
BIO5	max temperature warmest month	32.3	57.6
BIO6	min temperature coldest month	19.6	5.1
BIO12	annual precipitation	6.9	23

Figure Captions:

Figure 1: Spatial distribution of Red Shiner presence records. Native species' records were obtained from the Global Biodiversity Information Facility (GBIF) and non-native records were compiled from the Nonindigenous Aquatic Species (NAS) database. The native distribution of Red Shiner in North America is shown in dark gray (Miller et al. 2005; NatureServe 2004).

Figure 2: Model projections of Red Shiner potential distribution based on recent historical climates (contemporary), low future carbon emissions (B2), and high emissions (A1B) scenarios. The maps display the average habitat suitability from the three climate models, CCCma, CSIRO, and HadCM3. The color scale indicates relative habitat suitability which ranges from 0 to 1. Areas shaded in gray define regions with negative multivariate environmental similarity surface (MESS) values (i.e. extrapolation into novel climate space).

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Figure 1

presence locations

Spatial distribution of Red Shiner presence records. Native species' records were obtained from the Global Biodiversity Information Facility (GBIF) and non-native records were compiled from the Nonindigenous Aquatic Species (NAS) database. The native distribution of Red Shiner in North America is shown in dark gray (Miller et al. 2005 ; NatureServe 2004) .

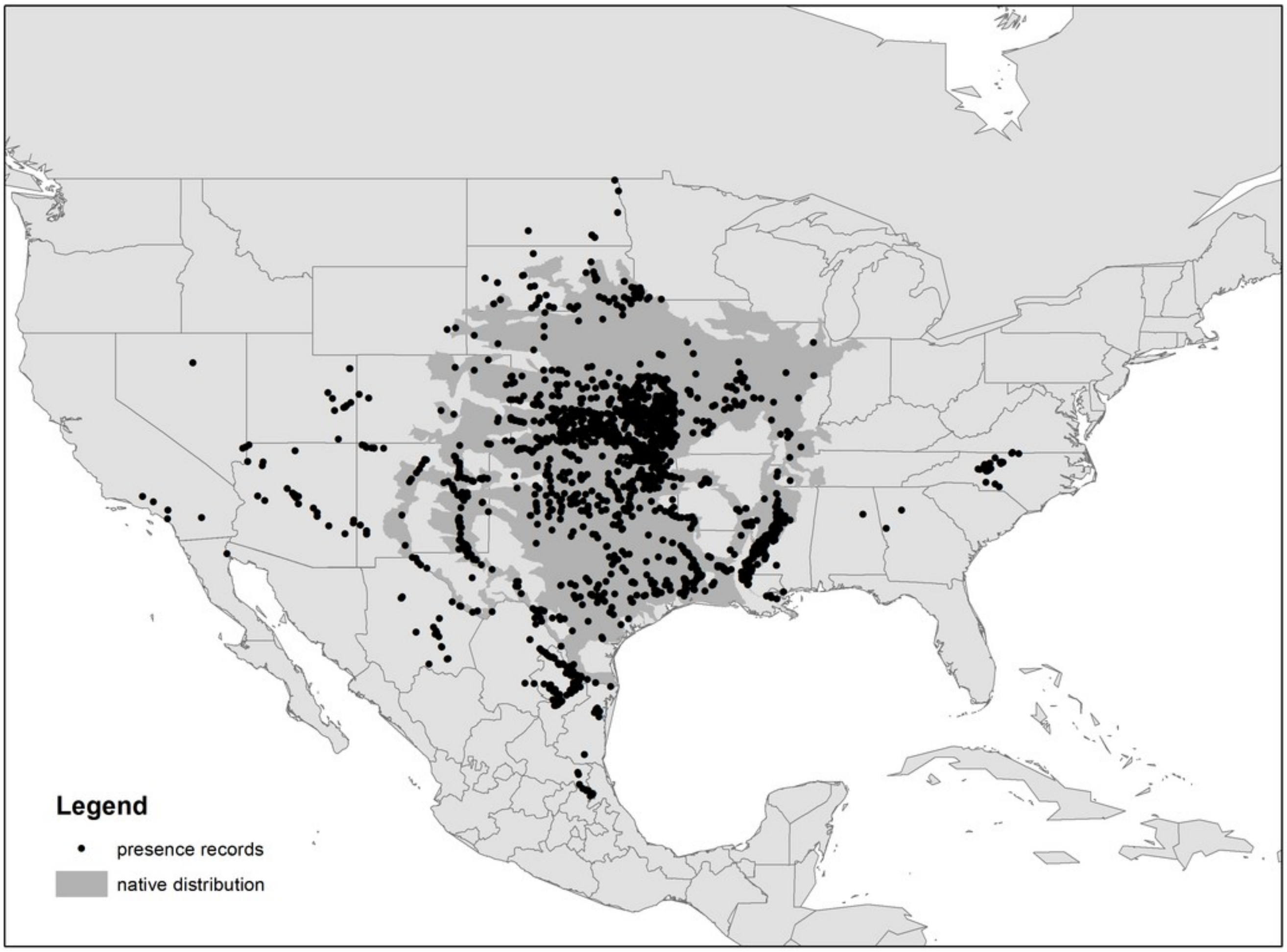

Figure 2

Distribution map

Model projections of Red Shiner potential distribution based on recent historical climates (contemporary), low future carbon emissions (B2), and high emissions (A1B) scenarios. The maps display the average habitat suitability from the three climate models, CCCma, CSIRO, and HadCM3. The color scale indicates relative habitat suitability which ranges from 0 to 1. Areas shaded in gray define regions with negative multivariate environmental similarity surface (MESS) values (i.e. extrapolation into novel climate space).

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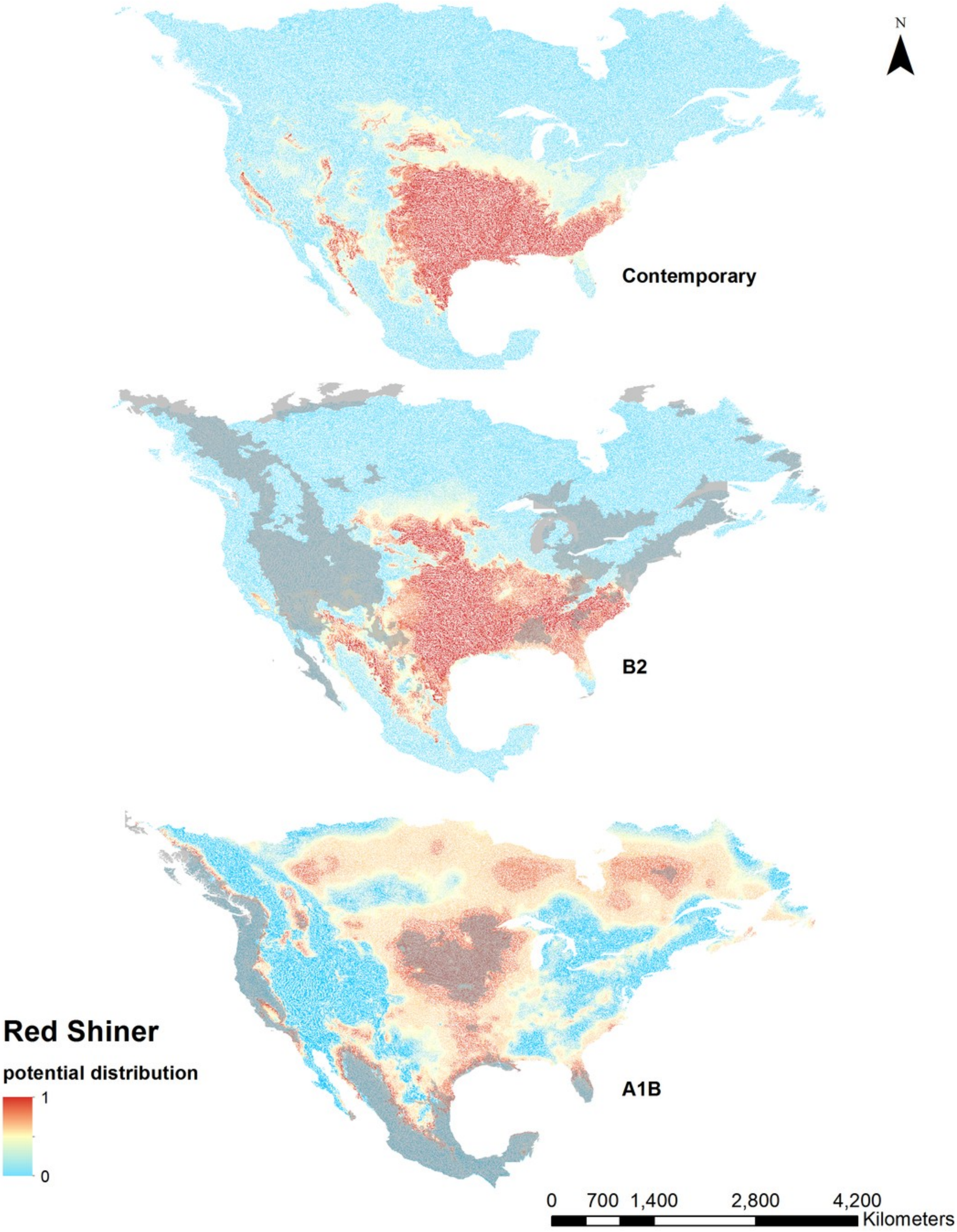

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