

Catchment-scale determinants of nonindigenous minnow richness in the eastern United States

Brandon K. Peoples¹ | Stephen R. Midway² | Jefferson T. DeWeber³ | Tyler Wagner⁴

¹Department of Forestry and Natural Resources, Purdue University, West Lafayette, IN, USA

²Department of Oceanography and Coastal Sciences, Louisiana State University, Baton Rouge, LA, USA

³Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR, USA

⁴U.S. Geological Survey, Pennsylvania Cooperative Fish & Wildlife Research Unit, Pennsylvania State University, University Park, PA, USA

Correspondence

Stephen R. Midway, Department of Oceanography and Coastal Sciences, Louisiana State University, Baton Rouge, LA, USA.
Email: smidway@lsu.edu

Present address

Brandon K. Peoples, Department of Forestry and Environmental Conservation, Clemson University, Clemson, SC, USA

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Abstract

Understanding the drivers of biological invasions is critical for preserving aquatic biodiversity. Stream fishes make excellent model taxa for examining mechanisms driving species introduction success because their distributions are naturally limited by catchment boundaries. In this study, we compared the relative importance of catchment-scale abiotic and biotic predictors of native and nonindigenous minnow (Cyprinidae) richness in 170 catchments throughout the eastern United States. We compared historic and contemporary cyprinid distributional data to determine catchment-wise native/nonindigenous status for 152 species. Catchment-scale model predictor variables described natural (elevation, precipitation, flow accumulation) and anthropogenic (developed land cover, number of dams) abiotic features, as well as native congener richness. Native congener richness may represent either biotic resistance via interspecific competition, or trait preadaptation according to Darwin's naturalisation hypothesis. We used generalised linear mixed models to examine evidence supporting the relative roles of abiotic and biotic predictors of cyprinid introduction success. Native congener richness was positively correlated with nonindigenous cyprinid richness and was the most important variable predicting nonindigenous cyprinid richness. Mean elevation had a weak positive effect, and effects of other abiotic factors were insignificant and less important. Our results suggest that at this spatial scale, trait preadaptation may be more important than intrageneric competition for determining richness of nonindigenous fishes.

KEYWORDS

Cyprinidae, Darwin's naturalisation hypothesis, fish, invasive species, stream

1 | INTRODUCTION

Biological invasions threaten human economies and biodiversity. Efforts to prevent and reduce impacts of invasive species cost the global economy billions of dollars annually (Simberloff, 2013). Moreover, invasive species are one of the leading contributors to global biodiversity loss and biotic homogenisation (McGeoch et al., 2010; Sala et al., 2000). The biodiversity crisis is quite urgent in freshwater ecosystems. Freshwater fishes and mussels are disproportionately imperilled, relative to other taxa (Jelks et al., 2008; Ricciardi & Rasmussen, 1999), and freshwater fish communities around the world are becoming

increasingly homogenised (Leprieur, Beauchard, Hugué, Grenouillet, & Brosse, 2008; Rahel, 2000; Villéger, Blanchet, Beauchard, Oberdorff, & Brosse, 2011). Understanding the mechanisms driving freshwater fish invasions will better equip ecologists with tools to prevent and manage nonindigenous species introductions.

Numerous factors affect invasion success, including environmental attributes, species composition of recipient communities, differential human introduction effort and traits of the invaders themselves (Barney & Whitlow, 2008; Catford, Jansson, & Nilsson, 2009). To successfully establish a population, individuals of nonindigenous species must pass through a series of biophysical filters that operate across

hierarchical spatial scales (Poff, 1997; Rahel, 2007) along sequential phases of introduction, colonisation and spread (Blackburn et al., 2011). Numerous conceptual models of biological invasions (invasion hypotheses) emphasise ecosystem properties as contributors to invasion success (i.e. ecosystem “invasiveness”) (Davis, Grime, & Thompson, 2000). Moreover, ecologists have identified a suite of both natural and anthropogenic abiotic variables contributing to establishment success and species richness of nonindigenous freshwater fishes. A few prominent examples include watershed-scale disturbance (Marchetti, Light, Moyle, & Viers, 2004; Stewart, Walters, & Rahel, 2016), native species richness (Gido, Schaefer, & Pigg, 2004), affinity for human use (Howeth et al., 2015), and a suite of functional species traits (García-Berthou, 2007).

Much research focuses on relationships between species richness of native and non-native species. The classic concept of “biotic resistance” suggests communities with higher species richness will be more likely to deter colonisation by nonindigenous species via greater likelihood of competitive exclusion (Kennedy et al., 2002). More specifically, Charles Darwin’s “naturalisation hypothesis” posits that nonindigenous species will be less likely to establish in an ecosystem in which native congeneric species are already present because phylogenetically conserved trait similarity will ensure fundamental niche overlap and thus competitive exclusion. On the other hand, congeners may have a positive association with establishment and richness of nonindigenous invaders because they share similar traits, and therefore, can likely inhabit similar environments; this alternative to Darwin’s naturalisation hypothesis is known as “trait preadaptation” (Thuiller et al., 2010). Relationships between native and nonindigenous freshwater fish species richness have been found to be both negative and positive among various systems and spatial scales (Gido et al., 2004; Guo & Olden, 2014; Stewart et al., 2016). Likewise, mixed evidence exists for the role of phylogeny as a predictor of freshwater fish invasions (Strecker & Olden, 2014), although the effects of native congener richness on nonindigenous species richness are largely understudied (Ricciardi & Mottiar, 2006).

Stream fishes provide an excellent model taxon for examining mechanisms that contribute to biological invasions. Unlike plants or most other mobile vertebrates, distributions of stream fishes are naturally restricted to hydrologic catchments. This creates a hierarchical network in which native distributions of fish species can be separated by great fluvial distances, but short overland distances (Leprieur, Olden, Lek, & Brosse, 2009; Lowe, Likens, & Power, 2006). Accordingly, most nonindigenous fishes in a given catchment of eastern North America are not native to other continents, but rather to nearby hydrologically disconnected catchments (Guo & Olden, 2014) or connected but historically unsuitable habitats which are becoming more favourable through environmental change (Scott & Helfman, 2001). Among North American stream fishes, minnows (Cyprinidae) are an ideal taxon for comparing invasion mechanisms. Cyprinidae is the most diverse freshwater fish family in the world (Howes, 1991), and cyprinids comprise a substantial portion of overall species richness in North American streams (Scott & Helfman, 2001). Accordingly, Cyprinidae is represented by some of the most

geographically ubiquitous and restricted fishes in North America. For example, Southern Redbelly Dace *Chrosomus erythrogaster* is distributed throughout the Mississippi River basin, while its congener, Clinch Dace *C. sp. cf. saylori*, is restricted to a few streams in two counties of Virginia (White & Orth, 2014). Consequently, some of the most harmful invaders (e.g. Red Shiner *Cyprinella lutrensis*) and highly imperilled fishes (e.g. Topeka Shiner *Notropis topeka*) in North America are cyprinids. Lastly, because many species are readily captured and/or cultured for bait, cyprinids are among the most transported and widely introduced fishes in North America (Drake & Mandrak, 2014).

Parsing out the relative roles of biotic and abiotic predictors of nonindigenous fish richness can contribute to development of more effective conservation strategies, as well as to our knowledge of biological invasions in general. Many studies of freshwater fish invasions focus on species invasiveness (see García-Berthou, 2007 for a review), and trait-based risk assessment is the basis for most screening and conservation efforts (Bomford, Barry, & Lawrence, 2010; Copp et al., 2009; Howeth et al., 2015). However, identifying factors contributing to ecosystem invasibility is also critical for fully understanding freshwater fish invasions. In this study, we estimate the relative importance of abiotic and biotic predictors of nonindigenous cyprinids in catchments throughout the eastern United States. In doing so, we identify catchment-scale predictors of cyprinid introductions, as well as hot spots of nonindigenous cyprinid species richness.

2 | MATERIALS AND METHODS

We sought to identify abiotic and biotic variables that influence nonindigenous cyprinid species richness in 170 catchments of the eastern USA (Figure 1). We collected fish data representing both historic and contemporary distributions from state, federal and nongovernmental monitoring programmes. We summarised predictor variables approximating geophysical processes, climate and anthropogenic stress from a variety of public sources. We then used generalised linear mixed modelling (GLMM) to identify the relative roles of abiotic and biotic predictors of nonindigenous cyprinid richness at the catchment (HUC8, the eight-digit hydrologic unit code) scale.

2.1 | Fish species richness data

Native cyprinid richness was determined using the NatureServe Digital Distribution of Native Fishes by U.S. catchment (NatureServe 2010). NatureServe is an organisation that collects and evaluates data from multiple sources, and makes it publicly available for download. NatureServe species distribution data are the product of published primary and secondary literature, state agency sampling and expert professional opinion. All NatureServe data are reviewed for accuracy by numerous professional ichthyologists and ecologists with in-depth expertise on regional stream fish biogeography. The native status of a few species in certain portions of their ranges of a few cyprinids may be debated. However, the stringent review process greatly decreases chances of major errors in assignment of native status. This data set

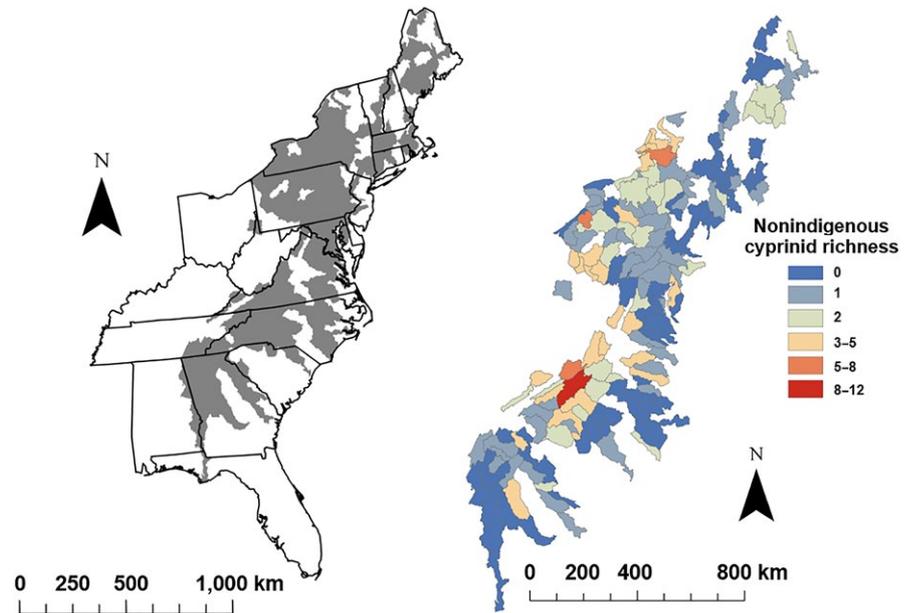


FIGURE 1 (a) The eastern United States, with study catchments shown in grey; (b) the number of nonindigenous cyprinids in 170 HUC8-level catchments throughout the eastern United States.

thus represents the best possible information on native stream fish distribution at the HUC8 scale and has been used in numerous other biogeographic studies to represent native freshwater fish diversity at the catchment scale (Guo & Olden, 2014; Muneeppeerakul et al., 2008; Stohlgren et al., 2006). NatureServe data were available at the HUC8 level. Prior to analysis, we subset the list of species to include only cyprinids that inhabit Wadeable streams (Barbour, Gerristen, Snyder, & Stribling, 1999;).

To calculate nonindigenous cyprinid richness, we compared native cyprinid distributions to a collection of ongoing (contemporary) stream fish community sampling programmes from state agencies in the eastern USA (see Appendix S1 in Supporting Information). We included state sampling programmes based on strict criteria that: (i) they sampled sufficiently long stream reaches to characterise presence/absence (i.e. typically 20–30 times mean stream width or more; Moulton, Kennen, Goldstein, & Hambrook, 2002); (ii) sampling and subsequent identification were carried out by professional biologists knowledgeable of the species and systems being sampled; and (iii) they were stream community sampling programmes intended to characterise species richness and diversity, and not targeting specific taxa, such as game species. Detection probabilities of some cyprinids that are not numerically abundant can be low in electrofishing surveys (Albanese, Peterson, Freeman, & Weiler, 2007; Peoples & Frimpong, 2011; Pregler, Vokoun, Jensen, & Hagstrom, 2015). Accordingly, we only included HUC8s in which ≥ 2 separate sites were sampled, or if only one site was sampled, ≥ 3 sampling events needed to take place over ≥ 3 years; this was to help ensure that recently established but numerically rare nonindigenous cyprinids were detected. Further, the number of introduced species was not correlated with the number of sampling occasions in a HUC8 ($r < 0.10$), suggesting that potential under-sampling of catchments is not contributing to under-detection of nonindigenous cyprinids. We coarsened the reach-scale contemporary data to the HUC8 scale to make it comparable to the NatureServe data. We calculated nonindigenous cyprinid richness

in each catchment as the total number of cyprinid species found in the contemporary data set that were not present in the native species list. Drawbacks to using such data sets have been noted by previous authors: they contain uneven information on survey effort, and surveys are rarely spatially homogenous (Hortal, Lobo, & Jiménez-Valverde, 2007; Sánchez-Fernández, Lobo, Abellán, Ribera, & Millán, 2008). However, these issues were minimised by (i) the diversity of sources from which they were derived, (ii) the criteria that they came from professional entities staffed by well-trained ecologists and (iii) our criteria for sampling intensity within a HUC (Guo & Olden, 2014). All species included in both data sets are present in Appendix S2.

2.2 | Predictor variables

We identified potential catchment-scale determinants of nonindigenous cyprinid richness based on findings from previous studies (Gido et al., 2004; Marchetti, Light et al., 2004; McKinney, 2001; Murphy, Grenouillet, & García-Berthou, 2015). We first obtained a shapefile of HUC8s for which NatureServe data were available from the United States Geological Survey Watershed Boundary Dataset (Simley & Carswell, 2009), and then calculated six predictor variables for each HUC8. We first used the national elevation data set to calculate *average elevation* in each catchment. We then used the 2011 version of the National Land Cover Database (Jin et al., 2013) to calculate cumulative proportions of anthropogenically developed land cover types (e.g. urban, suburban and planted/cultivated) in each HUC8 (hereafter, “*development*”). Anthropogenic land cover development is often positively associated with ecosystem invasibility, whether by habitat degradation or by increasing the probability of species introductions (Didham, Tylianakis, Hutchison, Ewers, & Gemmill, 2005; McKinney, 2002). Likewise, we used the National Hydrography Dataset Plus version 2 (United States Environmental Protection Agency 2012) to calculate the total number of dams and weirs in each HUC8. This metric (hereafter, “*dams*”) approximates anthropogenic impact to natural

hydrologic regimes, which can increase invasibility of freshwater ecosystems (Marchetti, Light et al., 2004). A drawback to this approach is that it cannot account for characteristics of individual dams. For example, fish communities can be affected differently depending on the size and operational structure of a dam (McManamay, Peoples, Orth, Dolloff, & Matthews, 2015). However, at the HUC8 scale, the number of dams serves as a useful measure of hydrologic impoundment or alteration in a catchment.

For each HUC8, we calculated three predictor variables from the near-global spatial data sets of freshwater environmental variables (1-km resolution) derived by Domisch, Amatulli, and Jetz (2015). We first calculated *maximum temperature*, the maximum value of monthly weighted average temperature for each HUC8. We then calculated *maximum precipitation*, the maximum value of the monthly sum of precipitation in a HUC8. Domisch et al. (2015) derived these two variables from the WorldClim climatology database (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). We also calculated *flow accumulation*, the number of upstream grid cells at the most downstream point in a HUC8; this metric approximates catchment size and total flow accumulation at the HUC8 scale (Domisch et al., 2015).

Lastly, we included one biotic predictor variable, *congeners*—a direct measure of the number of native congener species a nonindigenous cyprinid could potentially encounter in a given catchment (calculated from the NatureServe data set). For each species identified as nonindigenous in a given catchment, we calculated the number of native species in the same genus that occurs in the catchment. We made no hypothesis on the direction in which *congeners* might affect nonindigenous cyprinids because studies have shown both positive and negative effects of this variable (Thuiller et al., 2010).

2.3 | Statistical analyses

We used a Poisson generalised linear mixed model (GLMM) with a log link and took the general form of

$$S_i \sim \text{Poisson}(\lambda_i) \\ \log(\lambda_i) = \alpha_{j|i} + \mathbf{X}_i \mathbf{B}$$

where S_i is the nonindigenous species richness count in HUC8 i distributed as a Poisson random variable with expected value λ_i , where α_j are group-specific intercepts, $\alpha_j \sim N(\mu_\alpha, \tau^2)$, μ_α is the fixed intercept, τ^2 is the among-HUC4 variance in mean species richness, \mathbf{X}_i is a matrix of regression predictor variables, and \mathbf{B} is a matrix of slope coefficients. To account for some of the spatial clumping in cyprinid richness caused by potential movement among hydrologically connected HUC8s, we included HUC4 ($n = 36$) as a random intercept (α_j) in the models (Chrobotek et al., 2013; Mahoney et al., 2015). HUC4s are cumulative drainage basins in which HUC8s are nested. Prior to analysis, we scaled and centred all variables to mean = 0 and variance = 1, and screened them for multicollinearity ($r > .70$). We excluded *maximum precipitation* from GLMM analysis because (i) it showed little gradient among catchments and (ii) it was highly correlated with *flow accumulation* ($r = .99$).

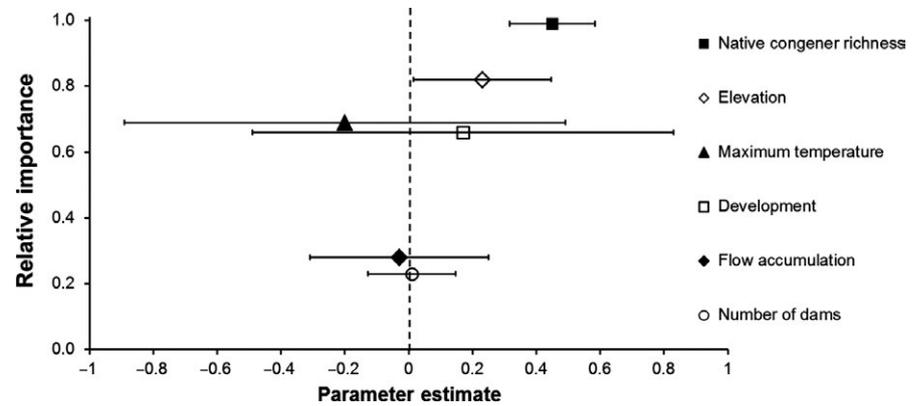
We used the `glmer` function in the `lme4` package of R version 3.2.3 (R Development Core Team, 2015) to fit a single GLMM including all predictor variables. We interpreted statistical significance of parameter estimates based on whether or not their 95% confidence interval bounded zero; this is analogous to a null hypothesis test at $\alpha = .05$. We also calculated pseudo- R^2 for the GLMM as a metric of the amount of variation in nonindigenous cyprinid richness explained by the model. An analog to R^2 in fixed-effects regression, pseudo- R^2 for mixed-effects models can be decomposed into marginal (variation explained by fixed effects only) and conditional (variation explained by both fixed and random effects) components.

We then calculated relative importance of each predictor variable using the sum of Akaike weights (SW) approach described by Burnham and Anderson (2002). This approach involves running separate GLMMs for all possible subsets of variables with estimated fixed effects from the global model. Akaike weights (w_i) are computed for each model. To calculate relative variable importance, values of w_i are summed across models containing that variable. The most important variables have higher values because they are in more models with higher Akaike weights. Relative variable importance ranges from zero (low importance) to one (high importance) for each variable, but is not additive to 1.0 among variables because Akaike weights sum to 1.0 among all models. We interpreted variable effect sizes from the global model only; model averaging was not used. We did not use the SW approach to draw inference from any one particular candidate model as a whole, but rather as a complimentary tool to interpreting effect sizes computed from the global model.

3 | RESULTS

Most (92 of 170, 54%) catchments had zero nonindigenous cyprinids, and 53% of invaded catchments (49 of 92) had only one nonindigenous cyprinid species. However, nonindigenous cyprinid richness was high in several catchments, reaching up to 39% (12 nonindigenous of 20 total species) of observed cyprinid richness in the upper New River (Ohio River basin) of North Carolina and Virginia (Figure 1). The GLMM predicting nonindigenous cyprinid richness fit the data reasonably well, with a marginal R^2 (fixed effects only) of .31 and a conditional R^2 (fixed + random effects) of .47; 13% of the variation in nonindigenous cyprinid richness was explained by spatial clumping in HUC4s. Two variables significantly (i.e. with 95% confidence intervals that did not bound zero) predicted nonindigenous cyprinid richness: *congeners* and *average elevation*; both of these variables had a positive effect. *Congeners* had the highest relative variable importance (1.0), and *average elevation* had relative importance of .82. *Development*, *flow accumulation* and *dams* were much less important predictors of nonindigenous cyprinid richness (relative importance < .40). With zero-bounding 95% confidence intervals, these variables were not significantly associated with nonindigenous cyprinid richness (Figure 2). Results of all models contributing to calculation of relative variable importance are presented in Appendix S3.

FIGURE 2 Parameter estimates ($\pm 95\%$ confidence intervals) of abiotic and biotic predictors of nonindigenous cyprinid species richness in 170 HUC8-level catchments throughout the eastern United States. Estimates with confidence intervals that do not bound zero are considered statistically significant at the 95% confidence level.



4 | DISCUSSION

We found that both abiotic and biotic variables were significant predictors of nonindigenous cyprinid richness in catchments of the eastern USA. The most influential variable was native congener richness. The strong positive effect of this variable suggests that at the catchment scale, fish communities are seldom-saturated and biotic resistance does not strongly deter establishment of nonindigenous species (Gido & Brown, 1999; Ruesink, 2005). This finding also lends support for trait preadaptation, rather than Darwin's naturalisation hypothesis. Studies of many systems have supported both Darwin's hypotheses of naturalisation (Jiang, Tan, & Pu, 2010; Van Wilgen & Richardson, 2011) and trait preadaptation (Mahoney et al., 2015; Park & Potter, 2013). Studies from freshwater fish communities have produced inconsistent results for the role of biotic resistance and Darwin's hypotheses in the invasion process. Our results corroborate some studies that have directly examined effects of native congeners and/or phylogenetic distance (Strecker & Olden, 2014), as well as other studies that have found positive relationships with overall native and nonindigenous fish species richness (Gido et al., 2004; Guo & Olden, 2014; Marchetti, Light et al., 2004; Stewart et al., 2016). However, other studies have found negative relationships between native and nonindigenous fish species richness (Alcaraz, Vila-Gispert, & García-Berthou, 2005; Olden, Poff, & Bestgen, 2006; Ricciardi & Atkinson, 2004), and some evidence suggests that native congener richness is much less important than propagule pressure and abiotic factors (Ricciardi & Mottiar, 2006).

One reason for this disparity in findings on the relationship between native and nonindigenous fish species richness may stem from differences in spatial scales at which studies were conducted (Thuiller et al., 2010). Thus far, broader-scale (e.g. continental) studies tend to support naturalisation (suggesting a role for negative biotic interactions), while intermediate-scale studies (e.g. among HUC4–8) support trait preadaptation. For instance, at the global scale, Ricciardi and Atkinson (2004) found that the most impactful invaders were from genera that were unique to a given system. Within major basins, Alcaraz et al. (2005) and Olden et al. (2006) found successful invaders were phylogenetically distinct from the native species pool. In addition to the present study, however, intermediate-scale (i.e. among

catchments) studies of freshwater fish invasions generally support trait preadaptation of nonindigenous species. This is illustrated best by Strecker and Olden (2014), who found that although nonindigenous fishes were dispersed around a phylogenetically clustered recipient community, environmental filtering facilitated success of phylogenetically similar invaders with preadapted traits to survive in novel habitats. Further, Guo and Olden (2014) identified positive native–nonindigenous relationships at the catchment scale, but hump-shaped relationships within stream reaches. Multiscale approaches will be necessary to elucidate mechanisms driving scale-dependent differences in the native–nonindigenous fish species relationship (Diez, Sullivan, Hulme, Edwards, & Duncan, 2008).

Average elevation was the only abiotic predictor variable affecting nonindigenous cyprinid richness. Higher-elevation catchments had greater nonindigenous cyprinid richness; this relationship is most clearly a reflection of cyprinid life history. Firstly, most cyprinids are relatively stenohaline; few species tolerate high salinities associated with low-elevation estuarine or marine systems (Howes, 1991). Secondly, most cyprinids of eastern North America exhibit life history strategies that tend towards the “opportunistic” portion of the life history spectrum (Winemiller & Rose, 1992). As opportunistic strategists, cyprinids optimise population generation time at the expense of reduced survivorship and fecundity. Accordingly, many of these species are uniquely adapted to persist and diversify in highly variable environments (Winemiller, 2005) such as headwater/high-elevation streams (Schlosser, 1987).

Interestingly, we found no significant relationship between nonindigenous cyprinid richness and either of our metrics of anthropogenic impact—percentages of developed land cover and the number of dams in a catchment. Anthropogenic perturbation is generally found to facilitate invasions by creating new habitats which are favourable to exotic species, or by extirpating native species and thus creating niche space (although our observed positive native–nonindigenous cyprinid richness relationship belies the latter argument). Reach-scale studies have found several measures of anthropogenic disturbance that make strong contributions to predicting nonindigenous species richness (Marchetti, Light et al., 2004; Stewart et al., 2016). This may be because the nonindigenous species in the study areas (California and Wyoming respectively) were phylogenetically and morphologically distinct from natives, and thus, were better adapted to changing

abiotic conditions associated with anthropogenic development. Few of the nonindigenous cyprinids in this study are the broadly tolerant trophic and habitat generalists often identified as strong invaders (see García-Berthou, 2007; for a review); they would thus likely fail to establish in highly degraded catchments due to poor environmental match (Bomford et al., 2010).

Given the plausibility of the trait preadaptation hypothesis in this system, taxa and spatial scale, it is intuitive to expect a positive relationship between average elevation and native cyprinid richness. The bivariate correlation between these two variables was sufficiently low ($r = .42$) for both variables to be included as predictors in the same model without running the risk of collinearity. However, a *post hoc* GLMM using the same “natural” independent variables as in the analysis of nonindigenous cyprinid richness (i.e. excluding *development* and *number of dams*) revealed that the only significant predictor of native cyprinid richness was *average elevation* ($\beta = 0.09 \pm 0.04$). This evidence lends support to the trait preadaptation hypothesis at this spatial scale. Moreover, coupled with the insignificant effects of anthropogenic variables on nonindigenous cyprinid richness, it is possible that the factors controlling observed native fish diversity at this scale are likely the same as those affecting nonindigenous fish diversity (Stewart et al., 2016).

Differences in geographic resolution may influence how our results relate to other studies (Olden & Poff, 2004). Analyses of invasion success often seek to draw inference at broad spatial scales, typically focusing on intercontinental comparisons (e.g. Gallagher, Randall, & Leishman, 2015; González-Suárez, Bacher, & Jeschke, 2015). At these scales, factors are often measured at relatively coarse resolutions. Accordingly, native and nonindigenous ranges of introduced species usually are separated by great distances. This increases potential for (i) phylogenetic dissimilarity between nonindigenous species and recipient community members and (ii) different climate match between the nonindigenous and native range. In contrast, most nonindigenous species in our study are not native to other continents (Fausch, Taniguchi, Nakano, Grossman, & Townsend, 2001; Jeschke & Strayer, 2006) or regions of North America (Marchetti, Moyle, & Levine, 2004; Olden et al., 2006). Instead, they are native to nearby (via overland measurements) catchments, despite being separated by great fluvial distances and unsuitable marine habitats. This may help to explain the strong signal of native congener richness indicating trait preadaptation: Euclidean distance from the native distribution, and thus phylogenetic dissimilarity, is likely to be minimal for the nonindigenous cyprinids in the catchments we studied.

Patterns of steam fish invasions are much less thoroughly studied than in other taxa. Further, much of our knowledge on freshwater fish invasions is drawn from only a subset of ecosystem types such as Mediterranean streams (Cobo, Vieira-Lanero, Rego, & Servia, 2010; Marchetti, Moyle et al., 2004; Marr et al., 2010, 2013; Ribeiro, Elvira, Collares-Pereira, & Moyle, 2008) and the Laurentian Great Lakes (Howeth et al., 2015; Kolar & Lodge, 2002; Rixon, Duggan, Bergeron, Ricciardi, & Macisaac, 2005; Snyder, Burlakova, Karatayev, & MacNeill, 2014). The high diversity and nested distributional patterns of stream fishes in the eastern USA present a unique opportunity for testing

conceptual hypotheses of invasion ecology, and this study represents a step towards understanding stream fish invasions in these systems. Unfortunately, stream fish communities in most eastern U.S. streams are not routinely monitored unless they contain endangered species or sportfishes. Consequently, virtually no quantitative information exists on the number of nonindigenous fish introductions these streams receive. In eastern North America, nonindigenous cyprinids (as well as other taxa) are most often transported via unreported bait bucket introductions (Drake & Mandrak, 2014). These events are usually only identified years after the actual introduction and are thus difficult to quantify (Ludwig, Herbert, & Leitch, 1996). The number of introduction attempts and the number of individuals introduced per attempt (collectively, “propagule pressure” sensu Lockwood, Cassey, & Blackburn, [2005]) can be critical drivers of freshwater fish invasions (Copp, Templeton, & Gozlan, 2007; Duggan, Rixon, & MacIsaac, 2006; Ruesink, 2005), and it is possible that catchment proximity to potential nonindigenous colonist pool plays a role in nonindigenous cyprinid richness in catchments of the eastern USA. Lastly, high morphological similarity among many cyprinids complicates species-level identification; identifying new cyprinid introductions in these systems often requires highly technical taxonomic skills and detailed catchment-specific knowledge of species distributions. These factors highlight the need for improved awareness, monitoring and communication of nonindigenous fish introductions in temperate streams of the eastern USA.

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SUPPORTING INFORMATION

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