Illinois-Indiana Sea Grant Final Report for Funded Research Project Section A. Summary.

Title: Methods Development to Predict Establishment Risk of Emerging Freshwater Invasive Species in the Great Lakes Basin

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Abstract: Species distribution models (SDMs) are one common tool used to identify which organisms could establish non-native populations in new regions. Unfortunately, scientific consensus has increasingly confirmed that these SDMs rarely extrapolate accurately to new areas. Native ranges often do not predict the non-native ranges subsequently invaded by nuisance species, and early occurrence records in a non-native range often fail to predict the full invasive extent after spread. One solution to the extrapolation problem of SDMs is to transfer niche shifts from well-established invasive species to emerging invasive species, in order to anticipate the magnitude to which native ranges under-estimate the total global habitat suitability for an organism of interest. Here, I demonstrate this "avatar" invader and iassociated niche shift concept using the globally invasive red swamp crayfish Procambarus clarkii as a well-studied taxa and the yabby Cherax destructor as an emerging invasive species of concern to the Great Lakes basin. I first characterize the extent to which the native range under-estimates all known non-native occurrences for P. clarkii globally, and then transfer this niche shift to the native range model of C. detructor. I found that the native range only predicted a minority of global introduced occurrences for P. clarkii and predicted none of the Great Lakes basin as suitable for this species, whereas an SDM that incorporated a niche shift to include 90% of known introduced occurrences predicted a large proportion of the Great Lakes basin as suitable for this species. When this same, avatar niche shift was transferred to the native range model of C. destructor, predicted suitable habitat for this emerging crayfish invader was expanded from omitting the Great Lakes basin to include substantial portions of the southern Great Lakes basin. I demonstrate one approach here to improved risk assessment for emerging freshwater invasive species, and identify locations that may benefit from surveillance and monitoring of both P. clarkii and C. destructor populations.

<u>Keywords</u>: avatar species, *Cherax destructor*, ecological niche modeling, Mahalanobis distance, *Procambarus clarkii*, red swamp crayfish, species distribution modeling, yabby

<u>Lay Summary</u>: Anticipating where harmful invasive species may live outside of their native range is difficult. My work proposes that we should use information from well-studied invasive species to make precautionary predictions of how different of an environment an emerging invasive species can tolerate relative to their native range.

Section B. Accomplishments

Introduction: The Laurentian Great Lakes and their watershed are among the most invaded ecosystems in the world, with at least 182 non-native freshwater species establishing populations in this region since 1840 (Ricciardi 2006). Many of these non-native species have manifested unwanted economic damages and ecological effects as invasive species (Pimentel et al. 2005, Madenjian et al. 2015). In response, management agencies and policy makers seek to identify species that could establish populations, spread, and cause negative impacts in the Great Lakes Basin in the future, in order to prohibit these organisms from deliberate trade and to monitor for their accidental presence in transport vectors and pathways like oceanic shipping (Lodge et al. 2016).

One tool used to identify which species could establish non-native populations in new regions is species distribution (or ecological niche) modeling (Peterson 2003, Jiménez-Valverde et al. 2011). Given that most species lack adequate physiological data to define the environmental tolerances that limit their distributions, risk assessment for invasive species instead routinely relies on a combination of presence-only occurrence data, GIS environmental data, and approaches like machine-learning algorithms to estimate suitable habitat for organisms (Elith and Leathwick 2009). These models are then extrapolated to the non-native range of interest to evaluate whether a prospective invader should be considered for regulatory prohibition under a black list or approval under a white list (Lodge et al. 2016). For example, the U.S. Fish and Wildlife Service uses an in-house SDM, the Risk Assessment and Mapping Program (RAMP), to evaluate establishment likelihood of prospective invasive species in the United States in guiding actions like listing injurious wildlife under the Lacey Act (https://www.fws.gov/science/pdf/RAMPPeerReview20150831.pdf).

Unfortunately, scientific consensus has increasingly confirmed that these species distribution models (SDM) rarely extrapolate accurately to new geographic regions (Broennimann et al. 2007, Medley 2010, Early and Sax 2014). Native ranges often do not predict the non-native ranges subsequently invaded by nuisance species (e.g., Fitzpatrick et al. 2007), and early occurrence records in a non-native range often fail to predict the full invasive extent after spread (e.g., Václavík and Meentemeyer 2012). Several mechanisms may explain this shortcoming of SDMs when applied to invasive species. The first is the possibility that species experience "niche shifts" during the invasion process, in which their relationship to abiotic factors changes (potentially through evolutionary mechanisms) between native and non-native ranges (Broennimann et al. 2007, Early and Sax 2014). The second is that models simply cannot extrapolate between one geographic region (e.g., native) and another (e.g., non-native) if climate or environmental conditions between these regions are too dissimilar (Petitpierre et al. 2012), particularly if these models are over-fit to training data or use environmental predictors that do not actually limit species distributions (Wenger and Olden 2012, Petitpierre et al. 2017).

Regardless of cause, the potential inability of native range distribution records to anticipate non-native distributions is highly problematic, particularly for emerging invaders that lack sufficient non-native range data to parameterize models or evaluate model transferability between native and non-native ranges. As an example, the temperate Australian crayfish *Cherax destructor* is a species of potential concern in the Great Lakes Basin due to its use in the aquaculture industry and impacts as a an invader

on its home continent (e.g., Beatty et al. 2005). Could *C. destructor* establish in the Great Lakes Basin? Unfortunately, past experiences with other invasive crayfish species suggest that the currently available occurrence records for *C. destructor* are inadequate to build an SDM that can predict everywhere this organism might live globally (Larson et al. 2010, Larson and Olden 2012). The same is undoubtedly true for a variety of freshwater taxa like aquatic macrophytes, mollusks, and fish that could become invasive in the Great Lakes in the future. At present, risk assessment for Great Lakes Basin aquatic invasive species is severely impaired by the well-documented extrapolation limitations of SDMs for estimating risk of establishment of emerging invasive species (Early and Sax 2014, Larson et al. 2014).

Larson and Olden (2012) proposed as a solution to the extrapolation problem of SDMs the idea of transferring niche shifts from well-established invasive species to emerging invasive species, in order to anticipate the magnitude to which native ranges under-estimate the total global habitat suitability for an organism of interest. Larson and Olden (2012) termed this idea "avatar" species, as one species (the avatar) is used to simulate a worst-case scenario invasion process for a data-poor, emerging invasive species. Larson et al. (2014) subsequently tested whether this avatar invader concept improved SDMs for a series of globally invasive terrestrial plants, finding that niche shifts transferred from other invaders improved native range extrapolation to non-native ranges for these species. Yet to date, the avatar invader concept has not been revisited or widely implemented, particularly for freshwater invasive species. Here, I demonstrate the avatar invader concept for a potential Great Lakes Basin invasive species, in order to generate preliminary data and results to expand this idea to a broader suite of prospective freshwater invasive species in a future grant application.

I use the globally invasive red swamp crayfish *Procambarus clarkii* as an avatar invader, characterizing the extent to which its native range under-estimates all known non-native occurrences for this species globally. I expand on past use of *P. clarkii* as an avatar invader in Larson and Olden (2012) by using new, high resolution, freshwater-specific GIS layers at a global extent by Domisch et al. (2015), rather than the terrestrial climate proxies more routinely used in past SDM applications to freshwater species. I estimate the extent to which the native range of *P. clarkii* under-estimates its total range habitat associations using Mahalanobis distance per Larson and Olden (2012) and Larson et al. (2014). I then collect native range occurrence records for the prospective invasive crayfish *C. destructor* from Australia, transfer the observed niche shift for *P. clarkii* above to the native range niche of *C. destructor*, and extrapolate its suitable habitat post-avatar niche shift to the Great Lakes Basin. I provide a transparent workflow for transferring avatar niche shifts to prospective emerging freshwater invasive species for managers or policy makers interested in implementing this technique for other taxonomic groups.

<u>Project Narrative:</u> I first collected occurrence records for the focal species, *P. clarkii* and *C. destructor*. I used the native and non-native range occurrences of *P. clarkii* from Larson and Olden (2012), and updated this dataset to include new post-2012 records for the United States (U.S.) from the U.S. Geological Survey's (U.S.G.S.) Non-indigenous Aquatic Species (N.A.S.) database (https://nas.er.usgs.gov/viewer/omap.aspx?SpeciesID=217). I included new global records for *P. clarkii* from Oficialdegui et al. (2019). For *C. destructor*, I used native range records from the Global



Figure 1. Native (n=319) and introduced (n=379) range occurrences for P. clarkii and native range occurrences for C. destructor represented globally (A) and for the Great Lakes basin (B) with flow lines from the EarthEnv environmental layers of Domisch et al. (2015).

Biodiversity Information Facility (GBIF; https://www.gbif.org/species/4417558). I did not use non-native records for *C. destructor*, as my modeling exercise specifically sought to demonstrate transferring total range (native and introduced) niche shifts from a well-studied invader (*P. clarkii*) to the native range niche of an emerging invader (*C. destructor*). Further, non-native records for *C. destructor* are almost exclusively from Australia, as the species has not yet become widely established globally. Cumulatively, I used 319 native range records for *P. clarkii*, 379 invasive range records for *P. clarkii*, and 64 native range records for *C. destructor* (Figure 1). All occurrence records were snapped to the nearest EarthEnv flow layer from Domisch et al. (2015; below).

Domisch et al. (2015) developed near-global (i.e., omitting high northern latitudes) environmental data layers for freshwater ecosystems in a relatively fine 1 km resolution

(https://www.earthenv.org/streams), termed the EarthEnv dataset. EarthEnv data layers include climate, topography, land cover, geology, and soil data specific to freshwater surfaces, as opposed to terrestrial environmental proxies like WorldClim (Fick and Hijmans 2017). I chose to model the global native and total range niches of P. clarkii and C. destructor using four environmental layers from EarthEnv: maximum estimated water temperature of the warmest month (Max T; C), minimum estimated water temperature of the coldest month (Min T; C), freshwater flow accumulation of the wettest month (Max P; mm), and freshwater flow accumulation of the driest month (Min P; mm), consistent with Larson et al (2014). I anticipated that the four chosen climatic variables are all associated with thresholds for survival of target species at a global extent and relatively coarse modeling grain size or resolution (1 km). Specifically: maximum and minimum temperature may set upper and lower bounds for survival or reproductive success throughout a year (Egly et al. 2019), whereas flow accumulation between wettest and driest seasons represents size and permanence of freshwater habitats. Too small of freshwater habitats may exclude species by disturbances like drought and complete drying of the habitat, whereas too large of freshwater habitats may exclude some species due to vulnerability to predators like fish (Dorn and Trexler 2007). Further, as Mahalanabois distance incorporates covariance between all predictor variables, seasonality between environmental conditions is also implicitly accounted for in these models.

I used LandFacet Corridor Designer (Jenness et al. 2011) in ArcMap 10.3.1 to calculate Mahalanobis distance at all native *P. clarkii* occurrences, and then converted Mahalanobis distance to χ^2 p-values as the probability of habitat being suitable for *P. clarkii*. This assumes that crayfish responses to environmental predictors approximate normal distributions (Clark et al. 1993). I chose a p-value > 0.10 as a threshold for identifying locations suitable for occurrences of *P. clarkii* based on the species native range (Figure 2, Figure 3), rather than a more conventional significance threshold of 0.05, in order to account for the potentially high proportion of presence-only occurrence data that could either represent data errors or sink populations without *P. clarkii* reproduction (Capinha et al. 2013). Notably, a native range-only Mahalanobis distance model at a suitability threshold of 0.10 did not predict any of the Great Lakes basin as suitable for *P. clarkii* (Figure 2), despite known introduced populations from this region (Figure 1).

Larson and Olden (2012) and Larson et al. (2014) identify multiple prospective ways to characterize niche shifts from native to total (native and introduced) ranges using Mahalanobis distance. Both papers demonstrate using Mahalanobis distance to characterize the change in mean, varianace, and covariance structures between all predictors as ratios between the total and native range data, but this method carries some risks of non-transferable niche changes between species (e.g., sign changes in covariance structure; Larson et al. 2014). An alternative method of transferring niche shifts from an avatar to emerging invaders proposed by Larson et al. (2014) was to use the avatar invader to identify habitat suitability thresholds that capture the majority (e.g., 90%) of non-native or introduced occurrence records from just the native range model. In other words, this approach would use the above native range model, but relax the habitat suitability threshold to capture all but 10% of non-native occurrences,



Figure 2. Suitable habitat for P. clarkii from its native range occurrences (Figure 1) estimated as χ^2 p-values > 0.10 from a Mahalanobis distance calculation on Max T, Min T, Max P, and Min P (Figure 3).

and then transfer this magnitude of habitat suitability threshold relaxation to the emerging invader's native range only model.

Notably, the *P. clarkii* native range threshold of χ^2 p-value > 0.10 would only predict 137 (36%) of nonnative range occurrences as suitable for this species, omitting 242 (64%) non-native range occurrences, including all of those in the Great Lakes basin (Figure 1, Figure 2). The native range χ^2 p-value would need to be relaxed from 0.10 to 0.00000000000000007 to identify 342 (90%) of non-native range occurrences as suitable for the species (Figure 3, Figure 4). Although this threshold relaxation is large by magnitude, it still omits many low-latitude tropical or high-latitude polar regions as unsuitable for *P. clarkii* (Figure 4). Further, this niche shift is most evident as an increase in both the maximum and



Figure 3. Relationships between Max T, Min T, Max P, and Min P for 10,000 random global points from the EarthEnv dataset, coded as conditions predicted to be suitable for P. clarkii from a Mahalanobis distance model with a χ^2 p-values > 0.10 threshold (dark red), and coded as conditions predicted to be suitable when this threshold is relaxed to instead capture 90% (omitting 10%) of non-native occurrences (light red; Figure 4). This represents the avatar niche shift from habitat estimated suitable from only native range occurrences (dark red) to including introduced range occurrences (light red).

minimum temperatures tolerated by the species relative to estimates from its native range, whereas minimum and maximum flow accumulation have seemingly little effect on the species' distribution (i.e., both small and large aquatic habitats support *P. clarkii* populations; Figure 3). When projected spatially, the *P. clarkii* avatar niche shift from a 0.10 to 0.000000000000007 habitat suitability threshold predicts much of the southern Great Lakes basin as suitable for this species, including eastern Wisconsin, the lower peninsula of Michigan, southern tributaries to Lake Erie, and some southern tributaries to Lake Ontario (Figure 4). This prediction corresponds with many observed non-native *P. clarkii* occurrences in the Great Lakes basin (Figure 1), and identifies specific waterbodies for ongoing surveillance of new invasions. This large niche shift still excludes the majority of Ontario and the upper peninsula of Michigan as unsuitable for the species, along with some locations in upstate New York and Wisconsin (Figure 4).



Figure 4. Suitable habitat for *P*. clarkii following an avatar niche shift in which habitat suitability from the native range model (Figure 2) is relaxed by threshold to include 90% (omitting 10%) of non-native range occurrences (Figure 3). Habitat suitable from the native range model is in dark red, whereas habitat predicted suitable from the avatar niche shift is light red.

Transferring an avatar niche shift from a well-studied invader (e.g., *P. clarkii*) to an emerging invader of interest (e.g., *C. destructor*) requires first characterizing the native range niche of the emerging invader. I followed the same Mahalanobis distance-based methodology for the native range of *C. destructor* as above for *P. clarkii*, again applying a suitability threshold of χ^2 p-value > 0.10 (Figure 5). This native range model did not predict any of the Great Lakes basin as suitable for *C. destructor*, but as evidenced above for *P. clarkii*, this may be a case in which the native range of a species under-estimates the locations where it could actually survive. In the absence of global non-native occurrence records for *C. destructor*, we instead apply a niche shift observed from our avatar invader *P. clarkii*, to simulate suitable non-native habitat for *C. destructor*.





Figure 5. Suitable habitat for C. destructor from its native range occurrences (Figure 1) estimated as χ^2 p-values > 0.10 from a Mahalanobis distance calculated on Max T, Min T, Max P, and Min P (Figure 6).

Relaxing the suitable habitat threshold for *C. destructor* from a χ^2 p-value > 0.10 to >0.0000000000000000 (Figure 6), consistent with the magnitude of niche shift observed for *P. clarkii*, resulted in a similarly large increase in global habitat predicted to be suitable for this species, and expanded suitable habitat to include much of the Great Lakes basin (Figure 7). Like *P. clarkii*, the niche shift for *C. destructor* was most pronounced for both maximum and minimum temperature, whereas a broad range of maximum and minimum flow accumulations were seemingly suitable for the species from its native range, with little effect of the avatar niche shift (Figure 6). Expanded habitat suitability predictions for *C. destructor* from the avatar niche shift included much of the lower peninsula of Michigan, both southern and northern tributaries to Lake Erie, and more southern tributaries to Lake Ontario than observed for *P. clarkii*. Alternatively, this niche shift did not include as suitable habitat any of Wisconsin (Figure 7).



Figure 6. Relationships between Max T, Min T, Max P, and Min P for 10,000 random global points from the EarthEnv dataset, coded as conditions predicted to be suitable for C. destructor from a Mahalanobis distance model with a χ^2 p-values > 0.10 threshold (dark red), and coded as conditions predicted to be suitable when this threshold is relaxed to a lower value per observed for the avatar invader, P. clarkii (Figure 3). This represents the avatar niche shift from habitat estimated suitable from only native range occurrences (dark red) to what would represent all introduced range occurrences from a similar invasive species that has more non-native occurrences to evaluate niche shift potential from (light red).

Cumulatively, this study demonstrates that: 1) native ranges can under-estimate where invasive species can establish and survive, per the failure of a native range distribution model for *P. clarkii* to represent its introduced occurrences both globally and in the Great Lakes; 2) in the absence of abundant non-native occurrence data, avatar niche shifts can be transferred from well-studied to emerging invaders, in order to provide precautionary or worst case scenario estimates of habitat suitability for data-poor prospective invasive species; 3) this "avatar invader" concept can be applied using freshwater rather than terrestrial climate and environmental data, like the EarthEnv dataset of Domisch et al. (2015); 4) avatar niche shifts may be transferred by adjusting habitat suitability thresholds to include non-native occurrences from a native range model, rather than transforming the mean, variance, and covariance



Figure 7. Suitable habitat for C. destructor following an avatar niche shift in which habitat suitability from the native range model (Figure 5) is relaxed by threshold to resemble that of the well-studied invader P. clarkii (Figure 3). Habitat suitable from the native range model is in dark red, whereas habitat predicted suitable from the avatar niche shift is light red.

structures of Mahalanobis distance itself, which can have some complications in niche shift transfer between species (Larson et al. 2014).

Results of my analysis have Great Lakes-specific applications, as these models identify large but specific areas where invasive species monitoring and surveillance might be directed for both *P. clarkii* and *C. destructor*, potentially through emerging methodologies like environmental DNA (Larson et al. 2017) or citizen science (Larson et al. in press).

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<u>Potential Applications, Benefits and Impacts:</u> This study demonstrates the avatar invader concept for a Great Lakes-focused audience, with relevance to invasive species risk assessment. This study also demonstrates the use of global freshwater environmental layers for GIS modeling of species distributions, given that these datasets remain relatively poorly known in contrast to terrestrial equivalents like WorldClim.

<u>International Implications</u>: The avatar invader concept is intended for use in invasive species distribution modeling and risk assessment globally.

<u>Data Management Plan</u>: Data will be published as either the supplement or appendix to a resulting peerreviewed scientific manuscript, or will be posted to the University of Illinois data bank if the journal does not support online supplementary materials. Data published will include *P. clarkii* and *C. destructor* occurrence records.

Section C. Outputs

Media Coverage: None to report

<u>Publications, Theses, Dissertations:</u> A resultant manuscript reporting the above study is anticipated for submission to the *Journal of Great Lakes Research* during winter 2019/2020.

<u>Undergraduate/Graduate Names and Degrees:</u> No student work was supported by this grant.

<u>Other Outputs</u>: I anticipate presenting on this research at the Association for the Science of Limnology and Oceanography (ASLO) and Society for Freshwater Science (SFS) joint meeting in Madison, Wisconsin, during summer 2020. I anticipate pursuing grant writing to support further development of the avatar invader concept through student or postdoc salary in the future.

Patents/Licenses: None to report.

Project Partnerships: None to report.

<u>Related Projects</u>: I have several species distribution modeling projects in progress with graduate student researchers that may incorporate concepts from this avatar invader modeling approach. This includes in particular a student working on non-native eastern banded killifish *Fundulus diaphanus diaphanus* establishment and spread in the western Great Lakes basin. I have a grant in-review on invasive crayfish distributions in the western United States that might use concepts reported here.

Awards and Honors: None to report.