

Which Traits Predict Invasive Success in Lake and Stream Environments in the Laurentian Great Lakes Basin?

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Abstract

Freshwater ecosystems are experiencing environmental and socio-economic impacts from nonindigenous species that are causing losses in ecosystem services. Lake and stream ecosystems have fundamental differences in abiotic and biotic factors such as flow, water temperature, and depth. These environmental differences can filter which species are most successful in each of these ecosystems by favoring certain traits. However, it is not well-understood which species traits (e.g., body size, fecundity, habitat breadth, or temperature) allow species to more successfully invade lake versus stream ecosystems. Focusing on the Great Lakes Basin, I address the following questions about nonindigenous freshwater species: (1) Are different traits associated with nonindigenous species occurring more often in lakes versus streams?, (2) Which traits predict which species will spread farther across freshwater taxa?, (3) Which traits predict which species will spread farther among fish species?, and (4) Do lake or stream species spread farther? I performed stepwise multiple regression between traits and two spread measures: the number of Great Lakes sub-basins colonized and the distance spread by each species. Traits including body size, life history traits, and environmental tolerances are associated with nonindigenous species occurring more often in lakes versus streams. I found that nonindigenous freshwater taxa, generally, and fishes, specifically, with smaller maximum size occurred more often in lakes than streams. When looking at life-history traits across broad nonindigenous taxa, I found that species in lakes had lower fecundity while nonindigenous fish species in lakes had a higher age at maturity. Large body size predicted high spread distance across nonindigenous freshwater taxa while I found the opposite result when only looking at fish species. In terms of life history traits, I found that nonindigenous freshwater taxa with high fecundity spread farther. While, nonindigenous fish species with high fecundity, high maximum lifespan, and high age at maturity also spread farther. Nonindigenous freshwater taxa that spread farther displayed generalist traits such as wide depth range, wide habitat breadth, and wide temperature range. Nonindigenous freshwater taxa and fish species that occurred more often in streams had spread farther compared to taxa and species in lakes. Understanding the traits that are favorable for nonindigenous species in lakes versus streams can be used to manage the spread of invaders and predict future invaders.

Keywords

nonindigenous species; life history traits; invasive success; lakes vs streams; Great Lakes Basin

Introduction

Humans are increasingly facilitating the spread of nonindigenous and invasive species in freshwater ecosystems which, in turn, has significant negative impacts on ecosystems and the services they provide to humans (Pimentel et al. 2005; Robertson et al. 2020; Diagne et al. 2021). Nonindigenous freshwater taxa (including fishes, crustaceans, mollusks, other invertebrates, vascular plants, and algae) are numerous in freshwater ecosystems across the world in lakes (Ricciardi 2006) and streams (Strayer 2010), and are costing the global economy over \$23 billion annually (Cuthbert et al. 2021; Diagne et al. 2021). The Great Lakes Basin has been experiencing nonindigenous species introductions since the early 1800s in both lake and stream environments. The GLB holds about 20% of the world's surface freshwater and supports an economy worth about \$4.1 trillion USD (Campbell et al. 2015). Nonindigenous species often have larger impacts on freshwater than terrestrial ecosystems because freshwater ecosystems have high invasibility (i.e., the ability of a nonindigenous species to survive in a new location) and are more susceptible to negative environmental and socio-economic impacts when invaded (Moorhouse & Macdonald 2015). Further, meta-analysis of experiments across systems indicates freshwater communities have lower biotic resistance to nonindigenous species than terrestrial or marine ecosystems (Alofs & Jackson 2014).

Life history traits and habitat preferences are important for determining invasive success in freshwater ecosystems and I can use traits (e.g., body size, fecundity, or physiological tolerances) to provide mechanistic explanations for variation in invasive success in lakes and streams. Ecologists have repeatedly used species traits to study nonindigenous freshwater fish invasions (Scott & Helfman 2001; Vila-Gispert et al. 2005; Olden et al. 2006; García-Berthou 2007; Buckwalter et al. 2020), as well as species distribution and abundance patterns, and a variety of anthropogenic impacts (Frimpong & Angermeier 2009). Species traits are often used to predict nonindigenous species success in novel freshwater environments because abiotic (e.g., depth or temperature) and biotic environmental factors (e.g., predation or competition) often favor traits such as larger body size (Vila-Gispert et al. 2005), higher fecundity (van Kuijk et al. 2021), or wide habitat breadth (Frimpong & Angermeier 2010; Buckwalter et al. 2020). Nonindigenous freshwater plants (i.e., macrophytes) have traits such as a high growth rate and high phenotypic plasticity that allows for better adaptation to environmental conditions which leads to high impacts on native species in lakes (Schultz & Dibble 2012). Nonindigenous fish species with longer maximum lifespans and larger body size have a higher dispersal ability and therefore can spread further (Marchetti et al. 2004b; Blanchet et al. 2010), while high growth rates lead to higher establishment success in both lakes and streams (Kolar & Lodge 2002; Howeth et al. 2016).

There have been numerous studies on demographic traits, life-history traits, and habitat preferences that favor invasive success of species in streams (Poff et al. 2002; Vila-Gispert et al. 2005; Buckwalter et al. 2020; Frimpong & Angermeier 2010) and lakes (Kolar & Lodge 2002; Marchetti et al. 2004b; Ruesink 2005; Strayer 2010; McKnight et al. 2017; Su et al. 2020). Broad physiological tolerances (such as temperature, salinity, and depth ranges) can increase nonindigenous establishment in both stream (Olden et al. 2021) and lake species (Kolar & Lodge 2002; Marchetti et al. 2004b) because there is a greater chance that a nonindigenous species' environmental requirements are met if they have broad tolerances. Life history traits such as large size, long lifespan, late maturity, and high fecundity are common characteristics in nonindigenous freshwater fish species in streams (Vila-Gispert et al. 2005). Longer maximum

lifespans give species more time to grow to larger sizes and more time to reproduce which can increase their spread. Successful nonindigenous crayfish that mostly occur in lakes are characterized by traits such as large body size, high fecundity, broad environmental tolerances, high aggression level, and the ability to migrate long distances (van Kuijk et al. 2021). Traits including high parental care, benthic feeding strategy, longer residence time, and high temperature tolerance can also support the establishment and spread of nonindigenous fishes in streams (Buckwalter et al. 2020).

Freshwater lakes and streams differ in their abiotic conditions which can lead to differences in the traits of species occurring in these environments, such as body size (Jackson et al. 2001), temperature tolerance (Olden et al. 2021), parental care (Buckwalter et al. 2020), and life history strategy (Olden et al. 2006; Comte et al. 2020). Lakes and low-flow stream environments are characterized by slow-moving water velocity and warmer water temperatures which favor nonindigenous species (Olden et al. 2006). Successful nonindigenous species in low-flow stream environments typically have a generalist life-history strategy with a wide diet breadth (Olden et al. 2006). Temperature is a limiting factor in fish distributions, but both lake and stream ecosystems typically offer thermal refugia where fish species can avoid high temperatures (Jackson et al. 2001). However, shallow lakes have less thermal stratification and shallow streams experience a greater extreme of conditions which limits cold-water fish species' ability to survive high summer temperatures (Jackson et al. 2001). Shallow lakes and streams also suffer from oxygen depletion which can limit fish distributions, but streams are more prone to decreased oxygen levels because they have less oxygen-rich areas (Jackson et al. 2001). Since streams suffer more from oxygen depletion, this may lead to smaller bodied fish being more successful because they can survive with less oxygen (Jackson et al. 2001). However, lakes also suffer from oxygen depletion due to their warm water and slow water velocity. Abiotic factors such as water velocity create more longitudinal variation in streams than lakes which leads to higher habitat heterogeneity (e.g., pools, runs, and riffles) in streams which can lead to more specialized species traits such as narrow habitat and diet breadth (Jackson et al. 2001). Streams also have increased connectivity compared to many lakes which can lead to higher spread in nonindigenous freshwater taxa due to dispersal in the stream network (Heino et al. 2015).

Disturbance promotes nonindigenous freshwater species invasion and streams experience more natural variation and anthropogenic disturbances than lakes. Natural disturbances such as high/low flows and temperature seasonality can be harmful for habitat specialists while habitat generalists can survive more easily (Marvier et al. 2004). Species with larger body size are better suited to survive and utilize natural disturbance because it encourages dispersal, which favors larger species, and smaller species may not be able to survive the increased water velocity (Terui et al. 2021). Anthropogenic disturbances also promote invasions in stream ecosystems such as land-use conversion (agriculture/urbanization) and hydrological alteration by dams (Olden et al. 2021). For example, nonindigenous crayfish, amphibians, and fishes have higher abundances in disturbed river ecosystems due to urbanization compared to undisturbed ecosystems (Riley et al. 2005). Impoundments in streams slow water velocity and increase water temperature, fine sediment, and nutrients, conditions which often favor nonindigenous species (Buckwalter et al. 2020). Nonindigenous plant species also have higher abundance in dam-regulated rivers compared to native species (Stromberg et al. 2007).

In addition to abiotic differences, lake and stream environments have fundamental differences in biotic interactions which play a role in structuring freshwater fish communities (Jackson et al. 2001). Predation has strong effects on fish community assemblages in lake

ecosystems because predators can limit the coexistence of smaller fish species (Jackson et al. 1992; Chapleau et al. 1997). In streams, predation can cause prey species to move to different habitat types (Jackson et al. 2001). Predation has species-level effects which can select for species with higher fecundity and shorter age at maturity in both lake and stream fish species (Ricciardi & Rasmussen 1998; Alcaraz et al. 2005). High fecundity allows species to produce more young annually, which increases the likelihood of more young surviving to adulthood, which can increase their spread and impact on other species. Shorter age at maturity allows species to reproduce at a younger age which means species can reproduce before spending a lot of time facing the effects of predation, competition, and harsh abiotic conditions. Predation pressure can also lead to increased parental care (Buckwalter et al. 2020). Competition also plays a role in structuring fish communities in lake ecosystems because lakes provide more stable abiotic conditions; competition likely has less impact in streams where species traits are typically determined by abiotic factors (e.g., variability and disturbance) and predation (Jackson et al. 2001). Lakes have higher biotic resistance than streams which means that streams may be more susceptible to invasions (Alofs & Jackson 2014). Consumption is more important than competition for determining biotic resistance in freshwater environments, so predation and herbivory likely creates the stronger biotic resistance found in lakes. Disturbance often has a larger effect than predation, and since disturbance is less common in lakes, it makes sense that predation has larger effects on lake communities.

It is not well-understood whether differences in species traits are important for determining invasive success in lake versus stream environments. There have been numerous studies on demographic traits, life-history traits, and habitat preferences that favor invasive success of species in streams and lakes. However, I do not know if there are different traits that make nonindigenous species successful in lakes versus streams or if there are traits of freshwater nonindigenous species that are generalized across freshwater habitats. I investigated how species' invasive success differs in lakes and streams through the lens of differences in demographic traits, life history traits, and habitat preferences by comparing the traits of non-indigenous species that occur in lake and stream environments in the GLB, which is one of the most invaded regions in the world (Ricciardi 2006).

I addressed the following questions about nonindigenous freshwater species in the Great Lakes Basin: (1) Are different traits associated with nonindigenous species occurring more often in lakes versus streams? (2) Which traits predict which freshwater taxa will spread farther? (3) Which traits predict which fish species will spread farther? and (4) Do lake or stream species spread farther? I used two spread measures: the number of Great Lakes sub-basins colonized and the distance spread by each species. I predicted that nonindigenous freshwater taxa which spread farther in lake ecosystems will have smaller body size, wider habitat breadth, and a broader diet than those species with high spread in streams. I predicted lake species to have smaller body size because they experience more oxygen depletion and do not experience as much disturbance as stream species. I also predicted lake species to have wider habitat breadth and broader diet because slow water velocity often leads to a generalist life history strategy (Olden et al. 2006). However, I predicted that certain traits will favor species which spread farther in both lakes and streams, including life history traits (e.g., higher fecundity, shorter age at maturity, or longer maximum lifespan), fewer known predators, and traits related to temperature tolerance and habitat depth. I predicted that both lake and stream species would have high fecundity and short age at maturity because species have a better chance to establish and spread further when they produce many offspring at a young age. Finally, I predicted that both lake and stream species

would have wide temperature tolerance and depth range because physiological tolerances make it easier for nonindigenous species to survive in new environments.

Methods

Study System

I focused on freshwater habitats throughout the Laurentian Great Lakes Basin (GLB) including lakes Huron, Ontario, Michigan, Erie, and Superior, and their connecting water bodies; as well as inland lakes and tributaries. I examined the relationship between traits and the degree of invasiveness in the 183 nonindigenous freshwater taxa which have been recognized in the GLB including fishes (N=26), plants (N=54), algae (N=28), crustaceans (N=24), mollusks (N=17), parasites (N=14), invertebrates (N=13), bacteria (N=3), amoeba (N=3), and a freshwater hydroid (N=1). I analyzed all possible nonindigenous freshwater taxa regardless of whether they were intentionally introduced or not and whether they have established, spread, and strongly impacted ecosystems such that they are considered 'invasive' (Olden et al. 2021)

Species Occurrence in Lake versus Stream Species

To examine relative use of lake versus stream habitats by each species using reported occurrences from the Great Lakes Aquatic Nonindigenous Species Information System (GLANSIS) I needed to account for the uneven number of observations in lakes versus streams (7998 versus 1769). Therefore, I adjusted the number of lake (or stream) observations for each species by dividing by the total number of lake (or stream) observations across species before calculating the adjusted proportion of a species occurrences in lake habitats. Overall this proportion is calculated as:

$$\frac{\# \text{ of lake obs for species } n / \# \text{ of lake obs for all species}}{(\# \text{ of lake obs for species } n / \# \text{ of lake obs for all species}) + (\# \text{ of stream obs for species } n / \# \text{ of stream obs for all species})}$$

Measures of the Spread of Nonindigenous Species

I used two measures to assess the spread of nonindigenous species: number of sub-basins invaded and distance spread. First, I summed the number of Great Lakes sub-basins (HUC 8) that each species had colonized, similarly used by Bell et al. (2021). Second, With ArcGIS Pro, I calculated the straight-line euclidean distance between the two point observations that were farthest apart for each species.

Species Traits

I primarily used the Nonindigenous Aquatic Species (NAS) Database from the Great Lakes Aquatic Nonindigenous Species Information System (GLANSIS), United States Geological Survey (USGS) to collect trait data on freshwater taxa and fish species. Most other trait data came from the FishTraits database (Frimpong & Angermeier 2009). Gaps were filled with trait data from the AnimalDiversity database, FishBase database, and government and state agencies; as well as from various species-specific peer-reviewed articles (Hopp et al. 1997; Keller et al. 2007; Phong et al. 2008; Sousa et al. 2008; Choi et al. 2013; Burnett et al. 2018; Jin et al. 2019; Soussi et al. 2021).

Because some traits were not analogous across taxa or were not available in the literature, I compiled three sets of traits for analysis: body size (which was the most broadly available species trait, $n = 134$); 11 traits for a subset of 40 freshwater species (including maximum size, maximum lifespan, age at maturity, fecundity, habitat breadth, maximum depth, minimum depth, depth range, maximum temperature, minimum temperature, and temperature range); and for 22 fish species, 13 traits including those in the previous dataset and adding diet breadth and predator breadth (number of different predator types) (Table 2). Habitat breadth was calculated as a sum of habitat types ranging from mucky substrate to large woody debris (Frimpong & Angermeier 2009). Diet breadth was also calculated as a sum of habitat types including algae, detritus, invertebrates, and small fish. Predator breadth was calculated as a sum of different predator types including humans, small fish, large fish, and birds.

Statistical Analyses

All statistical analyses were conducted in R 1.4.1717 (R Core Team). I used two Principal Coordinate Analyses (PCoA) ordinations of Gower dissimilarity matrices to visualize variation in species traits across freshwater taxa and fish species in multivariate space. To compare species traits among freshwater taxa and fish species, I performed stepwise multiple regression (both forwards and backwards) to predict habitat occurrence, e.g. how often species occur in lakes versus streams (calculated as the adjusted proportion of occurrences in lakes), using traits as predictors. I performed stepwise multiple linear regression to predict each of my two measures of nonindigenous success using the three trait data sets: body size, broad set of traits across freshwater taxa, and fish species traits. In addition to species traits, I included the proportion of species occurrences in lakes and time since introduction to the GLB as additional predictors. I included time since introduction because it can limit spread distance if a species was introduced a long time ago and is no longer spreading throughout the region (Buckwalter et al., 2020). I examined correlations between continuous predictor variables and removed variables which were highly correlated (determined by Pearson's $r > 0.75$). No predictor variables were highly correlated in the body size dataset (Appendix S3: Table 1). For the broad set of species traits across freshwater taxa, I removed age at maturity (positively correlated with maximum size), maximum depth (positively correlated with depth range), and temperature range (positively correlated with maximum temperature) (Appendix S3: Table 2). For the set of fish traits, I removed maximum lifespan (positively correlated with fecundity), maximum depth (positively

correlated with depth range), and temperature range (positively correlated with maximum temperature) (Appendix S3: Table 3). All continuous traits were log transformed and standardized (subtracted mean and divided by the standard deviation) before performing the stepwise multiple regression. The models with the lowest Akaike Information Criteria (AIC) were selected as the final model. All models within $\Delta 4$ AIC are presented in the Appendix S3 since they were indistinguishable from the final model.

Results

Species Occurrence in Lakes versus Streams - Principal Coordinates Analysis

Species were sorted across ordination space by taxonomic groups (fish and molluscs), but there was no significant pattern across species based on the time since introduction for each species and how often each species occurs in lakes versus streams. In the PCoA of freshwater taxa (Fig. 1), the first and second principal coordinates explained 42.0% and 24.5% (respectively) of the variation among species traits. Maximum size, age at maturity, maximum lifespan, fecundity, maximum depth, minimum depth, and depth range contributed more towards PCo 1 and were all negative vectors. Fecundity had the longest vector while maximum size, age at maturity, maximum lifespan, maximum depth, minimum depth, and depth range all had shorter but similar vector lengths. Maximum temperature, minimum temperature, temperature range, and habitat breadth contributed more towards PCo 2. Maximum temperature and temperature range were positive vectors while minimum temperature and habitat breadth were negative vectors. Maximum temperature and temperature range had the longest vectors and were about twice as long as minimum temperature which was again about twice as long as habitat breadth. The left side of the ordination consisted mostly of fish species while the right side consists mostly of mollusk species for the principal coordinate analysis of freshwater taxa (Fig. 2). Fish separated from molluscs primarily along the PCo 1 and this separation was explained by larger maximum size, higher age at maturity, longer maximum lifespan, higher fecundity, higher maximum depth, higher minimum depth, wider depth range, and narrower habitat breadth. There was no distinction between fish and molluscs along the PCo 2 which was explained by maximum temperature, minimum temperature, and temperature range.

In the PCoA of the 22 fish species (Fig. 3), the first and second principal coordinates explained 33.9% and 23.6% (respectively) of the variation among species traits. Maximum size, minimum depth, temperature range, age at maturity, fecundity, maximum temperature, habitat breadth, and minimum temperature contributed more towards PCo 1. Maximum size, minimum depth, temperature range, age at maturity, fecundity, and maximum temperature were positive vectors while habitat breadth and minimum temperature were negative vectors. Age at maturity, fecundity, and minimum temperature had the longest vectors followed by maximum size, temperature range, maximum temperature, and habitat breadth which were slightly shorter. Number of predator types, maximum depth, depth range, and diet breadth contributed more towards PCo 2. Number of predator types, maximum depth, and depth range were positive vectors while diet breadth was a negative vector. Maximum depth, depth range, and diet breadth had the longest vectors while the number of predator types had a slightly shorter vector. Maximum lifespan contributed to both PCo 1 and PCo 2.

Fish species were sorted into groups based on their habitat (lakes versus streams) where the top right side consisted mostly of fish species that occur more often in lakes while the bottom right side consisted mostly of fish species that occur more often in streams (Fig. 4). Based on visual examination of the ordination, lake species were characterized by higher number of predator types, wider depth range, higher maximum depth, larger maximum size, lower minimum temperature, and narrower habitat breadth. Stream species were characterized by high age at maturity, high fecundity, high maximum temperature, long lifespan, and wide diet breadth. Both lake and stream species were characterized by high minimum depth and wide temperature range.

Predicting nonindigenous species occurrence in lake versus stream habitats - Stepwise multiple regression

Nonindigenous species with smaller maximum size occurred more often in lakes than streams across both the body size and fish data sets (Table 3). No other traits were included in more than one of the final models predicting habitat occurrence across data sets. In the final model of habitat occurrence (lowest AIC) for the body size dataset comparing 134 freshwater taxa ($AIC = -226.781$, $F_{1,132} = 3.981$, $p = 0.048$, $Adj. R^2 = 0.02$), maximum size was included as a predictor (Appendix S3: Table 4). Maximum size was significant ($p=0.048$) and had a negative effect size (effect size (β) = -2.00) indicating species found more often in lakes had a smaller maximum size. Stepwise multiple regression showed one other model within $\Delta 4$ AIC. The alternative model included time since introduction but the factor was not a significant predictor of how often species occur in lakes versus streams (Appendix S3: Table 5.).

In the final model of habitat occurrence fitted using a broad set of traits for freshwater taxa ($AIC = -86.05$, $F_{2,37} = 7.069$, $p = 0.003$, $Adj. R^2 = 0.24$) fecundity and maximum temperature were included as predictors (Appendix S3: Table 6). The effect of fecundity ($\beta = -3.63$) was more than twice as strong as maximum temperature ($\beta = 1.54$), where species in lakes had lower fecundity and higher maximum temperature than species in streams. Fecundity was also the only predictor in the final trait-based model that was significant ($p<0.001$). There were three other models within $\Delta 4$ AIC but none of the additional traits included in those models were significant predictors of how often species occur in lakes versus streams (Appendix S3: Table 7).

In the final model of habitat occurrence for fish traits ($AIC = -68.91$, $F_{6,15} = 4.346$, $p = 0.010$, $Adj. R^2 = 0.49$); maximum size, age at maturity, diet breadth, predator breadth, minimum temperature, and time since introduction were included as predictors (Appendix S3: Table 8). Each predictor in the best model was significant. Diet breadth ($\beta = -3.51$; $p=0.003$) was the strongest predictor of species occurring in lakes more frequently than streams where species in lakes had narrower diet breadth than species in streams. While age at maturity ($\beta = 2.54$; $p=0.023$), predator breadth ($\beta = 2.54$; $p=0.028$), time since introduction ($\beta = 2.19$; $p=0.045$), maximum size ($\beta = -2.91$; $p=0.011$), and minimum temperature ($\beta = -2.49$; $p=0.025$) had smaller but similar effects on predicting species occurring in lakes more frequently than streams; where species in lakes had higher age at maturity, higher number of predator types, longer time since introduction, smaller maximum size, and lower minimum temperature. Stepwise multiple regression showed two other models within $\Delta 4$ AIC, but none of the additional traits included in those models were significant predictors of how often nonindigenous species occur in lakes versus streams (Appendix S3: Table 9).

Predicting how far nonindigenous species spread with body size

Stepwise multiple regression using the body size dataset resulted in a final model that predicted the number of Great Lakes sub-basins colonized ($AIC = 765.687$, $F_{3,130} = 11.04$, $p = <0.001$, $Adj. R^2 = 0.18$) using maximum size, proportion of species in lakes, and time since introduction as predictors (Appendix S3: Table 10). Maximum size was significant ($p=0.001$) while proportion of species in lakes and time since introduction were not significant. Maximum size was the strongest predictor of the number of Great Lakes sub-basins colonized. The effect of maximum size ($\beta = 3.30$) was more than twice as strong as proportion of species in lakes ($\beta = -1.57$) and time since introduction ($\beta = 1.48$), where species that colonized more great lakes sub-basins had large maximum size, occurred more often in streams, and had a long time since introduction. There were no other models within $\Delta 4$ AIC and the null model was also the final model.

In the final model that predicted spread distance ($AIC = 1596.942$, $F_{1,132} = 15.08$, $p = <0.001$, $Adj. R^2 = 0.10$), time since introduction was included as a predictor (Appendix S3: Table 11). Species with longer time since introduction spread farther in the GLB and this positive relationship ($\beta = 3.88$; $p<0.001$) was significant. Stepwise multiple regression showed two other models within $\Delta 4$ AIC, but none of the additional traits included in those models were significant predictors of spread distance (Appendix S3: Table 12).

Predicting how far nonindigenous species spread for the broad set of species traits across freshwater taxa - stepwise multiple regression

In the final model that predicted the number of Great Lakes sub-basins colonized ($AIC = 243.15$, $F_{1,38} = 16.06$, $p = <0.001$, $Adj. R^2 = 0.28$), fecundity was included as a predictor (Appendix S3: Table 13). Fecundity was significant ($p<0.001$). Fecundity ($\beta = 4.01$) was the strongest predictor of the number of Great Lakes sub-basins colonized, where species that colonized more Great Lakes sub-basins had high fecundity. Stepwise multiple regression showed five other models within $\Delta 4$ AIC, none of the additional traits included in those models were significant predictors of the number of Great Lakes sub-basins colonized (Appendix S3: Table 14).

In the final model that predicted spread distance ($AIC = 470.00$, $F_{5,34} = 3.557$, $p = 0.011$, $Adj. R^2 = 0.25$); depth range, maximum temperature, minimum temperature, habitat breadth, and proportion of species in lakes were included as predictors (Appendix S3: Table 15). Depth range was significant ($p=0.023$), minimum temperature and habitat breadth were close to significant ($p<0.10$), and maximum temperature and the proportion of species in lakes were not significant. Depth range ($\beta = 2.39$) was the strongest predictor of spread distance while maximum temperature ($\beta = 1.68$), habitat breadth ($\beta = 1.77$), minimum temperature ($\beta = -1.93$), and proportion of species in lakes ($\beta = -1.68$) had slightly smaller but similar effects, where species that spread farther had wide depth range, high maximum temperature, wide habitat breadth, low minimum temperature, and occurred more often in streams. Stepwise multiple regression showed three other models within $\Delta 4$ AIC, but none of the additional traits included in those models were significant predictors of spread distance (Appendix S3: Table 16).

Predicting how far nonindigenous species spread for fish species - stepwise multiple regression

In the final model that predicted the number of Great Lakes sub-basins colonized ($AIC = 145.13$, $F_{8,13} = 1.418$, $p = 0.277$, $Adj. R^2 = 0.14$); maximum size, age at maturity, fecundity, predator breadth, maximum temperature, minimum temperature, proportion of species in lakes, and time since introduction were included as predictors (Table 17). None of the predictors in the best model were significant ($p < 0.05$); but predator breadth, proportion of species in lakes, and time were close to significant ($p < 0.10$). The effects of time since introduction ($\beta = 2.15$) and number of predator types ($\beta = 1.97$) were more than one and half times stronger than minimum temperature ($\beta = -1.26$); while the effects of age at maturity ($\beta = 1.51$), fecundity ($\beta = 1.52$), maximum size ($\beta = -1.60$), maximum temperature ($\beta = -1.65$), and proportion of species in lakes ($\beta = -1.82$) were similar. Therefore, species which colonized a large number of Great Lakes sub-basins had a long time since introduction, high number of predator types, low minimum temperature, high age at maturity, high fecundity, small maximum size, low maximum temperature, and occurred more often in streams. Stepwise multiple regression showed three other models within $\Delta 4$ AIC, but none of the additional traits included in those models were significant predictors of the number of Great Lakes sub-basins colonized (Appendix S3: Table 18).

In the final model that predicted spread distance ($AIC = 266.88$, $F_{2,19} = 3.85$, $p = 0.040$, $Adj. R^2 = 0.21$); age at maturity and predator breadth were included as predictors (Appendix S3: Table 19). Both predictors in the best model were significant. The effects of age at maturity ($\beta = 2.27$; $p = 0.035$) and number of predator types ($\beta = 2.17$; $p = 0.043$) were similar, where species that spread farther had high age at maturity and high number of predator types. Stepwise multiple regression showed three other models within $\Delta 4$ AIC, but none of the additional traits included in those models were significant predictors of spread distance (Appendix S3: Table 20).

Discussion

Traits including body size, life history traits, and environmental tolerances are associated with nonindigenous species occurring more often in lakes versus streams. I found that nonindigenous freshwater taxa and fishes, specifically, with smaller maximum size occurred more often in lakes than streams. Looking at life-history traits across broad nonindigenous taxa, I found that species in lakes had lower fecundity and fish species specifically had a higher age at maturity in lakes. Lake taxa were also characterized by broader environmental/physiological tolerances such as depth and temperature.

Large body size predicted high spread distance across nonindigenous freshwater taxa while I found the opposite result when only looking at fish species (Table 4). In terms of life history traits, I found that nonindigenous freshwater taxa with high fecundity spread farther. Nonindigenous fish species with high fecundity, high maximum lifespan, and high age at maturity also spread farther. Nonindigenous freshwater taxa that spread farther displayed generalist traits such as occurring across wide depth range, wide habitat breadth, and wide

temperature range. Nonindigenous freshwater taxa and fish species that occurred more often in streams spread farther compared to taxa and species in lakes.

Are different traits associated with nonindigenous species occurring more often in lakes versus streams?

Nonindigenous freshwater species in both lakes and streams commonly have large body size compared to native species, but large body size is typically associated with higher dispersal which is more common in streams (Su et al. 2022). Both in fishes and across broad nonindigenous freshwater taxa, I found that stream species were characterized by a larger body size compared to lake species. This similarity across freshwater taxa is driven by a few characteristic taxa. For example, Carolina fanwort (*Cabomba caroliniana*) has a large maximum size (1,000 cm) while occurring in lakes only 6% of the time. In addition, several species of algae (*Chaetoceros muelleri subsalsum*, *Chroodactylon ornatum*, *Contricribra guillardii*, and others) are all relatively small and are primarily found in lakes. Fourspine stickleback (*Apeltes quadracus*) had the smallest maximum size among fish species (6.4 cm) while occurring in lakes 67% of the observations. In addition, grass carp (*Ctenopharyngodon idella*) and common carp (*Cyprinus carpio*) have large body sizes while occurring in lakes only 44% and 41% of observations compared to streams. Bluespotted sunfish (*Enneacanthus gloriosus*) and margined madtom (*Noturus insignis*) also had small maximum sizes and occurred more often in lakes than streams. Brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) had large maximum sizes and they occurred more often in streams than lakes. Since streams tend to be more connected, it is possible that nonindigenous species with larger size can more easily disperse within stream systems. In addition, large body size may improve survival through frequent high flow disturbance events in stream habitats (Del Signore et al. 2016). There is also evidence that larger maximum size is common in nonindigenous stream species compared to native species (Vila-Gispert et al. 2005; Olden et al. 2021).

Successful freshwater species in both lakes and streams are typically characterized by high fecundity, early age at maturity, and rapid growth rate which make it easier to establish and spread (Koehn 2004). I expected nonindigenous species in both lakes and streams to have an opportunistic life history strategy with lower age at maturity because it allows species to reproduce and establish at an early age before experiencing predation, competition, and harsh abiotic factors, but I found that nonindigenous fish species in lakes had a higher age at maturity than those in streams. Since streams are more prone to disturbance compared to lakes, it is possible that species which mature earlier and reproduce before being impacted by disturbance are more successful in stream habitats. The stability of lake ecosystems makes it more advantageous for species to mature later in life and produce fewer young while investing more in parental care (Olden et al. 2006). I found similar results across nonindigenous freshwater species for fecundity, another reproductive trait, which was higher in streams than lakes. Further, the PCoA of fish species showed that stream species had high fecundity and long maximum lifespan. Maximum lifespan was strongly correlated with fecundity (and therefore removed from the fish traits analysis) which means that short lifespans could also drive invasive success in lake habitats. Stream species may be more likely to have higher fecundity to give species a higher number of offspring which can increase the chances of young surviving to maturity since streams face harsh environmental conditions due to seasonality and anthropogenic disturbance. A shorter

age to maturity for fish species in streams and a higher fecundity in freshwater stream species indicates that stream species display a combination of an opportunistic and periodic life-history strategy which allows them to quickly establish in a novel environment and recover from disturbance events (Winemiller & Rose 1992; Olden et al. 2006).

Nonindigenous freshwater species in both lakes and streams are typically more successful when they have broad environmental/physiological tolerances, but I found that nonindigenous lake species had wider physiological tolerances (temperature and depth) compared to stream species. Nonindigenous fishes that had lower minimum temperature were more likely to occur in lakes and tolerance for lower minimum temperatures can create a wider temperature range which can help nonindigenous species survive in a wide variety of conditions. Nonindigenous lake species were characterized by higher maximum temperature which is likely because lakes and areas of slow-moving water are often characterized by warmer water temperatures (Olden et al. 2006). Lake species had higher maximum depth and wider depth range compared to stream species likely because lakes are typically much deeper than streams. It appears that nonindigenous lake species are characterized by a generalist life-history strategy due to their tolerance for low and high temperatures as well as a wide depth range compared to stream species.

Slow moving water favors a generalist life-history strategy (Olden et al. 2006, 2021) which is found more often in lakes and can lead to a wider diet breadth. In contrast to this, I found nonindigenous fish species that occurred more often in lakes had a narrower diet breadth than stream species. It is also perhaps surprising that lake species had a narrower diet breadth since lake species have been in the GLB for a longer period of time which could allow lake species to adapt to eat a wider variety of prey (Carlsson et al. 2011). However, since streams vary more longitudinally than lakes, streams often have more microhabitats which may result in a more diverse selection of prey.

High-impact nonindigenous fish species in lake ecosystems are typically top predators (Eby et al. 2006; Cucherousset & Olden 2011), however, I found that nonindigenous lake fish species had a high number of predator types compared to stream species. This is unexpected given naive native predators may not recognize nonindigenous species as prey (Carlsson et al. 2011). However, native species can learn how to incorporate nonindigenous species into their diet over time. Since lake species were also characterized by a longer time since their introduction to the GLB than those occurring more often in streams, it is possible that more predators have adapted to consuming these species. For example, in the Hudson River, there was a time lag before the native blue crab (*Callinectes sapidus*) preyed and influenced the population structure of nonindigenous zebra mussels (*Dreissena polymorpha*) (Carlsson et al. 2011). Longer time since introduction for nonindigenous lake species was also surprising because the major pathway of introduction for nonindigenous species in the 1800s was deliberate release (Ricciardi 2006). Early deliberate releases include stocking of species such as brown and rainbow trout which were released in both lakes and streams about 140 years ago, while unintentional species introductions into lakes became more common compared to streams in the past 60 years due to ballast water exchange from international shipping. For example, brown and rainbow trout occurred in streams for 78.4% and 70.1% of observations and the species were introduced 138 and 145 years ago.

Which traits predict how far nonindigenous species spread across freshwater taxa and among fish species?

Across nonindigenous freshwater taxa, I found that taxa with larger body size colonized more Great Lakes sub-basins which aligns with my expectations because large body size is associated with high dispersal and long lifespan. I also expected freshwater taxa with a larger maximum size to spread farther compared to smaller species because size is a common trait found in successful nonindigenous plants (van Kleunen et al. 2010), crayfish (van Kuijk et al. 2021) and fish (Vila-Gispert et al. 2005; Howeth et al. 2016; Su et al. 2020). Many freshwater species which have spread across the most sub-basins are plants such as purple loosestrife (*Lythrum salicaria*) and eurasian watermilfoil (*Myriophyllum spicatum*) and a meta-analysis has shown large body size to be a common trait of nonindigenous plant species (van Kleunen et al. 2010). However, when only looking at fish species I found species with smaller maximum size colonized more Great Lakes sub-basins which does not fit with my expectations. I found this result despite the fact that the two species that colonized the most Great Lakes sub-basins were larger species (common carp and brown trout). In addition, multiple small fish species did not colonize many Great Lake sub-basins including fourspine stickleback, bluespotted sunfish, western mosquitofish (*Gambusia affinis*), orangespotted sunfish (*Lepomis humilis*), and margined madtom. Round goby (*Neogobius melanostomus*) is an outlier that may be driving this pattern in fish species because it has a small maximum size but it has colonized the third most Great Lakes sub-basins. There is support for smaller body size leading to higher establishment success for fish species (Ruesink 2005), but most studies show the opposite.

High fecundity (Havel et al. 2015; Su et al. 2022), long lifespan (Su et al. 2022), and late age at maturity (Vila-Gispert et al. 2005) are common reproductive characteristics often characterizing successful nonindigenous freshwater taxa. I found that nonindigenous freshwater taxa and fish species with higher fecundity colonized more Great Lakes sub-basins. Maximum lifespan was removed from the fish traits analysis because it had a high positive correlation with fecundity, so I can also say that nonindigenous fish species with higher maximum lifespan colonized more Great Lakes sub-basins. I also found that nonindigenous fish species with higher age at maturity colonized more Great Lakes sub-basins and spread further in the GLB. High fecundity but shorter age at maturity could increase success by allowing nonindigenous species to quickly establish a population, outcompete native species, and recover from disturbance events. For example, nonindigenous mollusk species such as zebra mussels and asian clams (*Corbica fluminea*) have shorter age at maturity, shorter maximum lifespans, and high fecundity because they are adapted to live in more disturbed or extreme environments where they can recover quickly (McMahon 2002). These traits may give nonindigenous species competitive advantages over North American mollusks which have longer maximum lifespans and lower fecundity because they have evolved to live in more stable environments.

Successful nonindigenous species are often characterized by generalized habitat traits including: wide habitat breadth (Kolar & Lodge 2002), wide depth range (Marchetti et al. 2004a), and a wide temperature range (Kolar & Lodge 2002; Marchetti et al. 2004a; García-Berthou 2007; Bates et al. 2013; Havel et al. 2015; Howeth et al. 2016; Olden et al. 2021). I found that nonindigenous freshwater taxa with a wider depth range and wider habitat breadth spread further in the GLB, adding to evidence that trophic generalism often indicates invasive success (Romanuk et al. 2009). In addition, nonindigenous freshwater taxa and fish species with broad environmental tolerances have had higher establishment success (Havel et al.

2015; Howeth et al. 2016). Accordingly, I found that across nonindigenous freshwater taxa with a low minimum temperature and high maximum temperature spread further in the GLB. A wide temperature range makes it more likely that the climate will match between an invader's native climate and the climate in the Great Lakes. This has been shown in variety of taxa including fishes (Bomford et al. 2010), terrestrial plants (Petitpierre et al. 2012), birds (Duncan et al. 2001), mammals (Forsyth et al. 2004), and reptiles and amphibians (Bomford et al. 2008; Van Wilgen & Richardson 2012). However, when only looking at fish species, I found that species with lower minimum temperature and lower maximum temperature colonized more Great Lakes sub-basins. There is some evidence that nonindigenous fishes that spread quickly have not succeeded in high water temperatures, but the majority of evidence indicates species with wide temperature ranges are more successful (Kolar & Lodge 2002).

Successful nonindigenous fish species typically have few predator types because invaders are successful when they are in a novel environment where they have no natural predators. However, I found that nonindigenous fish species with a high number of predator types colonized more Great Lakes sub-basins and spread further in the GLB. Like previously discussed, successful nonindigenous taxa are habitat generalists which potentially explains the high number of predator types because they encounter more potential predators (Welborn et al. 1996). It is possible that species that spread more throughout the Great Lakes have a high number of predators because they are encountering more predator types since they are occupying a larger area.

Long time since introduction has been shown to predict nonindigenous fish species colonization success (Buckwalter et al. 2020) and I found that nonindigenous freshwater taxa and fish species with a longer time since introduction colonized more Great Lakes sub-basins. Nonindigenous species often experience a time lag period where species maintain a population for a period of time before eventually exploding and spreading further in the invaded region (Crooks 2005; McKnight et al. 2017).

Do lake or stream species spread further?

Nonindigenous freshwater taxa and fish species that occurred more often in streams colonized more Great Lakes sub-basins and spread further distances, as would be expected for several reasons. First, streams may have higher connectivity than isolated or unconnected lakes which can lead to increased dispersal, although the dispersal through stream networks can be uneven, directional, and interrupted by dams (Anderson et al. 2020). Second, large maximum size is associated with high dispersal rates in fishes (Olden et al. 2021), and stream species were characterized by larger maximum size compared to lake species. Finally, nonindigenous fish species with the ability to live in disturbed habitats have been shown to have higher establishment success (Marchetti et al. 2004a) and streams tend to experience more disturbance (Resh et al. 1988).

Limitations and Future Directions

My study had several methodological limitations that could be improved in future research. I measured how far species spread with euclidean distance spread over land, but

calculating water distance through a stream network and the Great Lakes would allow examining how species navigate through different habitat types and across barriers. Dams and other structures such as culverts are major barriers for spread throughout streams, but I was unable to account for these barriers when calculating spread. Additionally, many nonindigenous fish species are continually stocked (e.g., brown trout and rainbow trout) which may influence how far they spread, but I was not able to account for this additional propagule pressure. Stocked fish species are often selected by humans based on their recreational value which has led to nonindigenous fish having larger body sizes and laterally compressed bodies which are also better suited for lake environments (Su et al. 2020). While fish trait data were readily available, it was more difficult finding trait data, other than body size, to compare among the freshwater taxa which reduced sample size ($n = 40$) for comparing life history traits among freshwater taxa. Since there are over 180 nonindigenous freshwater species in the GLB, it would be helpful if future research was able to compile and compare life history traits (e.g., fecundity, lifespan, or maturity) and habitat-use traits (e.g., temperature or depth) for all the freshwater species.

Learning more about the traits that favor species invasions in lakes and streams, will allow us to profile future nonindigenous species that could be successful (Marchetti et al. 2004b). There are likely multiple types of successful nonindigenous species that have different sets of traits including species with high fecundity and short age at maturity and these nonindigenous species are successful because they can establish a population quickly and recover from disturbance by reproducing rapidly. While other successful nonindigenous species with large size and long lifespan can succeed by preying on smaller native species and establishing a population over multiple generations. Understanding the traits of successful nonindigenous species may also allow us to predict which current nonindigenous species will spread and have harmful effects in the future. Nonindigenous species are causing harm to ecosystems and economies in the Great Lakes (Steinman et al. 2017), so it is important to understand the traits of successful and impactful nonindigenous species.

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Tables

Table 1

Species trait	Description	Datasets
Maximum size	Maximum total length (centimeters)	1, 2, 3
Age at maturity	Mean age at maturity for females (years)	3
Maximum lifespan	Maximum lifespan based on life in the wild (years)	2
Fecundity	Maximum reported annual fecundity	2, 3
Diet breadth	The sum of all binary diet variables (see Appendix S1)	3
Predator breadth	The sum of all binary predator type variables (see Appendix S1)	3
Maximum depth	Maximum water depth	
Minimum depth	Minimum water depth	2, 3
Depth range	Difference between maximum water depth and minimum water depth	2, 3
Maximum temperature	Maximum water temperature	2, 3
Minimum temperature	Minimum water temperature	2, 3
Temperature range	Difference between maximum water temperature and minimum water temperature	
Habitat breadth	Sum of all binary habitat type variables (see Appendix S1)	2, 3
Time	Time since each species was introduced into the GLB	1, 2, 3
Proportion of species in lakes/streams	The proportion of how often a species was observed in lakes compared to streams. A value of 1 indicates the species was only found in lakes.	1, 2, 3

List of species traits for all datasets. 1 = Body size dataset, 2 = Broad set of species traits across freshwater taxa dataset, 3 = Fish species dataset

Table 2

Traits	Body size (133)	Broad set of species traits across freshwater taxa (40)	Fish (22)
Maximum size	-1.995**		-2.905**
Age at maturity			+2.538**
Maximum lifespan			
Fecundity		-3.630**	
Diet breadth			-3.507**
Predator breadth			+2.425**
Maximum depth			
Minimum depth			
Depth range			
Maximum temperature		+1.537	
Minimum temperature			-2.494**
Temperature range			
Habitat breadth			
Time			+2.192**

Summary of regression results for body size, broad set of species traits across freshwater taxa, and fish species dataset. Predicting how often species occur in lakes versus streams for aquatic taxa and fish species. * = $p < 0.10$. ** = $p < 0.05$. + = Larger/Higher in lakes (Smaller/Lower in streams). - = Smaller/Lower in lakes (Larger/Higher in streams).

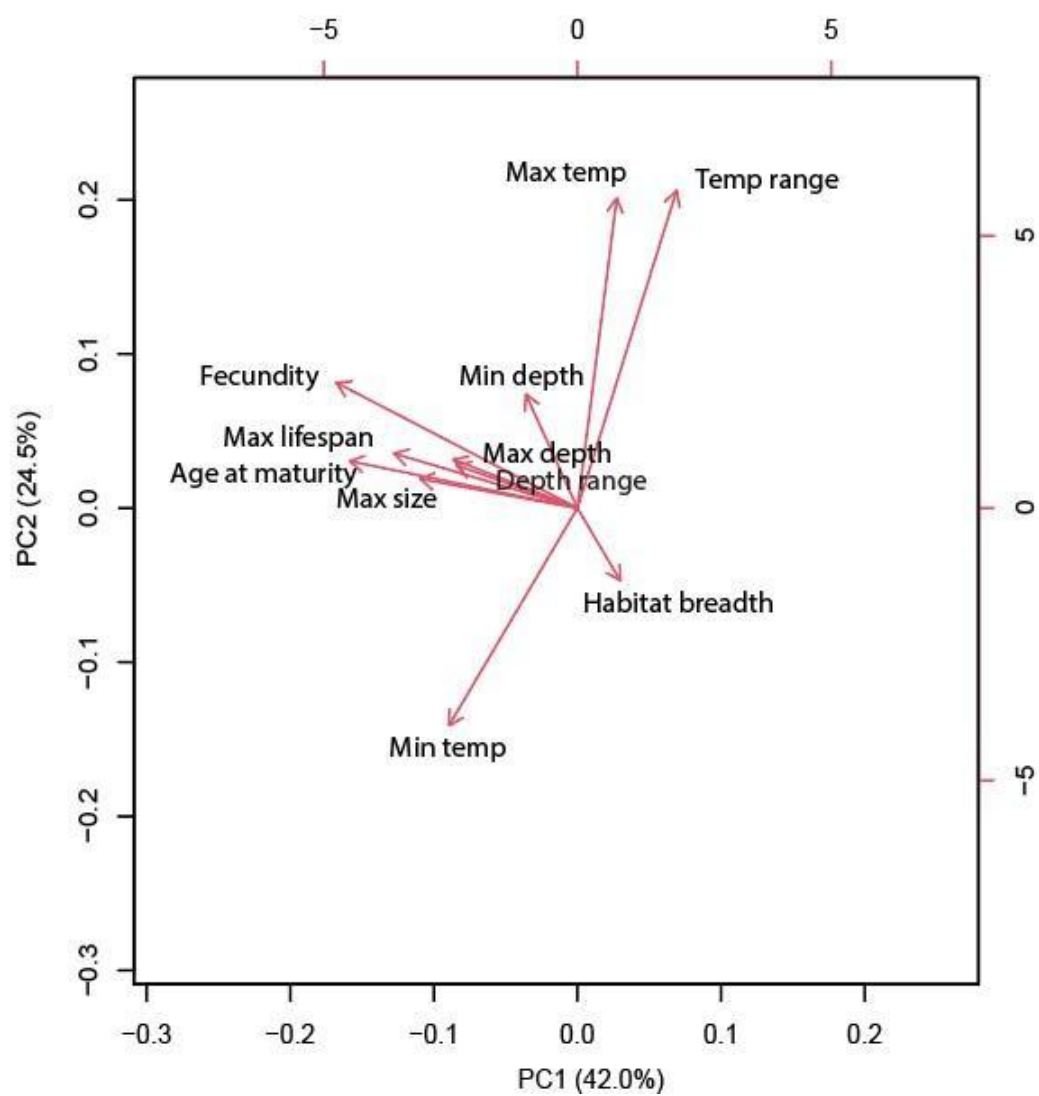
Table 3

Traits	Body size (N = 134)		Broad set of species traits across freshwater taxa (N = 40)		Fish (N = 22)	
	Sub-basins	Spread distance	Sub-basins	Spread distance	Sub-basins	Spread distance
Maximum size	+3.303**				-1.599	
Age at maturity					+1.505	+2.266**
Maximum lifespan						
Fecundity			+4.008**		+1.519	
Diet breadth						
Predator breadth					+1.968*	+2.171**
Maximum depth						
Minimum depth						
Depth range				+2.390**		
Maximum temperature				+1.676	-1.651	
Minimum temperature				-1.930*	-1.255	
Temperature range						
Habitat breadth				+1.768*		
Time	+1.484	+3.883*			+2.154*	
Lake/Stream	-1.574			-1.676	-1.822*	

Summary of regression results for aquatic taxa and fish species. Predicting spread and impact from species traits for aquatic taxa and fish species. + = positive effect size. - = negative effect size. * = $p < 0.10$. ** = $p < 0.05$. In the Lake/Stream row, + = positive effect size in lake species and - = negative effect size in stream species.

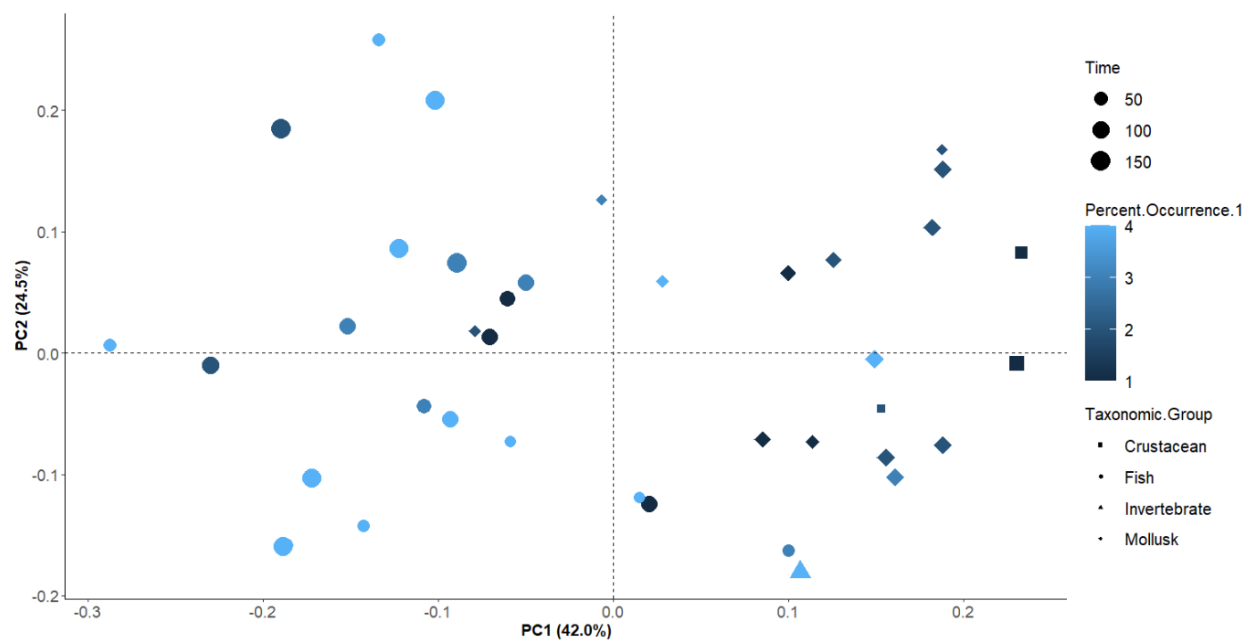
Figures

Fig. 1



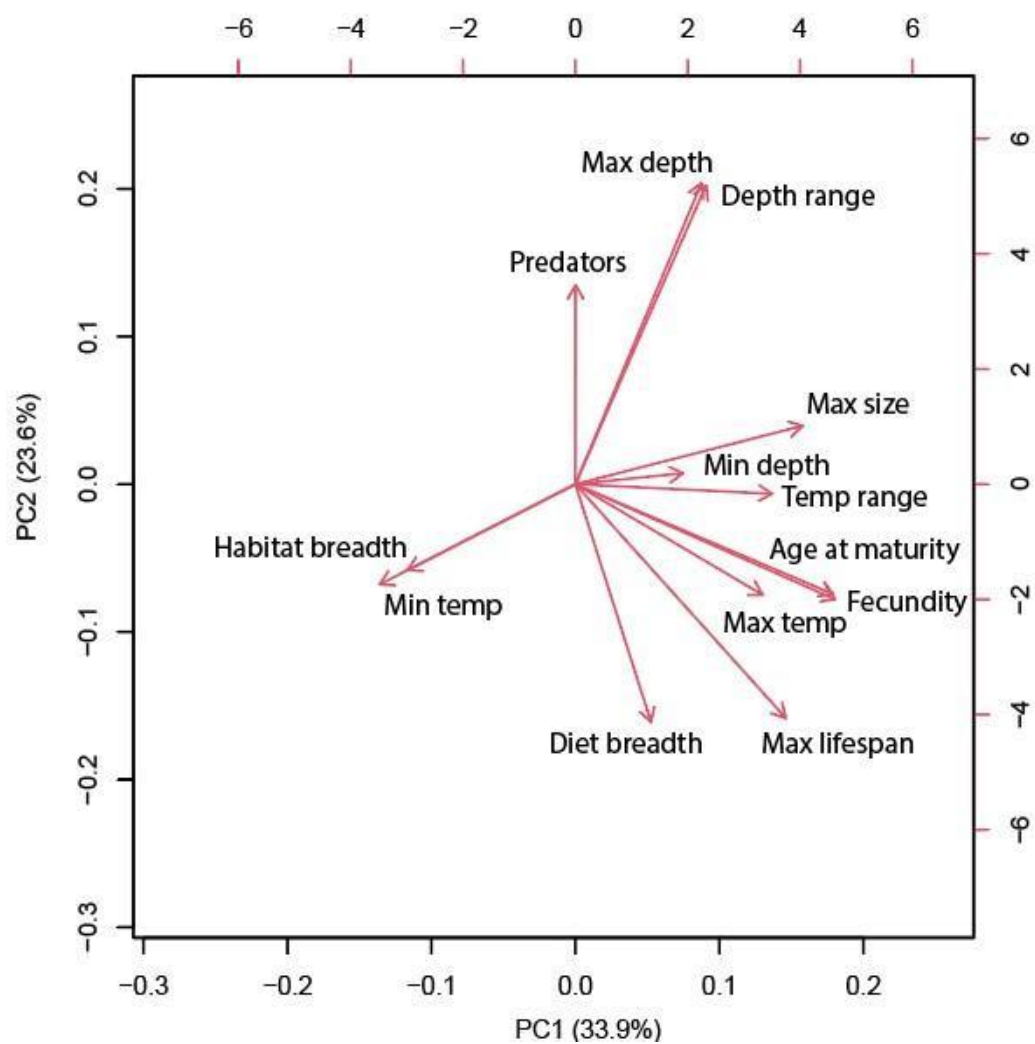
Broad set of species traits across freshwater taxa dataset Principal Coordinates Analysis (PCoA) with the vectors for the species traits.

Fig. 2



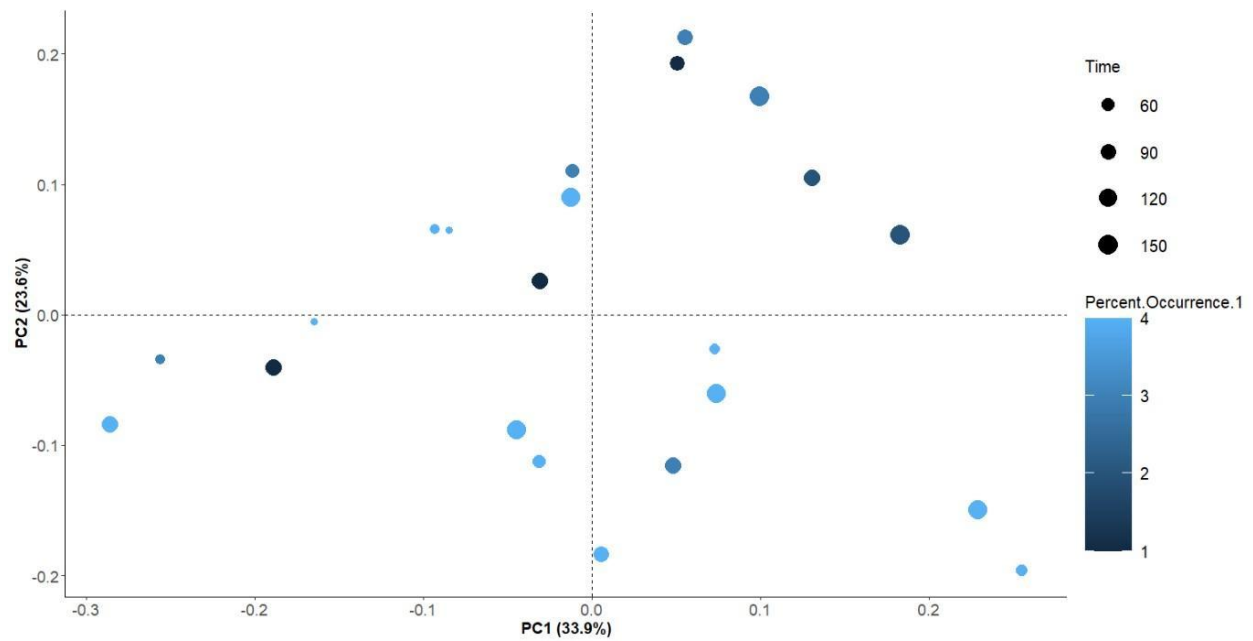
Broad set of species traits across freshwater taxa dataset Principal Coordinates Analysis with the points indicating different taxa. Rank scale: 1 = 0% observations in streams, 2 = 1-15% observations in streams, 3 = 16-30% observations in streams, 4 = 31-80% observations in streams.

Fig. 3



Fish species dataset Principal Coordinates Analysis (PCoA) with the vectors for the species traits.

Fig. 4



Fish species traits dataset Principal Coordinates Analysis (PCoA) with the points indicating different species. Rank scale: 1 = 0% observations in streams, 2 = 1-15% observations in streams, 3 = 16-30% observations in streams, 4 = 31-80% observations in streams.

Appendix S1

Table 1

Predictor	2	3
1. Maximum size	0.56	-0.17
2. Time	—	0.00
3. Lake/Stream		—

Correlation matrix of the body size dataset (n = 134) traits (Pearson's correlation). No traits were removed for high correlations.

Table 2

Predictor	2	3	4	5	6	7	8	9	10	11	12	13
1. Max Size	0.78	0.69	0.74	0.40	0.00	0.39	-0.01	0.31	-0.18	-0.19	0.17	-0.41
2. Age at maturity	—	0.73	0.70	0.31	0.13	0.30	0.04	0.36	-0.18	-0.19	0.21	-0.31
3. Max lifespan		—	0.70	0.02	0.06	0.01	0.06	0.28	-0.10	-0.07	0.25	-0.37
4. Fecundity			—	0.35	0.19	0.34	0.20	0.30	-0.02	-0.06	-0.01	-0.44
5. Max depth				—	0.22	0.99	-0.16	-0.09	-0.09	-0.18	0.02	-0.08
6. Min depth					—	0.20	0.12	0.00	0.07	-0.41	-0.25	-0.07
7. Depth range						—	-0.17	-0.08	-0.10	-0.17	0.03	-0.07
8. Max temp							—	-0.36	0.87	-0.07	0.16	0.10
9. Min temp								—	-0.72	0.02	-0.02	-0.34
10. Temp range									—	-0.01	0.15	0.27
11. Habitat breadth										—	0.16	0.07
12. Time											—	0.01
13. Lake/Stream												—

Correlation matrix of the broad set of species traits across freshwater taxa dataset (n = 40) traits (Pearson's correlation). Age at maturity, maximum depth, and temperature range were removed for high correlations.

Table 3

Predictor	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1. Max Size	0.68	0.49	0.65	0.26	0.32	0.53	-0.03	0.52	0.22	-0.39	0.25	-0.17	-0.10	0.47
2. Age at maturity	—	0.70	0.66	0.30	-0.28	0.21	0.37	0.19	0.25	-0.19	0.18	-0.37	-0.08	0.16
3. Max lifespan		—	0.75	0.37	-0.44	-0.10	0.14	-0.11	0.24	-0.18	0.15	-0.08	-0.35	0.18
4. Fecundity			—	0.25	-0.12	0.20	0.25	0.19	0.55	-0.17	0.36	-0.19	-0.18	0.34
5. Diet breadth				—	0.06	-0.36	-0.25	-0.36	0.28	-0.06	0.20	-0.04	-0.51	0.11
6. Predator breadth					—	0.36	-0.38	0.36	0.08	-0.23	0.19	-0.02	0.13	0.10
7. Max depth						—	0.20	0.99	-0.12	-0.30	0.06	-0.29	0.31	0.28
8. Min depth							—	0.18	0.15	-0.03	0.08	-0.57	0.23	-0.10
9. Depth range								—	-0.13	-0.29	0.05	-0.27	0.30	0.29
10. Max temp									—	-0.34	0.83	-0.20	0.16	0.35
11. Min temp										—	-0.74	0.27	-0.36	-0.23
12. Temp range											—	-0.20	0.41	0.36
13. Habitat breadth												—	-0.06	0.35
14. Lake/Stream													—	0.15
15. Time														—

Correlation matrix of the fish species dataset (n = 22) traits (Pearson's correlation). Maximum lifespan, maximum depth, and temperature range were removed for high correlations.

Table 4

Predictor	Coefficient	SE	T	P
Maximum size	-0.078	0.039	-1.995	0.048

Selected multivariate linear model summary table for the body size dataset. Summary table of the selected (see Appendix S3: Table 5) multivariate linear model results to predict the proportion of aquatic taxa in lakes (compared to streams) in response to species traits. Includes variable coefficients, standard error (SE), t value (T), and p-value (P).

Table 5

Predictors	NULL	1
Maximum size	0.018	0.048
Time	0.193	
AIC	-226.522	-226.781

Proportion of aquatic species in lakes (compared to streams) regression summary for the body size dataset. Summary of stepwise regression process for identifying the selected model (1, green) of the proportion of species in lakes in response to species traits. Model steps include the initial null model (all predictors) and all other models within Δ AIC (< 4.0). Values indicate the p-value for each predictor variable.

Table 6

Predictor	Coefficient	SE	T	P
Fecundity	-0.182	0.050	-3.630	<0.001
Maximum Temperature	0.086	0.056	1.537	0.133

Selected multivariate linear model summary table for the broad set of species traits across freshwater taxa dataset. Summary table of the selected (see Appendix S3: Table 7) multivariate linear model results to predict the proportion of aquatic taxa in lakes (compared to streams) in response to species traits. Includes variable coefficients, standard error (SE), t value (T), and p-value (P).

Table 7

Predictors	NULL	1	2	3	4
Maximum size	0.530	0.552	0.505		
Max lifespan	0.543				
Fecundity	0.098	0.079	0.042	<0.001	<0.001
Minimum Depth	0.758				
Depth range	0.258	0.331	0.202	0.239	
Maximum temperature	0.268	0.301	0.125	0.090	0.133
Minimum temperature	0.682	0.573			
Habitat breadth	0.815				
Time	0.700				
AIC	-75.203	-82.511	-84.131	-85.617	-86.051

Proportion of aquatic species in lakes (compared to streams) regression summary for the broad set of species traits across freshwater taxa dataset. Summary of stepwise regression process for identifying the selected model (4, green) of the proportion of species in lakes in response to species traits. Model steps include the initial null model (all predictors) and all other models within Δ AIC (< 4.0). Values indicate the p-value for each predictor variable.

Table 8

Predictor	Coefficient	SE	T	P
Maximum Size	-0.298	0.102	-2.905	0.011
Age at maturity	0.206	0.081	2.538	0.023
Diet breadth	-0.143	0.041	-3.507	0.003
Predator breadth	0.179	0.074	2.425	0.028
Minimum temperature	-0.108	0.043	-2.494	0.025
Time	0.104	0.047	2.192	0.045

Selected multivariate linear model summary table for the fish species dataset. Summary table of the selected (see Appendix S3: Table 9) multivariate linear model results to predict the proportion of fish species in lakes (compared to streams) in response to species traits. Includes variable coefficients, standard error (SE), t value (T), and p-value (P).

Table 9

Predictors	NULL	1	2	3
Maximum size	0.210	0.114	0.024	0.011
Age at Maturity	0.132	0.056	0.026	0.023
Fecundity	0.604	0.686	0.755	
Diet breadth	0.104	0.006	0.005	0.003
Predator breadth	0.255	0.121	0.044	0.028
Minimum depth	0.823			
Depth range	0.621			
Maximum temperature	0.611	0.786		
Minimum temperature	0.140	0.083	0.032	0.025
Habitat breadth	0.625			
Time	0.501	0.120	0.050	0.045
AIC	-59.973	-65.196	-67.067	-68.908

Proportion of fish species in lakes (compared to streams) regression summary for the fish species dataset. Summary of stepwise regression process for identifying the selected model (3, green) of the proportion of species in lakes in response to species traits. Model steps include the initial null model (all predictors) and all other models within Δ AIC (< 4.0). Values indicate the p-value for each predictor variable.

Table 10

Predictor	Coefficient	SE	T	P
Maximum size	6.445	1.951	3.303	0.001
Lake/Stream	-5.556	3.529	-1.574	0.118
Time	2.882	1.942	1.484	0.140

Selected multivariate linear model summary table for the body size dataset. Summary table of the selected multivariate linear model results to predict the number of Great Lake subbasins colonized in response to species traits. Includes variable coefficients, standard error (SE), t value (T), and p-value (P). Final model same as NULL model. AIC = 765.687.

Table 11

Predictor	Coefficient	SE	T	P
Time	138.62	35.70	3.883	<0.001

Selected multivariate linear model summary table for the body size dataset. Summary table of the selected (see Appendix S3: Table 12) multivariate linear model results to predict the spread distance in response to species traits. Includes variable coefficients, standard error (SE), t value (T), and p-value (P).

Table 12

Predictor	NULL	1	2
Maximum size	0.422		
Lake/Stream	0.344	0.423	
Time	0.007	<0.001	<0.001
AIC	1599.618	1598.284	1596.942

Spread distance regression summary for the body size dataset. Summary of stepwise regression process for identifying the selected model (2, green) of the spread distance in response to species traits. Model steps include the initial null model (all predictors) and all other models within Δ AIC (< 4.0). Values indicate the p-value for each predictor variable.

Table 13

Predictor	Coefficient	SE	T	P
Fecundity	12.244	3.055	4.008	<0.001

Selected multivariate linear model summary table for the broad set of species traits across freshwater taxa dataset. Summary table of the selected (see Appendix S3: Table 14) multivariate linear model results to predict the number of Great Lake subbasins colonized in response to species traits. Includes variable coefficients, standard error (SE), t value (T), and p-value (P).

Table 14

Predictors	NULL	1	2	3	4	5	6
Maximum size	0.810						
Max lifespan	0.259	0.237	0.273				
Fecundity	0.551	0.364	0.210	0.017	0.001	<0.001	<0.001
Minimum Depth	0.908						
Depth range	0.103	0.083	0.118	0.176	0.230		
Maximum temperature	0.365	0.373					
Minimum temperature	0.614						
Habitat breadth	0.116	0.065	0.085	0.119	0.127	0.195	
Lake/Stream	0.204	0.169	0.238	0.248			
Time	0.924						
AIC	253.219	245.725	244.703	244.140	243.685	243.311	243.152

Number of Great Lake subbasins colonized regression summary for the broad set of species traits across freshwater taxa dataset. Summary of stepwise regression process for identifying the selected model (6, green) of the number of Great Lakes subbasins colonized in response to species traits. Model steps include the initial null model (all predictors) and all other models within Δ AIC (< 4.0). Values indicate the p-value for each predictor variable.

Table 15

Predictor	Coefficient	SE	T	P
Depth range	143.87	60.21	2.390	0.023
Maximum temperature	104.41	62.30	1.676	0.103
Minimum temperature	-133.46	69.15	-1.930	0.062
Habitat breadth	149.25	84.44	1.768	0.086
Lake/Stream	-255.58	152.47	-1.676	0.103

Selected multivariate linear model summary table for the broad set of species traits across freshwater taxa dataset. Summary table of the selected (Appendix S3: Table 16) multivariate linear model results to predict the spread distance in response to species traits. Includes variable coefficients, standard error (SE), t value (T), and p-value (P).

Table 16

Predictors	NULL	1	2	3	4
Maximum size	0.719	0.737	0.537		
Max lifespan	0.865				
Fecundity	0.822	0.847			
Minimum Depth	0.955				
Depth range	0.049	0.031	0.027	0.028	0.023
Maximum temperature	0.189	0.177	0.145	0.164	0.103
Minimum temperature	0.157	0.134	0.102	0.052	0.062
Habitat breadth	0.249	0.191	0.183	0.152	0.086
Lake/Stream	0.106	0.097	0.088	0.106	0.103
Time	0.284	0.222	0.175	0.204	
AIC	477.445	473.487	471.535	470.018	470.003

Spread distance regression summary for the broad set of species traits across freshwater taxa dataset. Summary of stepwise regression process for identifying the selected model (4, green) of the spread distance in response to species traits. Model steps include the initial null model (all predictors) and all other models within Δ AIC (< 4.0). Values indicate the p-value for each predictor variable.

Table 17

Predictor	Coefficient	SE	T	P
Maximum size	-31.154	19.486	-1.599	0.134
Age at maturity	17.939	11.919	1.505	0.156
Fecundity	15.629	10.286	1.519	0.153
Predator breadth	23.668	12.026	1.968	0.071
Maximum temperature	-13.748	8.325	-1.651	0.123
Minimum temperature	-8.725	6.954	-1.255	0.232
Lake/Stream	-44.795	24.585	-1.822	0.092
Time	15.975	7.415	2.154	0.051

Selected multivariate linear model summary table for the fish species dataset. Summary table of the selected (see Appendix S3: Table 18) multivariate linear model results to predict the number of Great Lake subbasins colonized in response to species traits. Includes variable coefficients, standard error (SE), t value (T), and p-value (P).

Table 18

Predictors	NULL	1	2	3	4
Maximum size	0.282	0.223	0.238	0.185	0.134
Age at Maturity	0.315	0.207	0.222	0.236	0.156
Fecundity	0.441	0.409	0.305	0.220	0.153
Diet breadth	0.825				
Predator breadth	0.159	0.096	0.071	0.076	0.071
Minimum depth	0.388	0.378	0.327	0.524	
Depth range	0.579	0.591			
Maximum temperature	0.503	0.469	0.235	0.145	0.123
Minimum temperature	0.267	0.213	0.205	0.251	0.232
Habitat breadth	0.369	0.358	0.422		
Lake/Stream	0.164	0.078	0.072	0.082	0.092
Time	0.384	0.284	0.183	0.054	0.051
AIC	150.207	148.334	147.003	146.353	145.130

Number of Great Lake subbasins colonized regression summary for the fish species dataset. Summary of stepwise regression process for identifying the selected model (4, green) of the proportion of species in lakes in response to species traits. Model steps include the initial null model (all predictors) and all other models within Δ AIC (< 4.0). Values indicate the p-value for each predictor variable.

Table 19

Predictor	Coefficient	SE	T	P
Age at maturity	194.65	85.89	2.266	0.035
Predator breadth	227.29	104.70	2.171	0.043

Selected multivariate linear model summary table for the fish species dataset. Summary table of selected (see Appendix S3: Table 20) multivariate linear model results to predict the spread distance in response to species traits. Includes variable coefficients, standard error (SE), t value (T), and p-value (P)

Table 20

Predictors	NULL	1	2	3	4
Maximum size	0.859				
Age at Maturity	0.437	0.085	0.097	0.039	0.035
Fecundity	0.731				
Diet breadth	0.968				
Predator breadth	0.591	0.242	0.114	0.035	0.043
Minimum depth	0.751	0.510			
Depth range	0.396	0.325	0.380		
Maximum temperature	0.670				
Minimum temperature	0.936				
Habitat breadth	0.768				
Lake/Stream	0.440	0.324	0.226	0.315	
Time	0.918				
AIC	282.958	269.968	268.582	267.609	266.880

Spread distance regression summary for the fish species dataset. Summary of stepwise regression process for identifying the selected model (X, green) of the spread distance in response to species traits. Model steps include the initial null model (all predictors) and all other models within Δ AIC (< 4.0). Values indicate the p-value for each predictor variable.