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Predicting invasiveness of species in trade: climate match, trophic guild and fecundity influence establishment and impact of non-native freshwater fishes

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ABSTRACT

Aim Impacts of non-native species have motivated development of risk assessment tools for identifying introduced species likely to become invasive. Here, we develop trait-based models for the establishment and impact stages of freshwater fish invasion, and use them to screen non-native species common in international trade. We also determine which species in the aquarium, biological supply, live bait, live food and water garden trades are likely to become invasive. Results are compared to historical patterns of non-native fish establishment to assess the relative importance over time of pathways in causing invasions.

Location Laurentian Great Lakes region.

Methods Trait-based classification trees for the establishment and impact stages of invasion were developed from data on freshwater fish species that established or failed to establish in the Great Lakes. Fishes in trade were determined from import data from Canadian and United States regulatory agencies, assigned to specific trades and screened through the developed models.

Results Climate match between a species' native range and the Great Lakes region predicted establishment success with 75–81% accuracy. Trophic guild and fecundity predicted potential harmful impacts of established non-native fishes with 75–83% accuracy. Screening outcomes suggest the water garden trade poses the greatest risk of introducing new invasive species, followed by the live food and aquarium trades. Analysis of historical patterns of introduction pathways demonstrates the increasing importance of these trades relative to other pathways. Comparisons among trades reveal that model predictions parallel historical patterns; all fishes previously introduced from the water garden trade have established. The live bait, biological supply, aquarium and live food trades have also contributed established non-native fishes.

Main conclusions Our models predict invasion risk of potential fish invaders to the Great Lakes region and could help managers prioritize efforts among species and pathways to minimize such risk. Similar approaches could be applied to other taxonomic groups and geographic regions.

Keywords

Aquarium, biological invasions, classification tree, ecological impact, establishment success, exotic species, Laurentian Great Lakes, live food, risk assessment, water garden.

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INTRODUCTION

Increased intentional and unintentional transport of live organisms associated with international commerce has led to the establishment of many species well beyond their native geographic ranges (Levine & D'Antonio, 2003; Hulme, 2009). Biological invasions have subsequently altered patterns of biodiversity from local to continental scales (Wilcove *et al.*, 1998; Baiser *et al.*, 2012) and resulted in both ecological and economic impacts on entire ecosystems (Pimentel *et al.*, 2005; Strayer *et al.*, 2006). These impacts have motivated the development of risk assessment tools that identify non-native species likely to establish and have impact (Leung *et al.*, 2012; Ibáñez *et al.*, 2014). These tools can be used to prioritize both the species and geographic regions for which the risk of establishment and impact is greatest, thus facilitating more focused, efficient management actions that target prevention (Keller & Perrings, 2011; Jenkins, 2013).

Risk assessments for evaluating species imported via international trade have been under-utilized relative to the magnitude of the invasion threat posed (Keller & Lodge, 2007; Smith *et al.*, 2009). This is illustrated in freshwater ecosystems where the risk of species invasion is high (Padilla & Williams, 2004; Keller & Lodge, 2007), especially with respect to non-native fishes (Olden *et al.*, 2010). Risk assessments based on species' ecological traits associated with specific stages of invasion can offer scientifically rigorous support for efforts to prevent invasion (Marchetti *et al.*, 2004a; Leung *et al.*, 2012). Aggregating species assessment results across specific trade pathways can also help decision-makers determine which pathways pose the greatest risk of introducing new invaders, and thus deserve greater management or policy attention (Pysek *et al.*, 2011).

Fishes constitute approximately 90% of all individual animals imported into the United States annually (Smith *et al.*, 2009). Many of these fishes are sold through the aquarium, biological supply, live bait, live food and water garden trades (Keller & Lodge, 2007; Smith *et al.*, 2008). Some of these fishes are subsequently released by humans into the wild. For example, 2% and 3% of aquarium and water garden owners in the Great Lakes basin, respectively, release unwanted fishes (Marson *et al.*, 2009a,b). Further, >6% of aquarists in the northwestern United States have released live fishes (Strecker *et al.*, 2011). As different trade pathways select species for different purposes, it is likely that they pose different overall risks for the recipient ecosystems. For example, the water garden trade requires fishes that can survive in outdoor ambient conditions, while the aquarium trade imposes no such limitation. Knowledge of which trades introduce the most high-risk species would facilitate more efficient prioritization of management actions and policy improvements (Lodge *et al.*, 2006).

Traits that are highly predictive of non-native fish establishment differ across studies and geographic regions, but some traits are consistently correlated with establishment success (García-Berthou, 2007). For example, temperature tolerance (Kolar & Lodge, 2002; Bomford *et al.*, 2010), trophic status (Marchetti *et al.*, 2004b; Ruesink, 2005), spawning habitat requirements (Mandrak, 1989; Olden *et al.*, 2006) and history of invasion outside the native range (Kolar & Lodge, 2002; Ribeiro *et al.*, 2008) have emerged as robust indicators of establishment success. In contrast, traits associated with invasion *impacts* have exhibited greater variation across studies (García-Berthou, 2007), suggesting that additional understanding is required to model this stage of invasion.

The Laurentian Great Lakes of North America serve as an important region for developing and testing trait-based risk assessments of potentially invasive species. Hundreds of non-native species, including at least 65 freshwater fishes, have been introduced to the Great Lakes basin from multiple pathways over the last two centuries (Mandrak & Cudmore, 2010). The resulting invasions have altered ecosystem functions in undesirable ways and jeopardized valued services provided by the Great Lakes (Rothlisberger *et al.*, 2010, 2012). Major trade pathways, including the aquarium, biological supply, live bait, live food and water garden trades, have the potential to introduce many more unwanted non-native freshwater fishes to the Great Lakes region (Ricciardi, 2006; Keller & Lodge, 2007).

Here, we develop trait-based risk assessment tools for the establishment and impact stages of non-native fishes in the Great Lakes. We then use the models to identify traded non-native fishes that pose a threat of becoming invasive in the Great Lakes ecosystem and assess the relative risks of the aquarium, biological supply, live bait, live food and water garden trades for future invasions. We compare our analysis of trade pathway risks to historical patterns of non-native fish establishment in the Great Lakes to evaluate the relative contribution of trade to invasion over time and to identify which trades have historically supplied invaders with the highest rates of establishment success. In addition to advancing trait-based approaches, our results could inform current practices and future policies to prevent fish invasions via trade and thus safeguard the goods and services provided by the Great Lakes and other freshwater ecosystems.

METHODS

Predicting establishment and impact

We identified 65 non-native fish species introduced to the Great Lakes, 37 of which have established self-sustaining (reproducing) populations (Mandrak & Cudmore, 2010; see Table S1). The degree of ecological impacts associated with established non-native fishes is difficult to determine from literature because not all species have been studied and impacts differ across the region. Therefore, we evaluated the ecological impact of the 37 established species with a questionnaire (Appendix S1) distributed to university and government agency experts (Table S2) with experience in the

Great Lakes region and substantial knowledge of aquatic invasive species, fisheries and/or ecosystems. Experts were chosen based upon their specific expertise in particular lake basins to yield even, complete coverage of the Great Lakes region. The questionnaire asked experts to assign each species to one of four categories ranging from no perceived ecological impact to very high perceived ecological impact in the Great Lakes (definitions modified from Bradford *et al.*, 2009 and Mandrak *et al.*, 2012) and to assign either low or high confidence to their answer. Respondents could decline to rank a species if they were not familiar with its impact. A total of 33 experts in Canada and the United States received the questionnaire via electronic mail on 24 August 2011 and responses were received from 27 (82%) experts (Table S2). The 27 respondents cumulatively reported over 557 years of research experience in the Great Lakes, indicating that the impact scores come from a scientific community that is well-informed about fishes in the Great Lakes region.

We calculated the mean and 95% confidence interval (CI) of responses for each species and then ranked the species from lowest to highest impact based upon the upper CI value to incorporate variation in respondent answers. There were no obvious breaks in the impact rankings across the 37 species (i.e. impact ranks increased approximately linearly from lowest to highest). Therefore, for the analysis of impact, we compared the 12 species with the highest and lowest impacts, respectively (Table 1). This approach maximized our ability to detect differences in species traits and invasion risk parameters between low- and high-impact species.

Species traits and invasion risk parameters

From the literature, we identified 18 species traits and invasion risk parameters (details in Table S3) that have been previously associated with the establishment and impact stages of invasion (reviewed in García-Berthou, 2007) and for which sufficient data typically exist in publicly available databases. These 18 traits and parameters were categorized *a priori* as follows. Ecological traits included (1) diet breadth (sum of diet items, including algae/phytoplankton, vascular plants, detritus, aquatic/terrestrial invertebrates and larval fishes, fishes/crayfishes/crabs/frogs, blood, eggs); (2) macrohabitat association (lentic, lotic); (3) salinity tolerance (narrow, wide); (4) temperature tolerance [cold (10–17°C), cold/cool, cool (18–26°C), cool/warm, warm (>26°C)]; and (5) trophic guild (herbivore–detritivore, invertivore, invertivore–piscivore, omnivore, piscivore). Life history traits included (6) maximum total body length; (7) egg diameter; (8) fecundity (maximum reported per spawning season, per female); (9) larval size (length at hatching); (10) longevity (maximum life span); (11) maturation size (proportion, length of female at maturation as a function of maximum total length); (12) reproductive guild (non-guarders and open substratum spawners, non-guarders and brood hiders, guarders and substratum choosers, guarders and nest spawners, substrate indifferent); and (13) spawning frequency (batch, serial). Invasion risk parameters included (14) climate match [(measured with the online program CLIMATCH (Bureau of Rural Sciences, 2009) following a US Fish and Wildlife Service protocol (Appendix S2; Hoff, 2014) based upon Bomford *et al.*, 2010)]; (15) relatedness [absolute value of the difference in family-level rank (from Nelson, 2006) between the non-native species and the most closely related native or non-native species established in the first invaded Great Lake (from Mandrak & Cudmore, 2012)]; (16) phylogeny (description below); (17) prior establishment success (number of countries where the species has established); and (18) size of native range (area). Data for all variables were gathered from online databases, including FishBase (Froese & Pauly, 2014), FishTraits (Frimpong & Angermeier, 2009) and published literature (e.g. Kolar & Lodge, 2002; Mims *et al.*, 2010).

Given the broad taxonomic diversity of the species evaluated (27 families, 48 genera), ecological constraint is more likely to explain data patterns than phylogenetic constraint (Westoby *et al.*, 1995). However, to account for any impact of phylogenetic history (i.e. shared ancestral traits), we followed Grafen (1989) and calculated phylogenetic relatedness by ranking species according to their family membership [i.e. the degree of their derived characters, ordered from most ancient to most derived based on Nelson, (2006)].

Statistical analysis

We tested which subsets of the 18 variables were most strongly associated with the establishment and impact stages of invasion using a classification tree analysis in the program CART (v. 6.6, Salford Systems, San Diego, CA, USA). Classification tree analysis is a machine learning method that employs binary recursive partitioning to model categorical response variables (Breiman *et al.*, 1984). The tree is constructed by repeatedly splitting the data into two groups (nodes) defined by a threshold value (continuous data) or category (categorical data) of a single independent variable that maximizes homogeneity of outcome (e.g. established vs. not established) within the two groups created by the split (De'ath & Fabricius, 2000). Classification trees are particularly well suited for the analysis of complex ecological data sets that may support nonlinear relationships that interact hierarchically, and where data may be missing for some independent variables (De'ath & Fabricius, 2000).

We developed classification trees for each stage of invasion with binary-dependent outcomes: establish or fail for the establishment stage, and low or high for the impact stage. Node splitting criteria were based on the Gini homogeneity index, with no constraints on the minimum node size (De'ath & Fabricius, 2000). We chose the optimal classification tree by performing 10-fold cross-validation and selecting the smallest tree within one standard error of relative cost (misclassification rate).

Table 1 Established non-native fishes (n = 37 species) in the Great Lakes and their ecological impact based upon expert questionnaire results. The mean impact score (and 95% CI) and percentage of respondents that had high confidence in their answers are reported (n = 27 respondents). Species are listed in rank order from high to low impact based upon the upper 95% CI. The 12 species perceived to have the highest (impact class 'high') and the 12 species with lowest (impact class 'low') impact were used to develop the impact classification tree reported in Fig. 1. The intermediate impact species (impact class 'medium') not used in modelling are also reported.

Species	Common name	Impact class	Impact score (95% CI)	% high confidence
Petromyzon marinus Linnaeus 1758	Sea Lamprey	High	3.85 (3.68–4.00)	100
Alosa pseudoharengus Wilson 1811	Alewife	High	3.74 (3.53–3.95)	100
Neogobius melanostomus Pallas 1814	Round Goby	High	3.27 (2.94–3.59)	96
Osmerus mordax Mitchill 1814	Rainbow Smelt	High	3.04 (2.65–3.42)	93
Cyprinus carpio Linnaeus 1758	Common Carp	High	2.81 (2.24–3.39)	81
Oncorhynchus tschawytscha Walbaum 1792	Chinook Salmon	High	2.81 (2.45–3.16)	92
Morone americana Gmelin 1789	White Perch	High	2.46 (2.17–2.75)	81
Oncorhynchus mykiss Walbaum 1792	Rainbow Trout	High	2.40 (2.05–2.75)	84
Salmo trutta Linnaeus 1758	Brown Trout	High	2.25 (1.81–2.69)	75
Ctenopharyngodon idella Valenciennes 1844	Grass Carp	High	1.90 (1.31–2.48)	32
Oncorhynchus kisutch Walbaum 1792	Coho Salmon	High	2.12 (1.80–2.43)	73
Gymnocephalus cernua Linnaeus 1758	Ruffe	High	2.04 (1.75–2.34)	61
Scardinius erythrophthalmus Linnaeus 1758	Rudd	Medium	1.71 (1.33–2.08)	53
Gasterosteus aculeatus Linnaeus 1758	Threespine Stickleback	Medium	1.50 (0.96–2.04)	44
Esox niger Lesueur 1818	Chain Pickerel	Medium	1.62 (1.28–1.95)	46
Proterorhinus marmoratus Pallas 1814	Tubenose Goby	Medium	1.43 (0.97–1.89)	48
Aplodinotus grunniens Rafinesque 1819	Freshwater Drum	Medium	1.50 (1.14–1.86)	50
Salmo salar Linnaeus 1758	Atlantic Salmon	Medium	1.45 (1.07–1.84)	50
Oncorhynchus gorbuscha Walbaum 1792	Pink Salmon	Medium	1.50 (1.22–1.78)	64
Lepomis microlophus Gunther 1859	Redear Sunfish	Medium	1.33 (0.93–1.74)	50
Gambusia affinis Baird & Girard 1853	Eastern Mosquitofish	Medium	1.43 (1.14–1.72)	36
Gambusia holbrooki Girard 1859	Western Mosquitofish	Medium	1.43 (1.14–1.72)	36
Carassius auratus Linnaeus 1758	Goldfish	Medium	1.38 (1.13–1.62)	42
Noturus insignis Richardson 1836	Margined Madtom	Medium	1.18 (0.76–1.60)	55
Cyprinella lutrensis Baird & Girard 1853	Red Shiner	Medium	1.38 (1.16–1.59)	25
Morone mississippiensis Jordan & Eigenmann 1887	Yellow Bass	Low	1.22 (0.96–1.48)	44
Alosa aestivalis Mitchill 1814	Blueback Herring	Low	1.23 (0.99–1.47)	54
Enneacanthus gloriosus Holbrook 1855	Bluespotted Sunfish	Low	1.18 (0.91–1.45)	64
Lepomis humilis Girard 1858	Orangespotted Sunfish	Low	1.21 (1.00–1.43)	50
*Ictiobus cyprinellus** Valenciennes 1844	Bigmouth Buffalo	Low	1.17 (0.93–1.41)	58
Apeltes quadracus Mitchill 1815	Fourspine Stickleback	Low	1.18 (0.98–1.39)	27
Misgurnus anguillicaudatus Cantor 1842	Oriental Weatherfish	Low	1.14 (0.96–1.33)	43
Ictiobus bubalus Rafinesque 1818	Smallmouth Buffalo	Low	1.17 (1.10–1.32)	58
Ictiobus niger Rafinesque 1819	Black Buffalo	Low	1.17 (1.10–1.32)	58
Carpiodes carpio Rafinesque 1820	River Carpsucker	Low	1.10 (0.91–1.29)	50
Phenacobius mirabilis Girard 1856	Suckermouth Minnow	Low	1.00 (1.00–1.00)	11
*Clinostomus elongatus** Kirtland 1840	Redside Dace	Low	1.00 (1.00–1.00)	53

*Introduced beyond the species' native range in the Great Lakes.

Predicting invaders from trade

We compiled a list of species used in five trades that transport live non-native fishes into the Great Lakes region: aquarium, biological supply, live bait, live food (including aquaculture) and water garden (Keller & Lodge, 2007). We obtained Canadian and United States federal data sets that document live fishes imported through legal, permit-based processes. We compiled a list of Canadian live fish imports over the period 1 October 2004 to 30 September 2005 from data provided by the Canadian Border Service Agency's Facility for Information Retrieval Management, which covers all ports in Canada. From the United States Fish and Wildlife Service's Law Enforcement Management Information System, a database that tracks import and export data for all United States ports authorized to process live animal shipments, we obtained a list of live fish imports over the period 1 October 2004 to 30 November 2005 through a Freedom of Information Act request following Romagosa *et al.* (2009). For the Canadian and United States data sets, each species was assigned to one or more of the five trades based on information in the documents and/or from the importer's website. Our analysis excluded fishes imported for zoos or university research, fish species listed on the Convention on

International Trade of Endangered Species and not regularly traded, and marine fishes.

Next, we performed Internet searches for species in the biological supply, live bait and water garden trades because they were poorly represented in the federal importation species data sets. The search strings '*trade pathway name* supply' and '*trade pathway name* supply Canada' were used for each of the three trades. Vendors listed in up to the top 15 hits were used to obtain identities of species available from major suppliers. Four non-native species were documented for the live bait trade from Internet searches. We obtained additional bait species from published surveys of bait shops (Litvak & Mandrak, 1999; Drake & Mandrak, 2014). The final list of species in all five trades excluded fishes already in our established/failed data set (Table S1) or that were native to the Great Lakes. For the species in trade, climate match and trait data were collected using the methods described above. We used the establishment classification tree to predict which species would likely establish in the Great Lakes. For those species predicted to establish, we estimated impact using the impact classification tree. Trades posing the greatest threat to the Great Lakes were identified by the proportion and the absolute number of species predicted to establish and have high impact.

Historical patterns of establishment

We used data from Mandrak & Cudmore (2012) on the number of fish species both intentionally and unintentionally introduced to the Great Lakes between 1829 and 2012 to determine the contribution of different trades to past fish invasions relative to other introduction pathways (commercial shipping, natural dispersal, stocking, unknown). We evaluated the introduction pathway of 64 species in Table S1 (all species in Table S1 except *Gambusia holbrooki*, which has an unknown introduction date and pathway), in addition to four other fish species that have been introduced and have unknown establishment status (*Alosa chrysochloris, Ameiurus catus, Lepisosteus oculatus, Pimephales vigilax*), and three hybrid species bred and stocked for recreation that failed to establish (*Salvelinus fontinalis* × *S. namaycush*, *S. fontinalis* × *S. namaycush* × *S. namaycush*, *Salmo trutta* × *S. fontinalis*) (N. E. Mandrak, *unpublished data*). For those species introduced through trade, assignment of the specific trade pathway (aquarium, biological supply, live bait, live food, water garden) was accomplished by cross-referencing with the species list formulated in the *Predicting invaders from trade* subsection [above] in addition to reviewing information reported in the United States Geological Survey's Nonindigenous Aquatic Species Database (USGS, 2013). Six species (Table S1) could have originated from multiple trades and were represented in each possible pathway for the analysis.

To assess the contribution of the five trades collectively to non-native species introduction over time, we used linear regression to evaluate trends in the introduction frequency over 25-year time intervals. Additionally, for each of the five trades, we calculated the proportion of introduced species that established.

RESULTS

Predicting establishment and impact

The classification tree for the establishment stage indicates that a climatic match >71.7% between the native range of a fish and the Great Lakes region distinguishes species that established from those that did not (Fig. 1a; relative cost = 0.44, AUROC = 0.77). Cross-validation reveals that 81% of established fishes, and 75% of fishes that failed to establish, are correctly classified with this model. Likewise, the classification tree for the ecological impact stage accurately distinguishes low- versus high-impact species on the basis of trophic guild and fecundity (Fig. 1b; relative cost = 0.42, AUROC = 0.79). Under cross-validation, 75% of low impact invaders and 83% of high-impact invaders were correctly classified with this model. The tree branching sequence indicates that trophic specialization was the most important predictor of impact. Species in the top trophic levels (invertivore–piscivore, piscivore) had a large ecological impact, while the tree differentiates among impact levels of lower trophic level species with a split in fecundity. Species producing more than one million eggs per spawning season had a high impact, whereas species with lower fecundities had a low impact (Fig. 1b). An analysis evaluating the sensitivity of the impact model to a different number of low- and high-impact species indicates this reported model has the lowest relative cost (error) of five alternative models (Appendix S3). Further, trophic guild emerged as the root node in five of the six models tested, indicating this variable is a robust predictor of invasiveness.

Predicting invaders from trade

A total of 787 live freshwater fish species were traded in the United States and Canada, with 20 species occurring in multiple trade pathways (Table S4). Screening each of these species with the establishment classification tree suggests that 2 of the 13 species in the water garden trade, 2 of the 23 species in the live food trade and 4 of the 768 species in the aquarium trade are capable of establishing in the Great Lakes (Fig. 2a). No species from the biological supply trade ($n = 8$) are predicted to establish. The live bait trade contributed no species to the final trade species list, as all bait species identified were either native to the Great Lakes ($n = 3$), or already established ($n = 6$). Overall, seven non-native fish species are predicted capable of establishing in the Great Lakes from the five trades, and four of these are predicted to have a large impact (Table 2). All species predicted to establish from the water garden trade are predicted to have a large ecological impact, whereas only half of the

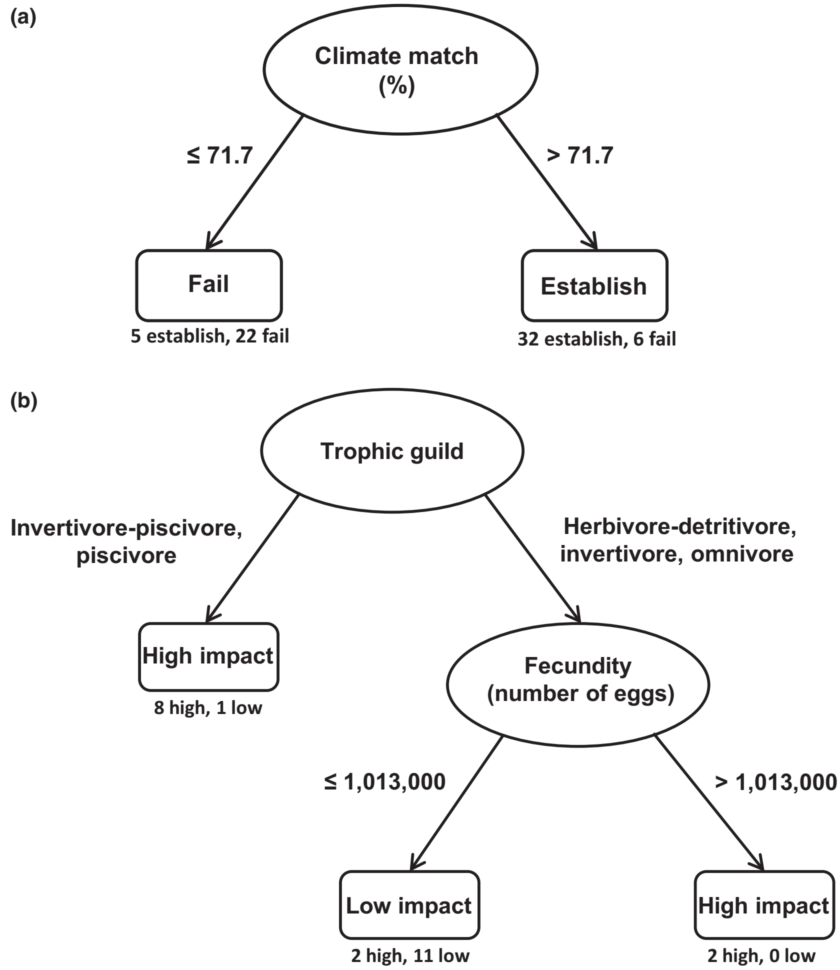

Figure 1 Classification trees predicting (a) establishment and (b) ecological impact of non-native fish species in the Great Lakes. The number of fish species from the model training data set located in each response category is indicated at every terminal node.

species predicted to establish from the aquarium and live food trades are predicted to have a large ecological impact (Fig. 2b).

Historical patterns of establishment

Since 1829, 45 non-native fish species have been introduced to the Great Lakes from pathways other than the five trades, including commercial shipping, natural dispersal, stocking and unknown sources. Introduction frequency of these fishes has not increased over time (linear regression; $y = 1.15x + 0.43$, $R^2 = 0.27$, $P = 0.19$, Fig. 3a). Over this same period, 25 fishes have been introduced through trade pathways with a significant linear increase in introduction frequency ($y = 1.30x - 2.71$, $R^2 = 0.78$, $P = 0.004$). Of the species successfully established from trade ($n = 10$), the majority originated from the live bait trade, followed by the biological supply and water garden trades (Fig. 3b). The aquarium and live food trades contributed the fewest established species. Of the fishes that failed to establish ($n = 14$), most originated from the aquarium trade with the remainder originating from the live food trade and biological supply trade (Table S1). All species introduced through the live bait and water garden trades successfully established in the Great Lakes, compared to 75% from biological supply, 33% from live food and 14% from the aquarium trade.

DISCUSSION

The present study provides a comprehensive evaluation of trait-based risks of establishment and ecological impact for non-native freshwater fishes in the Laurentian Great Lakes of North America, stratified by five global trade pathways. We identified climate match, trophic guild and fecundity as invasion risk factors that are most predictive of past establishment and impact, and subsequently applied these risk assessment tools to 787 fishes in international trade to identify species that present a significant invasion threat in the future. Application of the tools to these species in trade that are not yet known to have been released indicates that the water garden, live food and aquarium trades currently pose the greatest risk of introducing species that are likely to establish and generate impacts. These predicted outcomes parallel the historical importance of the trades in introducing non-native species to the Great Lakes over a period

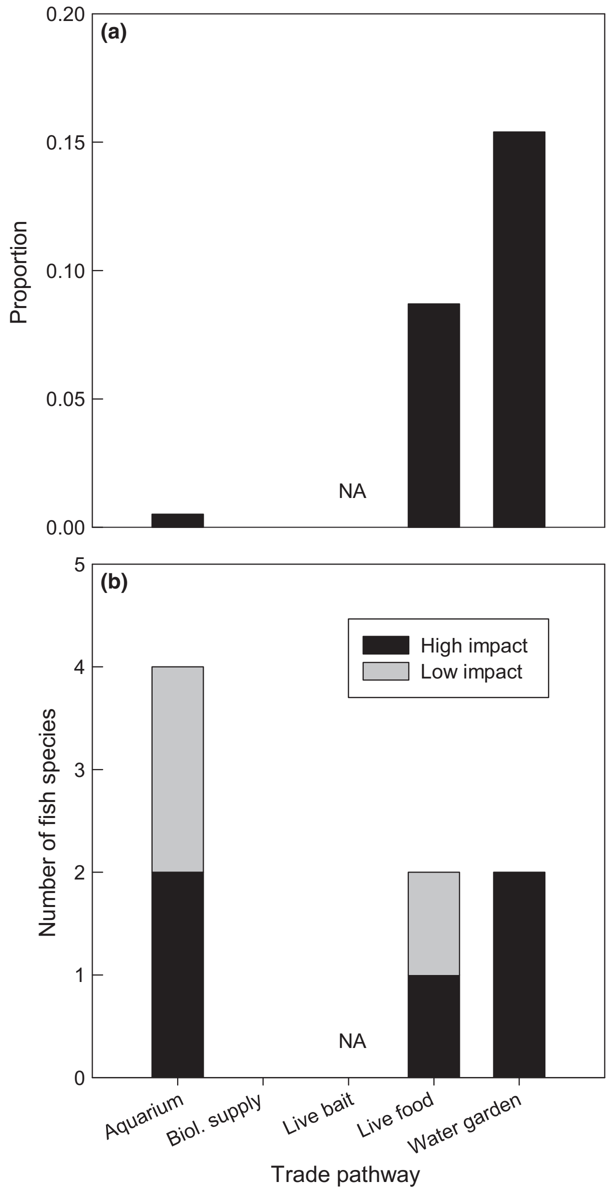

Figure 2 (a) Proportions of non-native fish species predicted to establish in the Great Lakes from the aquarium (n = 768), live bait (NA = no contributing species), biological (Biol.) supply (n = 8), live food (n = 23) and water garden (n = 13) trades. Identities of species in each trade pathway are in Table S4. (b) The number of fish species predicted to establish in each trade pathway and their corresponding predicted ecological impact. One species (*Leuciscus idus*) is represented in two trade pathways (aquarium, water garden). Identities of species in each trade pathway are in Table 2.

spanning almost 200 years. The projected importance of the water garden trade in particular parallels patterns of its historical contribution of introducing successful non-native fishes. The historical analyses further demonstrate that the live bait, biological supply, aquarium and live food trades have also contributed non-native fishes to the Great Lakes biota.

Table 2 Non-native fish species in trade predicted to establish in the Great Lakes, with corresponding prediction of ecological impact and associated trade pathway(s). Species were identified with the classification trees reported in Fig. 1 and are listed in alphabetical order.

Species	Common name	Impact	Trade pathway
Carassius carassius Linnaeus 1758	Crucian Carp	Low	Live food
Cobitis taenia Linnaeus 1758	Spined Loach	Low	Aquarium
Ictalurus furcatus Valenciennes 1804	Blue Catfish	High	Water garden
Leuciscus idus Linnaeus 1758	Ide	High	Aquarium, water garden
Misgurnus fossilis Linnaeus 1758	European Weatherfish	Low	Aquarium
Morone saxatilis Walbaum 1792	Striped Bass	High	Live food
Silurus glanis Linnaeus 1758	European Catfish	High	Aquarium

Accuracy and scientific basis of trait-based risk assessment tools

Not only did our risk assessment models accurately predict establishment and impact (75–83% accuracy) in most former species invasions, but they did so on the basis of only a few, readily available variables with known ecological relevance. The match between climate in a species' native range and the Great Lakes region proved sufficient to predict the establishment of introduced fishes, consistent with previous analyses of fishes (Bomford *et al.*, 2010) and other taxa including terrestrial plants (Petitpierre *et al.*, 2012), birds (Duncan *et al.*, 2001), mammals (Forsyth *et al.*, 2004), and amphibians and reptiles (Bomford *et al.*, 2009; Van Wilgen & Richardson, 2012). This is congruent with the generally recognized importance of physiological tolerance in shaping species distributions, often making climate match a robust predictor of non-native species establishment (Hayes & Barry, 2008). The predictive ability of climate match is unique relative to findings from previous invasion risk analyses of the Great Lakes using smaller data sets of introduced fish species and different predictors of establishment that exclude aspects of the regional environment (e.g. climate match) and biota (e.g. relatedness) included in this study (Kolar & Lodge, 2002; Snyder *et al.*, 2014). These analyses found positive associations between establishment status and higher growth rates, previous history of invasiveness, broad salinity tolerances, broad temperature tolerances and diet breadth.

The ecological impact model required information about a species' trophic guild and average fecundity. These ecological and life history traits are often important in interspecific interactions and population growth, respectively. Consistent with many observations of large top-down population and

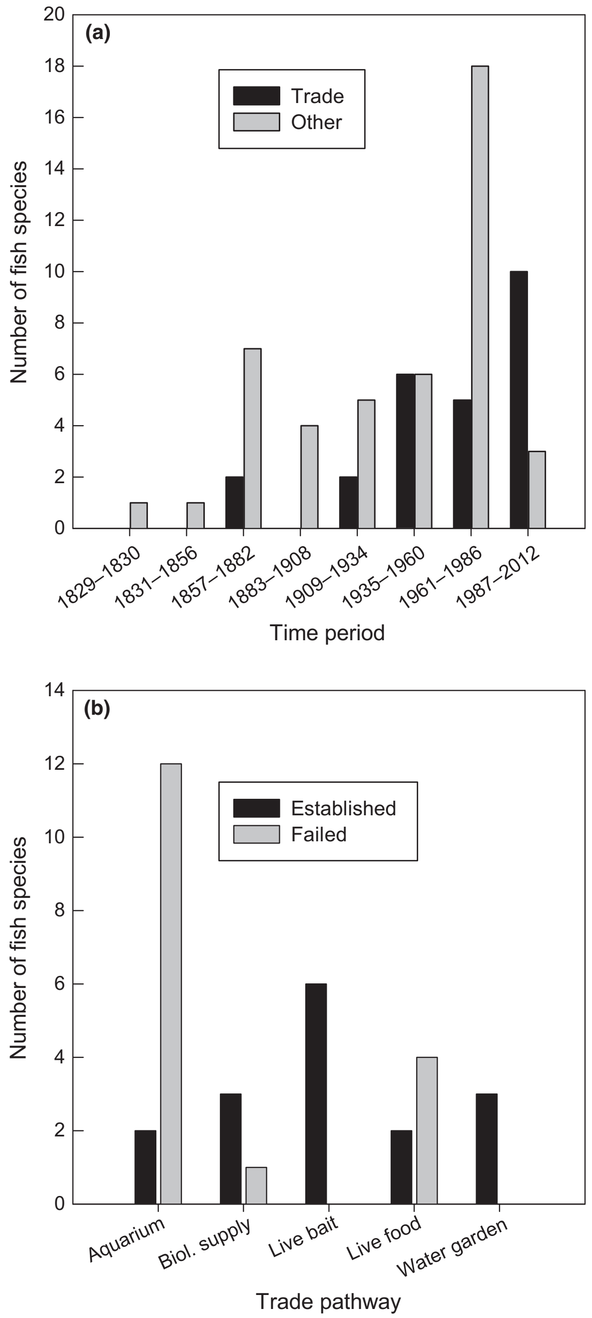

Figure 3 (a) The number of fish species introduced to the Great Lakes via different introduction pathways, for the time period 1829–2012. Data are grouped into 25-year bins, except for the oldest (2 years) grouping. Species were classified as being introduced from trade (i.e. commerce in living organisms) (black bars) or other pathways (grey bars). Analysis includes fish species that have established, or failed to establish, in the Great Lakes. (b) The number of fish species that have established (black bars) or failed to establish (grey bars) in the Great Lakes from trade, and their associated pathway, including the aquarium, live bait, biological (Biol.) supply, live food and water garden trade. Ten species have established, and 14 species have failed to establish from trade. Six of these species are represented in multiple trade pathways. Refer to Table S1 for trade pathway by species.

ecosystem impacts in lake food webs, high-impact non-native fishes are likely to be top predators (piscivores, invertivore–piscivores) (Eby *et al.*, 2006; Cucherousset & Olden, 2011). The impact model further predicted that for non-native species in the lower trophic levels (herbivore–detritivore, invertivore, omnivore), high fecundity species have a large ecological impact. This result aligns with other trait-based models that find fecundity to be a predictor of invasion success in aquatic species including crayfishes (Larson & Olden, 2010) and molluscs (Keller *et al.*, 2007a). The results differ, however, from previous trait-based impact studies of non-native freshwater fishes from the same and different ecosystems. For example, a study of invasive Great Lakes fishes using a different suite of ecological and life history traits found positive associations between nuisance status (defined as both ecological and economic impacts from expert opinion) and smaller egg size, wider salinity tolerance and survivorship in lower water temperatures (Kolar & Lodge, 2002). A related study of invasive Great Lakes fishes found associations between impact status (method not described) and egg size, minimum water temperature and history of invasiveness (Snyder *et al.*, 2014). A study of non-native freshwater fishes in California, United States, evaluating impact (defined as average abundance) found prior invasion success and propagule pressure as reliable indicators (Marchetti *et al.*, 2004b). The lack of consistency in impact predictors for freshwater fishes supports previous findings that mechanisms of impact often vary across studies (e.g. García-Berthou, 2007), as do the ways in which impact is perceived and measured (Cucherousset & Olden, 2011; Lapointe *et al.*, 2012). They further demonstrate that it is challenging to identify a single robust trait or variable that predicts impact of non-native freshwater fishes.

Consistency of the current relative risks of different trades with historical patterns

Since the early 20th century, the number of fish species introduced into the Great Lakes region from the live organism trades has increased relative to other pathways. In the past few decades, trade has introduced more fishes than all other pathways combined, reflecting an increase in commercial globalization and the importance of growing human populations and urban trade hubs (e.g. Chicago, Toronto) in the Great Lakes region.

The application of our models to species known to be traded but not known to be established in the Great Lakes revealed that among the live trades, the water garden trade has the highest proportion of species likely to establish (15%); all of which are predicted to have high impact. This is not surprising given that the water garden trade is restricted to species that survive well in outdoor ambient conditions. Accordingly, our historical analysis revealed that 100% of the non-native fish species originating from the water garden trade have established, paralleling a previous finding that the water garden trade has supplied the majority of established aquatic non-native plant species in the Great Lakes (Keller & Lodge, 2007).

Specifically, our risk assessment models identified Ide (*Leuciscus idus*) and Blue Catfish (*Ictalurus furcatus*) as water garden species predicted to become established and have an ecological impact if introduced in the Great Lakes. Blue Catfish has already established outside of its native range within North America (Bonvechio *et al.*, 2012). Additionally, Blue Catfish has been genetically crossed with Channel Catfish (*Ictalurus punctatus*) in the U.S. aquaculture industry to produce a high growth hybrid with increased disease resistance (Arias *et al.*, 2012; Bosworth & Waldbieser, 2014). Blue Catfish and its hybrids thus have the potential to hybridize with wild native Channel Catfish in the Great Lakes.

The live food trade represents the second-highest risk pathway in terms of proportion of species predicted to establish (9%). Similar to the water garden pathway, the live food trade often selects for species that survive well outdoors under high density conditions (Naylor *et al.*, 2001). Because major cities occur in and near the Great Lakes, there is heightened risk of non-native species sold in urban live fish markets being released alive into nearby habitats (Rixon *et al.*, 2005). For example, Crucian Carp (*Carassius carassius*) and Striped Bass (*Morone saxatilis*) are predicted to establish in the Great Lakes. Striped Bass commonly hybridize with White Bass (*M. chrysops*) in live food aquaculture, and both Striped Bass and its hybrids are frequently found in live fish markets in Ontario and Québec, Canada (Rixon *et al.*, 2005).

The aquarium trade ranked third in terms of proportion of species predicted to establish; but because of the great number of species imported by this pathway, it was tied for second in terms of the absolute number of species predicted to establish and cause high impact. Our analysis identified four aquarium species that are native to temperate regions of Europe and/or Asia that would likely establish if introduced to the Great Lakes: European Weatherfish (*Misgurnus fossilis*), Ide, Spined Loach (*Cobitis taenia*) and European Catfish (*Silurus glanis*). The impact model further predicted that European Catfish, a large-bodied piscivore that has been introduced outside of its native range in Europe (Copp *et al.*, 2009a), will become invasive in the Great Lakes if introduced and established. Eventual introduction of European Weatherfish to the Great Lakes seems likely, given that 10% of aquarium and pet stores in Michigan, USA, and Ontario, Canada, sell this species (Rixon *et al.*, 2005), and frequency of occurrence of fish species in stores positively correlates with regional establishment success (Duggan *et al.*, 2006).

Although the majority of aquarium species in trade are tropical in origin and thus predicted not to establish in the Great Lakes due to the current climate mismatch, we caution that the currently moderate threat posed by aquarium species may increase in the near future for two important reasons. First, increasing demand for unique fishes from hobbyists (Padilla & Williams, 2004) may bring new temperate fishes to the region (Keller *et al.*, 2011). Second, elevated regional temperature associated with climate change will increase the proportion of warmwater species that can successfully establish from the aquarium and other trade pathways (Stefan *et al.*, 2001). The biological supply and live bait trades pose lower invasion threats to the Great Lakes. No species from biological supply were predicted to establish; however, the pathway has historically supplied approximately one-fifth of successful invaders. Although no species currently in the bait trade and not already established in the region are predicted to establish, the bait trade has historically contributed approximately 40% of successful invaders. This is not surprising, as the bait trade has the highest propagule pressure stemming from the highest volume and release rates (30%; Drake & Mandrak, 2014) of all trades. While the use of non-native baitfishes is illegal in the Great Lakes basin, they do occur in trade (Drake & Mandrak, 2014), and the bait trade has the potential to become a high-risk pathway if contaminated with non-target invasive species (e.g. bigheaded carps, *Hypopthalmichthys* spp.; Cudmore *et al.*, 2012).

Applications and conclusions

The trait-based risk assessments presented here provide a science-based, quantitative method for predicting invasion risk from fish species that may be introduced to the Great Lakes. Because few parameters are required to achieve high model accuracy, they could readily be implemented for voluntary or regulatory decision-making to achieve the goal, adopted by United States and Canadian policy-makers, to reduce the introduction of and harm from invasive species over the long term (GLWQA, 2012). Currently, most states and provinces across the Great Lakes basin implement some form of risk assessment for fishes, but there is little consistency in approach. This leads to inconsistent outcomes in terms of the number and identity of species considered high risk. These alternative risk screening approaches include literature reviews (e.g. Cudmore *et al.*, 2012) and questionnaire-based assessments (e.g. Fish Invasiveness Screening Kit; Copp *et al.*, 2009b) which require more data and are thus more costly to implement (Leung *et al.*, 2012) than our approach. The speed with which the risk assessment framework developed in this study can be implemented offers the opportunity to adopt predictive models with minimal cost, and consequently with greater potential to coordinate preventative screening efforts among multiple jurisdictions (in this case, United States and the Canadian province of Ontario) (Gantz *et al.*, 2015). This result could also encourage the development of rapid trait-based assessments for application in other regions and countries.

Although our models are robust, there are at least four limitations to their management application. First, our establishment analysis assumes all non-native species have an equal probability of introduction from trade. There may be traits predictive of introduction probability in fishes, and these could differ among trades, but the data to evaluate this are lacking. Second, we lack direct measures of propagule pressure, which may differ among trades, species and localities. Propagule pressure is an important determinant of establishment success (Lockwood *et al.*, 2005; Drake & Lodge, 2006), yet is commonly missing from quantitative risk assessments (Leung *et al.*, 2012). The already high accuracy of our models might improve if data on propagule pressure become available in the future. For example, Northern Snakehead (*Channa argus*) is documented on our list of species that have failed to establish in the Great Lakes, but a previous study indicates the species could establish in the region based upon suitable climate match (Herborg *et al.*, 2007). Propagule pressure may explain the failed invasion of *C. argus* in the Great Lakes. Third, our data on species in trade were for only one year, and additional species that we have not screened have likely entered the marketplace in the last decade. Fourth, the history of success or failure in past introductions may become a less reliable guide to the outcome of future introductions, especially with respect to climate change. Fortunately, however, the models reported here could easily be developed under alternative assumptions about climate match. The climate match variable used in the establishment model is freely available and should facilitate application of this screening tool as climate continues to change.

For short-term application with long-term conservation implications, our results identify specific species and a subset of the live trade pathways that pose an imminent high risk to the Great Lakes. Results indicate that at least seven fish species currently traded in the water garden, live food and/or aquarium pathways are likely to establish in the Great Lakes if introduced. These trade pathways currently experience little voluntary or regulatory oversight with respect to risk assessment of commercial species (Fowler *et al.*, 2007). The risks of invasion could be lowered by improved management practices in the private sector and government agencies, and improved policies that are coordinated across the political jurisdictions surrounding the Great Lakes. Greater use of risk assessment tools, including those presented herein, would also likely deliver net economic benefits (Keller *et al.*, 2007b).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. List of introduced nonnative fish species documented to have established, or failed to establish, in the Great Lakes.

Table S2. Experts responding to a questionnaire regarding the perceived ecological impact of established nonnative fish species in the Great Lakes.

Table S3. List of 18 selected species traits and invasion risk parameters used for the establishment and impact classification tree analyses.

Table S4. Nonnative fish species (n = 787) used in trade and screened through the developed classification trees.

Appendix S1. Questionnaire regarding risk assessment of ecological impact by Great Lakes fishes.

Appendix S2. Climate match methods.

Appendix S3. Description and results of the sensitivity analysis for the ecological impact classification tree.

BIOSKETCH

This publication is a product of a North American working group interested in determinants of invasion success of freshwater fishes and the associated development of invasive species risk assessment tools. All authors met on three occasions to design the research. J.G.H and C.A.G collated and analysed species trait and invasion risk parameter data and conducted the screening analysis. P.L.A, E.A.F, M.H., N.E.M and J.D.O. contributed trait data. N.E.M contributed historical data on the Great Lakes and the CBSA import data set. C.R.M contributed the LEMIS import data set. D.M.L and R.P.K funded the study. J.G.H. led writing of the manuscript, with contributions to the conceptual framework and revisions from all authors.

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