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Refining species distribution model outputs using landscape-scale habitat data: Forecasting grass carp and *Hydrilla* establishment in the Great Lakes region

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ABSTRACT

Forecasts of the locations of species invasions can improve by integrating species-specific climate and habitat variables and the effects of other invaders into predictive models of species distribution. We developed two species distribution models (SDMs) using a new algorithm to predict the global distributions of two nonindigenous species, grass carp (*Ctenopharyngodon idella*) and Hydrilla (*Hydrilla verticillata*), with special attention to the North American Great Lakes. We restricted the projected suitable habitat for these species using relevant habitat data layers including accumulated Growing Degree Days (GDD), submersed aquatic vegetation (SAV), wetlands, and photic zone. In addition, we restricted the grass carp niche by the projected *Hydrilla* niche to explore the potential spatial extent for grass carp given a joint invasion scenario. SDMs showed that climate conditions in the Great Lakes basin were often suitable for both species, with a high overlap between the areas predicted to be climatologically suitable to both species. Restricting *Hydrilla* regions by GDD and photic zone depth showed that the nearshore zones are primary regions for its establishment. The area of predicted habitat for grass carp increased greatly when including *Hydrilla* niche as a potential habitat for this species. Integrated risk maps can provide a means for the scientifically informed prioritization of management resources toward particular species and geographic regions.

Introduction

Biological invasions of freshwater ecosystems cause significant impacts on community structure and ecosystem function (Havel et al., 2015). The effects of freshwater invasive species occur globally, in part because of their ability for widespread dispersal through both natural pathways (e.g., active or passive movement through connected waterways) and human-mediated mechanisms (e.g., intentional stocking, accidental releases, hitchhiking on vessels or equipment). Often these human-mediated vectors are associated with commercial and recreational activities. It is expected that the effects of aquatic invasive species will increase as human populations and associated commerce and recreation also increase (Lockwood et al., 2013).

As a major center of commercial and recreational activity, the Great Lakes Basin represents a unique confluence of nonindigenous aquatic species (NAS) from across the globe (Rothlisberger and Lodge, 2013). Multiple pathways of introduction of NAS to the Great Lakes include transport on ship hulls, contamination of ballast tanks, regional overland movement from inland waterbodies on recreational boats, aquarium and horticulture trade, accidental release, or passage through waterway connections (MacIsaac et al., 2001). As a result, the Great Lakes have been subject to over 180 nonindigenous species establishments, some of which have caused irreversible ecological shifts and significant economic damages (Mills et al., 1993; Ricciardi and MacIsaac, 2000; Rothlisberger et al., 2012). As resources to manage biological invasions are typically scarce, there is value in understanding where NAS may establish prior to their establishment. Further, the ability to understand how different NAS may facilitate future invasions may also

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provide useful information for managers prioritizing prevention or control strategies.

A number of tools have been developed to forecast invasive species distributions based on the concept of the environmental niche (Guisan and Zimmermann, 2000). Termed "environmental niche model" or "species distribution model" (hereafter referred to as SDM), these correlative predictive models combine known geographic locations or occurrences of a species with environmental data (often climate data such as temperature or precipitation) to predict species potential geographic distributions in novel environments (Elith and Leathwick, 2009; Hutchinson, 1958; Jiménez-Valverde et al., 2011; Pulliam, 2000). SDMs have been used in a wide range of applications such as locating rare and threatened species and habitats, predicting the spread of invasive species, and estimating the response of species to global climate change (Guisan and Thuiller, 2005). In the Great Lakes, SDMs have been used to anticipate invasions from the Caspian Sea (Fitzpatrick et al., 2013), assess suitable climate conditions for an organism in trade, grass carp (*Ctenopharyngodon idella*) (Wittmann et al., 2014), and to estimate the potential range expansion of common reed (*Phragmites australis*) (Carlson Mazur et al., 2014).

While SDMs are useful tools to estimate species distributions based on climate variables, they have been criticized for the lack of the integration of species-specific habitat information in model specification (Araújo and Peterson, 2012; Elith and Leathwick, 2009). The ability to incorporate specific habitat information is typically not possible because of the absence of relevant data at the appropriate spatial resolutions or extents (Gies et al., 2015). Further, predicting which combinations of species and habitats may facilitate or prevent biological invasions is difficult (Romanuk et al., 2009). In part, this is due to uncertainties in forecasting how nonindigenous species may interact with one another, and with their environments in invaded ecosystems (Grosholz et al., 2000; Johnson et al., 2009).

Here, we forecast biological invasions by combining an SDM algorithm and a recently developed spatially explicit habitat classification database to assess sole and joint invasion scenarios for two nonindigenous species that threaten the Great Lakes ecosystem, grass carp and *Hydrilla* (*Hydrilla verticillata*). First we apply "range bagging", a new technique of species distribution modeling that uses only species presence data (Drake, 2015) to predict suitable climate conditions for these species. Range bagging draws on the concept of a species' environmental range and is inspired by the empirical performance of ensemble learning algorithms (e.g., boosted regression trees) in other areas of ecological research (Elith et al., 2008). Second, we evaluate localized habitat suitability for each of these species using Great Lakes habitat data layers (Wang et al., 2015) specific to the physiological limitations of these species as found in the published literature. Finally, we investigated the intersection of the restricted niches of both species to understand how the predicted suitable habitat for *Hydrilla* might enhance grass carp distribution.

The goal of this study was to identify potential habitat for two invasive species that currently threaten the Great Lakes region. For our specific study species, *Hydrilla* and grass carp, we tested the following three hypotheses for the Great Lakes region: (1) that there is suitable habitat for the potential invasion of *Hydrilla* and (2) grass carp, and that (3) the presence of *Hydrilla* can increase the amount of habitat in which grass carp could persist. We propose that the incorporation of habitat specific information in SDMs can focus management efforts on the locations where prevention, management, and monitoring programs will be most effective.

Methods

Study species

A number of nonindigenous aquatic species currently threaten to invade the Great Lakes region (USACE, 2011). Due to their proximity to the Great Lakes and the documented negative impacts in other systems, grass carp (*Ctenopharyngodon idella*) and *Hydrilla* are of particular concern (Langeland, 1996; Michelan et al., 2014; Wittmann et al., 2014). Grass carp is a large cyprinid fish native to eastern Asia, with a native range extending from northern Vietnam to the Amur River along the Russia-China border (Fuller et al., 1999). An herbivore, it has been globally introduced for nuisance aquatic plant control and is also cultivated in China and other countries as a food source. Despite its widespread introduction and use as a biocontrol agent for nuisance aquatic macrophytes, there has been a great deal of uncertainty about its ecological risk—particularly in the Great Lakes Region (Wittmann et al., 2014). Currently, both diploid and triploid grass carp remain widely available for stocking in the U.S., and feral, reproducing populations have been reported in the Illinois and Mississippi Rivers (Raibley et al., 1995), Lake Erie, and some tributaries of Lake Erie and Lake Michigan (Chapman et al., 2013; Wittmann et al., 2014).

Hydrilla is a submersed aquatic macrophyte native to central Asia and Australia (Cook and Lüönd, 1982). *Hydrilla* was first detected in Florida in the 1960s (Steward et al., 1984) and is now considered invasive and naturalized in the United States as well as much of temperate North America. Introduced populations also occur in Central and South America, Africa, Europe, and New Zealand (Langeland, 1996). *Hydrilla* often has unwanted impacts such as impeding water conveyance, impairment of recreation activities, displacement of native plants, and alteration of nearshore community structure (Gordon, 1998; Langeland, 1996). The monoecious form of *Hydrilla* has been found in waterways with a direct connection to the Great Lakes in New York and Ohio as recently as 2012 (Jacono et al., 2014). The Great Lakes has experienced a number of native aquatic macrophyte declines of ecologic and cultural importance, including wild celery (*Vallisneria americana*) and Wild rice (*Zizania palustrus*) (Schloesser and Manny, 2007; Sierszen et al., 2012). Concern about sensitive wetland species like these in the Great Lakes continues to increase as *Hydrilla* is discovered in adjacent watersheds because studies have shown that *Hydrilla* can competitively exclude these and other native aquatic macrophytes when they are co-located (Chadwell and Engelhardt, 2008; Langeland, 1996; Rybicki and Carter, 2002). Due in part to its life history, *Hydrilla* is extremely difficult to eradicate (Rejmánek and Pitcairn, 2002). Grass carp prefers *Hydrilla* as a food source, and is commonly used as a biocontrol agent for *Hydrilla* in the southern US, Texas and other regions where the plant is a nuisance (Chilton et al., 2008; Pine and Anderson, 1991; Shireman and Maceina, 1981).

Species distribution model

We predicted regions of suitable climate conditions for grass carp and *Hydrilla* by estimating statistical relationships between a widely-used set of global climate variables and species occurrence records using a new SDM method called "range bagging" (Drake, 2015). Range bagging is a form of boundary estimation, considering the limits of the environmental space where a species can persist. The range bagging algorithm efficiently estimates the range limits in a multi-dimensional space of environmental variables using bootstrap aggregation. By repeatedly defining the convex hull of occupied environments in 2 of n dimensions at a time it is possible to determine how often a given environment occurs inside these niche boundaries. The resulting measure, called "niche centrality", refers to the proportion of times an environment occurs within the environmental range of a species across the bootstrapped combinations of environmental variables. Range bagging compares well to other species distribution models in traditional SDM contexts (Drake, 2015) and for invasive species (Cope et al., in review) with the distinct advantages of not requiring pseudo-absence points for fitting and having an ecologically relevant interpretation (Drake, 2015; Cope et al., in review).

The range bagging models were trained on a random partition of 80% of the occurrence data. Performance was reported as the area

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