



Invasion success of a freshwater fish corresponds to low dissolved oxygen and diminished riparian integrity

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Abstract Invasions are a common occurrence in many ecosystems but predicting the establishment and impacts of the invader can be difficult. Understanding how and why invasion progresses can improve efforts to prevent spread and mitigate invasion impacts. Recent efforts have sought to design forecasting methods to identify the environmental context of invasions to help identify areas vulnerable to future invasions. We suggest there are predictable environmental characteristics that affect the probability of successful establishment of invasive species. Specifically, we hypothesize that degraded habitat and water quality facilitate successful invasion, as indicated by high abundances of the invader, due to multiple interacting stressors in the invaded ecosystem. To test this hypothesis, we assessed seven rivers in a temperate region of North America undergoing round goby (*Neogobius melanostomus*) invasion via fish surveys, water quality assessments, and land

cover analyses over three years (2015–2017). Mixed effect random forest models were used to identify commonalities among biotic, physical, chemical, and landscape parameters associated with the relative abundance of round goby among fish assemblages. Low dissolved oxygen and lower proportions of wetland and wetted area land cover in the riparian corridors were associated with highly invaded sites. Results were consistent with prior works suggesting identification of sites with diminished riparian integrity and water quality may help prioritize stream reaches for monitoring to aid in early detection.

Keywords Aquatic-terrestrial interaction · Context dependency · Environmental forecasting · Great Lakes · Land cover · Multiple stressors

Introduction

Invasive species can cause declines in native biodiversity, negatively affect water quality, and disrupt food webs and ecological processes (e.g., Ricciardi et al. 1998). The economic consequences of invasion can also be significant; for example, recreational fisheries alone are an estimated \$190 billion per year global industry (World Bank 2012) but have seen dramatic declines in some areas due in part to species invasions (e.g., Lauber et al. 2020). Invasions can also alter water quality and availability for drinking water and hydropower (Pejchar and Mooney 2009)

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and decrease property values (Horsch and Lewis 2009). The introduction of nonnative species is thus one of the foremost concerns for aquatic conservation (Wilcove et al. 1998; Tickner et al. 2020). Effective prevention is by far the most suitable method of addressing invasive species problems compared to trying to control them after establishment, as mitigation and removal are more difficult and costly (Rout et al. 2011). This dilemma has motivated researchers to identify the environmental context in which invasion is most likely to occur to allow forecasting and better allocation of management resources.

The concept of ‘invasibility’, or how likely any system is to be invaded, evolved from ideas about competitive equilibria for species (MacArthur 1970) and was adopted for terrestrial species by Crawley (1987). Since this time, retrospective studies (e.g., Moyle and Light 1996; Gido and Brown 1999) have provided some indication of how these theories apply to freshwater habitats. The biology of the invader itself can dictate how likely it is to establish in new locations (Marchetti et al. 2004). However, likelihood of nonnative establishment can be difficult to determine based solely on information derived from a species’ native range (Kornis and Vander Zanden 2010). Collectively, low native community diversity (Moyle and Light 1996), available niche space (Davis et al. 2000), and environmental similarity to the nonnative species’ native range are commonly identified as key characteristics of areas likely to be invaded (Shea and Chesson 2002). Given this understanding, direct observation of the environmental conditions of an invasion can assist in understanding factors that facilitate invasion.

Human alterations of ecosystems are also an important component of invasion potential (Leprieur et al. 2008). Nonnative introductions may occur over a large gradient of anthropogenic influence and some areas may be more vulnerable than others specifically due to human influence. The effects of human population size (McKinney 2006), contaminants (Hillery et al. 1997), nutrient runoff (Anderson et al. 2002), previous invasions (Glon et al. 2017), and nonnative propagule pressure (Lockwood et al. 2005) can impact invasion potential. Identifying the mechanisms that govern native community response can be difficult when multiple stressors are present due to the potential for stressor interactions (Bianchi and Morri 2000). Regardless, the potential for invasion may be

exacerbated when native communities experience multiple stressors (Strayer 2010). Byers (2002) found that anthropogenic alteration of habitats through eutrophication or trophic restructuring created an environment where nonnative species were favored because advantages associated with local adaptation were eliminated. Changes in land cover can also impact ecosystems through multiple mechanisms across a landscape (Wolter et al. 2006). Specifically, there can be large-scale effects from urban and agricultural development that have multiple, long-lasting consequences for freshwater biota (Chen and Olden 2020). Because altered land cover can impact ecosystems through a suite of specific and potentially interacting mechanisms, it can be an important metric for overall degradation (Foley et al. 2005). For example, this approach of quantifying land cover change as a measure of ‘cumulative stress’ has been instrumental in the Laurentian Great Lakes for identifying widespread, landscape-scale impacts on freshwater ecosystems, alongside many other stressors (Allan et al. 2013).

The complex and interacting nature of environmental factors that influence invasion potential have made implementation of best practices for conservation and management efforts difficult. For example, funding and personnel limitations sometimes limit our ability to measure critical system attributes at appropriate time- and spatial- scales (Simberloff et al. 2012). However, understanding these characteristics, or the ‘context dependency’ for invasion, can help prioritize management resources to limit the degree and extent of consequences imposed by invasive species (Dick et al. 2017). While the specifics of any invasion can vary dramatically from one instance to another, the physical, chemical, biotic, and anthropogenic factors surrounding invasion create common opportunities that contribute to the establishment of nonnative species and may act as potential indicators for vulnerable sites.

Here we identify the environmental factors relevant to invasion success and develop a method to characterize the biotic and abiotic context of a successful invasion. We focus on round goby (*Neogobius melanostomus*) invasion in the Laurentian Great Lakes as an example. The round goby was introduced to North America from the Ponto-Caspian region of Europe around 1990 (Jude et al. 1992). Like the round goby’s invasion outside its native

range in Europe (Kornis et al. 2012), it has become one of the most prolific invaders in the Laurentian Great Lakes and has undergone secondary spread into inland waters (Kornis and Vander Zanden 2010; Campbell and Tiegs 2012). In its introduced range, the round goby has engaged in egg predation of native fishes including economically important game species and species of conservation interest including lake trout (*Salvelinus namaycush*), lake sturgeon (*Acipenser fulvescens*), walleye (*Sander vitreus*), and smallmouth bass (*Micropterus dolomieu*), (Kornis et al. 2012), though associated population declines have not been reported. However, the round goby has been linked to population decreases in native benthic fishes which are the likely competitors in invaded streams including a suite of percid species and mottled sculpin (*Cottus bairdii*) (French and Jude 2001; Lauer et al. 2004; Poos et al. 2010; Burkett and Jude 2015). In stream habitats, the round goby has induced shifts in diet composition in native benthic species due to competition for resources (Stauffer et al. 2016). However, in some systems, round goby has established with no apparent negative consequences for native fish abundances or assemblage composition thus far (Riley et al. 2008; Kornis et al. 2013). Because round goby establishment has been so successful, there is concern regarding the potential impact of round goby on native ecosystems, and investigations that may contribute to more effective prevention strategies are timely.

Given the environmental differences between previously invaded lake habitats, and the river ecosystems that are the current locations of secondary spread in the Great Lakes, we set out to identify characteristics common to Great Lakes tributaries that are experiencing initial invasions and expansions of round goby populations. Specifically, we sought to (1) describe the nature of current secondary spread of round goby into Great Lakes tributaries, and (2) identify common features of the habitats hosting the largest populations of round goby as a means to facilitate prediction of locations vulnerable to future invasions. Due to the uncertainty surrounding round goby impact on native ecosystems, a more thorough understanding of invasion potential, particularly in lotic waters, can provide important context for management of invasions.

Methods

To determine the environmental context of round goby invasion, we conducted surveys in seven rivers experiencing active round goby invasion (Fig. 1). Each river is a tributary to one of the Laurentian Great Lakes in the state of Michigan (USA; Table S1) and this suite of rivers was chosen to represent a variety of watershed types (land cover dominated by urban development, agriculture, forest, or wetland; Krabbenhoft 2019). Sampling occurred once per year at three wadeable stream reaches in each watershed in the spring and summer from 2015 to 2017; however, the Ocqueoc River and Stony Creek were not sampled in 2015. Sampling occurred in the spring as soon as water temperatures were conducive to full sampling of the fish assemblage (late April to early May of each year – see Table S1) and continued in a south-to-north fashion until all rivers had been sampled (thus ensuring each river was sampled under similar temperature conditions each year). Reach locations were chosen based on representative habitat from each section of the river. Reach lengths were designed to account for ten times the reach width where possible, or else contained at least two distinct geomorphic habitat types along the length to ensure a representative sample of the fish assemblage (e.g., riffles, pools, meanders; Lyons 1992).

Biotic parameters

We conducted annual fish surveys for approximately one hour at each site (from downstream to upstream) to identify the composition of the fish assemblage at each location. Fish were captured using a 3 × 1.5 m nylon seine (3.18 mm mesh) using a combination of sweeps and kick seining as appropriate for the habitat. Seines were chosen as the ideal sampling device in this instance because the rivers in this study are largely sand or gravel bottom, and electrofishing has been known to exclude small-bodied individuals (Wiley and Tsai 1983) which made up a majority of the species in fish assemblages in these rivers (Fig. S1). Individual fish were identified on site and released, except a subset which were euthanized via an overdose of MS222 (tricaine methanesulfonate) and preserved as vouchers for further analyses.

To complement this study's data on round goby distribution, past fish survey data were gathered from

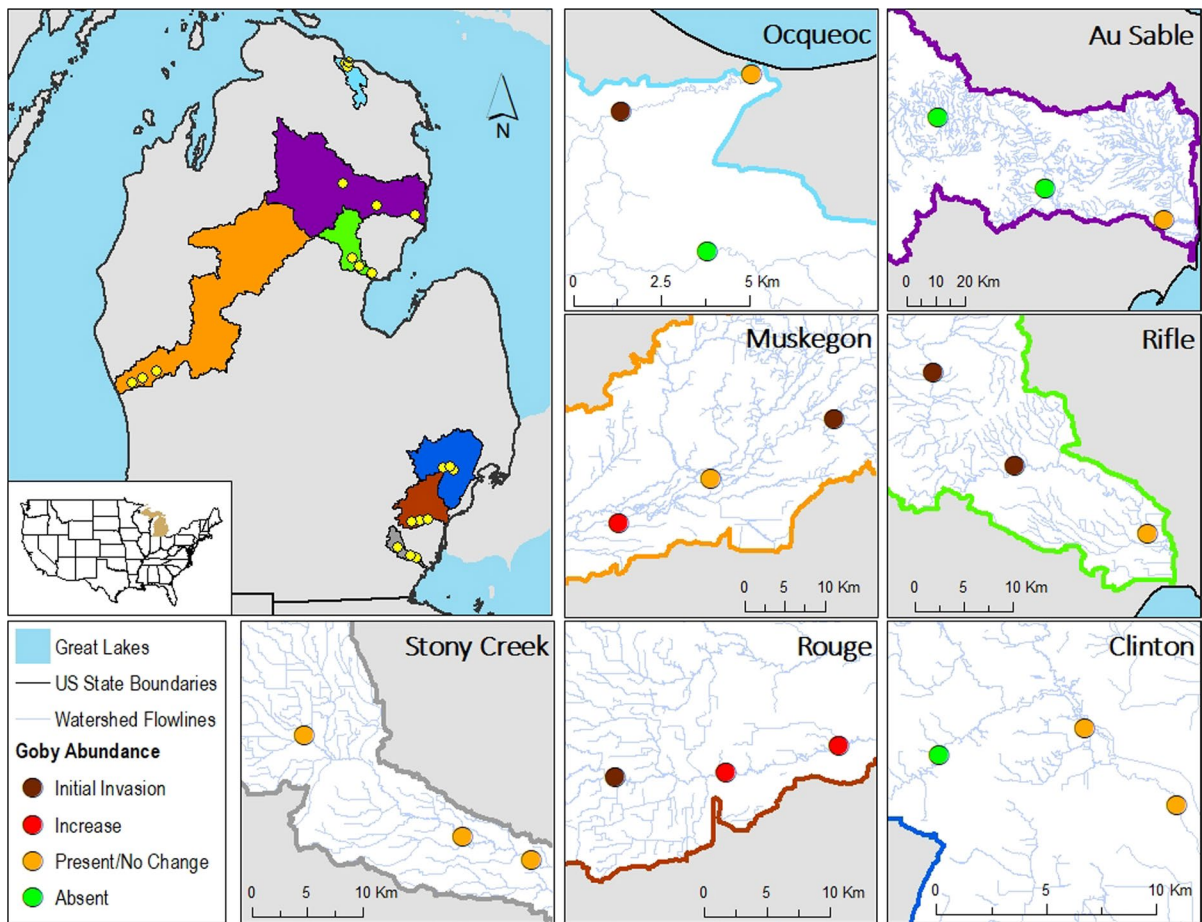


Fig. 1 Seven watersheds in the lower peninsula of Michigan sampled from 2015 to 2017. Sample sites are indicated by yellow points in the top left panel. Smaller maps show sample sites in each watershed. Flowlines show streams, rivers, canals, and ditches (USGS 2017). Coloration of sample points on

watershed maps illustrates round goby abundance throughout our study: goby absent for the entire study (green); goby present but did not change in abundance over time (orange); goby increased in abundance over time (red); initial invasion was observed during this study (dark red)

several sources to narrow down timing of initial invasion for each site (Table S2). Fish collection information was gathered from the FishNet2 repository (FishNet2 2018), the University of Michigan Museum of Zoology Fish Division catalog (UMMZ 2018), the Midwest Invasive Species Network (MISIN 2017), the Great Lakes Aquatic Nonindigenous Species Information System (GLANSIS 2018), and the Global Biodiversity Information Facility (GBIF 2018). In addition, collection records from fisheries surveys and scientific permits were obtained from the Michigan Department of Natural Resources (MI DNR) (personal communication – T. Goniea and K. Wehrly, Michigan DNR). Where necessary, individual

watershed status reports were obtained from the MI DNR (Francis and Haas 2006). All collection records that included round goby were assessed for spatial relevance to our sample locations; a collection record was deemed spatially relevant if it occurred at or upstream of a study site, indicating that round goby had invaded or surpassed that site by the time of the collection. The dates of all records were interpreted as minimum estimates of initial invasion (acknowledging that invasion timing may have occurred earlier than these survey events). At sites where collection records did not report round goby, timing of invasion was informed by survey data from this study. Initial invasion timing ranged from 2002 to 2017, and four

sites were uninvasioned by the conclusion of surveys for this study (Table S3).

Physical parameters

In addition to fish surveys, a suite of water chemistry and physical variables were measured at the time of sampling. Temperature, dissolved oxygen, conductivity, and pH were measured using a YSI multiparameter instrument. Average stream depth was estimated at the conclusion of sampling and average stream width was estimated for the reach using the Google Earth distance tool (Google 2018). In addition to basic water chemistry, we collected fifteen mL water samples, preserved with concentrated nitric acid- HNO_3 , for analysis of copper concentration (Van Metre and Mahler 2003). Copper was chosen as a metric for contamination associated with urbanization as concentrations tend to be higher in freshwaters near areas with high human population density due to copper shed from tires and brake linings (Paul and Meyer 2001), runoff from rooftops (Van Metre and Mahler 2003), and contaminated sewage discharge (Sodré et al. 2005). Dissolved copper (Cu) was measured using a Shimadzu AA-7000 Atomic Absorption Spectrophotometer. Concentrations were calculated from an average of three concurrent runs of each sample based on a calibration curve of laboratory standards at 0, 0.5, 1.0 and 1.5 mg L^{-1} . Using ArcGIS, landscape-scale habitat factors were measured, including the distance in river kilometers (rkm; linear distance along the stream flowline) to the river mouth and the overall area of each watershed (m^2).

Land cover parameters

Finally, as a large-scale indicator of anthropogenic influence on invasions, 30-m resolution land cover data were obtained from the National Land Cover Database (NLCD; Homer et al. 2015). Twenty land cover types defined by the NLCD were binned into five categories relevant to stream integrity (e.g., Ahearn et al. 2005; Table S4). Land cover information from 2011 (Homer et al. 2015) and 1992 (Vogelman et al. 2001) were used to represent how the current and past (legacy effects) landscape compositions influenced patterns of invasion, respectively. Land cover was quantified for each watershed inside a 100 m riparian buffer zone (from each

bank) following the flowline of the stream (National Hydrography Dataset – USGS 2004) using ArcGIS. Isolating the riparian buffer allowed us to account for the land area most directly affecting stream form and function (Allan 2004). In addition, each watershed was clipped along the streamline such that only the land area upstream of each site was considered. Upstream buffer clipping resulted in the downstream-most site incorporating the largest land area, so land cover data were converted to proportional abundances for each site.

Data analysis

All analyses were completed using the statistical software package, R (R Core Team 2016), with additional packages for specific analyses as indicated below.

Assemblage data from fish surveys were analyzed for assemblage diversity using the adjusted Shannon's diversity index proposed by Chao and Shen (2003), which applies a maximum likelihood correction for rare species potentially missed during sampling. For various reasons (e.g., instrument failure), occasional missing data points existed for the water quality data (temperature, dissolved oxygen, conductivity, pH, and copper). Because missing data can skew results, missing points were imputed by multiple imputation using the R package, 'missMDA' (Josse and Husson 2016).

Model building

All physical, biotic, and land cover parameters (Table 1) were assessed for their predictive power of round goby proportional abundance using longitudinal Mixed Effect Random Forests (Capitaine et al. 2021). Mixed Effects Random Forests (MERF) use a Classification and Regression Tree (CART) approach to build regression trees that partition the variable space of the explanatory variables by randomizing the explanatory variables at each step, and then average the predictions made by individual trees (see Hajjem et al. 2011). This approach allows estimation of prediction error (out-of-bag error) of the model response variable based on a learning data set and predictions made for observations from trees built on the bootstrapped data. Estimated errors are also used to assign variable importance which is calculated from the increase in mean error incurred in the final model by the iterative removal of each predictor variable. The

Table 1 Variables included in the Mixed Effects Random Forest model for identifying the environmental context of round goby populations. Independent variables are listed by category; the dependent variable was round goby abundance as calculated from fish assemblage surveys

Variable category	Variable names	Description
Biotic	H_adjusted	Shannon's diversity index adjusted for rare species
	Invasion_year	Estimated year of invasion plus one
Physical	Mouth_distance	Distance from sample site to the mouth of the river (km)
	Width	Mean reach wetted channel width (meters)
	Depth	Mean reach water depth (meters)
	Watershed_area	Total area of the entire watershed for each river (m ²)
Water chemistry	Temp	Water temperature (°C)
	Cond	Specific conductivity (μS cm ⁻¹)
	DO	Dissolved oxygen (mg L ⁻¹)
	pH	pH
	Copper	Concentration of dissolved copper (mg L ⁻¹)
Land cover	Ag_2011	Percent agricultural riparian land cover in 2011
	Urban_2011	Percent urban riparian land cover in 2011
	Forest_2011	Percent forested riparian land cover in 2011
	Water_2011	Percent water riparian land cover in 2011
	Wetland_2011	Percent wetland riparian land cover in 2011
	Ag_1992	Percent agricultural riparian land cover in 1992
	Urban_1992	Percent urban riparian land cover in 1992
	Forest_1992	Percent forested riparian land cover in 1992
	Water_1992	Percent water riparian land cover in 1992
	Wetland_1992	Percent wetland riparian land cover in 1992
Response variable	Goby_density	Number of round goby present divided by the total number of fish from the assemblage survey

addition of stochastic processes and application to longitudinal data provided by Capitaine et al. (2021) adjusts this model to incorporate change in covariance among variables over the range of observations, and takes into account repeated measures to increase understanding of within variable variance in addition to variation among variables.

Using the R package, 'longituRF' (Capitaine et al. 2021), we built longitudinal MERF models with a stochastic process to account for fixed (site and river) or random variables (all other parameters) in our sample design. This process builds trees with a subsample of the original dataset that has been bootstrapped to allow calculation of out-of-bag (OOB) observation error rates with all data points. Our original model contained 21 physical, biotic, and land cover parameters (Table 1). We used a model simplification function (see Jiang et al. 2004) to eliminate variables with the least amount of contribution to the dependent variable variance based on mean out-of-bag error across all iterations of the random forests. Updated model parameters (less the bottom 20% of variables)

were then iteratively rerun until only two explanatory variables remained. All models with a mean out-of-bag error within one standard error of the full model were deemed comparable (Hansen et al. 2015), and the model with the maximum percent variation explained was chosen as the final model. All models were calculated using 1000 trees, a delta value of 0.01 to prevent overfitting (resulting in either 26 or 27 iterations), and a maximum number of trees used for splitting at each node ('mtry') equal to one third of the number of explanatory variables in each model (in order to tune each model to correspond with the number of independent variables). Partial dependence plots were generated for the most important parameters by predicting the outcomes of all variables in the model while holding the variable of interest to a single value; this procedure was then repeated across the entire range of the predictor variable values to generate plots illustrating the relationships between predictor variables and the response variable (Cutler et al. 2007). Partial dependence plots are a useful way of illustrating the effect a single independent variable

has on the outcome of the machine learning model when all other parameters are held constant.

Results

Biotic parameters

Fish surveys identified 4,663 fish of 57 species (Data S1). Fish assemblages varied among sites, watersheds, and years and largely consisted of cyprinids, percids, centrarchids, and catostomids (Figure S1; Data S1). The midstream site in the Rifle River had the lowest Shannon diversity (1.08), while the highest was at the upstream site in the Muskegon (2.05). The lowest watershed-level diversity was observed in the Rouge River (1.48), while the highest was in the Muskegon River (1.91). Round goby was present at 40 of 57 sites over three years and comprised an average of 16% of the fish assemblage, where present (Fig. 2). The proportional abundance of round goby and the number of sites at which it was present increased over time. The greatest overall abundances were observed in the Rouge River and Stony Creek, the two southern-most watersheds in this study. Over the three years in this study, initial round goby invasion (the invasion front) was identified at five sites across four rivers: the Rouge, Muskegon, Rifle, and Ocqueoc Rivers.

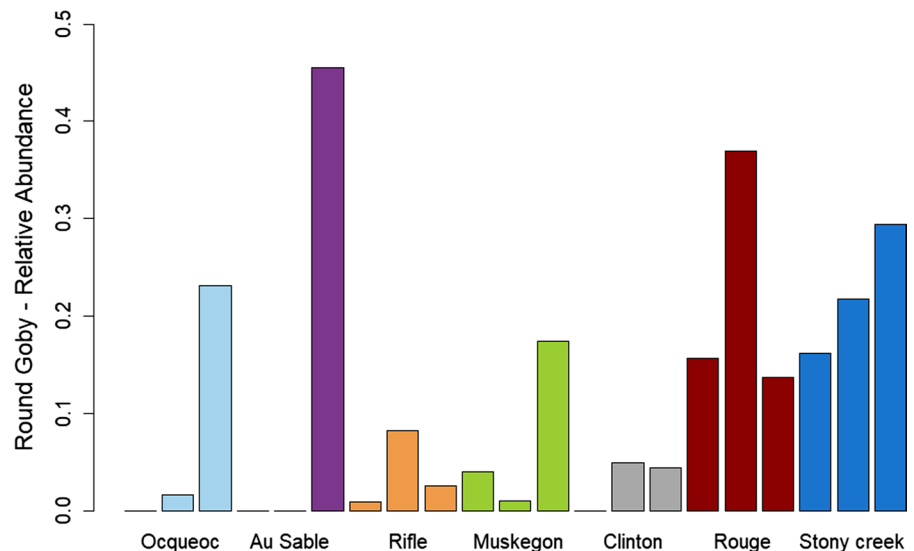
Fish collection information from online databases, reports, and survey information yielded 385

collections that were spatially relevant to this study including 48 round goby collections (Table S2). Combined with our survey data, an approximate time of initial invasion was assigned to each site in the study (Table S3).

Physical parameters

Mean water depth at all sampled reaches was 0.95 m and mean reach width was 28.5 m. Dissolved oxygen ranged from 5.4 to 13.0 mg L⁻¹ and was lowest in the most agriculture-dominated watershed (Stony Creek; Krabbenhoft 2019). Water chemistry parameters were relatively similar during fish surveys among years (within sites) and water temperature varied within a site by a maximum of 4.6 °C among years (upstream site in the Rifle; Data S1). pH was similarly consistent among years and the highest values recorded were in the Rouge and Clinton Rivers (the most urban watersheds; Krabbenhoft 2019). Conductivity was similarly high in urban and agricultural reaches (Data S1). Contrary to our expectations, dissolved copper concentrations were fairly low for all sites (mean 0.102 mg L⁻¹). Some of the highest values occurred in the Au Sable (0.251 mg L⁻¹) and Ocqueoc Rivers (0.214 mg L⁻¹) while there were samples with undetectable concentrations from both the Rouge and Clinton Rivers (the most urban watersheds).

Fig. 2 Round goby relative abundance (expressed as a proportion of the fish assemblage) at each of the three sites in each watershed (from left to right, sites are listed from upstream to downstream; rivers are listed from north to south). Abundances are shown as a mean per site across all sampling years (2 years for the Ocqueoc River and Stony Creek; 3 years for all others)



Land cover

Binned riparian land cover was summarized by the percent area of the riparian buffer for all streamlines upstream of each site (Figure S2). The Rouge and Clinton River watersheds were by far the highest in urban development, while Stony Creek had a relatively high proportion of agricultural land use. The Au Sable, Rifle, and Ocqueoc had the most forested riparian areas. The Ocqueoc and Au Sable Rivers also had notable proportions of wetland in the riparian buffer. Forest, wetlands, and water decreased as agriculture and urban development increased over time, suggesting expansion of anthropogenic land uses across all watersheds, particularly for urban development (Table S5). Variation in riparian land cover among sites within a river differed for each watershed. For example, in the Muskegon and Ocqueoc Rivers, all three sites had relatively similar land cover composition, while the other rivers showed gradients in land cover change from upstream to downstream (Table S6). The Rouge River and Stony Creek had the highest percentage of agricultural land cover at the upstream-most site, while the Clinton River had the highest percentage of urban land cover at the upstream site. The Rifle and Au Sable (two northern, forested watersheds) had relatively similar compositions of urban and agricultural land cover among sites but had the greatest proportions of wetland at their upstream sites.

Mixed effects random forest (MERF) model

The MERF model largely identified land cover variables as among the most important factors related to round goby abundance (Fig. 3). The final simplified MERF model for environmental conditions associated with round goby abundance had a mean out-of-bag error of 0.001 and explained 94.38% (standard error 0.017) of the variance (Table S7). The model was built from 26 iterations of the bootstrapped data and contained four variables: dissolved oxygen and three riparian land cover variables –water, wetland, and forest from 2011.

Partial dependence plots were fitted to each explanatory variable to indicate the direction and degree of the relationship between each of the independent variables in the final model and the

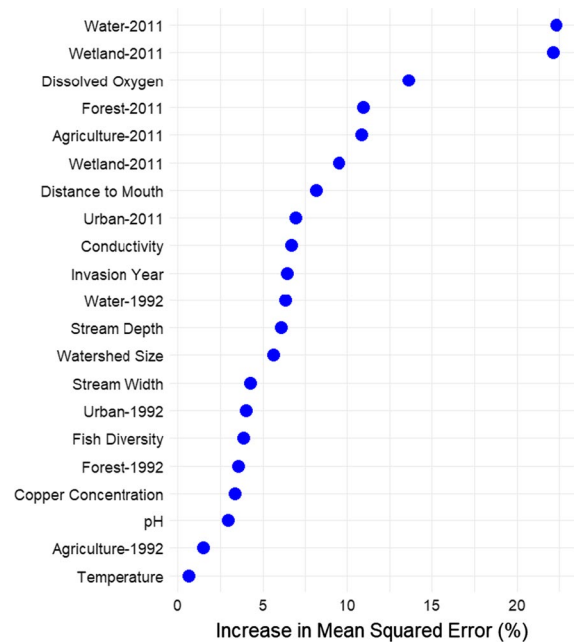
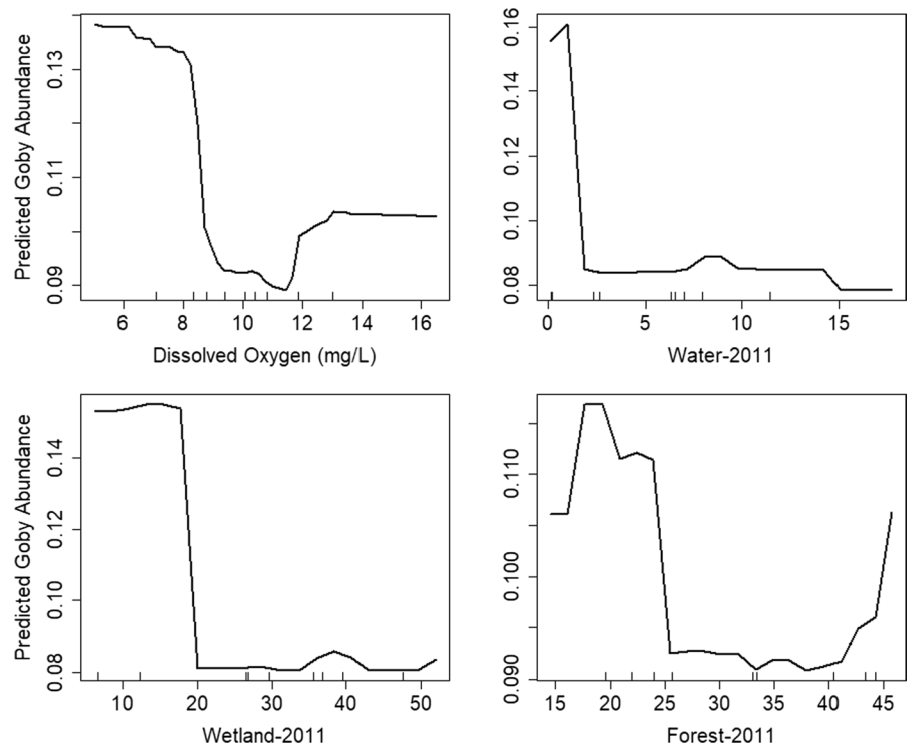


Fig. 3 Relative importance of the independent variables in the Mixed Effects Random Forest model. Variables are listed from top to bottom relative to the percent increase in mean squared error incurred by removal of each parameter when it is permuted. Riparian land cover categories are listed with their respective years noted

relative abundance of round goby in the fish assemblage (Fig. 4). These relationships collectively indicate that round goby is lower in abundance in areas where dissolved oxygen is moderate, wetted area and wetland composition of the riparian area are high, and the proportion of forest in the riparian area is moderately high. Both dissolved oxygen and percent forest cover had non-monotonic relationships with round goby, where round goby abundance was greater at the extreme ends of each distribution. It is also of note that partial dependence plots do not consider interactions among variables. It is therefore possible that additional variation within our model that cannot be explained by these four variables alone, may be due to their interactions and contribute to additional variance in round goby abundance in our model.

Fig. 4 Partial dependence plots for the four most important variables in the final Mixed Effects Random Forest model. Lines represent the predictions for round goby proportional abundance relative to an increase in each parameter along the x-axis. Vertical lines along the x-axis show the distribution of the independent variable (deciles). Note that y-axes differ among plots



Discussion

Here we incorporate physical, chemical, and biotic parameters to identify the environmental context common to streams where round goby has successfully invaded and persisted. Physical and landscape characteristics reflected variation in overall site quality, largely corresponding to a north-to-south gradient across the state of Michigan. As demonstrated by Krabbenhoft and Kashian (2019), more densely populated areas in southern Michigan typically had the lowest habitat quality and the highest urban and agricultural land use. Despite large differences in site quality, stream morphometry, and landscape composition, round goby has successfully invaded all rivers in this study. This finding is in line with previous results suggesting the round goby's broad environmental tolerance has allowed it to become a prolific invader in North America (Kornis et al. 2012).

Our model selection procedure identified several variables that had minimal impact on the mean squared error of the model when removed. While logistic factors like propagule pressure (Lockwood et al. 2005) have typically been identified as important in invasion success, time since invasion and

distance to the propagule source were only moderately informative in our final model. Native species diversity was not among the most predictive factors in goby invasion in these rivers, similar to previous findings for round goby invasion in Lake Michigan tributaries (Kornis et al. 2013). These findings are contrary to standing ecological theory (Elton 1958), which suggests that native diversity may increase system resistance to invasion, but may reflect variations in this relationship across spatial scales (Von Holle 2013). In particular, our approach to site selection that intentionally incorporated a gradient in riparian land cover types may have reinforced the importance of land cover over factors typically associated with invasion success (e.g., native diversity and propagule pressure). This finding is also interesting given that some native species, particularly native benthic fishes, have often been shown to decline in response to round goby invasion (e.g., Janssen and Jude 2001; Lauer et al. 2004; Balshine et al. 2005; Krabbenhoft 2019). This disparity suggests context-dependence may be a critical factor in governing the relationships among environment, native community composition, and round goby invasion and that interactions among these factors may be more informative. Other aspects

of the invasion context that were not investigated in this study (e.g., invader genetic diversity (Roman and Darling 2007) and niche breadth (Vazquez 2006) may also influence both invasion and changes in native diversity. However, Wicks (2020) found that genetic diversity of round goby among these systems was relatively low, while differences in gene expression among sites was high. The interaction between native diversity and invasion potential may thus be indirect and difficult to measure.

Physical data corresponding to watershed and stream size and morphometry were also largely uninformative in our model, contrary to previous findings for round goby (Kornis and Vander Zanden 2010; Kornis et al. 2013). Both stream depth and width as well as watershed area were removed during our model simplification procedure. We suggest this pattern may be due to the relatively high influence of human-mediated movement across the landscape. This area of southern Michigan has a large population of anglers (Krabbenhoft et al. 2019) and bait bucket transfer of round goby may be high, as has been proposed elsewhere (Brownscombe et al. 2012; Mueller et al. 2017). Spatial barriers which have often precluded initial introductions may only provide short-term barriers to range expansion as human activities act as vectors for movement of individuals across the landscape (Davidson et al. 2017). In this case, the regularity of human transfer across inland waterscapes may have aided dispersal, rendering the influence of habitat and watershed size negligible in our final model. Similarly, Raab et al. (2018) identified distance to the nearest downstream impoundment was an important factor in secondary spread of round goby in inland waters, but we excluded this variable in our modeling procedure because our sample design necessitated that sites were concentrated to downstream reaches, in many cases because dams had thus far impeded upstream invasion (though not in all cases). As such, vulnerable sites that are upstream of existing barriers should continue to be monitored, despite current exclusion of natural upstream migration of round goby populations.

Our final model found that round goby relative abundance was related primarily to dissolved oxygen concentrations and land cover composition of the riparian corridor. Specifically, round goby was lowest in abundance in areas with moderate levels of dissolved oxygen and a high degree of wetted

area, wetlands, and forest cover in the riparian buffer. Round goby have a relatively wide tolerance for dissolved oxygen (Tang et al. 2020), but avoid habitats with consistently low dissolved oxygen concentrations (<60% saturation; Cooper et al. 2009). In contrast, relatively high-quality habitat (e.g., high dissolved oxygen, undisturbed riparian land cover) that benefits native taxa may also facilitate invaders at large spatial scales (Von Holle 2013), thus making the relationship to some of these variables non-monotonic. However, correlation between land cover and human population density in Michigan could be masking the relationship between round goby abundance and propagule pressure (due to a concentration of human development around Great Lakes port cities). Thus, these relationships should be further investigated in additional watersheds. While wetland and wetted area could simply correspond to stream size, the parameters for depth, width, and watershed size were excluded as variables in our final model, suggesting the importance of land cover in our findings may be a result of the extent of floodplain connections and aquatic-terrestrial habitat linkages. For example, loss of aquatic-terrestrial linkages via channelization and urban stream burial, as well as the impact this has had on stream function, is well documented in the Rouge River (Napieralski et al. 2015; Beam and Braunscheidel 1998). Although the relative impact of land cover, compared to other variables, might fluctuate with further sampling (e.g., additional replicates within each land cover type), our findings support the idea that land cover alteration in a watershed is correlated with, and potentially can facilitate, invasion. This has previously been shown in freshwater invertebrate invasion (Früh et al. 2012). Because land cover types impact streams through different mechanisms (Allan 2004), land cover alone may be a poor predictor of overall fish assemblage composition (Tóth et al. 2019). However, we demonstrate here that a potential consequence of loss of natural land cover is an increased incidence of invasive species. This underscores the importance of considering ecosystem function in an urban planning and landscape development context. Specifically, maintaining natural land cover (and thus minimizing disturbance) in riparian corridors may decrease the potential for aquatic invasions.

Our study illustrates a relationship between environmental variables and round goby invasion. Though the heterogeneity in the relative abundance of round

goby in the fish assemblages at each site is similar to studies from tributaries in Wisconsin (USA), the driving factors in our final model showed greater emphasis on water quality (oxygen) and land cover than variables identified by Kornis et al. (2013). This shift in the priority of environmental factors related to round goby relative abundance may be due to the time since invasion (e.g., residence time) in our study (5–10 years later), differences in sampling strategies (repeated sampling in a few invaded streams representing specific land cover types vs. a large number of sites with broad land cover types), and/or differences in the variables measured (e.g., Kornis et al. (2013) did not account for dissolved oxygen). We thus echo their concerns about the lag time and associated effects of round goby invasion, as well as the changing role of landscape and habitat variables in regulating round goby populations in invaded streams. The impacts of this invasion are variable and context-dependent, but there is concern that as round goby becomes more established in tributary habitats, there will be greater consequences for native communities as has been seen in other invasions (Crooks and Soulé 2001). The consequences of this invasion warrant further study, particularly in lotic habitats that have lagged in investigation relative to round goby populations in the Great Lakes.

Round goby distribution expanded over the course of this study and as shown here, populations have not yet decreased following initial invasion (e.g., boom-bust invasion dynamics; Strayer et al. 2017). As round goby invasion continues in these tributaries, we expect they will further integrate with native communities, as has been observed in lake populations (Foley et al. 2017). The adjustment of piscivorous fish species to include round goby in their diet may offer some form of future population regulation (Madenjian et al. 2011). However, there is still much to be gained by curtailing round goby invasion where possible to minimize their impact on native species. In this study, we identified four environmental factors related to round goby invasion in Laurentian Great Lake tributaries. The biological, physical, and chemical contexts associated with this invasion correspond to long-standing ecological hypotheses that highlight the importance of riparian integrity and water quality for structuring aquatic communities (e.g., aquatic-terrestrial linkages), such as the role of habitat loss and human development. Though we cannot tease apart

correlation vs. causality in our data, our findings suggest that reaches with a high degree of development in riparian corridors and poorer water quality may be vulnerable to aquatic invasions. Our results add to a body of evidence that conservation and restoration activities may promote system resistance to invasion. We also suggest that an understanding of linkages between environmental factors and invasion success can help management entities maximize their return from limited resources by helping to prioritize monitoring efforts for early detection and conservation efforts for invasion prevention. These lessons should be broadly applicable across species and could aid conservation of native ecosystems and species in the face of increasing global species introductions.

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Author contributions CAK and DRK conceived the study. CAK obtained funding through fellowships, conducted field and laboratory work, performed data analyses, and wrote the manuscript. DRK conducted field work, obtained funding for supplies, and provided revisions to the manuscript. Both authors contributed to the drafts and gave final approval for publication.

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Data availability All data are available in the manuscript supplement data file.

Code availability Source code was used as indicated in the methods of the manuscript.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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