Title: Reconciling the invasion paradox: biotic resistance in freshwater fish communities depends on richness of donor and recipient basins

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Abstract:

Evidence for the theory of biotic resistance is equivocal, with experiments often finding a negative relationship between invasion success and native species richness, and large-scale comparative studies finding a positive relationship. Our analysis of global and regional datasets for fishes in river and stream reaches demonstrates that invasion patterns are consistent with biotic resistance. A negative relationship between native and non-native species richness in local assemblages was found at the global scale, while regional patterns revealed the opposite trend. At both spatial scales, however, nearly all non-native species originated from river basins with higher native species richness than the basin of the invaded community. These findings imply that distinct evolutionary histories in different regions strongly influence invasion of intact communities that are relatively un-impacted by human actions. Both ecological and evolutionary perspectives are required for understanding invasion patterns, and together may explain conflicting evidence for biotic resistance at different scales.

Introduction

The theory of biotic resistance predicts that more diverse communities are more resistant to invasion by non-native species (Elton 1958; Levine & D'antonio 1999). The current reorganization of the earth's flora and fauna through species introductions presents a critical test of this theory; however, evidence for biotic resistance is equivocal. Experiments conducted on small spatial scales have found some support for biotic resistance to invasion (Stachowicz *et al.* 1999; Naeem *et al.* 2000; Fridley *et al.* 2007; Carey & Wahl 2010). In contrast, analyses of regional and global patterns often have found positive correlations between numbers of native and non-native species (Stohlgren *et al.* 1999; Davies *et al.* 2005), and strong influence of species responses to abiotic conditions (Moyle & Light 1996; Roura-Pascual *et al.* 2011). This discrepancy of positive or no relationship between native and exotic richness at large spatial scales versus mixed, sometimes negative, relationships found at small spatial scales has been referred to as the invasion paradox (Renne & Tracy 2003; Fridley *et al.* 2007).

Multiple scale-dependent factors could produce the invasion paradox, including spatial heterogeneity, neutral processes, immigration rates, response to disturbance, or even statistical artifacts (Tilman 2004; Fridley *et al.* 2007; Melbourne *et al.* 2007; Clark & Johnston 2011; Clark *et al.* 2013). Greater environmental heterogeneity at the landscape scale may promote beta-diversity that results in the positive correlations between richness of native and non-native species at large spatial scales (Davies *et al.* 2005). Variation in resource availability across spatial scales could also shift species richness relationships of natives and non-natives (Byers & Noonburg 2003). Focusing on a different component of scale, Clark and Johnston (2011) found that temporal changes in species response to disturbance caused a shift in pattern between scales. Human activity (*e.g.*, habitat alteration) is strongly associated with regional and global distributions of non-native species (Leprieur *et al.* 2008; Pysek *et al.* 2010), and differences in anthropogenic disturbance across studies may explain some discrepancies. Indeed, the relative influence of anthropogenic and environmental factors on non-native species richness has been shown to vary across biogeographic realms; yet, evidence for biotic resistance at regional scales remains lacking (Blanchet *et al.* 2009; Roura-Pascual *et al.* 2011).

Contrasting relationships could also arise if datasets for different spatial scales reflect different phases of the invasion process (Dietz & Edwards 2006; Melbourne *et al.* 2007; Clark *et al.* 2013). The invasion process is generally thought to be composed of at least three phases: introduction, establishment, and spread (Shea & Chesson 2002). Experiments conducted on relatively small spatial scales have been used to examine how species interactions affect invasion success in local communities (*i.e.*, establishment), whereas comparative studies conducted at regional scales (*e.g.*, number of introduced and native taxa per country, ecoregion, watershed unit, *etc*.) examine a combination of the three phases of invasion. Because it is generally difficult to disentangle different phases of invasion based on regional survey data, such large-scale comparative analyses, perhaps unsurprisingly, find little evidence for biotic resistance. Comparative tests of biotic resistance need to be performed with assemblage data collected at local scales that are relevant for species interactions.

Freshwater fishes provide an excellent model system to test hypotheses of biotic resistance because dispersal between drainage basins is highly restricted and therefore biogeography can be inferred with confidence (Abell *et al.* 2008; Léveque *et al.* 2008; Brosse *et al.* 2013). Certain regions of the world (*e.g.*, Western North America, Europe, Australia) contain high percentages of non-native freshwater fishes, whereas other regions report few (Leprieur *et al.* 2008). Interestingly, the regions that tend to report high numbers of introduced species are also those with relatively low native diversity, suggesting that biotic resistance may play a role even at broad spatial scales. Nonetheless, evidence for biotic resistance in lotic ecosystems at any scale is limited. A recent meta-analysis of small-scale experimental studies in aquatic systems found strong evidence for biotic resistance in lentic habitats, but little support for biotic resistance in lotic habitats (Alofs & Jackson 2014). This may be partly explained by a bias toward pond mesocosm experiments in the literature (Thomsen *et al.* 2014). Previous studies of broad scale patterns of freshwater fish invasions in rivers have generally inferred significant influence of environmental suitability, including the degree of human impact, and little evidence for biotic resistance (Moyle & Light 1996; Gido & Brown 1999; Leprieur *et al.* 2008; Blanchet *et al.* 2009). However, these studies have generally analyzed species checklists at the sub-basin or basin scale. A study analyzing reach-scale data of fishes in the United States found support for a negative relationship between natives and non-natives (Mitchell & Knouft 2009), suggesting that comparison of reach-scale data that reflect species establishment and coexistence may provide a more valid test of biotic resistance. Comparisons based on species presence/absence at large spatial scales may include accounts of non-native release without population establishment, and present a skewed depiction of community composition because local assemblages of potentially interacting species are small subsets of the regional species pool.

Using comparative data that reflect local species interactions offers a potential ecological explanation for the invasion paradox; however, both ecological and evolutionary processes are known to influence community assembly (Cavender-Bares *et al.* 2009). Species identity and evolutionary history may also explain conflicting results for studies conducted at different spatial scales. Species that evolved in association with more diverse fauna should be superior competitors with a relative advantage when introduced into areas of lower diversity (Vermeij

1991; Sax & Brown 2000; Tilman 2011; Fridley & Sax 2014). Comparative studies of invasion patterns have rarely considered invader origins, mostly because specific invasion pathways are unknown. In cases where the details of non-native introductions are known, differences in niche characteristics of the invaders relative to those of the recipient community ultimately dictate invader success (Shea & Chesson 2002; Azzurro *et al.* 2014; Skóra *et al.* 2015). For example, Azzurro *et al.* (2014) showed that successful fish invaders tend to exist on the periphery of community morphological space. Similarly, non-native pest plants tend to be more distantly related to species in the receiving community than introduced plants that fail to become pests (Strauss *et al.* 2006). While specific invasion pathways or functional trait data are not uniformly available on a global scale, broad-scale patterns in fish biogeography are well understood, and relative differences in species richness between donor and receiving fauna can serve as a proxy of relative competitive abilities of non-native species.

To address these issues, the present study analyzes global and regional patterns of non-native and native freshwater fishes based on reach-scale surveys of fishes in rivers and streams. Because species interact within habitats, the stream reach is the most relevant spatial scale for documenting invasion success. To test the hypothesis that more species-rich communities should be more resistant to invasion, we compare the number of native and established non-native fish species found within a given stream or river reach, as well as compare the species richness of the basin of origin for the invader with the species richness of the basin of the invaded community. Separate analyses were performed on two sets of reach-scale data: one global and one regional. Our regional analysis included rivers and streams within the state of Texas, USA, a region with strong gradients of native fish species richness and endemism among seven major river basins that flow to the Gulf of Mexico. Our hypotheses for biotic resistance are two-fold: 1) the number of non-native species is negatively correlated with the number of native species present at local sites, and 2) species originating from basins with more native species are more likely to become established when introduced into communities in regions with lower species richness. Specifically, the frequency distribution of established non-natives should be strongly skewed in favor of species that originated from more diverse faunas in relation to the fauna of the recipient community.

Methods

Data Collection

Habitats impacted by human activities tend to have more introduced species (Johnson *et al.* 2008; Leprieur *et al.* 2008; Roura-Pascual *et al.* 2011). To increase the chance of detecting the influence of biotic resistance, we focused on fish survey data from relatively unaffected stretches of rivers and streams. Reach-scale surveys of fishes in lotic ecosystems (including both main channel and floodplain habitats) were compiled from the literature and natural history collection databases into global and regional datasets (*Supporting Information*). Sites were selected to maximize geographic coverage and evenness, as well as to capture a range of stream and river sizes within each region. Priority was given to sites where established invasive species are known to occur. Our goal was to develop a balanced global survey across habitat types, impact categories and climatic regimes. Nonetheless, data availability was skewed toward well-studied regions, such as Europe, Australia, and North and South America. We attempted to select studies conducted as recently as possible to reflect current invasion status (survey dates range from 1970–2009, with most studies in the 2000s).

For the purposes of this study, we loosely defined a reach as a segment of a stream or river, ranging from 500 m to 10 km in length. Only surveys that reported effort sufficient to obtain a representative sample of the entire fish community within the reach were included in the analysis. Between-site differences in reach size and survey effort are unavoidable. Here, we assumed that variation in survey methods and effort affects the probably of finding native and exotic species equally. For studies conducted at multiple sites within a basin, the reach with the highest recorded species richness was retained in the database for analysis. In general, we did not include river reaches located within reservoirs, but for a few highly impacted basins this was unavoidable.

The list of species recorded from each study was obtained and the total number of native and introduced species was recorded. Only established, self-sustaining exotic populations were counted; introduced species incapable of sustaining a population (*e.g.*, *Oncorhynchus mykiss*, rainbow trout, stocked for recreational fisheries) were not included in richness estimates. Hybrid species were only included if the parental forms were absent from the system. Species whose native status was considered questionable or species transplanted between sub-basins within the same major basin were considered native species. These criteria should facilitate counting introduced non-native species that are established and sufficiently common to have reasonable probabilities of detection during surveys. Exclusion of hybrids and species of questionable geographic origin ensured that species counted as non-native did not evolve with the local ichthyofauna of the receiving community. Each survey location was classified as a small (< 30 m wide), medium (< 200 m wide), or large river (> 200 m wide), and as temperate, subtropical, or tropical. Additionally, each site was assigned to one of three human impact categories: low (relatively natural landscapes with few apparent impacts, such as some areas with livestock grazing), moderate (watersheds with grazing and crop lands, rural dwellings and towns, and/or with a few dams), and high (watersheds with extensive agricultural and urban development, pollution, and/or extensively dammed). For the regional analysis of Texas streams and rivers, impact categories were assigned as either ‘low’ or ‘high’ given the shorter impact gradient compared to the global analysis.

We also compared native species richness of the river basin of origin of successful invaders and the river basin of the recipient community. For invader species with broad geographic ranges that encompass multiple river basins, the basin of origin was the basin with greatest native species richness. Here, we assume that more diverse basins are acting as a “center of origin” (*i.e.*, the donor fauna). In other words, even though the specific geographic source of many introductions was unknown, the introduced individuals likely evolved within the biotic environment associated with the center of diversity within their native range. While this assumption yields a coarser analysis, it does not bias results. In almost all cases, the differences between the richness of donor and receiving fauna were large enough (*e.g.*, Amazon vs. Mississippi basin) that trends were robust to slight differences between alternative basins of origin for non-native species with large ranges. References for basin richness and native ranges of introduced species were compiled from multiple sources, including online databases, compendia, and primary literature (*Supporting Information*). For basins with multiple reported estimates of species richness, the most recently published estimate was used. For several sites in smaller basins (*e.g.*, in Patagonia and parts of Asia), species richness estimates for the basin were unavailable so the nearest geographic basin in Brosse *et al.* (2013) was used.

Statistical Analysis

A generalized linear modeling (GLM) approach was used to determine whether the number of non-native species is negatively correlated with the number of native species at a given location. The number of non-native species was modeled as a negative binomial distribution, and a truncated zero hurdle model that treated non-native presence vs. absence as a binomial distribution was included to account for the high number of zeros in the dataset. Number of native species, impact category, and habitat type were included as explanatory variables. Modeling was conducted via backwards selection and the model with the lowest cross-validation error was chosen. Models were run using the pscl package in R (Zeileis *et al.* 2008). The explanatory variable ‘climate’ was excluded from analyses to deal with issues of collinearity, as it essentially described a gradient of increasing native richness from temperate to tropical sites. The remaining explanatory variables did not show signs of significant collinearity based on examination of the scatter plot matrix and calculation of the condition index ($\lambda_{max} / \lambda < 2$), where λ_{max} represents the dominant eigenvalue and λ the remaining eigenvalues (Quinn & Keough 2002). Due to issues of collinearity between explanatory variables within the regional Texas analysis, the GLM approach described above was not appropriate. Instead, these data were analyzed by principal components regression using a quasipoisson distribution.

A null model for the global analysis was created following the approach presented in Gido and Brown (1999) to test whether observed patterns of non-native species differed from expectations based on random invasion. A presence-absence matrix was created from the observed occurrences of non-native species within reach-scale sites. To avoid pseudoreplication, only one reach-scale site (maximum native diversity) was modeled for each river basin. Each non-native species was allowed to invade sites outside of their native range at random, with number of sites invaded equaling the number of occurrences in the observed data. This approach maintained interspecific differences between species, but allowed for equal colonization of all river basins. Null simulations were conducted in R (version 3.1.3). Simulations were run 1000 times to obtain a mean and maximum number of introduced species for each site. The percentage of sites where the observed number of non-natives was greater than expected by random was compared across high (≥ 80 species) and low diversity sites using a binomial proportions test with continuity correction.

To determine whether established non-native species originate from regions of higher fish diversity, a one-way chi-squared analysis was performed on the number of occurrences where a non-native species came from an area of higher or lower fish diversity. To avoid pseudoreplication, only one instance of a given non-native species was counted per river basin. A log-linear model with a poisson distribution was used to test for potential interactions between number of native species, impact category, and habitat type. Modeling was performed via backwards selection until removal of non-significant terms significantly increased residual deviance.

Results

A total of 226 reach-scale surveys were included in the global analysis (*Supporting Information*). There was large variation in the number of non-native species found in sites with low native diversity, whereas high diversity sites contained few, if any, non-native species (Fig. 1). A significant negative relationship was found between the number of non-native species and number of native species at a site, as well as a larger positive relationship between the number of non-native species and human impact (Table 1). On average, highly impacted sites contained more non-native species, but the number of non-natives decreased with increasing native diversity. The zero hurdle model showed a significant negative relationship between the presence of non-native species and native species richness, as well as a significant influence of habitat type, with medium and large rivers more likely to contain non-native species than small rivers. Impact level was not significantly correlated with the absence of non-native species (Table 1).

To test the potential influence of several highly diverse tropical sites included in the dataset, a subset that only included cases with native richness ≤ 200 was analyzed. This subset excluded five large, relatively pristine, tropical rivers from Venezuela and Guyana (Cinaruco, Caura, Casiquiare, Apure, and Rupununi). Results from this subset were identical to the model run with the full data set (*Supporting Information*). Therefore, the full data set was retained for subsequent analyses.

Null simulations in which species were allowed to invade sites at random showed no evidence for a relationship between number of native species and mean number of non-native species (Fig. 1; slope = 0.00015, SE = 0.0001, $P = 0.135$). The proportion of sites with an observed number of non-native species greater than the mean random expectation was significantly lower in high (≥ 80 species) than in low native diversity sites (Table 2). No significance difference was found between high and low native diversity sites for the proportion of sites greater than the maximum random expectation (Table 2), although some sites with low native diversity contained nearly twice as many non-native species as predicted from the null model (Fig. 1). A significant proportion of sites with high native diversity contained fewer non-native species than mean expectations based on null simulations ($\chi^2 = 27.03$, $df = 1$, $P < 0.0001$).

A total of 145 species accounted for the 458 cases of non-native establishment in the data set. Most of these cases involved a small number of cosmopolitan species introduced into multiple river basins. Significantly more cases ($n = 429$) involved establishment of non-native species that originated from basins more species rich than the receiving basin (Fig. 2; $\chi^2 = 349.35$, $df = 1$, $P < 0.0001$). A log-linear model was used to test for interactions between covariates. There was a significant interaction between invader origin (from more diverse *vs.* less diverse community) and habitat type (slope = –1.64, SE = 0.59, z = –2.79, $P = 0.005$), whereas the interaction between invader origin and impact was non-significant. The three-way interaction term was not significant, indicating a similar interaction between invader origin and impact across habitat types. Most of the cases in which established non-native species came from a more diverse basin than the receiving basin were highly impacted sites, reflecting the significant positive relationship between human impact and number of non-natives.

The regional analysis included a total of 55 reach-scale surveys of Texas rivers and streams. The relationship between the number of native and non-native species was weaker than the one obtained for the global analysis. PC1 was significantly correlated with number of non-natives (parameter estimate = –0.932, SE = 0.281, $t = –3.322$, $P = 0.002$). All three variables loaded roughly equally on PC1 (number native species = –1.44, human impact = –1.44, habitat size = –1.78), and were therefore all positively correlated with number of non-natives. While highly impacted sites tended to have more non-native species for a given habitat category, the relationship between non-native and native species richness varied from no correlation for large and small rivers to a positive correlation for medium-sized rivers (Fig. 3). A total of 38 non-native species accounted for the 77 cases of non-native establishment in the regional analysis. Similar to the global analysis, most of these introductions involved a small number of cosmopolitan species. Significantly more cases ($n = 68$) involved non-native species originating from a river basin that was more diverse than the receiving basin (Fig. 4; $\chi^2 = 54.37$, $df = 1$, $P <$

0.0001). There was no significant interaction between invader origin and habitat type, or invader origin and level of human impact.

Discussion

Contrary to previous comparative studies that analyzed species assemblage data at large spatial scales, we found evidence to suggest that high native species richness inhibits establishment of non-native species originating from less diverse river basins. Though human impact and habitat size influence the number of non-native species, there was a consistent trend of declining numbers of non-native species as a function of native species richness within streams and rivers in our global analysis (Fig. 1). The observed negative trend was significantly different from random expectations based on a null model (Fig. 1). A significant proportion of high diversity (≥ 80 native species) sites were found to contain fewer non-native species than the mean value predicted by null simulations (Table 2). In addition, some low diversity sites contained almost twice the maximum number of non-native species predicted by the null model. The vast majority of non-native species in both the global and regional analyses originated from river basins with higher native species richness than the basin of the recipient community (Figs. 2, 4), a trend consistent with previous regional analyses of freshwater and marine fishes (Vermeij 1991; Gido *et al.* 2004; Fridley & Sax 2014). This high proportion of successful invaders originating from a more diverse fauna than the receiving fauna suggests that coevolved ecological interactions in species-rich systems inhibit establishment of non-native species.

Discrepancies in the observed relationship between native and non-native species richness for the regional and global analyses could be partially explained by unequal competitive environments between donor and receiving faunas. The large amount of variation in numbers of non-natives established in local assemblages with low native diversity suggests that native species richness alone is a poor predictor of invasion success (Fig. 1). Results from the regional analysis of Texas rivers indicated a positive to no relationship between native diversity and the number of non-native species (Fig. 3). However, when placed in the context of the global analysis, this regional relationship becomes nested within the decreasing pattern displayed along a much greater diversity gradient (Fig. 1). Because a significant portion of non-native species in the regional analysis originated from a basin with higher native diversity than the invaded basin, the observed regional trends are not necessarily in conflict with the theory of biotic resistance. Both native and non-native species of a local assemblage are exposed to the same abiotic and biotic factors, which suggests that niche differences between natives and non-natives probably determine invasion success, rather than some aspect of native diversity alone (Shea & Chesson 2002).

While previous attempts to explain the invasion paradox have shown that patch dynamics (Shea & Chesson 2002; Davies *et al.* 2005) and temporal dynamics (Clark *et al.* 2013) can explain the shift in pattern across scales, we suggest that data on a scale appropriate for species interactions and consideration of invader origin may provide a more complete explanation. Changes in resource or habitat heterogeneity across scales or response to temporal changes in disturbance cannot explain the mixed results found in small-scale observational studies (Fridley *et al.* 2007; Clark & Johnston 2011). Consideration of invader origin (*i.e.*, invader identity), however, may be able to account for some of these discrepancies. Sun *et al.* (2015) recently showed that the relationship between native plant diversity and invader performance differs between species introduced from the same regional species pool and alien species introduced from a different continent. This suggests that characteristics of the invading species relative to the recipient community are critical in determining invasion success. Nonetheless, patterns produced comparing species richness of donor and receiving communities remain highly dependent on spatial scale. Jeschke and Strayer (2005) analyzed invasion success in vertebrates moving between Europe and North America and found similar rates of invasion in both directions; however, their study compiled lists of non-native species on a continental scale. Using reach-scale data that should better reflect species interactions, our study shows that numerous fishes have successfully established in both directions, but invaders tend to establish in river basins that are less diverse than their native basins. So while consideration of relative differences in competitive environments between donor and receiving communities may explain unresolved discrepancies in observational studies, prior explanations based on differences in the spatial and temporal scales of studies remain equally important to consider.

Using species richness of river basins in the native and introduced ranges of species as a proxy of competitive differences presents some difficulties. For example, some non-natives are found in only part of a river basin, and therefore co-occur only with a subset of the basin's fish species. However, this would bias results in the opposite direction of the observed trend. In our dataset, a non-native species sometimes was recorded as invading a local assemblage within a river basin more diverse than its basin of origin, when in fact the species had only established within small headwater streams having relatively depauperate local assemblages (e.g., *Oncorhyncus spp.*). In addition, our analysis may have been biased because we selected the highest diversity basin within the native distribution of a species to represent the basin of origin. However, in almost all cases, differences between the richness of donor and receiving basins were sufficiently large that trends should be robust. Although it is possible that species-rich basins contain recent invaders that evolved within adjacent basins and later dispersed into a basin with higher native richness, it is likely that the great majority of species have their evolutionary history within the basin having greatest native richness and later dispersed outward to adjacent basins.

A potential confounding factor affecting results of our study is unequal propagule pressure between high diversity and low diversity sites. For example, many tropical species pass through the aquarium trade to Europe and the United States, creating opportunities for introductions. Fewer temperate fishes are kept in aquaria, particularly in tropical countries. However, there are other opportunities for introductions into tropical regions. Many Asian and African fishes are available in pet stores in Brazil, yet successful introductions only occur in severely impacted waters (Leandro M. Sousa, *personal communication*). In contrast, armored catfish (*Pterygloplichthys* spp.) and other Neotropical fishes popular in the aquarium trade have become established in streams in tropical Asia (Ann *et al.* 2013), a region with a less diverse ichthyofauna. Farming of African tilapia (*Oreochromis*, *Sarotherodon* and *Tilapia* spp.) is widespread in the Neotropics, yet tilapia captures are rarely reported in streams and rivers of the Amazon, Orinoco, and Paraná basins and appear to be restricted to reservoirs (K.O.W., *personal observation*). This pattern is consistent with our results, as well as a previous study that suggested limited propagule pressure was not a cause for the low number of exotic vascular plants established in diverse tropical areas (Rejmanek 1996). It appears that the low number of established non-native species in diverse tropical regions reported for a variety of taxa across freshwater, marine, and terrestrial communities (Rejmanek 1996; Sax 2001) likely reflects aspects of those communities that inhibit establishment of species from less diverse regions.

The spread of cosmopolitan non-natives and concomitant loss of native species has been shown to cause biogeographic homogenization at regional (Rahel 2000) and global scales (Baiser *et al.* 2012). Our findings for freshwater fish counter the argument that homogenization is global. In the absence of impacts to habitat, it appears unlikely that temperate-zone fishes can successfully invade tropical habitats with high species richness. Moreover, most tropical fishes are incapable of invading most temperate and sub-polar regions due to physiological intolerance of low temperatures. Interestingly, a recent study analyzing homogenization patterns for several major taxonomic groups across several spatial scales found strong support for homogenization for all taxa at all scales, with the exception of fishes (Baiser *et al.* 2012). Regional patterns of homogenization in fishes reveal that tropical regions have experienced low levels of homogenization (Villeger *et al.* 2011). However, invasion of high diversity fluvial ecosystems could be facilitated by habitat degradation caused by dams, water diversions, pollution, and other impacts that alter native communities (Johnson *et al.* 2008). In fact, habitat alteration may partly explain why tests of biotic resistance based on analyses conducted at coarse spatial scales have not inferred greater invasion resistance in more species-rich assemblages.

Fridley *et al.* (2007) identified a need for theories that create precise, falsifiable predictions of species invasions at large scales. We propose that one component of such a theory would involve some form of a biotic establishment term: $S_{\text{native range}} / S_{\text{invaded range}}$, where S represents species richness and values ≥ 1 represent circumstances where establishment within an invaded community is possible. Of course, other proxies of competitive differences between regions (*e.g.*, genetic potential) may also prove useful (Fridley & Sax 2014). Clearly, no single explanation can account for all biological invasions, and hierarchical frameworks to predict invasion are appropriate (Catford *et al.* 2009; Gurevitch *et al.* 2011). Environmental heterogeneity, dispersal limitation, functional traits, and anthropogenic drivers undoubtedly influence invasion success in addition to biotic interactions. Identifying how these factors interact to form a general theory of invasion remains a key challenge.

Our findings imply that coevolution and niche relationships strongly affect invasion success in freshwater fishes. However, biotic resistance alone cannot explain invasion success or failure. Anthropogenic environmental impacts have major influence, in part because they shift the composition and structure of native assemblages and hence the strength of biotic resistance. While other factors may mask or alter the effects of competitive interactions, the global trends for freshwater fishes are consistent with the theory of biotic resistance. Recent theories have emphasized that distinct evolutionary histories of different biotic regions may create competitive advantages for species evolving in areas of higher genetic potential (Tilman 2011; Fridley & Sax 2014). Consideration of both the ecological and evolutionary aspects of community assembly is critical to understanding invasion patterns, and may explain some of the discrepancies previously noted in the relationship between native and non-native species richness across spatial scales.

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Table 1 Results from a generalized linear model of number of non-native species per site for global freshwater fish invasions. Number of non-native species was modeled as a negative binomial distribution and a truncated zero hurdle model was included to account for the high number of sites where no non-native species were found. Number of native species, level of human impact (categorized as low, moderate, or high) and habitat size (categorized as small, medium, or large) were included as explanatory variables. Details of the categorization criteria are provided in Material and Methods.

Model	Variable	Parameter estimate	Standard error	z	p-value
Count Model	Intercept	0.785	0.423	1.855	0.064
	Number Native	–0.021	0.007	–2.880	0.004 *
	Impact (moderate)	–0.575	0.616	–0.934	0.350
	Impact (high)	1.254	0.566	2.216	0.027 *
	Habitat (medium)	0.090	0.482	0.187	0.851
	Habitat (large)	–11.310	108.023	–0.105	0.917
Zero Hurdle	Intercept	0.190	0.390	0.487	0.626
	Number Native	–0.028	0.006	–4.282	< 0.001 *
	Impact (moderate)	–0.133	0.554	–0.239	0.811
	Impact (high)	0.168	0.001	0.012	0.990
	Habitat (medium)	1.138	0.519	2.191	0.028 *
	Habitat (large)	1.207	0.752	1.605	0.109

Table 2 Percentage of sites in global analysis with a greater number of non-native species than mean and maximum values obtained from 1,000 random simulations. Low and high diversity categories were selected following Gido & Brown (1999). Comparisons between low and high diversity sites were conducted using a binomial proportions test with continuity correction.

	Percentage of sites with more non-native species than predicted by random	
Native Species Richness	Mean	Maximum
Low (< 80 spp.)	22.84%	6.60%
High (≥ 80 spp.)	0.00%	0.00%
Chi-squared	6.9009	0.99570
p-value	0.0040 *	0.15900

Figure Captions

Figure 1. Relationship between the number of native and non-native species for global freshwater fish invasions. Upper panel shows a generalized linear model in which the number of non-native species was modeled as a negative binomial distribution with a zero hurdle. Number of native species, habitat size (small, medium, large), and human impact (low, moderate, high) were included as explanatory variables. Significant trend lines are presented for each combination of habitat size and human impact, with line type reflecting habitat categories and line color representing impact categories. Lower panel shows the null expectation (1,000 simulations) when species are allowed to randomly colonize any drainage outside of their native range. Trend lines represent least squared regression lines of minimum, mean, and maximum number of non-native species per site. Slopes of all three statistics were not significantly different from zero. Points represent observed values from the data.

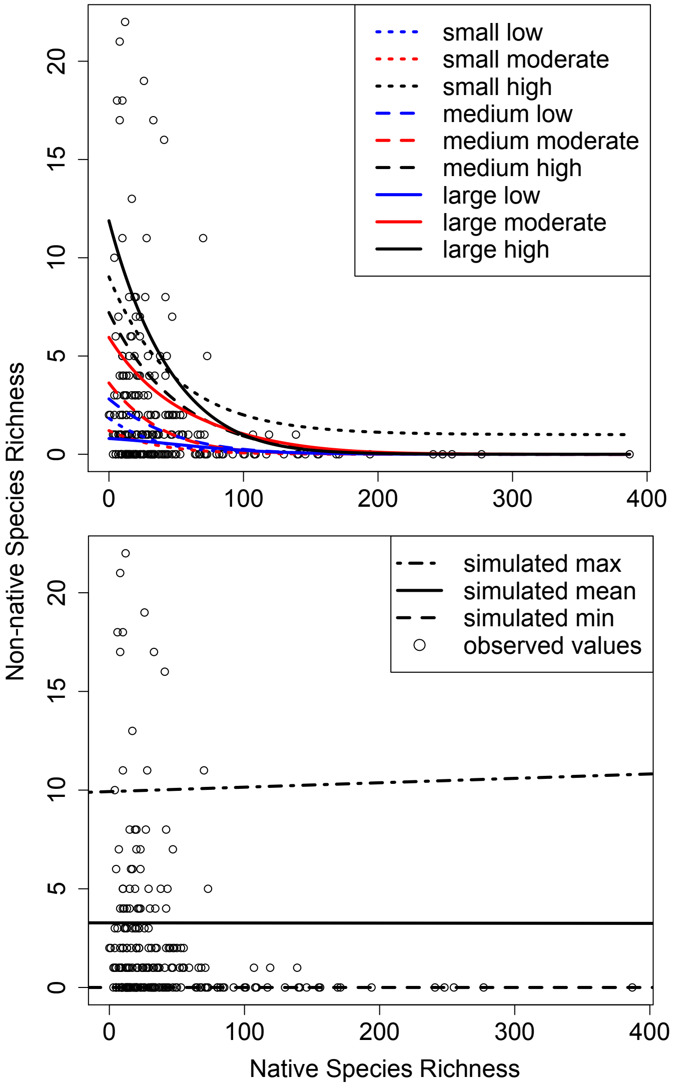
Figure 2. Number of cases in the global dataset in which an observed non-native species originated from a more or less diverse native ichthyofauna. Significantly more cases (n = 429) involved establishment of non-native species that originated from basins more species rich than the receiving basin ($\chi^2 = 349.35$, $df = 1$, $P < 0.0001$). Number of cases in which no non-native species was found is presented for reference only and was not included in the Chi-squared analysis. Shadings represent the number of cases for each of the three habitat sizes (upper panel) and impact categories (lower panel).

Figure 3. Relationship between the number of native and non-native species for freshwater fish invasions in the state of Texas, USA. Principal components regression, with number of non-

native species modeled as a quasipoisson distribution, was used to test the relationship. PC1 was significantly correlated with number of non-native species (parameter estimate = –0.932, SE = 0.281, $t = -3.322$, $P = 0.002$). Number of native species, habitat size (small, medium, large), and human impact (low, moderate, high) loaded negatively on PC1 (number native species = –1.44, human impact = –1.44, habitat size = –1.78), making all three positively correlated with number of non-native species. Lines for each combination of habitat size (line type) and human impact (line color) do not represent true regression lines and are presented only to show general trends across categories.

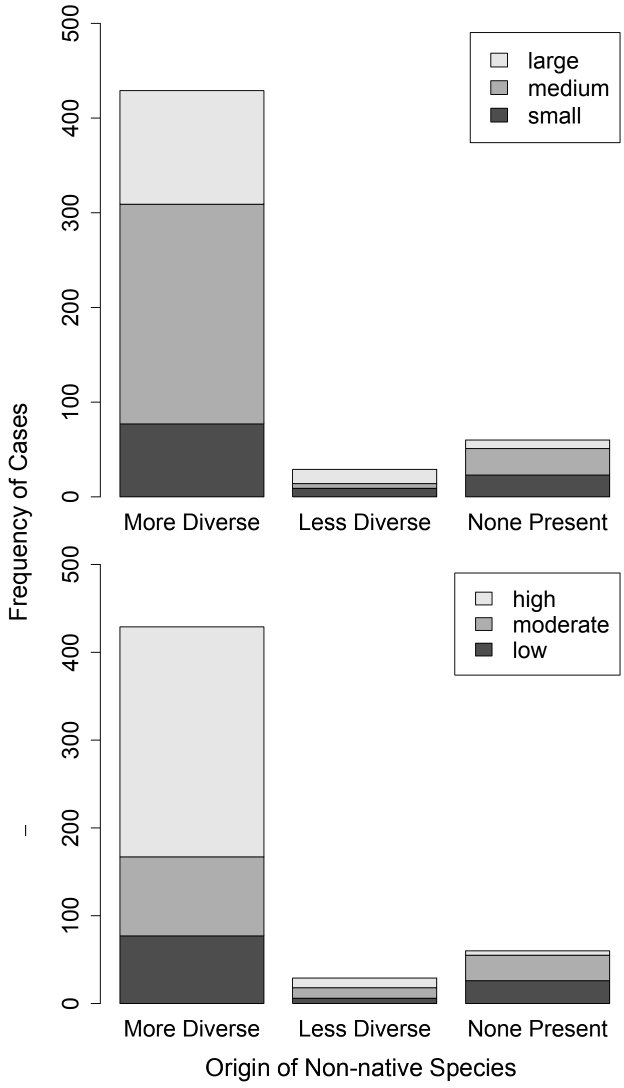
Figure 4. Number of cases in the regional dataset for the state of Texas, USA in which an observed non-native species originated from a more or less diverse native ichthyofauna. Significantly more cases ($n = 68$) involved non-native species originating from a river basin that was more diverse than the receiving basin ($\chi^2 = 54.37$, $df = 1$, $P < 0.0001$). Number of cases in which no non-native species was found is presented for reference only and was not included in the Chi-squared analysis. Shadings represent number of cases for each of the habitat sizes (upper panel) and impact categories (lower panel).

Fig 1.



small low
small moderate
small high
medium low
medium moderate
medium high
large low
large moderate
large high
simulated max
simulated mean
simulated min
observed values
Non-native Species Richness
Native Species Richness
0
5
10
15
20
0
100
200
300
400

Fig. 2


500
400
300
200
100
0
large
medium
small
More Diverse
Less Diverse
None Present
Frequency of Cases
500
400
300
200
100
0
high
moderate
low
More Diverse
Less Diverse
None Present
Origin of Non-native Species

677

Fig. 3

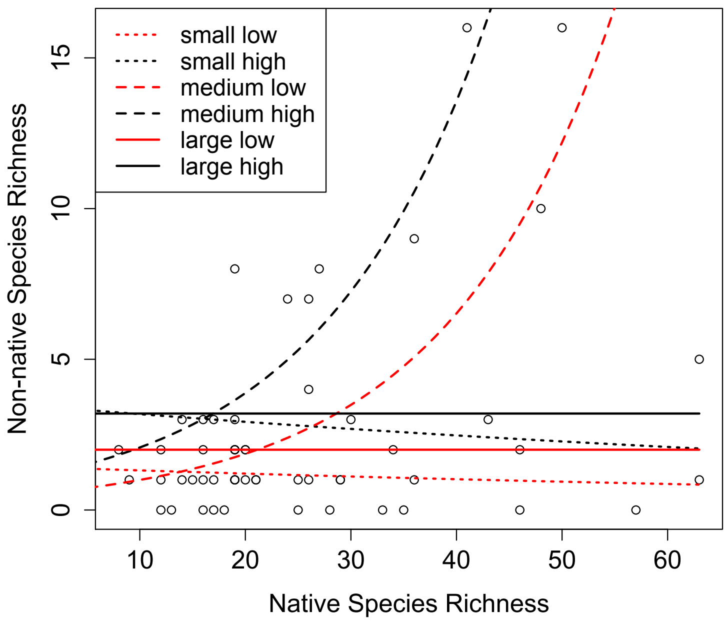
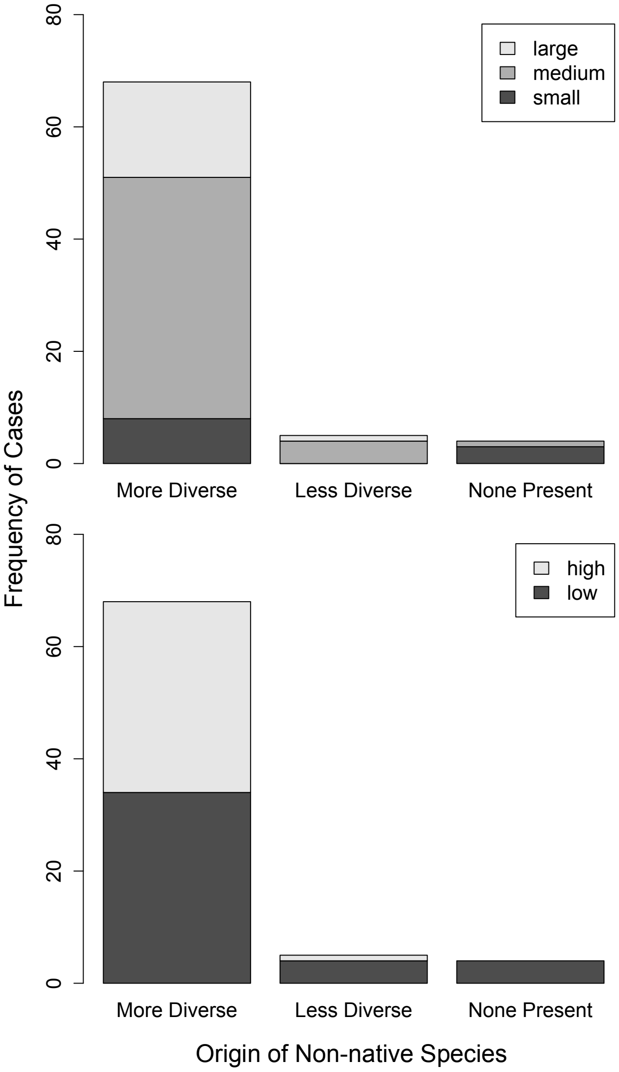

small low
small high
medium low
medium high
large low
large high
Non-native Species Richness
0
5
10
15
Native Species Richness
10
20
30
40
50
60

Fig. 4



Frequency of Cases
0
20
40
60
80
large
medium
small
More Diverse
Less Diverse
None Present
0
20
40
60
80
high
low
More Diverse
Less Diverse
None Present
Origin of Non-native Species

679