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The Potential Impact of Climate Change on the Distributions of *Eleutherodactylus cystignathoides* and *E. planirostris* (Anura: Eleutherodactylidae)

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THE POTENTIAL IMPACT OF CLIMATE CHANGE ON THE DISTRIBUTIONS OF
ELEUTHERODACTYLUS CYSTIGNATHOIDES AND *E. PLANIROSTRIS*

(ANURA: ELEUTHERODACTYLIDAE)

A Thesis

by

REBECCA T. CHASTAIN

Submitted in Partial Fulfillment of the

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ABSTRACT

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Eleutherodactylus cystignathoides and E. planirostris (Anura: Eleutherodactylidae) Master of
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Climate change is inducing changes in the distributions of many species, causing range shifts and habitat loss as well as facilitating invasions. It is a broad contributor to global amphibian decline, already causing mass extinctions and extirpations of amphibian populations, a phenomenon which is expected to continue. The understudied direct-developing frog *Eleutherodactylus cystignathoides* is a notable outlier, having rapidly expanded its distribution in recent years. This is of particular interest given that other eleutherodactylids, such as *E. coqui* and *E. planirostris*, have already shown propensity for rapid dispersal and invasion. Originally found in the southernmost tip of Texas, USA and northeastern Mexico, *E. cystignathoides* has established populations far into northeastern Texas, in addition to southern Louisiana, USA, and Alabama, USA. This expansion has been assumed to be ecologically neutral due to lack of evidence of negative impact, but no confirmational investigation has occurred. The dearth of information about this species' dispersal and ecology, coupled with the documented negative impacts of other successful eleutherodactylid invaders, warrants investigation that preempts waiting for any potential consequences of this geographical expansion to make themselves known. To conduct an investigation into the potential range limits of this species as they are defined by bioclimatic variables, we used spatially rarefied occurrences and selected future

climate models to develop Maxent projections of potentially suitable habitat of *E. cystignathoides*. These methods were repeated with the better-studied congener *E. planirostris*, a Cuban frog with an introduced range from Florida to Texas, for the purposes of contextualization and comparison. Our models suggest the existence of currently non-invaded potentially suitable habitat across the southeastern USA under both current and future models for *E. cystignathoides*, but widespread range contractions for *E. planirostris*. The models additionally predict habitat loss in the native ranges of each species under future climate conditions.

DEDICATION

To Mom and Dad, for teaching me who I am; to Corneshea Halton and Jody Musgrove, for teaching me how to speak; to Pat Person and Carlos de Oro, for teaching me how to listen; to Bill Topich, Megan Abbott, Jim Kilfoyle, and Michael Saenger, for teaching me how to write; to Ben Pierce, Max Taub, and Romi Burks, for teaching me how to research; and to Jo, for teaching me why it matters.

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CHAPTER I

INTRODUCTION

The global effects of climate change on biological systems have already made themselves apparent in the form of natural disasters (Berlemann and Steinhardt 2017, Islam 2018, Benevolenza and DeRigne 2019), acidified oceans (Hoegh-Guldberg et al. 2017, Rheuban et al. 2018, Stewart-Sinclair et al. 2020), desertified lands (Shukla et al. 2019, Burrell et al. 2020), destructive biological invasions (Hellmann et al. 2008, Mainka and Howard 2010), and other global tragedies, but even as researchers rush to quantify and identify these alterations to the Earth, the full extent of the impact remains unknown. However, in the absence of individual power to stop the process of anthropogenic climate change remains the responsibility to prepare for it. For example, through the use of predictive climate change-based modeling, it is possible to identify populations at risk of decline (Razgour et al. 2018) or anticipate temporal and spatial changes in issues tied to human welfare such as wildfires (McKenzie and Littell 2017) or vector-borne diseases (Tjaden et al. 2018). Another potential application is species distribution modeling with future climate change projections (Ramirez-Cabral et al. 2017, Silber et al. 2017, Dyderski et al. 2018, Morán-Ordóñez et al. 2018, Kurpis et al. 2019, Peterson et al. 2019, Garza et al. 2020, Li et al. 2020). While many such studies have focused on endangered, rare, and endemic species, others have focused on modeling the potential for climate change to facilitate the dispersion of invasive species to new areas, such as fire ants (Sung et al. 2018), small hive

beetles (Cornelissen et al. 2019), or golden apple snails (Lei et al. 2017). Predicting the spread of these invasive species is productive for aiding in the identification of potential threats as well as effective preventative actions (Wallingford et al. 2020).

Although amphibians are declining globally (Grant et al. 2019), some species have shown aptitude for invasion instead, such as the cane toad (Urban et al. 2008) or the Cuban tree frog (McGarrity and Johnson 2009). Some studies have even modelled the potential impact of climate change on amphibian invaders' distributions. For example, one paper posited that the year 2070 will see a 1.2% increase in the proportion of land that represents suitable habitat for the invasive American bullfrog (Johovic et al. 2020); another predicted an expansion of suitable habitat for the Cuban tree frog under future climate change conditions (Rödder and Weinsheimer 2009).

A few studies have focused on successful introduced populations of eleutherodactylid (*Eleutherodactylus*: Eleutherodactylidae) frogs, a large group of direct-developing Neotropical frogs known for their unique, high-pitched calls. The most well-known of these frogs is likely *E. coqui* (common coquí), which, despite its cultural significance in its native range in Puerto Rico, USA, is considered a pest in its introduced range, particularly in Hawaii, USA, where they achieve high population densities and impact local insect biodiversity and abundance (Beard et al. 2009). Distribution modeling for this species has been able to produce predictions about the potential distribution of *E. coqui* within Hawaii (Bisrat et al. 2012) as well as other regions throughout the tropics (Rödder 2009). Similarly, the distribution potential of *E. johnstonei* (Johnstone's whistling frog), a prominent and widespread invader in Central and South America (Ernst et al. 2011, Leonhardt et al. 2019), has been modelled under current climate projections in order to aid in informed conservation policymaking (Rödder 2009b), as has that of *E.*

planirostris, a native of the Caribbean which is known to carry disease and otherwise negatively impact communities in its invasive range (Rödder and Lötters 2010).

Such modeling efforts have not yet been applied to the under-studied *E. cystignathoides* (Rio Grande chirping frog), a small frog (~16–22mm SVL) with a native range in northeastern Mexico and the southernmost tip of Texas, USA (Hayes-Odum 1990). It is associated with anthropogenic sources of moisture, such as ditches and watered lawns, thought to be territorial, and known to climb vegetation at night while utilizing underground habitat during the day (Hayes-Odum 1990). As one of only two *Eleutherodactylus* native to the USA (alongside *E. marnockii* of central Texas), it represents a unique part of the herpetofauna of the region. There is only one publication dedicated to the ecology and life history of *E. cystignathoides* (see Hayes-Odum 1990), representing a concerning dearth of information considering the rapid dispersal of this species documented in recent years. In 1987, there were only two counties (Bexar and Harris counties, Texas) which were known to host introduced populations (Dixon 1987), but by 2000, they had been documented in 11 counties (Dixon 2000), and by 2013, their confirmed distribution included 24 counties (Dixon 2013). Their current documented distribution ranges north nearly to the Texas–Oklahoma, USA border, at least as far west as Bandera County, Texas, USA, and eastward into coastal Louisiana, USA and Alabama, USA (GBIFa 2021, Lott 2019).

Despite a growing number of new records of this rapidly expanding species, there is virtually no published research into the potential impact or extent of this spread. It is unknown whether *E. cystignathoides* might negatively impact invertebrate densities or diversity like *E. coqui* is known to (Beard 2007), as the diet of the *E. cystignathoides* has not been documented past anecdotal evidence (Lott 2019). Similarly, it is unknown if *E. cystignathoides* has the

potential to spread pathogens such as *Batrachochytrium dendrobatidis* to previously unexposed amphibian populations, as has been a concern with invasive *E. coqui* and *E. planirostris* populations (Beard and O'Neill 2005). It is also unclear how far *E. cystignathoides* may spread, which areas are at risk, or what factors might constrain their dispersion.

The current study aims to address some of these unanswered questions through the first investigation into the current and future potential distribution of *E. cystignathoides*. This investigation is juxtaposed with an identical analysis of *E. planirostris*, an eleutherodactylid from the Caribbean which is considered invasive from Florida, USA through southern Texas and northern Mexico and overlaps with populations of *E. cystignathoides* (Olson et al. 2012). Together, these two species constitute all the introduced eleutherodactylids established in the southeastern USA, allowing for a comprehensive picture of the potential impact of introduced eleutherodactylids in this region. Additionally, overlap of their introduced ranges is of immediate conservation concern should the diseases carried by *E. planirostris* spread to *E. cystignathoides*, possibly enabling them to spread disease to native populations in their own range. We used positive occurrence data from the Global Biodiversity Information Facility database as well as bioclimatic variables from WorldClim to develop potential distribution models for *E. cystignathoides* and *E. planirostris* in Maxent under current climate parameters as well as several climate change projections for the years 2050 and 2070.

CHAPTER II

MATERIALS AND METHODS

Target species

Eleutherodactylus cystignathoides

Eleutherodactylus cystignathoides is a small (~16–22 mm SVL; females larger than males), terrestrial, direct-developing eleutherodactylid native to the lower Rio Grande Valley in extreme southern Texas, USA and northeastern Mexico (Conant 1975). They are readily identifiable by their high-pitched call, consisting alternately of short, birdlike chirps and ascending trills, which can be heard throughout the year given appropriately warm/wet conditions (indicating they are unlikely to be seasonal breeders), and tend to be locally abundant (Hayes-Odum 1990, Lott 2019, personal observation). Despite their ease of identification and abundance, they remain an understudied organism, meaning their ecological and life history background is incomplete, perhaps due in part to the relative difficulty of locating individuals in the field. This difficulty is largely attributable to their small size and proclivity to hide in under cover objects, but it should be noted that high-frequency calls such as those emitted by *E. cystignathoides* are difficult to localize (Lott 2019). Most of what is known about these frogs originates from its sole dedicated research paper (see Hayes-Odum 1990) and anecdotal evidence, which sometimes contradict and often draw from similar types of data. For example, Hayes-Odum (1990) concludes that *E. cystignathoides* are likely to be territorial based on

observations of “several instances” of males displacing each other, while Lott (2019) suggests that they are unlikely to be territorial based on “occasional” observation of groups clustered together under debris. Nevertheless, there exists information that appears to be uncontested, such that *E. cystignathoides* are known to climb and call from perches raised off the ground (Hayes-Odum 1990), or that they utilize cracks and tunnels in the earth, likely to avoid desiccation (Hayes-Odum 1990, Lott 2019).

Closely associated with human development and well-watered lawns throughout their introduced range, it is assumed that *E. cystignathoides* is dispersing via the horticultural trade (Lott 2019). It is difficult to determine exactly when and where introductions have occurred in the last several decades due to a paucity of published records; for example, Lott (2019) cites a personal observation of *E. cystignathoides* in Bexar County, Texas that predates official records by several years. In 1987, a Texas-specific field guide presumably drawing upon all available official records indicated only two Texan counties with introduced populations, Bexar and Harris (Dixon 1987). The 2000 edition of the same guide additionally cited records in Tarrant, Walker, Smith, Liberty, Fayette, Nueces, and San Patricio Counties (Dixon 2000), while the 2013 edition adds Crockett (which appears to have never been substantiated by further observations and may not represent an established population), as well as Burnet, Wilson, Dallas, Austin, Nacogdoches, Brazos, Grimes, Montgomery, San Jacinto, Brazoria, Galveston, and Live Oak Counties (Dixon 2013). Notes published in *Herpetological Review* in subsequent years have added Bastrop (Jackson et al. 2012), Duval, Goliad, Jim Wells, Kleberg (Cox et al. 2012), Comal (Lee 2014), Guadalupe (Harvey et al. 2014), Travis (Powell 2014), Colorado (Farr and Forstner 2015), Bell, Hays (Magno-Naoe et al. 2015), Fort Bend (Hickel et al. 2015), Robertson (MacLaren et al. 2015), Kendall (Swanson et al. 2016), Bandera (Mock et al. 2016), Caldwell

(Lee et al. 2016), Matagorda (Swanson and Swanson 2017), Aransas (Ruppert and Davis 2019), Colin (McDaniels 2020), Waller (Bassett and Forstner 2020), Calhoun, Kenedy, Starr, Willacy (Guadiana et al. 2020), DeWitt, Victoria (Davis 2021), and Rockwall (Bassett et al. 2022) counties. It has additionally been documented in Alabama, USA (McConnell et al. 2015) and Louisiana, USA (Boundy and Gregory 2012).

Eleutherodactylus planirostris

Eleutherodactylus planirostris is also a small (~34 mm SVL for males, ~36 mm for females), terrestrial, direct-developing eleutherodactylid thought to be native to Cuba, the Bahamas, the Cayman Islands, and other islands in the Caribbean (Conant 1975). It occupies similar habitats and possesses a similar appearance and call to *E. cystignathoides* (Conant 1975), but it is far from understudied, likely due to its success as an invasive species. It has been established in Florida for well over a century, and in that time, it has spread, presumably through the nursery trade, to establish populations in Louisiana, Alabama, Georgia, USA, Mississippi, USA, and Texas (Rödder and Lötters 2010, Simpson et al. 2019). It has also been introduced and become established in Hawaii, USA, Guam, Jamaica, Mexico, Colombia, Hong Kong, Costa Rica, El Salvador, Honduras, the Philippines, and likely elsewhere (Rödder and Lötters 2010, Olson et al. 2012, Barquero and Araya 2016, Lee et al. 2016, Sy and Ibañez 2020, Antúnez-Fonseca et al. 2021, Cubillos-Abrahams et al. 2021).

Unlike *E. cystignathoides*, there is published evidence that *E. planirostris* impacts native communities in its introduced range. For example, it is known to negatively impact invertebrate populations in Hawaii (Beard et al. 2009, Olson et al. 2012), but perhaps more pressingly, it is

known to carry diseases such as *Batrachochytrium dendrobatidis* (Goodman et al. 2019), which is a known contributor to worldwide amphibian decline (Lips et al. 2006).

Distributional data

We obtained a total of 1,228 presence-only occurrence data for *E. cystignathoides* and 3,299 for *E. planirostris* from the Global Biodiversity Information Facility (GBIFa 2021, GBIFb 2021); observations deposited after the dates these datasets were collected were not included. These geographical datasets (decimal longitude/latitude) were cleaned through removal of outliers (the most distant observations in each direction, in order to create a more conservative dataset) and duplicates. In order to reduce geographic correlation bias, we then used SDM Toolbox Pro (Brown 2014) to spatially rarefy the occurrence data at a distance of 10km following the methods outlined in Kurpis (2019). This dataset was reduced to 271 occurrence records for *E. cystignathoides* and 417 for *E. planirostris*.

Climatic variables

Following the procedures developed in Kurpis et al. (2019) and Garza et al. (2020), we obtained data at 30s spatial resolution representing 19 global bioclimatic variables from WorldClim (Table 1). These variables, used here to approximate the current global climate, were created using aggregated climatic data collected from around the world between the years 1950 and 2000. Additionally, we obtained datasets for the same 19 bioclimatic variables at the same resolution for three general circulation models (CM3 from the Geophysical Fluid Dynamics Laboratory, CMIP5 from the Coupled Model Intercomparison Project, and HadGEM2 from the Hadley Centre for Climate Prediction and Research) averaged between the years 2040–2060

(representing approximately the year 2050) and 2060–2080 (representing approximately the year 2070). Selection of these models was based on the work of Garza et al. (2020). For each of these, we obtained versions with two representative concentration pathways, RCP4.5 and RCP8.5, which represent intermediate and severe climate change scenarios, respectively.

Modeling and analysis

In order to remove highly correlated bioclimatic variables which may create bias in the data, we conducted a band collection statistics analysis in ArcGIS Pro (Table 1), which identifies amounts of redundancy among the variables. This analysis was applied to the training model of each species, geographically limited to the range represented by the spatially rarefied occurrence data (approximately 19–34°N, 90–101°W for *E. cystignathoides* and 13–39°N, 72–97°W for *E. planirostris*). Variables with a correlation above 0.8 were removed from the model, reducing the total number of variables included in the analysis. This resulted in the inclusion of nine variables each for *E. cystignathoides* and *E. planirostris*, seven of which were shared (see Table 1). A jackknife test in Maxent version 3.4.4 was used to quantify the relative influence of each remaining variable on the distribution of these species (Table 1).

Each current and future potential distribution model was run with 20 replicates in Maxent, a maximum entropy algorithm chosen for its use of presence-only data and prediction accuracy, using default parameters and the bootstrap function. Each replicate within a given set of 20 was weighted by its estimated accuracy, represented by the Area Under the Curve (AUC) value produced by Maxent, and averaged together using the raster calculator spatial analyst tool in ArcGIS Pro to produce a consensus map. By this method, derived from Kurpis et al. (2019) and Garza et al. (2020), a consensus map of currently suitable habitat was generated using

rarefied species occurrence data and a base-map of the area encompassing said occurrence data (approximately 13–44°N, 64–107°W). This extent was selected for the base map because it contains the native ranges of both *E. cystignathoides* and *E. planirostris* as well as the areas where it is plausible they may disperse to from their current introduced ranges. The resulting consensus map for each species formed the baseline against which future modeling scenarios were compared.

Although AUC scores were used to determine the weight of each replicate in each set, there has been some criticism of their use in evaluating the accuracy of statistical models (Lobo et al. 2008). We therefore opted to report partial receiver operating characteristics (pROC) as a measure of each current potential distribution model's accuracy, such that a score ≥ 1.80 is considered well supported. Each pROC value and its corresponding standard deviation (SD) was calculated using the SDM performance function in NicheToolBox (Osorio-Olvera et al. 2020). The pROC value is only applicable to current projection models.

To draw consistent comparisons between different models, the reclassify spatial analyst tool in ArcGIS Pro was used to convert the current distribution models into binary maps in which presence = 1 and absence = 0, using the 10th percentile training presence omission value produced by Maxent as the threshold, chosen for its relatively conservative criteria (Pearson et al. 2007, Radosavljevic and Anderson 2013).

Table 1. Description of the WorldClim bioclimatic variables used to model current and future species distribution, accompanied by percent contribution to the modeling of each species if used. Temperature is measured in Celsius, and precipitation is measured in millimeters.

| Variable | Definition | Percent contribution to <i>E. cystignathoides</i> modeling | Percent contribution to <i>E. planirostris</i> modeling |
|--------------|--|--|---|
| <i>bio_1</i> | Annual Mean Temperature | | 16 |
| | Mean Diurnal Range | | |
| <i>bio_2</i> | (Mean of monthly (max temp–min temp)) | 28.7 | 1.4 |
| <i>bio_3</i> | Isothermality ($\text{bio}_2/\text{bio}_7$)*100 | 2.3 | 1.4 |
| <i>bio_5</i> | Max Temperature of Warmest Month | 2.2 | 10.7 |
| <i>bio_6</i> | Min Temperature of Coldest Month | 28.4 | |
| <i>bio_8</i> | Mean Temperature of Wettest Quarter | 19.4 | 43.7 |

Table 1, cont.

| Variable | Definition | Percent contribution to <i>E.</i> <i>cystignathoides</i> modeling | Percent contribution to <i>E.</i> <i>planirostris</i> modeling |
|---------------|---------------------------------------|--|---|
| <i>bio_9</i> | Mean Temperature of Driest Quarter | 8.8 | 10.1 |
| <i>bio_12</i> | Annual Precipitation | 1.1 | 1.4 |
| <i>bio_13</i> | Precipitation of Wettest Month | 5.4 | |
| <i>bio_14</i> | Precipitation of Driest Month | 3.6 | 1.1 |
| <i>bio_18</i> | Precipitation of Warmest Quarter | | 14.2 |

CHAPTER III

RESULTS

Current potentially suitable habitat

Eleutherodactylus cystignathoides

The current potentially suitable habitat for *E. cystignathoides* (Fig. 1) showed high performance (pROC = 1.93, SD = 0.01). A jackknife test revealed the relative contribution of each bioclimatic variable to the models' distribution of potentially suitable habitat (Table 1), with the highest contributions from bio_2 (Mean Diurnal Range, 28.7%), bio_6 (Min Temperature of Coldest Month, 28.4%), and bio_8 (Mean Temperature of Wettest Quarter, 19.4%; Table 1). The current projection identified 657,029 km² of potentially suitable habitat out of the 9,473,303 km² of land included in the model for *E. cystignathoides* (Table 2). The distribution of current potentially suitable habitat for *E. cystignathoides* includes much of its known introduced and native range along the Gulf Coast as well as in central Texas, USA (Fig. 1). However, areas which are not currently known to host this species are also predicted to be potentially suitable habitat, particularly southern Florida, USA and coastal Mississippi, USA, Georgia, USA, North Carolina, USA, and Virginia, USA.

Eleutherodactylus planirostris

The *E. planirostris* current potentially suitable habitat (Fig. 2) was similarly well supported (pROC = 1.94, SD = 0.01), with the highest contributions from bio_8 (Mean Temperature of Wettest Quarter, 43.7%), bio_1 (Annual Mean Temperature, 16%), and bio_18

(Precipitation of Warmest Quarter, 14.2%; Table 1). The projection identified 592,884 km² of potentially suitable habitat out of the 9473303km² included in the model (Table 3). Like *E. cystignathoides*, the distribution of current potentially suitable habitat for *E. planirostris* includes much of its known native range in the Caribbean and invasive range along the Gulf Coast from Florida to Texas and Mexico (Fig. 1). This projection does not support the scattered observations found in the GBIF database of individuals observed farther north, in areas such as in Memphis, Tennessee, USA or St. Louis, Missouri, USA (GBIF 2021), suggesting that these occurrences may represent introduced individuals or errors rather than established populations.

Future potentially suitable habitat

Eleutherodactylus cystignathoides

Generally, the CM3 projections (Fig. 3) of potentially suitable habitat for *E. cystignathoides* show a northward expansion along the eastern coast as well as a contraction from the non-coastal portions of its current introduced and native habitat. Most visually striking is the loss of habitat in central Texas, where robust introduced populations of this species are known, but it is of note that all CM3 projections predict the loss of native habitat in south Texas. The most conservative projection, representing the year 2050 under an intermediate emissions scenario, predicts the existence of potentially suitable habitat as far north as the southern portion of the Delmarva Peninsula (Fig. 3A). Both the high emissions scenario for the same year (Fig. 3B) and the same emissions scenario for year 2070 (Fig. 3C) predict further expansion of potentially suitable habitat to parts of New Jersey, USA and Long Island, New York, USA. The most extreme projection, CM3-RCP8.5-2070 (Fig. 3D), does not expand coastal habitat further north, but rather predicts greater habitat gain inland from the coast and around the Great Lakes in the northeastern USA. Finally, the CM3-RCP4.5-2050, CM3-RCP8.5-2050, and CM3-RCP4.5-

2070 projections (Figs. 3A–C) all predict loss of habitat in southern Florida. The CM3 model predicts less total area of potentially suitable habitat than the other two models (Table 2).

Unlike the projections produced by the CM3 model, the CMPI5 projections (Fig. 4) predict the existence of potentially suitable habitat farther inland, retaining non-coastal habitat in Texas in the current introduced range. Interestingly, sizeable pockets of suitable habitat are predicted in the areas near Little Rock, Arkansas, USA and Memphis, Tennessee. Loss of potentially suitable habitat is seen along the Gulf Coast between Florida and Louisiana, USA as well as in southern Florida. In contrast to model CM3 as well as the current projection, habitat is not predicted in the southern portion of the Delmarva Peninsula. Additionally, unlike the aforementioned projections, the CMIP5-RCP4.5-2050 and CMIP5-RCP4.5-2070 projections (Figs. 4A, C) suggest nearly contiguous habitat along the east coast approximately from West Palm Beach, Florida to the Chesapeake Bay area. The CMIP5-RCP8.5-2070 projection (Fig. 4D) is similar apart from indicating the loss of habitat along much of the eastern Florida coast, while the CMIP5-RCP4.5-2070 projection (Fig. 4C) shows a gap along the coast of the Carolinas. All four projections predict loss of potentially suitable habitat in coastal Mississippi, USA and Alabama, USA as well as the Florida panhandle.

Similar to the CM3 model, the HadGEM2 projections (Fig. 5) predict loss of potentially suitable habitat in central Texas and parts of the native range in Mexico. The HadGEM2-RCP8.5-2050 and HadGEM2-RCP4.5-2070 projections (Figs. 5A, C) also predict the loss of suitable habitat in the native range in Texas. The pattern of inland potentially suitable habitat is continued from the CMIP5 projections, with the largest patches found in the same approximate areas around Little Rock, Arkansas and Memphis, Tennessee, though they are accompanied by an area around Dallas, Texas, as well. These HadGEM2 projections (Fig. 5) predict suitable

habitat in southwest Louisiana, USA that is not found in the current projection. They also predict loss of potentially suitable habitat in southern Florida as well as coastal Alabama and Mississippi, like the CMIP5 projections (Fig. 4) and the CM3-RCP4.5-2050, CM3-RCP8.5-2050, and CM3-RCP4.5-2070 projections (Figs. 3A–C). Akin to what was seen in the CMIP5 projections (Fig. 4), the HadGEM2 projections (Fig. 5) suggest contiguous potentially suitable habitat along the East Coast from Florida to Delaware, USA, though with more area inland of the coast included. Out of the three models used in the present study, the projections for HadGEM2 predict the largest total areas of potentially suitable habitat (Table 2).

Eleutherodactylus planirostris

In contrast to the projections for *E. cystignathoides*, future projections for *E. planirostris* show dramatic decreases in potentially suitable habitat. The CM3 projections (Fig. 6) predict the loss of potentially suitable habitat in the majority of this species' native and invasive range. All four projections indicate virtually total loss of potentially suitable habitat in the continental southeastern USA as well as in the northern islands of the native Bahamas. Notably, much of the native range in Cuba is predicted to become bioclimatically unsuitable as well. As was the case with *E. cystignathoides*, the CM3 projections predict less total area of potentially suitable habitat than those produced by the other two models.

The CMIP5 projections (Fig. 7) also predict massive losses of potentially suitable habitat both in the invasive continental USA range and in the native Caribbean range. Rather than total loss as seen in the CM3 projections, however, potentially suitable habitat is variably retained in coastal Mississippi and Alabama (Figs. 7B–C), parts of Louisiana (Figs. 7A–C), and parts of the east coast of Florida (Fig. 7). Similarly, somewhat more potentially suitable habitat is retained in northern Cuba and the Bahamas (Figs. 7). While the current distribution of potentially suitable

habitat for *E. planirostris* does not range much further north than Charleston, South Carolina, USA (Fig. 2), the CMIP5 projections (Figs. 7) indicate future potentially suitable habitat along the coast into North Carolina, USA. Potentially suitable habitat appears to expand in eastern Honduras and Nicaragua in these projections as well.

Habitat loss is widespread in the HadGEM2 projections (Fig. 8) for *E. planirostris*. The HadGEM2-RCP4.5-2050 projection (Fig. 8A) shows potentially suitable habitat along parts of the east coast from South Carolina, USA to Virginia, similar to the CMIP5- RCP4.5-2050 projection (Fig. 7A), and only small parts of Florida. Habitat loss is again observed in the native Cuban range, particularly in the northern portion. In accordance with the CMIP5 projections (Fig. 7), potentially suitable habitat is predicted in Nicaragua and Honduras, though the HadGEM2-RCP4.5-2050 projection (Fig. 8A) shows this potential habitat range farther inland. Habitat is further restricted in the intermediate scenarios represented by the HadGEM2-RCP4.5-2070 and HadGEM2-RCP8.5-2050 projections (Figs. 5B–C), in which all potentially suitable habitat in South Carolina is lost, but not to the extent observed in the HadGEM2-RCP8.5-2070 projection (Fig. 8D), which predicts virtually no suitable habitat within the continental USA or northern Cuba.

Table 2. Changes in potentially suitable habitat for *E. cystignathoides* (measured in km² and as percent change relative to contemporary distribution) for each climate scenario in 2050 and 2070.

| | <i>Present</i> | 2050 | | | | | |
|----------------------------------|----------------|----------------|--------------|----------------|----------------|--------------|----------------|
| | | RCP 4.5 | | | RCP 8.5 | | |
| | | CM3 | CMIP5 | HadGEM2 | CM3 | CMIP5 | HadGEM2 |
| Suitable area (km ²) | 657029 | 297122 | 502126 | 465058 | 387096 | 510929 | 572988 |
| Change (%) | | -54.78% | -23.58% | -29.22% | -41.08% | -22.24% | -12.79% |
| | | <hr/> | | | | | |
| | <i>Present</i> | 2070 | | | | | |
| | | RCP 4.5 | | | RCP 8.5 | | |
| | | CM3 | CMIP5 | HadGEM2 | CM3 | CMIP5 | HadGEM2 |
| Suitable area (km ²) | 657029 | 376625 | 512392 | 560996 | 671634 | 469470 | 612932 |
| Change (%) | | -42.68% | -22.01% | -14.62% | 2.22% | -28.55% | -6.71% |

Table 3. Changes in potentially suitable habitat for *E. planirostris* (measured in km² and as percent change relative to contemporary distribution) for each climate scenario in 2050 and 2070.

| | <i>Present</i> | 2050 | | | | | |
|-------------------------|----------------|----------------|--------------|----------------|----------------|--------------|----------------|
| | | RCP 4.5 | | | RCP 8.5 | | |
| | | CM3 | CMIP5 | HadGEM2 | CM3 | CMIP5 | HadGEM2 |
| Suitable | | | | | | | |
| area (km ²) | 592884 | 88072 | 209295 | 216360 | 97609 | 194784 | 207574 |
| Change | | | | | | | |
| (%) | | -85.15% | -64.70% | -63.51% | -83.54% | -67.15% | -64.99% |
| | <i>Present</i> | 2070 | | | | | |
| | | RCP 4.5 | | | RCP 8.5 | | |
| | | CM3 | CMIP5 | HadGEM2 | CM3 | CMIP5 | HadGEM2 |
| Suitable | | | | | | | |
| area (km ²) | 592884 | 95580 | 196993 | 227187 | 57745 | 173530 | 163614 |
| Change | | | | | | | |
| (%) | | -83.88% | -66.77% | -61.68% | -90.26% | -70.73% | -72.40% |

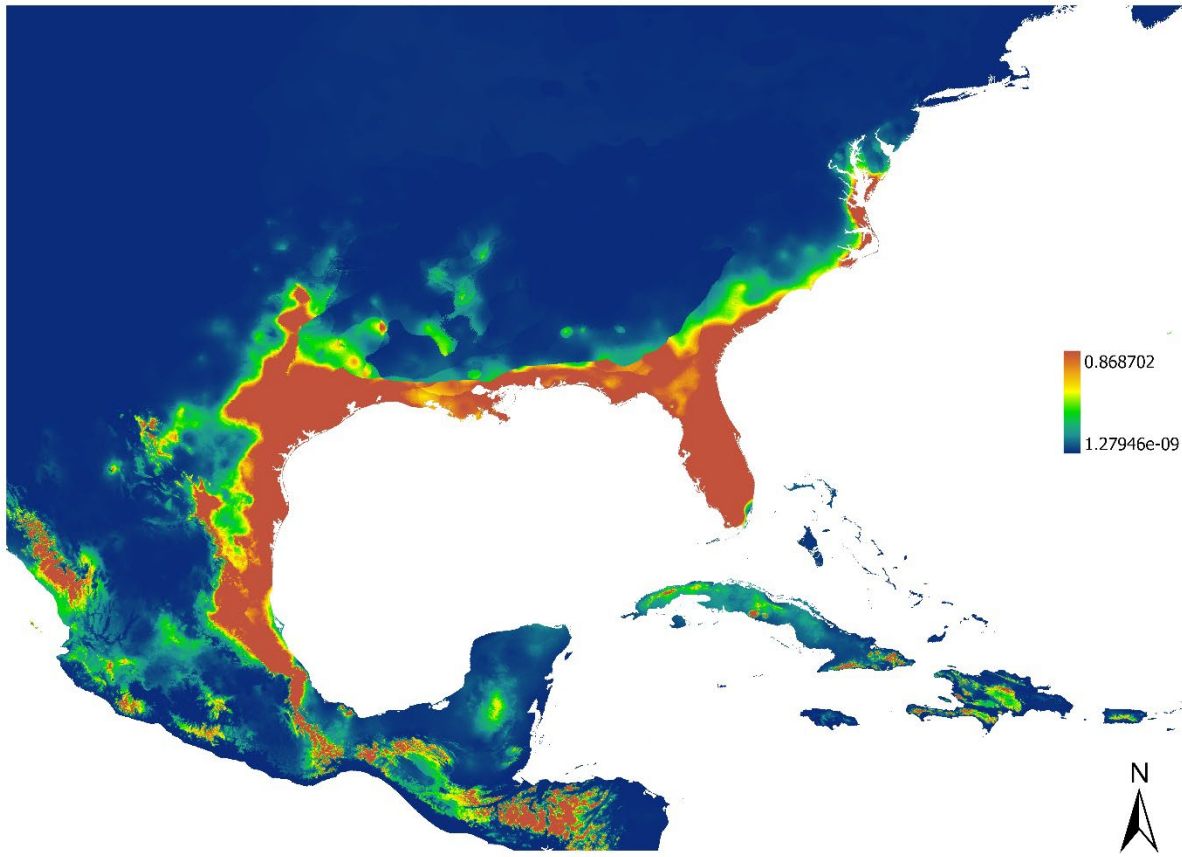


Figure 1. Consensus model of current geographic distribution of potentially suitable habitat for *E. cystignathoides* based on selected bioclimatic variables and rarefied occurrence data. Blue represents habitat predicted to be unsuitable while red represents potentially suitable habitat; green and yellow suggest partial suitability.

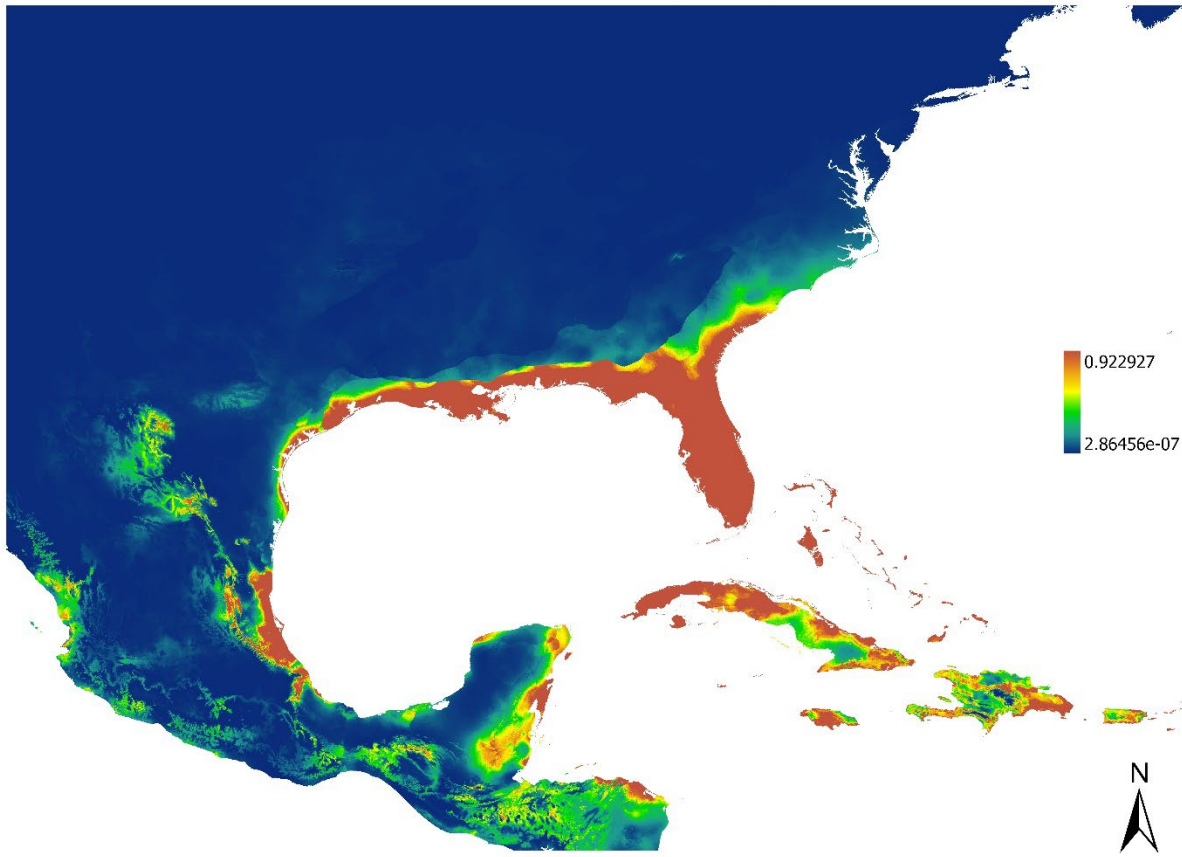


Figure 2. Consensus model of current geographic distribution of potentially suitable habitat for *E. planirostris* based on selected bioclimatic variables and rarefied occurrence data. Blue represents habitat predicted to be unsuitable while red represents potentially suitable habitat; green and yellow suggest partial suitability.

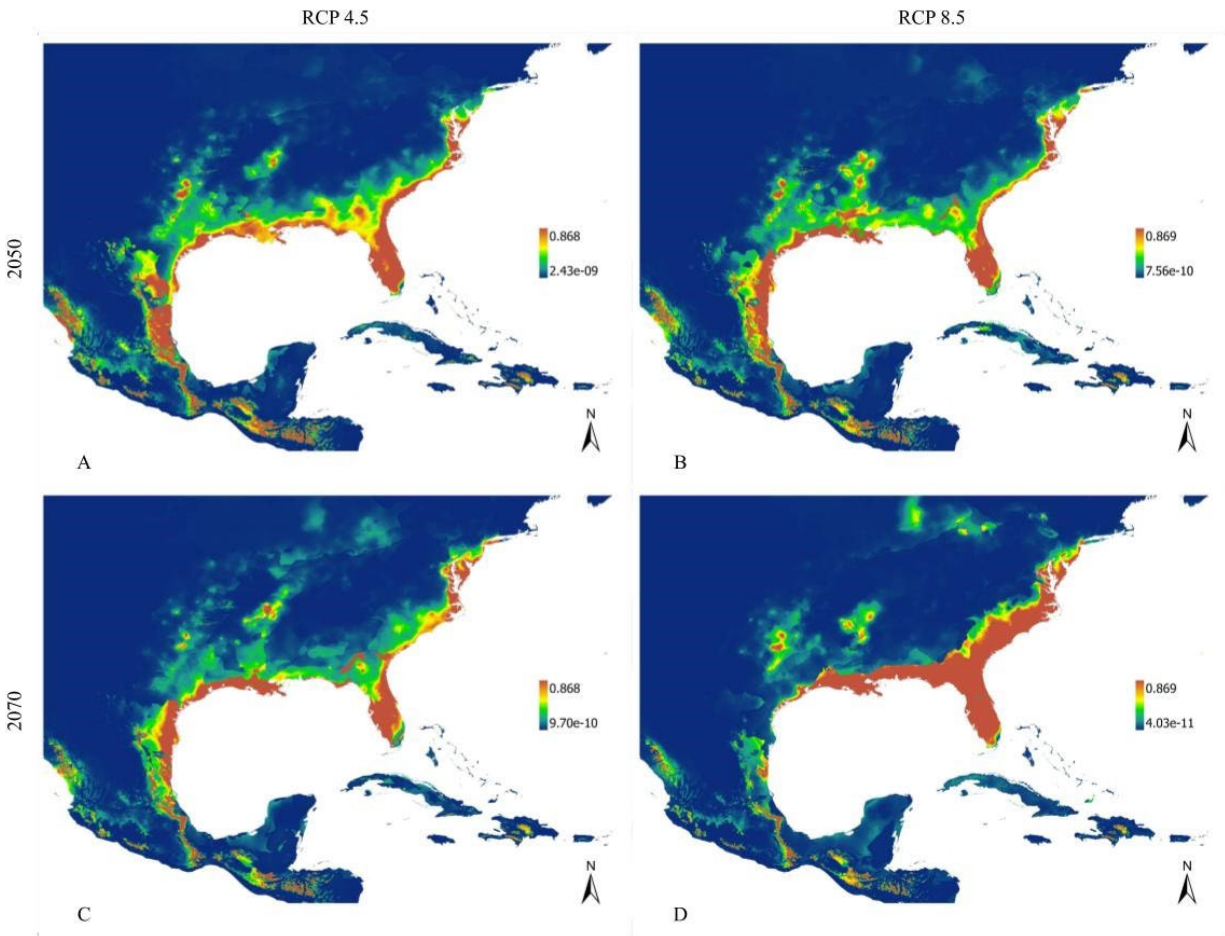


Figure 3. The CM3 consensus models of projected future geographic distribution of potentially suitable habitat for *E. cystignathoides* based on selected bioclimatic variables and rarefied occurrence data. The intermediate emissions scenario (RCP4.5) is on the left while the high emissions scenario (RCP8.5) is on the right; the projections made to approximate the year 2050 are on the top while those approximating the year 2070 are on the bottom. Blue represents habitat predicted to be unsuitable while red represents potentially suitable habitat; green and yellow suggest partial suitability.

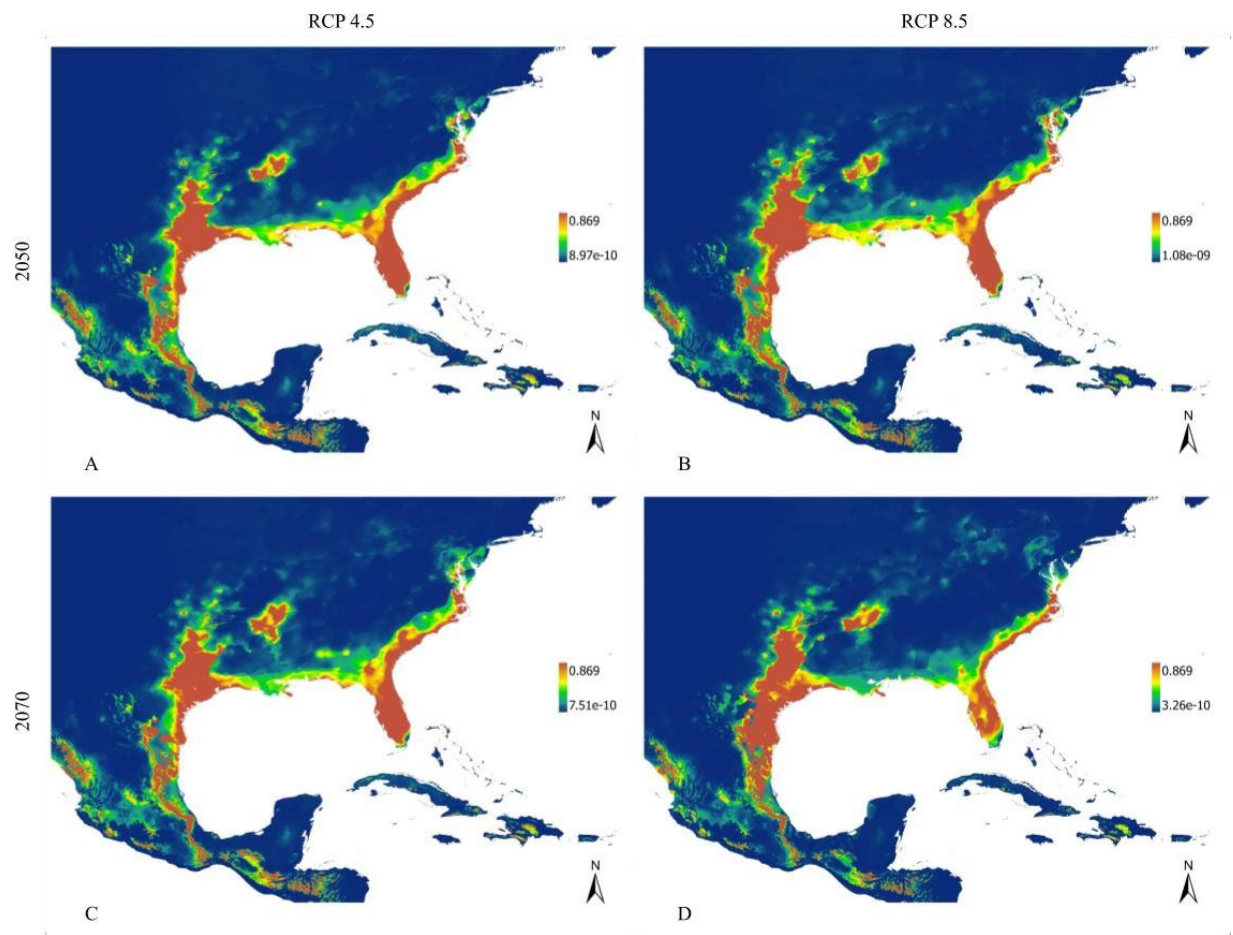


Figure 4. The CMIP5 consensus models of projected future geographic distribution of potentially suitable habitat for *E. cystignathoides* based on selected bioclimatic variables and rarefied occurrence data. The intermediate emissions scenario (RCP4.5) is on the left while the high emissions scenario (RCP8.5) is on the right; the projections made to approximate the year 2050 are on the top while those approximating the year 2070 are on the bottom. Blue represents habitat predicted to be unsuitable while red represents potentially suitable habitat; green and yellow suggest partial suitability.

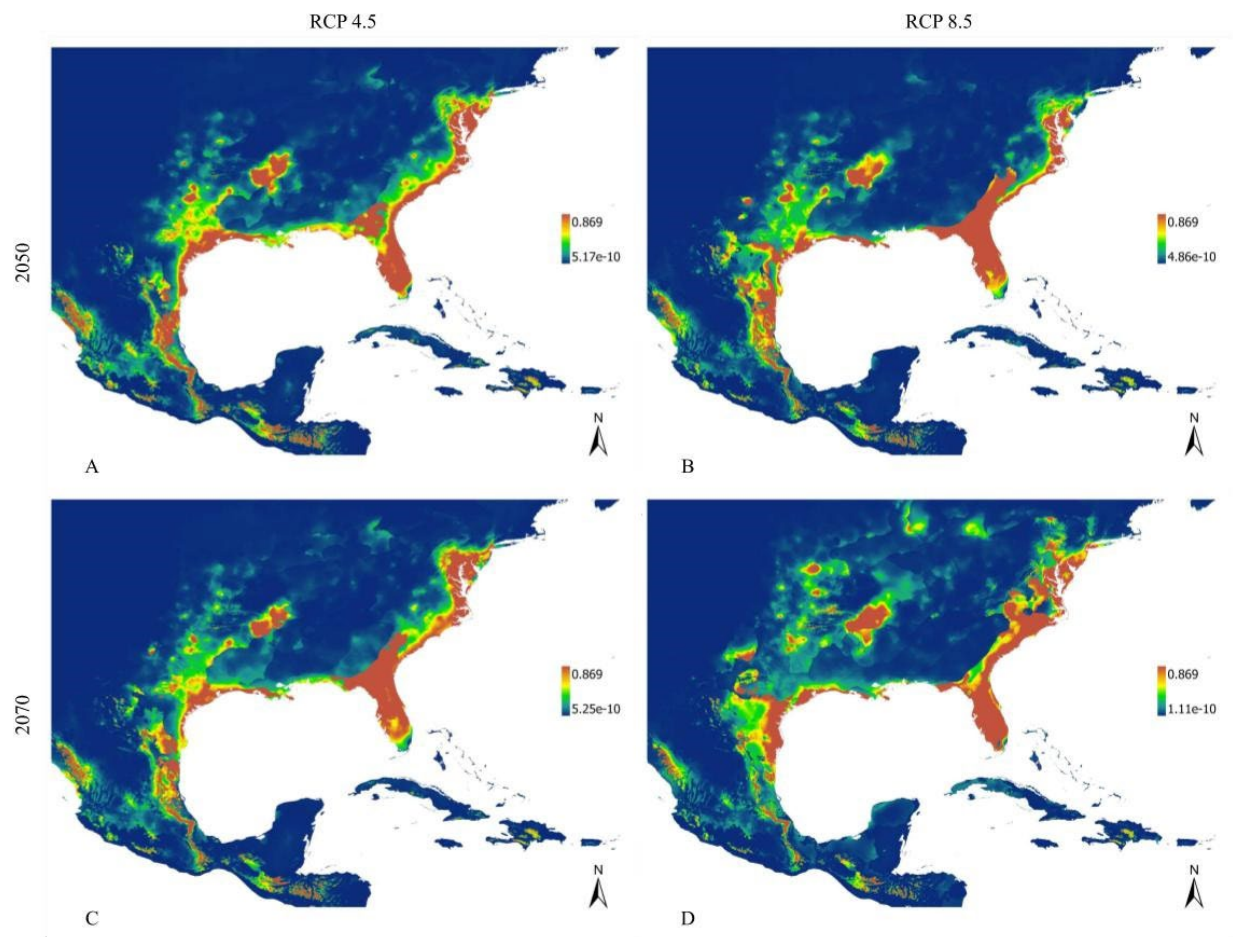


Figure 5. The HadGEM2 consensus models of projected future geographic distribution of potentially suitable habitat for *E. cystignathoides* based on selected bioclimatic variables and rarefied occurrence data. The intermediate emissions scenario (RCP4.5) is on the left while the high emissions scenario (RCP8.5) is on the right; the projections made to approximate the year 2050 are on the top while those approximating the year 2070 are on the bottom. Blue represents habitat predicted to be unsuitable while red represents potentially suitable habitat; green and yellow suggest partial suitability.

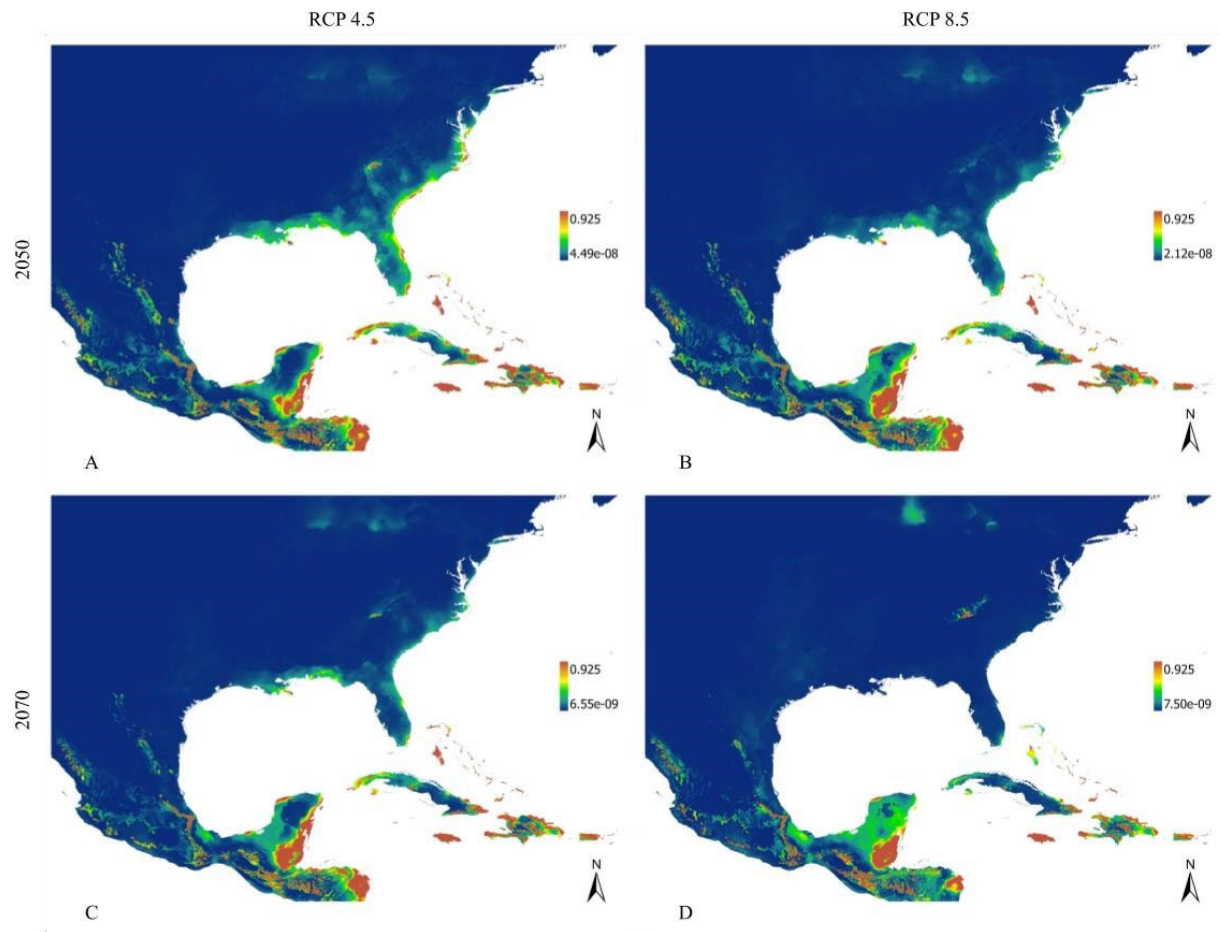


Figure 6. The CM3 consensus models of projected future geographic distribution of potentially suitable habitat for *E. planirostris* based on selected bioclimatic variables and rarefied occurrence data. The intermediate emissions scenario (RCP4.5) is on the left while the high emissions scenario (RCP8.5) is on the right; the projections made to approximate the year 2050 are on the top while those approximating the year 2070 are on the bottom. Blue represents habitat predicted to be unsuitable while red represents potentially suitable habitat; green and yellow suggest partial suitability.

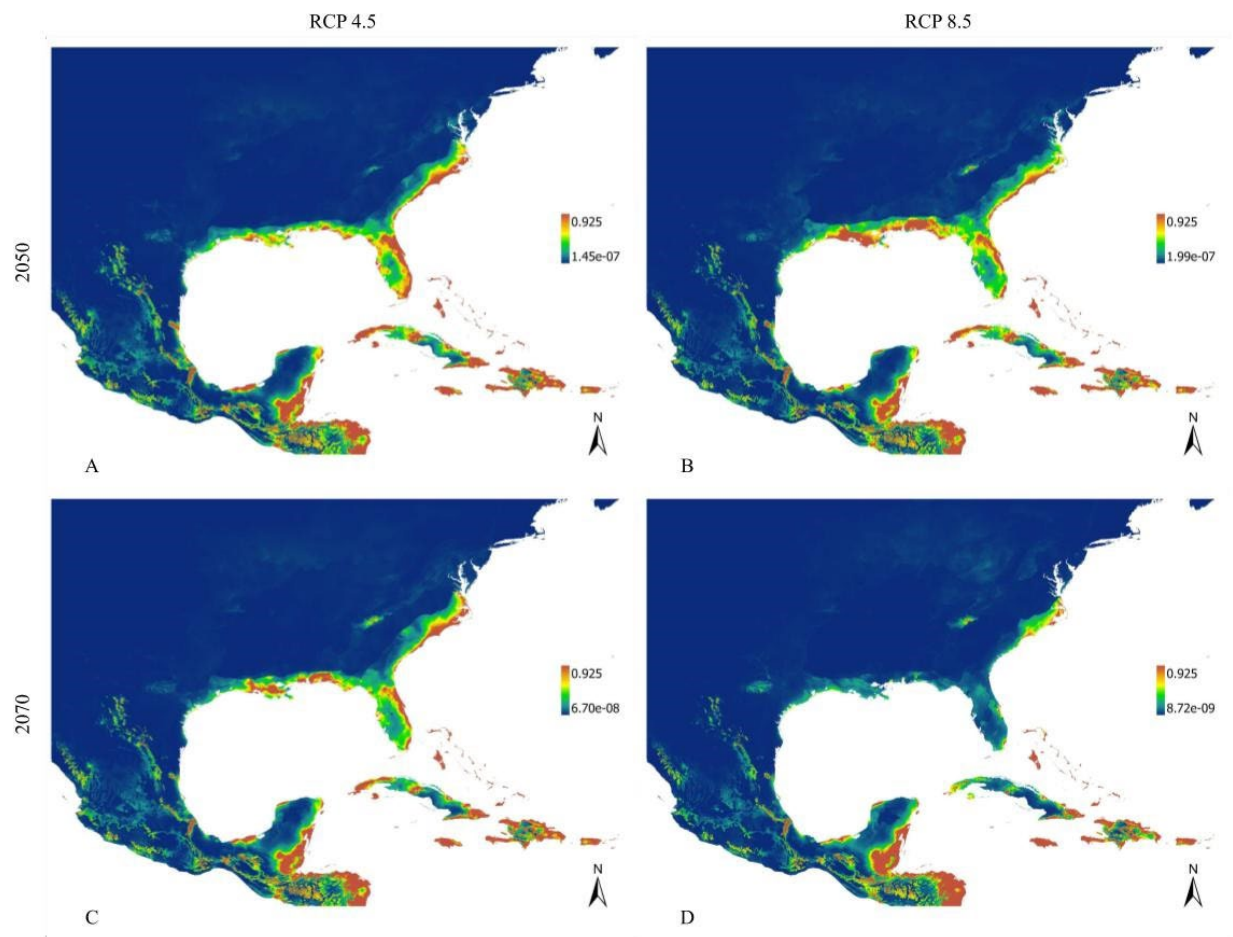


Figure 7. The CMIP5 consensus models of projected future geographic distribution of potentially suitable habitat for *E. planirostris* based on selected bioclimatic variables and rarefied occurrence data. The intermediate emissions scenario (RCP4.5) is on the left while the high emissions scenario (RCP8.5) is on the right; the projections made to approximate the year 2050 are on the top while those approximating the year 2070 are on the bottom. Blue represents habitat predicted to be unsuitable while red represents potentially suitable habitat; green and yellow suggest partial suitability.

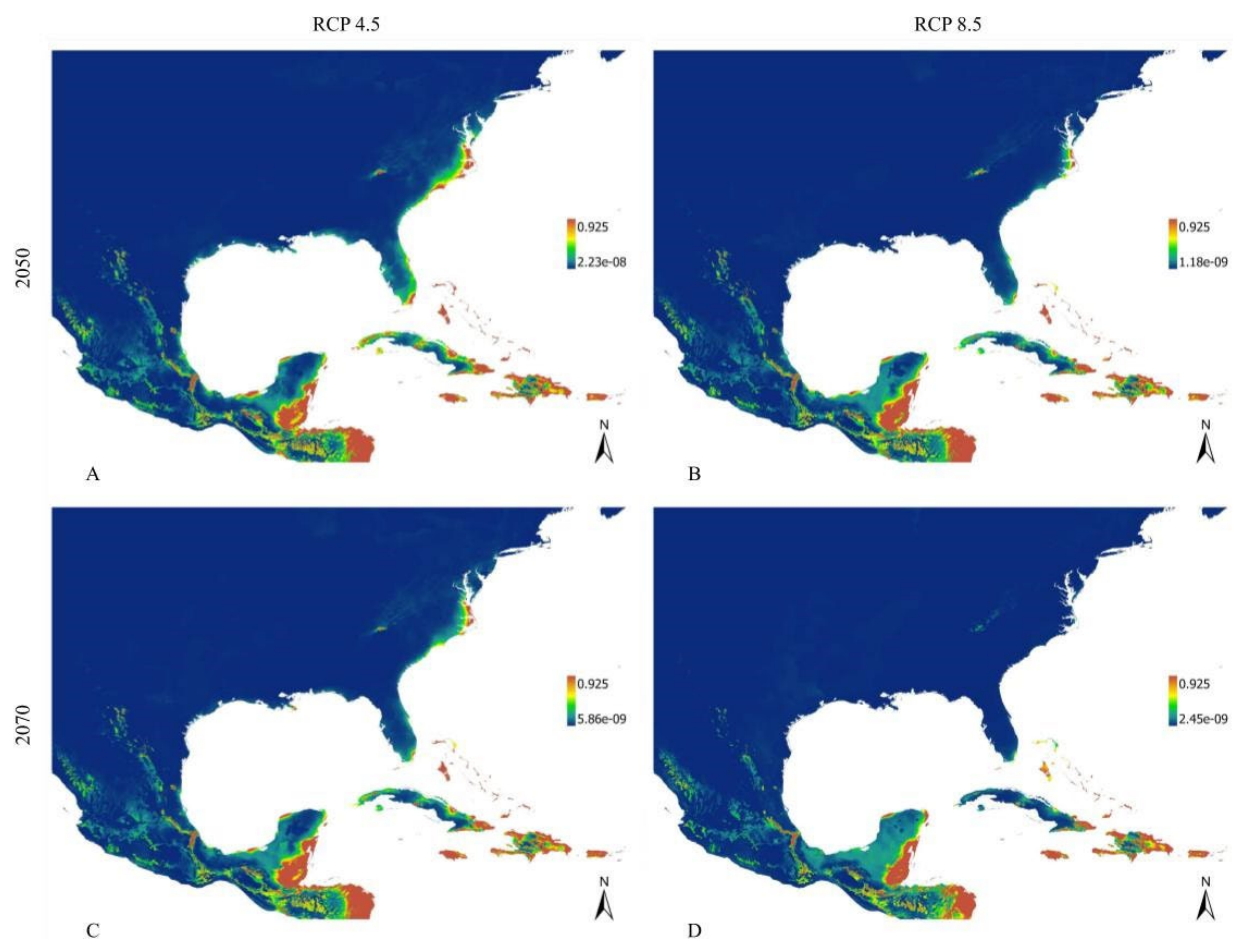


Figure 8. The HadGEM2 consensus models of projected future geographic distribution of potentially suitable habitat for *E. planirostris* based on selected bioclimatic variables and rarefied occurrence data. The intermediate emissions scenario (RCP4.5) is on the left while the high emissions scenario (RCP8.5) is on the right; the projections made to approximate the year 2050 are on the top while those approximating the year 2070 are on the bottom. Blue represents habitat predicted to be unsuitable while red represents potentially suitable habitat; green and yellow suggest partial suitability.

CHAPTER IV

DISCUSSION

Current potentially suitable habitat

Eleutherodactylus cystignathoides

The current projection for *E. cystignathoides* (Fig. 1, pROC = 1.93, SD = 0.01) predicts potentially suitable habitat based on bioclimatic variables in most of the currently recognized distribution of the species, although with several exceptions. The spatially rarefied occurrence data includes nearly a dozen occurrences in Louisiana, USA, where multiple populations are thought to be established, but very little of this habitat qualified for the cutoff imposed by the training threshold. There is also a notable set of occurrences outside of the potentially suitable habitat range in northeastern Texas, USA. Other occurrences outside the predicted range exist, but they are more isolated. This suggests that the model may be conservative in predictions made about the limiting nature of some of the included bioclimatic variables, with type II error favored over type I. Some occurrences which have been validated but which represented outliers unsupported by additional observations were excluded from the model to reduce the chances of including observations which do not represent established populations. However, the model predicted the existence of suitable habitat encompassing certain excluded occurrences which were distant from the rest of the species' known range, such as in southern Alabama, USA (GBIFa 2021). This observation provides additional support for the predictive power of the

model when projected over areas excluded from the training map and suggests that some of those isolated observations might represent established populations.

Additional potentially suitable habitat was predicted east of the current known range of *E. cystignathoides*, including coastal Mississippi, USA and Georgia, USA, parts of coastal Louisiana and Alabama, and much of Florida, USA, as well as north along the Atlantic Coast, encompassing parts of South Carolina, USA, North Carolina, USA, Virginia, USA, and Maryland, USA. These findings are surprisingly far north given that *E. cystignathoides* is a neotropical species, but it should be noted that its thermal limitations have not been studied. While no such research has been conducted on *E. cystignathoides*, there is a study which examines critical thermal minimum temperature (defined as the cooled frog being unable to right itself within 10 sec of being placed on its back) in *E. coqui*, a tropical invasive from the same genus (Haggerty 2016), which found that the critical minimum occurred between $\sim 3^{\circ}\text{--}8^{\circ}\text{C}$, meaning the individuals were still capable of movement in temperatures approaching freezing. Notably, no deaths resulted from reducing the temperature of the *E. coqui* into this range (Haggerty 2016). Additionally, there has been anecdotal evidence that the extreme winter weather which impacted North America in February of 2021 did not negatively impact the *E. cystignathoides* populations in areas such as central Texas, where temperatures fell below 0°C for nearly a week straight (T. J. LaDuc personal communication 2021). Perhaps *E. cystignathoides* is able to withstand more extreme winter weather than is found in its native range, as was suggested in Lott (2019). Further research into the thermal limitations of this species could elucidate this aspect of its biology and allow for a better understanding of the range limits of this species.

Eleutherodactylus planirostris

The current projection for *E. planirostris* (Fig. 2, pROC = 1.94, SD = 0.01) does not predict the existence of much potentially suitable habitat beyond known occurrences, though there is some, namely in the island of Hispaniola as well as Puerto Rico, USA and the southern islands of the Bahamas. Introductions in those areas may be a cause for concern. In the continental USA, however, the distribution of potentially suitable habitat largely aligns with the occurrence data in pattern, with many of the small gaps between occurrences filled in. The potentially suitable habitat is virtually contiguous from the coast of South Carolina to just south of the USA–Mexico border in the lower Rio Grande Valley. The total area estimated to be suitable for *E. planirostris* (592,884km²; Table 3) is less than that estimated for *E. cystignathoides* (657,029km²; Table 2). The two distributions exhibit a lot of overlap, meaning that much of the coastline in the southeastern USA is potentially vulnerable to simultaneous occupation by both species. The potential interactions between these two species and the combined effect of those interactions on communities and habitats where they are introduced is a topic which warrants further investigation.

Future potentially suitable habitat

The future projections for *E. cystignathoides* and *E. planirostris* are divided into three major categories based on the general circulation models they were based upon: CM3 (Figs. 3, 6), CMIP5 (Figs. 4, 7), and HadGEM2 (Figs. 5, 8). Within each of these general circulation models, alternative projections were produced for an intermediate (RCP4.5 2050 and RCP4.5 2070 of Figs. 3–8) and high (RCP8.5 2050 and RCP8.5 2070 of Figs. 3–8) emissions scenario, as well as the years 2050 (RCP4.5 2050 and RCP8.5 2050 of Figs. 3–8) and 2070 (RCP4.5 2070 and RCP8.5 2070 of Figs. 3–8). For both species, CM3 projections predict the smallest total

areas and therefore likely represent the most conservative prediction of potentially suitable habitat presented in this paper. The CMIP5 and HadGEM2 projections did not exhibit a particular pattern in relative area of habitat predicted to be suitable.

E. cystignathoides

The CM3 projections (Fig. 3) for *E. cystignathoides* showed agreement with the generally observed trend of species ranges shifting away from the equator in response to climate change (Parmesan and Yohe 2003), with potentially suitable habitat gained in more northern areas, such as along the eastern coast, and lost in southern areas, as is seen in southern Florida and Central America. As is argued by VanDerWal et al. (2013), range shifts are more complex than simple latitudinal movement. The CM3-RCP4.5-2050, CM3-RCP8.5-2050, and CM3-RCP4.5-2070 projections (Figs. 3A–C) predict the loss of habitat in central Texas, for example, apart from small patches near Dallas. There is a visible trend in all CM3 projections towards coastal areas, though the CM3-RCP8.5-2070 projection (Fig. 3D) predicts additional inland habitat. The CM3-RCP8.5-2070 projection (Fig. 3D) predicts loss of habitat in the native range. In the CM3-RCP8.5-2050 and CM3-RCP4.5-2070 projections (Fig. 3B–C), habitat absent from the current projection is predicted to be gained in coastal Louisiana, though the projections do not take into account the physical structure of the habitat; it is possible that such these wetlands represent unsuitable habitat for this terrestrial species.

By contrast, the CMIP5 future projections for *E. cystignathoides* (Fig. 4) do not align as closely with the pattern of coastal affiliation seen in Fig. 3. These projections predict maintenance of much of the Texas distribution of potentially suitable habitat, albeit with some losses towards the west, as well as an expansion in northeast Texas, where there are already a few recorded occurrences. There are additional areas of predicted suitable habitat farther inland,

along the Mississippi River Valley in Arkansas, USA and Tennessee, USA, as well as near Oklahoma City, Oklahoma, USA. Some of the distribution in Arkansas is also supported by the CM3-RCP4.5-2070 and, to a lesser extent, CM3-RCP8.5-2050 projections (Fig. 3B–C). The CMIP5 projections do not extend as far north as those produced for CM3, but they do predict the inclusion of more of the Atlantic Coast; the CMIP5-RCP4.5-2050 and CMIP5-RCP4.5-2070 projections (Figs. 4A, C) predict nearly contiguous potentially suitable habitat from Florida to Virginia. However, far less of the Gulf Coast is included in the predictions made by the CMIP5 projections than those of CM3. The CM3-RCP8.5-2050 and CM3-RCP4.5-2070 projections (Figs. 3B–C) predict habitat in most of southern Louisiana, while in the CMIP5 projections (Fig. 4), only the Louisiana coast west of Vermillion Bay and along the lowest lobe of the Mississippi River Delta are included. Similarly, far less habitat is predicted in coastal Mississippi, Alabama, and the Florida panhandle, with what little there is restricted primarily to the barrier islands and adjacent shorelines.

Like the projections presented in Fig. 3, the HadGEM2 projections (Fig. 5) predict the loss of suitable habitat in much of central Texas, although not to the same extent. In keeping with the other predictions (Figs. 3, 4), the HadGEM2 projections (Fig. 5) also suggests that parts of southern Florida will become bioclimatically unsuitable under future conditions, although some of this habitat is reclaimed in the most extreme projection (Fig. 5D), as is the habitat loss predicted in the native range by the more conservative projections. The HadGEM2 projections (Fig. 5) support the potentially suitable habitat identified previously in the Mississippi River Valley as well (Figs. 3B–C; Fig. 4).

Eleutherodactylus planirostris

In contrast with the projections produced for *E. cystignathoides*, those concerning *E. planirostris* predict dramatic habitat contraction in all future climate scenarios (Figs. 6–8), including the loss of virtually all inland habitat in the continental USA in some projections. For example, the CM3 projections (Fig. 6) for this species predict the loss of all USA habitat except small areas on the border of South Carolina and Tennessee (Fig. 6A), near Cape Canaveral, Florida (Fig. 6A), and around Cape Hatteras, North Carolina (Figs. 6A–B). The habitat near the South Carolina-Tennessee border and in Cape Hatteras represent novel potentially suitable habitat gains when compared to the current projection (Fig. 2). Notably, the CM3-RCP4.5-2070 projection (Fig. 6C) predicts no potentially suitable habitat in the continental USA at all. The CM3-RCP4.5-2050, CM3-RCP8.5-2050, and CM3-RCP4.5-2070 projections (Figs. 6A–C) also predict the loss of much of the current potentially suitable habitat in the native range of *E. planirostris* in Cuba. The overall trend in the region of the Antilles included in this analysis is an equatorward shift in potentially suitable habitat; for example, habitat is lost in northern Cuba, but retained in coastal southern Cuba and Jamaica (Figs. 6A–C).

The CMIP5 model projections for *E. planirostris* (Fig. 7) predict a similar pattern to that found in the CM3 projections (Fig. 6), but with more potentially suitable habitat found along the coasts of the USA. The CMIP5-RCP4.5-2050, CMIP5-RCP8.5-2050, and CMIP5-RCP4.5-2070 projections (Figs. 7A–C) predict disjointed habitat along the eastern coast of Florida and as far north as North Carolina, as well as in the Florida Keys. The CMIP5-RCP4.5-2050 projection (Fig. 5A) predicts a very small amount of potentially suitable habitat in the Florida panhandle, and while the CMIP5-RCP8.5-2050 and CMIP5-RCP4.5-2070 projections (Figs. 7B–C) agree with that prediction, they both expand upon it, suggesting the future presence of potentially

suitable habitat further inland and more widespread along the coast, particularly in coastal Alabama. Both of these scenarios predict an increase in potentially suitable habitat in coastal Louisiana as well, suggesting that climate change will have a nonlinear influence on habitat suitability at a fine scale along the coast. The CMIP5-RCP8.5-2070 projection (Fig. 7D) more closely resembles the CM3-RCP4.5-2050, CM3-RCP8.5-2050, and CM3-RCP4.5-2070 projections (Figs. 6A–C) when examining habitat within the USA, showing a near total loss of potential habitat with the exception of very small areas south of Cape Canaveral, near Miami, Florida, and in the Florida Keys. Most of the CMIP5 projections for this species (Figs. 7A–C) do not demonstrate the same southern shift seen in the Antilles in the CM3 projections (Fig. 6), instead seeming to favor movement towards the coasts. However, habitat loss is still predicted in the native Cuban range and the southern shift is predicted in the CMIP5-RCP8.5-2070 projection (Fig. 7D).

The HadGEM2 model (Fig. 8) future projections predict an intermediate amount of coastal territory in the USA compared to those produced by the CM3 (Fig. 6) and CMIP5 (Fig. 7) models. Looking along the East Coast, the HadGEM2-RCP4.5-2050 projection (Fig. 8A) resembles projections in the CMIP5 model (Fig. 7), with scattered habitat predicted in coastal North and South Carolina. Notably, however, the HadGEM2-RCP4.5-2050 projection (Fig. 8A) reaches further north than the other projections, into coastal Virginia. The HadGEM2-RCP4.5-2050 projection (Fig. 8A) also predicts habitat along the South Carolina–Tennessee border, as was seen in the CM3-RCP4.5-2050 projection (Fig. 6A). However, in examining the Florida coast, the HadGEM2-RCP4.5-2050 projection (Fig. 8A) more closely resembles the CMIP5-RCP4.5-2050, CMIP5-RCP8.5-2050, and CMIP5-RCP4.5-2070 projections (Figs. 7A–C), with habitat predicted in and around Cape Canaveral and Miami, Florida as well as the Florida Keys.

As was seen in projections from the CM3 and CMIP5 models (Figs. 6, 7), major habitat loss is predicted in the native range as well. The HadGEM2-RCP8.5-2050 and HadGEM2-RCP4.5-2070 projections (Figs. 8B–C) show further contractions of continental USA potentially suitable habitat, which is virtually lost altogether in the HadGEM2-RCP8.5-2070 projection (Fig. 8D). The same progressive pattern of potentially suitable habitat across the HadGEM2 projections loss is observed in western Cuba (Fig. 8).

Comparison

In summation, the future projections for *E. cystignathoides* and *E. planirostris* are decidedly divergent from one another, with potentially suitable habitat for *E. cystignathoides* predicted to see dynamic range expansions and contractions while potentially suitable habitat for *E. planirostris* is largely only predicted to contract. Relationships within each set of projections differ as well; the projections for *E. planirostris* resemble each other to a greater degree than do those for *E. cystignathoides*. Broadly, there are also similarities between the *E. cystignathoides* projections, but variation is notable in the amount of inland versus coastal habitat predicted as well as the predicted suitability of habitat in the native range (for example, compare Fig. 3 with Fig. 4).

The cause of this divergence is indeterminate given the ecological data—or lack thereof, in the case of *E. planirostris*—available to contextualize differences between these two species, inviting future research on the topic. However, some preliminary hypotheses may be posited based on differences in the relative contributions of various bioclimatic variables to modeling each species (Table 1). The two bioclimatic factors that most influenced the *E. cystignathoides* modeling were bio_2 (28.7%), which is defined as the average of the temperature range for each month, and bio_6 (28.4%), which represents minimum temperature of the coldest month (Table

1). The importance of bio_2 to modeling could be interpreted to suggest that *E. cystignathoides* is better suited to areas without large swings in temperature, while the high contribution of bio_6 might suggest that there is a temperature below which this species simply cannot survive, or that areas with lower minimum temperatures in their coldest month are more likely to have winters lasting too long for this species to persist. For the *E. planirostris* modeling, the most important factor was bio_8 (43.7%), representing the mean temperature of the wettest quarter, which could be interpreted to mean that *E. planirostris* requires rainy summers in order to reproduce. It has been documented that this species has the highest rate of egg survival at 100% humidity (Lazell 1989), which has been interpreted as evidence of reliance on heavy rainfall during reproductive activity (Rödger and Lötters 2010). Perhaps *E. cystignathoides*, which is naturally occurring in areas with frequent draughts, such as the lower Rio Grande Valley in southern Texas, is better suited for the decrease in precipitation and irregularity of rain events expected under climate change conditions.

In context

The projections reported here provide mixed support (with *E. cystignathoides* projections generally aligning and *E. planirostris* opposing) for the broad findings that under anthropogenic climate change, many species will or are already demonstrating shifts in distribution to higher elevations and more poleward habitat (Chen et al. 2011), supporting the supposition that complex responses to climate change should be expected (VanDerWal et al. 2013). Additionally, these projections support the finding that even those amphibians which demonstrate the capability of invasion and dispersal can show losses of potentially suitable habitat in other parts of their range (Lawler et al. 2010). These projections suggest that in the future, *E. cystignathoides* and *E. planirostris* may even join the ranks of other species which are ironically

both invasive outside their native range and threatened within it, such as the arapaima or the Monterey pine (Marchetti and Engstrom 2016).

However, it is vital to communicate that these models only suggest potentially suitable habitat based exclusively on the bioclimatic variables outlined in Table 1 and do not take into account any other potential influences of biotic or abiotic factors, such as the presence of urbanization and lawn maintenance, both of which have been implicated as facilitators in the spread of this species (Lott 2019). Additionally, projections onto different times and spaces cannot be free of other unknown variables or statistical limitations (Rödder and Lötters 2010). These caveats invite the question of what aspects of these projections are useful and realistic, particularly given the little information known about the ecology of *E. cystignathoides*. The exact dispersal method of this species is unknown, but it is thought to primarily occur in jump-dispersal events facilitated by the movement of potted plants via the horticultural trade (Lott 2019), similar to *E. planirostris*. This pattern would explain the city-outward trend seen over the last decades in the range expansion of these frogs, though of course the same trend could be explained via observation bias in more highly populated areas.

The horticultural trade is a profitable and robust sector of the Texas economy, and in Hidalgo and Cameron counties, which encompass much of the native range of this species in the USA, the sale of non-agricultural plants by growers in 2015 was estimated in the range of 10–25 and 25–50 million dollars, respectively (Palma and Hall 2019). How many of these plants are sold to out-of-state markets is not publicly accessible information. However, given the current global popularity of succulents and cacti (Haenni 2020) as well as the likelihood that drought- and heat-resistant ornamental plants (many of which are grown commercially in southern Texas as well) will see a rise in demand as the climate continues to make certain regions drier and

warmer (Webster et al. 2017), it is not unreasonable to think that some of these plants might end up being sold in areas with potentially suitable habitat and no currently established *E. cystignathoides* population. Such invasions due to nursery trade are not rare. For example, the trade of ornamental plants has recently been implicated in the introduction of *E. planirostris* to the Hong Kong region (Lee et al. 2016), but other examples of amphibians introduced via this pathway abound (Plenderleith et al. 2015, Barker and Rodríguez-Robles 2017, Measey et al. 2017, Padayachee et al. 2017, Lee et al. 2019, Sy and Ibañez 2020); for a review, see (Kraus 2007, 2009). Therefore, directing prevention and detection efforts to highly populated areas, with which this species is associated (Lott 2019), within the current and future potentially suitable habitat ranges would be prudent. For example, if one were interested in the status of this species in Florida, where the closely related *E. planirostris* has long been established as an invasive species (Olson et al. 2012), it would be pragmatic based on the models presented to listen for its distinctive call in the parks and suburbs of the Orlando metro area as well as to recommend precaution when importing plants from areas known to host *E. cystignathoides*.

As was discussed previously, it is not known what biological interactions *E. cystignathoides* may engage in or what broader impact they may have where they are introduced (see Lott 2019 for summary). Looking to the literature concerning other introduced *Eleutherodactylus* gives examples of both seemingly benign introduction and disruptive invasion, from the negative impact of *E. planirostris* and *E. coqui* on insect biodiversity in Hawaii, USA (Beard 2007, Beard et al. 2009, Olson et al. 2012) and as competitors for resources with native species or food sources for other non-native species (Olson et al. 2012) to the purportedly negligible impact of *E. johnstonei* in French Guiana (Ernst et al. 2011). Of particular

conservation concern is the question of whether *E. cystignathoides* will interact with other amphibians, particularly those which similarly occupy terrestrial microhabitats.

Hayes-Odum (1990) observed territorial behavior in *E. cystignathoides*, which has been interpreted as a potential cause of competition with fellow Texas endemic *E. marnockii* (Wallace 2005, Lott 2019). Wallace (2005), in addition to *E. marnockii*, lists other potential amphibian competitors with *E. cystignathoides*, including *Gastrophryne olivacea* and *Leptodactylus fragilis*, while also voicing the concern that *E. cystignathoides* may hybridize or spread diseases to *E. marnockii*. Whether the two species may hybridize is open for speculation, with no evidence thus far published which contradicts or supports this idea, nor any phylogenetic data available with which to attempt to evaluate the genetic divergence of the two species; however, it has been a frequently repeated concern about the expansion of *E. cystignathoides* since it became apparent that their distributions would overlap. While their known ranges coincide in central Texas, our models do not elevate concern for displacement or hybridization in habitat further west than what has already been observed. This does not preclude contact, however, and potential for the spread of pathogens to *E. marnockii* as well as other amphibian populations is still cause for concern.

Little research has been conducted into the diseases and parasites hosted by *E. cystignathoides*. Key exceptions include a study which tested five individuals collected as part of a larger survey in the mid-2000s for the presence of *Batrachochytrium dendrobatidis* (*Bd*) and found that they had all tested negative (Gómez et al. 2015) as well as a study which found widespread infection of *E. cystignathoides* near Houston, Texas with spiruroid parasites (McAllister and Freed 1992). Not much more is known about the pathogens of *E. marnockii*, which is only known to host one species of *Hannemania* mite (Malone and Paredes-Leon 2005), which has not been documented in *E. cystignathoides*. Other *Eleutherodactylus*, however, have

been demonstrated to host diseases of conservation concern. The invasive *E. coqui* and *E. planirostris*, for example, are known hosts of *Bd* and rat lungworm (*Angiostrongylus cantonensis*) in Hawaii (Beard and O'Neill 2005, Goodman et al. 2019); *E. planirostris* has additionally been observed to host *Bd* in its invasive range in Florida (Rizkalla 2010). This is of particular concern because *E. planirostris* and *E. cystignathoides* are already known to co-occur in Texas and our models predict both current and future potentially suitable habitat for *E. cystignathoides* in Florida, where *E. planirostris* is abundant (Figs. 1, 3–5). Should *E. cystignathoides* become infected with *Bd* in areas that overlap with *E. planirostris*, further introductions or re-introductions of *E. cystignathoides* could spread the disease in the parts of its introduced range which don't overlap, or even within the native range.

While outright alarm may be an inappropriate response to the findings presented here, caution and attention is warranted. Additional research into the ecology, dispersal, associated pathogens, and life history of *E. cystignathoides* is necessary to determine the relative risk—or, perhaps, lack thereof—posed by further introductions of *E. cystignathoides* into previously unoccupied habitats and communities. Furthermore, research into *E. cystignathoides* could facilitate a more informed comparison with *E. planirostris*, which may elucidate the question of why these two similar species demonstrate radically different trends in their future potentially suitable habitat predictions. This information in turn might enable asking broader questions about the factors that have caused the emergence of multiple successful invaders among the eleutherodactylids, connecting the ideas presented here to a general picture of the relationship between invasion and climate change among the amphibians looking forward.

APPENDIX A

APPENDIX A

RAREFIED OCCURRENCE DATASETS

The rarefied occurrence datasets for *E. cystignathoides* and *E. planirostris* used in the present paper are [have been made permanently available via Googles Sheets](#).

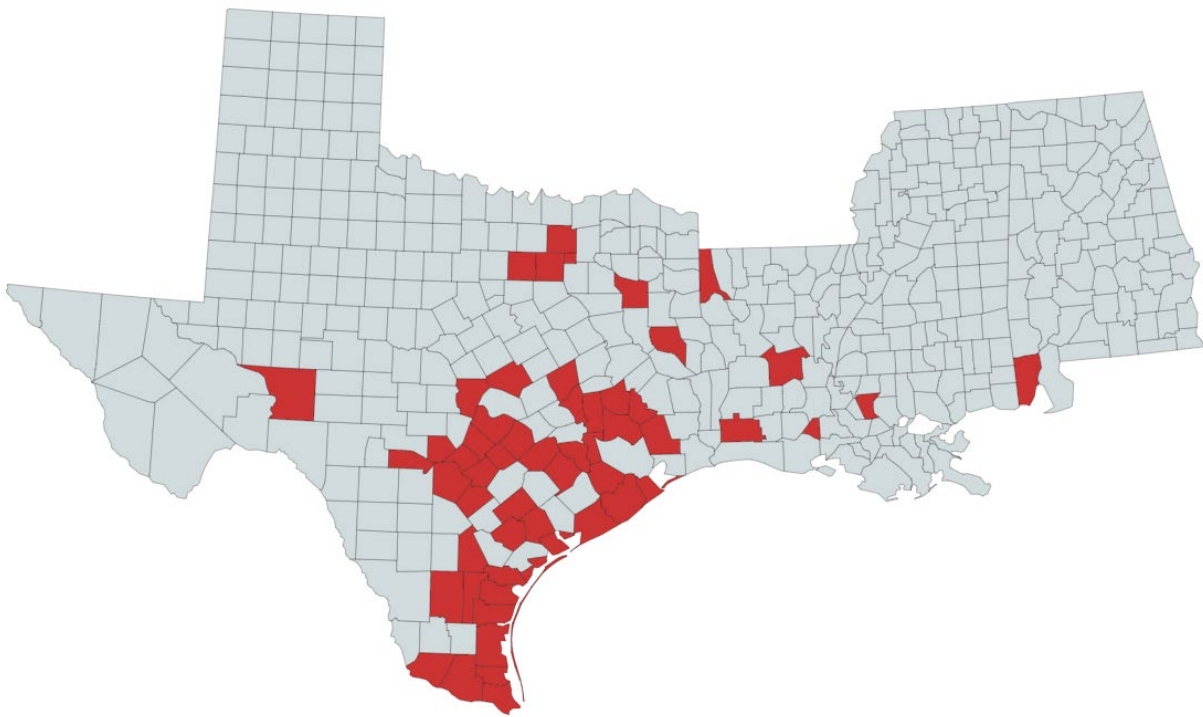
Plain text URL:

<https://docs.google.com/spreadsheets/d/1jBTaV2TxK-HuzDhtdLoHwOTjFu0NEg8sVrOdphiNPUE/edit?usp=sharing>

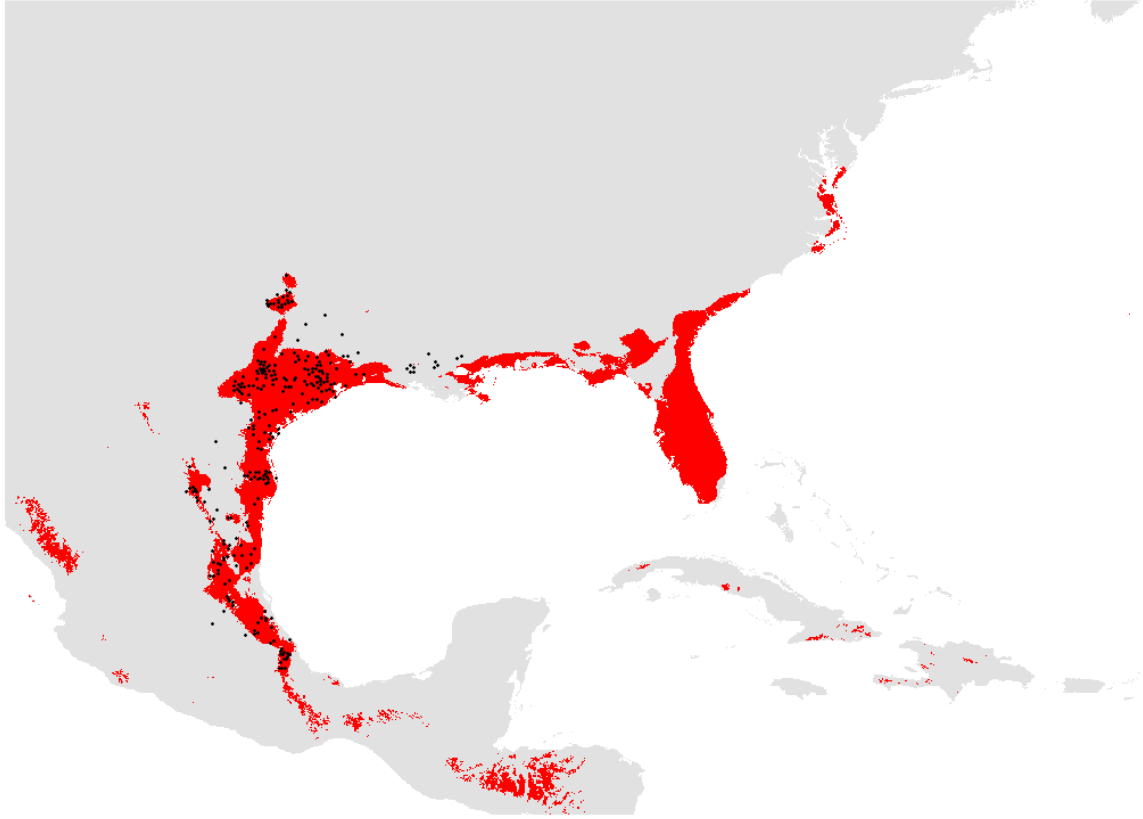
APPENDIX B

APPENDIX B

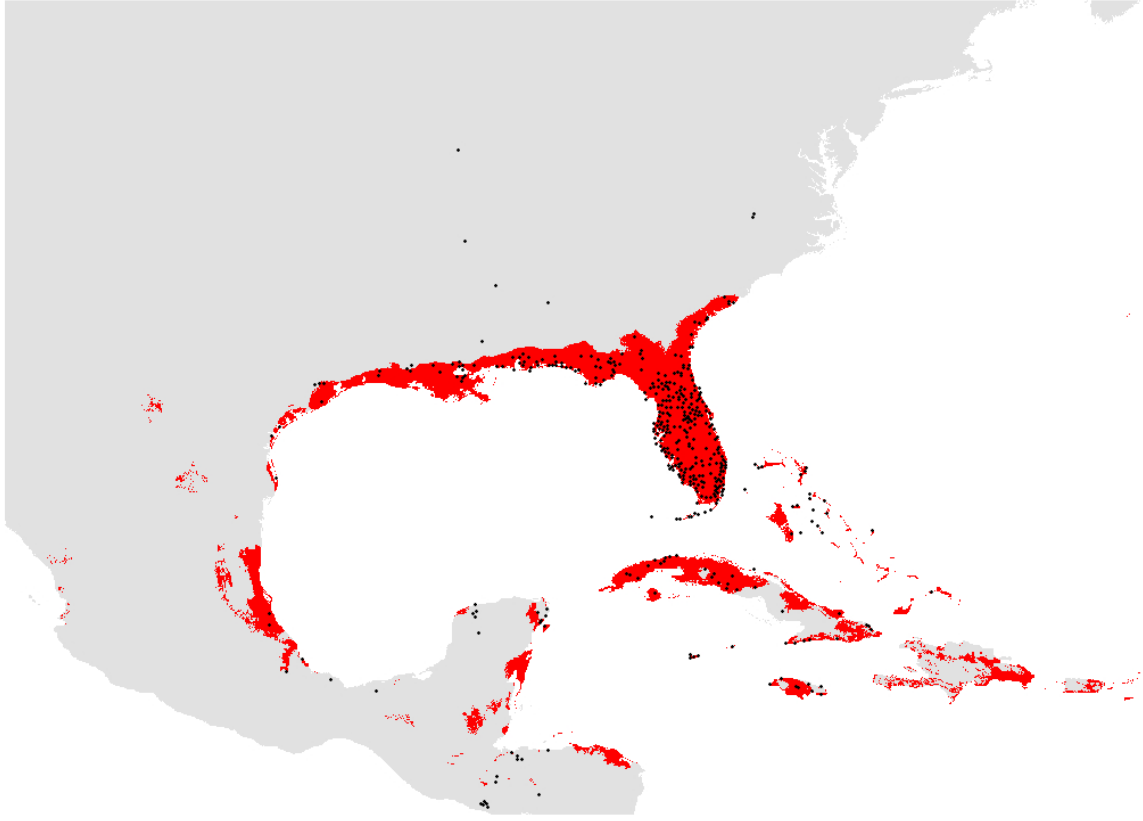
SUPPLEMENTAL FIGURES



Supplemental Figure 1. Map of official county/parish records for *E. cystignathoides* in the USA. Data from Herpetological Review and www.louisianaherps.com. Map generated with MapChart.



Supplemental Figure 2. Rarefied occurrence data for *E. cystignathoides* (n = 271) overlaid on a binary map of potentially suitable habitat modeled under current bioclimatic conditions.



Supplemental Figure 3. Rarefied occurrence data for *E. planirostris* (n = 417) overlaid on a binary map of potentially suitable habitat modeled under current bioclimatic conditions.

APPENDIX C

APPENDIX C

UNSUBSTANTIATED AND DISPUTED CLAIMS CONCERNING *E. CYSTIGNATHOIDES*

A brief, incomplete overview of claims about *E. cystignathoides* which have not been adequately substantiated or about which there is disagreement [has been made permanently available via Google Sheets](#). Investigation and research into these claims is encouraged.

Plain text URL:

https://docs.google.com/spreadsheets/d/12CH5DiM9Yewez1jOg07XHCCHIXjV9l_qaOtTKrMxwo0/edit?usp=sharing

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BIOGRAPHICAL SKETCH

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