Research Article

Climate match fails to explain variation in establishment success of non-native freshwater fishes in a warm climate region

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Abstract

For non-native species, climate can act as a primary filter limiting establishment. Numerous studies examining climate similarity between native and introduced regions have been completed for temperate areas, however we know little about how well climate matching performs for warmer regions. For non-native freshwater fish introduced to warm regions, one potential problem with climate matching is that fish from both temperate and tropical source regions could establish. Our goal was to examine whether climate matching can predict the establishment of non-native freshwater fish for a warm climate region. We used CLIMATCH, a widely applied climate matching program, to analyze climate similarity between source and target regions for 37 successfully established species and 36 species that have failed to establish. CLIMATCH was calculated in two ways for successfully established species, with Florida records included (*post hoc*) and without Florida records (*a priori*). The mean *post hoc* score for successful species was higher than that of failed species; however, the mean *a priori* score for successful species did not significantly differ from failed species. On average, *post hoc* scores were inflated 1.5 times over *a priori* scores. The *post hoc* result is tautological—the scores are high because the species is successful, and the species is successful because the scores are high. These results highlight two issues for climate matching: (1) as commonly done *post hoc*, degree of climate match and predictive power may be overestimated and (2) *a priori* applications may lack predictive power. We recommend consideration of these issues in the use and interpretation of CLIMATCH for prediction. Additional research into regional importance of climate variables (temperature and precipitation) is warranted, especially in warm climate regions.

Key words: CLIMATCH, Florida, risk assessment, ERSS, invasive species, non-native fish

Introduction

Predicting successful invaders is a central theme for invasion ecology, yet only three factors yield consistent associations with establishment success across regions and taxa: climate match, prior invasion success, and propagule pressure (Kolar and

Lodge 2001; Hayes and Barry 2008; Gallien and Carboni 2017). Of the three consistent predictors, climate match is the most fundamental because some degree of suitability is necessary for establishment (Hayes and Barry 2008; Olyarnik et al. 2009). Climate therefore provides a strong primary invasion filter (Chapman et al. 2014), reducing the pool of potential invaders to those species capable of surviving, reproducing, and spreading within the regional constraints of seasonal variation in temperature and precipitation.

Climate match is frequently associated with establishment success in freshwater fishes. An analysis of 280 species in 10 countries identified a simple model using climate match and invasion history to correctly categorize 78% of successfully established species (Bomford et al. 2010). The mean climate match for successfully established non-natives was greater than the mean climate match for failed introductions for each of the countries in their study (Bomford et al. 2010). For the heavily invaded Laurentian Great Lakes, climate match alone was predictive of establishment success with 75–81% accuracy (Howeth et al. 2016). This past success in incorporating climate match increases the confidence that risk managers can place in assessments (Hayes and Barry 2008).

Most regional studies assessing fish establishment success focus on temperate or cold climates of North America or Europe (Garcia-Berthou 2007), and global analyses have explained little variance in establishment success (e.g., 12%, Ruesink 2005) or have included few warmer climate locations (e.g., Bomford et al. 2010). More thorough investigation of warm climate regions is warranted to determine the consistency of climate match as a predictor of establishment. A broadening of geographic scale is needed in response to the growing numbers of freshwater fish introduced into tropical and warm temperate climate zones in Mexico (Espinosa-Pérez and Ramírez 2015), Central and South America (Britton and Orsi 2012; Esselman et al. 2013), Florida (USA) (Shafland et al. 2008; Robins et al. 2018), Africa (Ellender and Weyl 2014), south and southeast Asia (Arthur et al. 2010; Herder et al. 2012), and Australia (Lintermans 2004). Such studies can lead to better understanding of the complex process of invasion across geospatial scales and taxonomic diversity.

Florida (USA) is an important region for testing hypotheses related to non-native freshwater fish establishment, with at least 122 species reported, of which 48 species have achieved persistent, reproducing populations (Robins et al. 2018). Peninsular Florida has multiple invasion pathways, hotspots of dense human population, and abundant and diverse aquatic habitats, all factors thought to increase its vulnerability to non-native fish introduction and establishment (Hardin 2007). Importantly, the climate of peninsular Florida is considerably different than the rest of the continental United States. It has some of the warmest winters in the warm temperate climate zone (Cfa) and the only tropical zones (Af, Am, and Aw) in the region (Beck et al. 2018). The goal of our study was to test the accuracy of climate match in a warm climate region for distinguishing successful versus failed introductions using the introduced freshwater fish fauna of peninsular Florida. Our specific objectives were to (1) test for mean differences in climate match between non-native fish species that have successfully established (hereafter, 'successful') and those that have failed to establish (hereafter, 'failed') using existing protocols (Bomford et al. 2010; USFWS (United States Fish and Wildlife Service 2020. Standard operating procedures: How to prepare an "Ecological Risk Screening Summary". https://www.fws.gov/fisheries/ANS/pdf_files/ERSS-SOP-February2020-FINAL.pdf; hereafter, 'USFWS SOP') and (2) to determine if the climate match categories of the USFWS SOP could distinguish between successful and failed species. The results of this study can be used to evaluate the predictive ability of these climate match protocols and hence their utility for risk screening and assessment of potentially invasive species.

Methods

We developed lists of established and failed non-native freshwater fish species for peninsular Florida using a wide range of sources, including the U.S. Geological Survey's Nonindigenous Aquatic Species database (USGS 2023. http://nas.er.usgs.gov/), published literature (e.g., Shafland et al. 2008; Schofield and Loftus 2015; Robins et al. 2018), field collections of the authors, and consultation with colleagues. Species were excluded from both lists if they were native transplants except for the Rio Grande Cichlid *Herichthys cyanoguttatus* Baird & Girard, 1854, a species native to southern Texas but universally included in such lists (e.g., Schofield and Loftus 2015), or if the introductions were outside of peninsular Florida. Species were categorized as successful if they had one or more established or reproducing populations in the region. Failed species included formerly reproducing species or those reported without evidence of reproduction; however, species were excluded if all known populations were eradicated by humans or if they represented introductions of a single individual (Lawson and Hill 2021, 2022). The resulting list included 37 successful and 36 failed species.

We estimated climate match in two ways. First, following a test of climate matching for the Laurentian Great Lakes region (Howeth et al. 2016), we used CLIMATCH (ABARES (2020) Climatch v2.0 user manual. Australian Bureau of Agricultural and Resource Economics and Sciences, Canberra. https://climatch.cp1.agriculture.gov.au/) and a U.S. Fish and Wildlife Service (USFWS) protocol for Ecological Risk Screening Summaries (ERSS; USFWS SOP) that incorporates all native and non-native established populations as source data, including locations within the risk assessment area. This procedure results in a *post hoc* determination of climate match for successful species. Secondly, we ran the same analysis using CLIMATCH but omitted all Florida locations (Bomford et al. 2010) to determine an *a priori* climate match, a more useful scenario for risk assessment (i.e., determining if a species not already introduced might establish). CLIMATCH, a simple freely available web-based application, has become the climate-matching program of choice for many risk screening activities in the United States and worldwide (ABARES (2020) Climatch v2.0 user manual. Australian Bureau of Agricultural and Resource Economics and Sciences, Canberra. https://climatch.cp1.agriculture.gov.au/; Froese 2012). The USFWS ERSS previously utilized the program but has since developed a similar application for internal use (USFWS (United States Fish and Wildlife Service) (2019) Standard operating procedures for the Risk Assessment Mapping Program (RAMP). U.S. Fish and Wildlife Service. https://www.fws.gov/fisheries/ANS/pdf_files/RAMP-SOP.pdf). Both programs use temperature and precipitation data from land-based weather stations to determine similarity between a designated source region and a target region. As recommended in the protocols, we used the default set of 8 temperature and 8 precipitation variables (Suppl. material: table S1).

CLIMATCH analyses were completed for all species using source populations with (*post hoc*) and without (*a priori*) Florida locations for successfully established species. Location data were acquired through the Global Biodiversity Information Facility (GBIF 2023 https://www.gbif.org/), the U.S. Geological Survey Nonindigenous Aquatic Species database (USGS 2023. http://nas.er.usgs.gov/), taxonomic guides, and primary literature and assessed for accuracy before use. The target region was peninsular Florida, the part of Florida south and east of the Suwannee River system. The output of CLIMATCH includes similarity values for each weather station that range from 0 to 10, where 0 indicates no similarity and 10 indicates complete similarity (Bomford et al. 2010; USFWS SOP). The proportion of stations with a similarity of 6 or greater (Climate 6 Score = (Sum of counts for Climate Scores 6–10)/(Sum of all Climate Scores)) is the critical value, with values ≤ 0.005 indicating low climate match, those > 0.005 but < 0.103 indicating medium climate match, and values ≥ 0.103 indicating high climate match (Table 1; USFWS SOP). We tested for mean differences in climate 6 scores (1) between successful species (including Florida source locations) and failed species, and (2) between successful species (excluding Florida source locations) and failed species, using Wilcoxon Rank Sum tests in JMP Pro (V. 17.0, SAS Institute Inc., Cary, NC, USA). See Suppl. material: table S2 for species categories and Climate 6 scores and Suppl. material: table S3 for notes on species categorization.

Results

With Florida locations included (*post hoc*), mean climate match (± SE) of successful species (0.991 ± 0.004) was greater (χ^2 = 18.88, df = 1, P < 0.0001) than the mean climate match for failed species (0.574 ± 0.072; Fig. 1). Climate 6 scores

Table 1. Climate-match categories for failed and successful (a priori) non-native freshwater fishes in peninsular Florida. Climate 6 score categories from USFWS (2020).

Climate 6 Score	Climate Match Category	Failed Species	Successful Species
0 ≤ X ≤ 0.005	Low	3	2
0.005 < X < 0.103	Medium	4	3
≥ 0.103	High	29	32

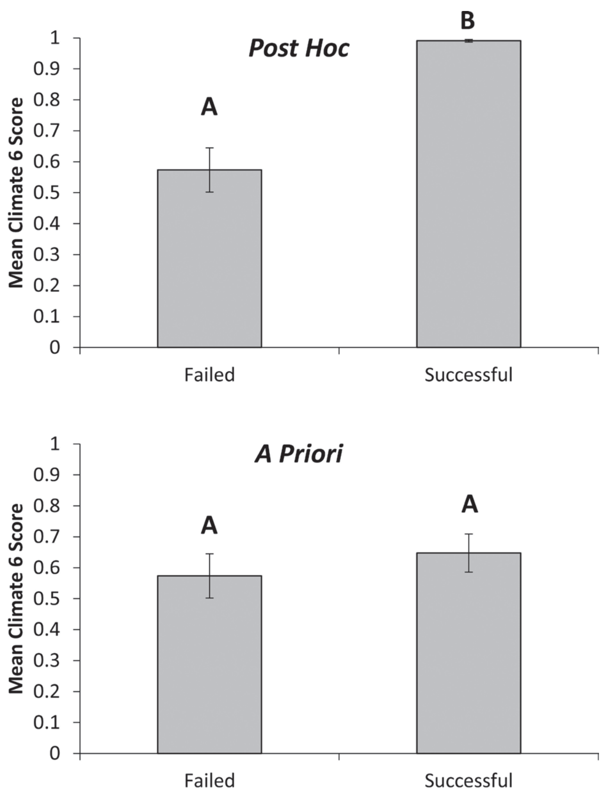

Figure 1. Mean Climate 6 scores (±SE) from CLIMATCH for failed and successful non-native fishes in peninsular Florida. The *post hoc* analysis includes data points from Florida for successful species and the *a priori* analysis omits data points from Florida for successful species. Different letters denote significantly different means (P < 0.05).

for successful species ranged from 0.87 to 1 and failed species from 0 to 1. Of all introduced species with Climate 6 scores ≥ 0.87, 72.6% were successful. In contrast, without Florida source locations (*a priori*), the mean climate match (± SE) for successful species (0.647 ± 0.062) was not significantly different ($\chi^2 = 0.0436$, df = 1, $P = 0.834$) from the mean climate match for failed species (0.574 ± 0.072). In this latter case, Climate 6 scores for successful species ranged from 0 to 1. On average, the inclusion of data from the target region inflated climate match scores 1.5 times (0.991 vs. 0.647).

All Climate 6 scores for successful species in the *post hoc* analysis were equal to or greater than those in the *a priori* analysis. Climate 6 scores for 11 successful species did not differ between *post hoc* and *a priori* analyses whereas Climate 6 scores of the remaining 26 successful species differed by values (Δ) ranging from 0.012 to 0.991 (Fig. 2). Mean Δ was 0.343 (SD = 0.365) for all 37 successful species. The most extreme example of the variation in *post hoc* versus *a priori* scores is the goldline snakehead *Channa aurolineata* (Day, 1870), a species native to Southeast Asia (Fig. 3). Using occurrence data from southeast Florida, the *post hoc* Climate 6 score was 1.0. Conversely, leaving out Florida source data (*a priori*) resulted in a much lower Climate 6 score of 0.009. Therefore, the *a priori* analysis indicated relatively little similarity between climates in Southeast Asia and peninsular Florida whereas the *post hoc* analysis suggested considerably more potential range of climate match in the risk assessment area.

Post hoc Climate 6 scores for successful species resulted in all 37 being classified as having a high climate match (>0.103) and *a priori* scores resulted in 32 species with a high climate match, 3 with medium match, and 2 with low match (Table 1). For failed species, 29 species had a high climate match, 4 had a medium match, and 3 had a low match (Table 1).

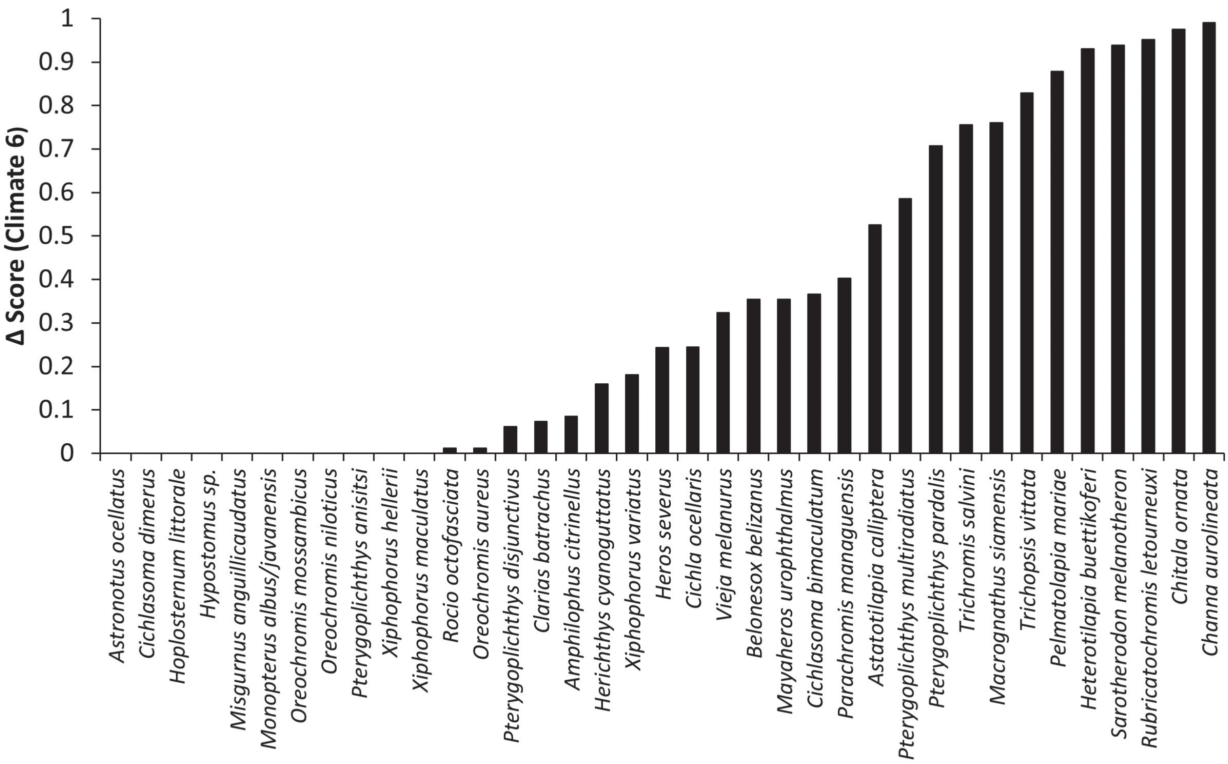

Figure 2. Mean difference (Δ) in *post hoc* and a *priori* Climate 6 scores for 37 successful non-native fishes in peninsular Florida. *Post hoc* values were always equal to or greater than *a priori* values resulting in positive Δ scores.

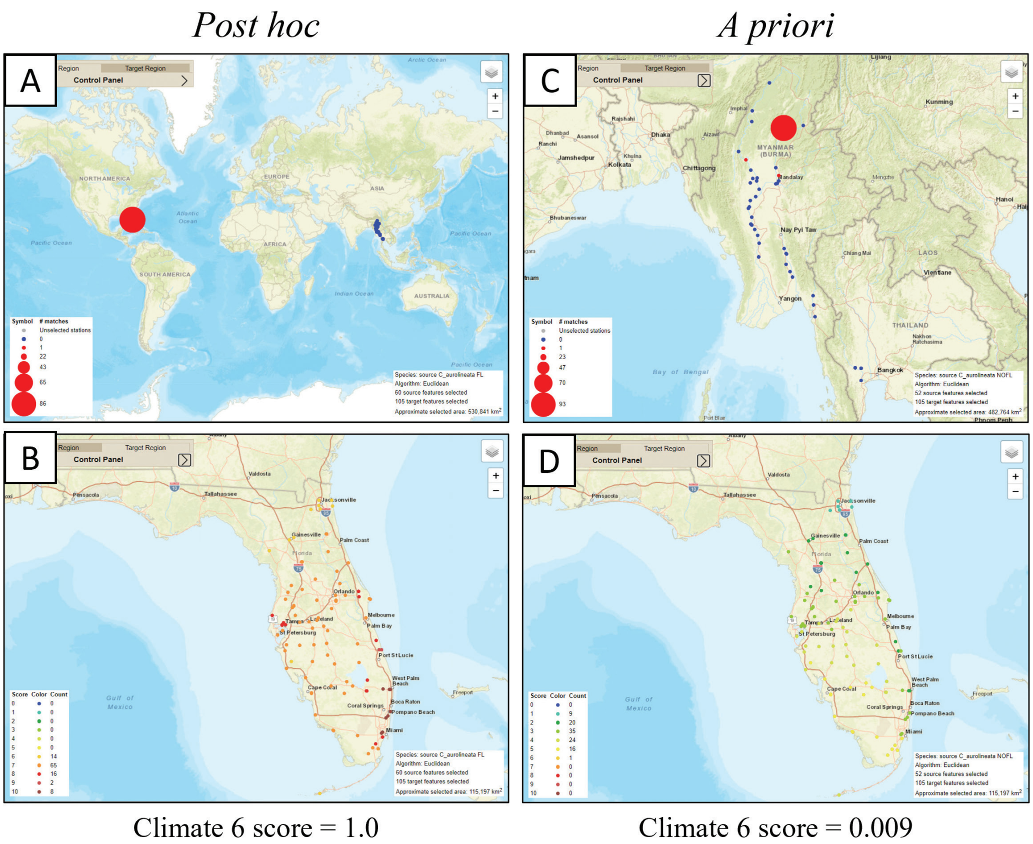

Figure 3. CLIMATCH maps showing source (A and C) and target (B and D) regions for goldline snakehead *Channa aurolineata* (Day, 1870). Source map A shows that location data were used from peninsular Florida, the target region for climate matching and therefore maps A and B show an *ad hoc* analysis. Maps C and D show an *a priori* analysis because no source data from the target region are used. Source maps indicate climate stations in native or established locations in blue or red. Blue dots indicate that the climate station did not contribute to match in the target region. Red dots contributed to match and the size of the red point indicates the relative contribution. Target maps indicate climate stations with a color code indicating match. Similarity values ≥ 6 indicate suitable climate and Climate 6 scores are the proportion of climate stations in the target region with ≥ 6 similarity to the source region.

Discussion

We found little evidence for the association between *a priori* climate match and establishment success of non-native freshwater fishes in peninsular Florida, a warm climate zone. This finding is in contrast to the robust consensus in the literature that climate match is a consistent predictor of invasion success for a wide range of taxa (Hayes and Barry 2008), including freshwater fishes (Bomford et al. 2010; Howeth et al. 2016). Following a similar protocol using data from the target region led to differing results of climate match—strongly predictive *post hoc* versus non-predictive *a priori* of establishment success using the same data set. However, the post hoc analysis is of limited utility for prediction because it is tautological—the scores are high because the species is successful, and the species is successful because the scores are high. Thus, the climate match procedure may strongly influence the outcome of analyses. Our results have considerable implications for the use of climate match as a predictive tool for freshwater fish invasions, risk assessment in general, and management of potentially invasive species.

Post hoc vs. *a priori*

Risk assessment has two prominent components, (1) the probability that a non-native species will establish within a specific region and (2) the consequences (i.e., impacts) resulting from establishment (Aquatic Nuisance Species Task Force (ANSTF) (1996) Generic Nonindigenous Aquatic Organisms Risk Analysis Review Process. https://www.anstaskforce.gov/Documents/ANSTF_Risk_Analysis.pdf; Orr 2003). If a species is already established in the region of interest, the assessment is reactive, and the first component is reduced to evaluating potential spread or increased density. Thus, the risk assessment becomes a hazard, impact, or injury assessment (Hope 2006). A more useful approach is proactive risk assessment (i.e., *a priori* or "true" risk assessment; Hope 2006) which is completed prior to the establishment of a non-native species within the risk assessment area. Further, if a climate match analysis includes data from part of the target region for which the risk assessment is being conducted, it conflates climate match with invasion history.

Our results show that using occurrence records in the target region such as in the USFWS SOP greatly inflates the climate score. This result is not surprising because CLIMATCH works by comparing temperature and precipitation variables between selected source and target region weather stations, with increasing scores assigned for increasing similarity (Bomford 2008). Weather stations within the target region that happen to be in the established range of a non-native are typically similar to those nearby and are of course identical to themselves (i.e., used in both sides of the analysis—source and target). This results in the tautological nature of the *post hoc* analysis. This analysis might prove useful for evaluating spread within the target region; however, Froese (2012) recommends CLIMATCH only for pre-entry analysis.

An uncritical acceptance of the USFWS SOP protocol would result in a considerably different view of the predictive power of CLIMATCH for distinguishing successful and failed Florida introductions. Using a *post hoc* analysis to develop a predictive relationship between climate match and invasion success would then result in a false indication that Climate 6 scores will have high predictive ability. For example, if we use the *post hoc* analysis for peninsular Florida, where 68% of species with a Climate 6 score ≥ 0.87 were successful, we overestimate the importance of Climate 6 score because *a priori* only 44% of successful species have a score exceeding this threshold. Furthermore, an evaluation of Climate 6 scoring thresholds is warranted considering that 81% of failed species had scores > 0.103, the threshold for a high match, suggesting that this value may be too sensitive.

Despite previous successful applications, our study calls into question the utility of using CLIMATCH as a predictor of potential establishment. At the very least, CLIMATCH should be applied and interpreted with caution (Froese 2012; present study), especially in the southeastern United States and perhaps other warm regions. Consideration should be given to underestimating as well as overestimating potential range in the target region. Species may possess greater thermal tolerances than evidenced by their native and non-native ranges (Broennimann et al. 2007; Jiménez-Valverde et al. 2008), resulting in an underestimation of climate match. Further, the presence of thermal refuges in the environment and adaptive behavior or variation in thermal tolerance among individuals may result in invasion and establishment of areas otherwise considered peripheral or unsuitable for establishment (Tuckett et al. 2016, 2021b; Purtlebaugh et al. 2020).

Potential limitations

CLIMATCH (Bomford et al. 2010; Howeth et al. 2016; USFWS SOP), uses 16 variables to measure climate, 8 based on air temperature and 8 based on precipitation. This full variable set was found to be the most predictive for freshwater fishes in early testing (Bomford 2008). However, the thermal regime of many aquatic systems can be complex and precipitation effects may be variable across habitats or species (Power et al. 1999; Logez et al. 2012). Determining which variables or suites of variables are important on a regional basis may improve the predictive ability of CLIMATCH.

A wide range of other factors unrelated to climate may limit the effectiveness of CLIMATCH as a predictor of potential establishment of non-native fishes in Florida and other warm climate regions. Life history traits are important determinants and predictors of invasion success in several regions of the United States (Kolar and Lodge 2001; Marchetti et al. 2004; Olden et al. 2006) including peninsular Florida (Lawson and Hill 2021, 2022). Biotic resistance from predators and aggressive competitors has also been shown to strongly influence invasion success of many small-bodied non-native fishes in Florida (Hill et al. 2011; Thompson et al. 2012; Hill 2016; Hill and Tuckett 2018). The influence of prior invasion history and propagule pressure, thought to be consistent predictors of invasion success (Hayes and Barry 2008), have not been evaluated in peninsular Florida, though some observations suggest that these factors may also not be as predictive in Florida as in other regions. For example, several species such as pike killifish *Belonesox belizanus* (Kner, 1860) and African jewelfish *Rubricatochromis letourneuxi* (Sauvage, 1880) have proven successful in Florida but have little or no invasion history elsewhere whereas several well-known invaders worldwide such as goldfish *Carassius auratus* (Linnaeus, 1758) and guppy *Poecilia reticulata* (Peters, 1859) have had little to no success in Florida (Lawson et al. 2015a; Tuckett et al. 2021a).

We acknowledge the importance of abiotic factors in influencing risks of establishment (Moyle and Light 1996; Garcia-Berthou 2007; Hayes and Barry 2008) and conclude that more research into the role of specific climate variables and their exploration via modeling approaches is warranted. The simple and rapid program is of great utility for risk screening, and we recommend efforts to better adapt CLIMATCH for Florida and other warm climate regions by testing other combinations of variables. Nevertheless, other, more complex species distribution models may be needed to capture the influence of interacting habitat and climate variables (Froese 2012). One particularly promising area for research is coupling empirical physiological tolerance experiments with realistic water temperature modeling to determine relative maximum occurrence as well as likely occurrence zones (Lawson et al. 2015b). Similarity algorithms such as used in CLIMATCH are unlikely to detect thresholds, which may be of prime importance in determining effective temperature barriers to establishment or spread. Finding such thresholds should lead to improved prediction.

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Author contribution

JEH, QMT, KML research conceptualization; JEH, QMT, KML sample design and methodology; JEH, QMT, KML investigation and data collection; JEH, QMT, KML data analysis and interpretation; JEH funding provision; JEH, QMT, KML writing - original draft; JEH, QMT, KML writing - review & editing.

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Supplementary material 1

Climate variables, species lists, climate scores, notes on species inclusion exclusion

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Data type: xlsx

Explanation note: **table S1.** Variables of temperature and precipitation used in CLIMATCH analyses. **table S2.** Climate 6 scores for non-native freshwater fish species in peninsular Florida. **table S3.** Notes for the categorization of select non-native freshwater fish species in peninsular Florida.

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