Fishing pressure and species traits affect stream fish invasions both directly and indirectly

Brandon K. Peoples¹ | Stephen R. Midway²

¹Department of Forestry and Environmental Conservation, Clemson University, Clemson, SC LISA

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

Correspondence

Brandon K. Peoples, Department of Forestry and Environmental Conservation, Clemson University, Clemson, SC, USA. Email: Peoples@Clemson.edu

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Abstract

Aim: We sought to identify direct and indirect effects of factors contributing to establishment and spread of 272 stream fish species.

Location: Two hundred and ninety-seven watersheds in the eastern United States.

Methods: We modelled two variables: (1) whether a species had become established outside its native range (establishment) and (2) the number of watersheds in which species established outside their native range (spread). We estimated these variables by comparing historical distributions to a rich data set of contemporary sampling. We calculated metrics of human use (indexing propagule pressure), and gathered species trait data from an open-access database. We then used piecewise path analysis to estimate direct and indirect effects of human use, native range size and species traits on the two metrics of species introductions.

Results: We identified a hierarchical causal structure in which native range size and fishing pressure were important direct determinants of introductions. Species traits had some direct effects, but played a more indirect role. Native range size was significantly affected by thermal tolerance and diet breadth. Likewise, fishing pressure was significantly affected by life history strategy: larger-bodied, longer-living and more fecund species were positively associated with fishing pressure.

Main conclusions: Functional traits can confer an advantage to some species during the establishment phase, but human use is important for subsequent dispersal throughout the non-native range. However, human use is non-random, and is largely a function of species traits. Considering both direct and indirect effects of traits across stages of the invasion process can help to elucidate the full role of traits in species invasions.

KEYWORDS

fish, fishing, indirect effects, invasive species, path analysis, traits

1 | INTRODUCTION

Functional species traits (sensu McGill, Enquist, Weiher, & Westoby, 2006) can be a strong determinants of biological invasions. In conjunction with propagule pressure (i.e., introduction effort; Lockwood et al. 2005) and abiotic factors, traits affect outcomes of species introductions at sequential stages of the invasion process (Hayes & Barry, 2008). Ecology is progressing towards a synthetic understanding of how traits determine invasions (Blackburn et al., 2011; Catford, Jansson, & Nilsson, 2009), but a gap still exists between conceptual models and the empirical studies that support them. Although studies examining only traits usually find significant differences between traits of invasive and native species (Davidson, Jennions, & Nicotra, 2011; van Kleunen, Weber, & Fischer, 2010), analyses including traits, propagule pressure and abiotic factors, which do not consider interactions between abiotic factors and

species traits (sensu Brown et al., 2014; Della Venezia, Samson, & Leung, 2018) almost invariably find a non-significant or diminished role of traits (Dawson, Burslem, & Hulme, 2011; Mahoney et al., 2015; McGregor, Watt, Hulme, & Duncan, 2012). Recognizing the indirect role of species traits can help to bridge this gap (Maurel, Hanspach, Kühn, Pyšek, & van Kleunen, 2016; Peoples & Goforth, 2017b; Pyšek et al., 2015). Traits may confer direct advantages to successful non-native species, but can also function indirectly by creating non-random patterns of propagule pressure (Capellini, Baker, Allen, Street, & Venditti, 2015; Zeng, Chong, Grey, Lodge, & Yeo, 2015) and native range size (Böhning-Gaese, Caprano, van Ewijk, & Veith, 2006; Pyšek et al., 2009). Considering invasions as a hierarchical, nonlinear process with a complex causal structure will help us to understand the full role traits play in determining species invasions.

North American freshwater fishes represent one of the richest yet imperiled faunas on earth (Jelks et al., 2008). Numerous traitonly approaches (Howeth et al., 2015; Keller, Kocev, & Džeroski, 2011) and meta-analyses (Liu, Comte, & Olden, 2017; McKnight, García-Berthou, Srean, & Rius, 2017) show distinct differences in trait values between native and non-native fishes. Yet like other groups, significant effects of propagule pressure, relative to traits, suggest a more complex causal structure may influence freshwater fish invasions (Jeschke & Strayer, 2006; Marchetti, Moyle, & Levine, 2004; Ruesink, 2005). Understanding indirect effects of traits and human use on freshwater fish introductions may lead to a better understanding of the underlying causal structure of the invasion process.

Another factor that must be considered is the spatial scale at which native status is considered (Colautti & MacIsaac, 2004; Richardson et al., 2000). Relative to its non-native range, an introduced species may be native to another continent, another region of the same continent, or even smaller spatial scales. Stream fishes are particularly well-suited to explore scale-dependency in native status because their distributions are separated by distinct boundaries created by watershed borders; non-native stream fishes may hail from disparate continents or simply an adjacent watershed. While the scale-dependent definition of native status is sometimes recognized (Peoples, Midway, DeWeber, & Wagner, 2017; Stewart, Walters, & Rahel, 2016), most macroscale analyses of non-native freshwater fishes consider only a continental-scale definition of native status (Davis & Darling, 2017; Liu et al., 2017) or within continents at large scales (e.g., Pacific vs. Mississippi/Atlantic drainages, sensu Marchetti et al., 2004; Olden, Poff, & Bestgen, 2006). Recognizing transfer among nearby watersheds as a source of species introductions may provide new insight into the establishment and spread of non-native species that may cause ecological impact.

In this study, we sought to identify direct and indirect effects of factors contributing to establishment and spread (or lack thereof) of 272 stream fish species in 297 watersheds of the eastern United States. We modelled two response variables: (1) whether a species had become established outside its native range (hereafter, *establishment*) and, if so, (2) the number of watersheds outside its native

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range in which the species established (hereafter, spread). We estimated these variables by comparing historical distributions to a rich data set of contemporary sampling. This allowed us to identify native and non-native status at the watershed scale. Our definitions are accompanied by some caveats: firstly, it is possible that detection of a non-native species does not equate directly to establishment. Detected non-native species may exist in population sinks and are on the verge of introduction failure. Likewise, our second response variable is not a measure of spread rate (number of established watersheds per time unit), but rather of all watersheds established to date (Jeschke & Straver, 2006: Pvšek et al., 2015). We calculated metrics of human use (indexing propagule pressure) and gathered species trait data from an open-access database. We then used piecewise path analysis to estimate direct and indirect effects of human use, native range size and species traits on the two metrics of species introductions.

2 | METHODS

2.1 | Fish occurrence data

Watersheds are organized using hydrologic unit codes (HUCs; Seaber, Kapinos, & Knapp, 1987); each watershed has a unique code that increases in length as watershed size decreases. We conducted this study at the HUC8 scale, which represents watersheds of 3,500-4,000 km². HUC8 is the most relevant scale for this analysis because it is the smallest scale at which ecologists can confidently assign native or non-native status. We determined native distributions (i.e., verified the historical presence in a watershed) using the NatureServe Digital Distribution of Native Fishes by US watershed (NatureServe, 2010). NatureServe collects and evaluates data from multiple sources, and maintains an open-access repository for download. NatureServe species distribution data are compiled from published primary and secondary literature, state agency sampling and expert professional consultation. NatureServe data are reviewed for accuracy by professional taxonomists and ecologists with in-depth expertise on regional fish biogeography. Although it is possible that native status in small portions of the ranges of a few species may be debated, the stringent review process greatly decreases the chances of major errors in assignment of native status. This data set 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 (Davis & Darling, 2017; Guo & Olden, 2014; Muneepeerakul et al., 2008).

To characterize non-native species distributions, we compared fish distributions to a collection of ongoing (contemporary) stream fish community sampling programmes from state agencies in the eastern United States. We included state sampling programmes based on strict criteria that: (1) they sampled sufficiently long stream reaches to characterize presence/absence (i.e., typically 20–30 times mean stream width or more; Moulton, Kennen, Goldstein, & Hambrook, 2002); 2) sampling and subsequent identification was carried out by professional biologists knowledgeable of the species



FIGURE 1 Watersheds of the eastern United States and sampling sites (dots) encompassing the contemporary fish occurrence data set

and systems being sampled; and 3) they were stream community sampling programmes intended to characterize species richness and diversity, and not targeting specific taxa, such as game species (see Appendix S1 in Supporting Information). This resulted in a total of 139,184 individual occurrence records. While most species captured in contemporary sampling were native to the conterminous United States, a few were not. Backpack electrofishing surveys can result in relatively low detection probabilities of some numerically low species (Peoples & Frimpong, 2011; Pregler, Vokoun, Jensen, & Hagstrom, 2015). Accordingly, we only included watersheds in which \geq 2 separate sites were sampled; this helped to ensure that recently established but numerically rare non-native species were detected (Figure 1). Furthermore, the number of introduced species was not correlated with the number of sampling occasions in a HUC8 (r < .10), suggesting that potential undersampling of catchments is not contributing to underdetection of non-native species.

Of course, combining these data sets must be accompanied by some caveats. Our conservative subsetting of the contemporary data accommodates for potential non-detection of species introduction, but not for potential non-detection in historical sampling. For example, if a species was somehow not detected in a watershed by historical sampling, we would incorrectly conclude it to be non-native in that watershed. This may be an issue for some species with naturally low abundance or highly restricted distributions within HUC8s. Moreover, certain traits, such as small body size or preference for difficult-to-sample habitats, may contribute to non-detection. However, we consider this situation because (1) NatureServe has made much effort to ensure the quality of its distribution data, (2) we coarsened the reach-scale contemporary data to the HUC8 scale to make it comparable to the NatureServe data and (3) HUC8s are quite large and have been sampled extensively throughout the historical data set. Measurement error of response variables is expected, but is also overcome by the number of species we modelled.

We calculated our first response variable, establishment (binary), as whether a species were detected in a watershed outside its native range. We calculated our second response variable, spread (a Poisson-distributed count variable), as the number of watersheds in which an established species was detected outside its native range. The number of units in which a species has established is a useful and common representation of non-native species spread rate (Marchetti et al., 2004; Pyšek et al., 2015). 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 minimized by (1) the diversity of sources from which they were derived, (2) the criteria that they came from professional entities staffed by well-trained ecologists, (3) our criteria for sampling intensity within a HUC8 and (4) our use of occurrence and not count data (Guo & Olden, 2014). All species included in both data sets are present in Appendix S2.

2.2 | Predictor variables

Estimates of propagule pressure are unavailable for most freshwater fishes because most introductions go undocumented, and are usually performed unintentionally by anglers discarding live bait. However, "human use indices" can serve as a meaningful surrogate of direct propagule pressure measures (Castro-Díez, Godoy, Saldaña, & Richardson, 2011; Thuiller, Richardson, Rouget, Proches, & Wilson, 2006). Human use indices are generally calculated as the number of entries in discipline-specific literature databases. For example, Proches, Wilson, Richardson, and Reimánek (2012) and McGregor et al. (2012) used the number of abstracts in the Centre for Agriculture and Biosciences International Forestry Compendium to index human use of introduced pine (Pinus) spp.; this variable explained 70.7% of variation in species naturalized range size (Proches et al., 2012). We calculated two indices of human use: fishing and aquaculture, by performing searches for each species in the Aquatic Science and Fisheries Abstracts (ASFA) database, hosted by the Food and Agriculture Organization of the United Nations. Searches included a Boolean combination of the species' scientific name and either the term, "fishing" or the term "aquaculture," respectively, and were not year-restricted.

We retrieved species traits from the FishTraits database (Frimpong & Angermeier, 2009), and included traits that have been previously shown to affect establishment and/or spread of nonnative fishes (Liu et al., 2017; McKnight et al., 2017; Olden et al., 2006). These include estimates of *native range size* (km²), as well as trophic and life history traits. Frimpong and Angermeier (2009) provide binary values for utilization of nine trophic items; we summed these to calculate *diet breadth* (sensu Peoples & Goforth, 2017a). We calculated *temperature range* by subtracting the minimum from the maximum temperature for each species. We included four traits representing key components of the trilateral life history **Diversity** and **Distributions**

continuum of freshwater fishes (Winemiller, 2005; Winemiller & Rose, 1992): maximum total length, age at maturation, maximum lifespan and fecundity. Because these variables were highly correlated with one another (.67 > r > .90 for all pairwise combinations), we reduced their dimensionality using principal coordinates analysis of Bray-Curtis distances and used the resultant eigenvector to represent life history in models. We used Pearson's correlations between the eigenvector and raw trait values to interpret the eigenvector. Finally, we calculated two morphometric ratios that have been found to influence stream fish invasion success (Olden et al., 2006). These include shape factor (the ratio of body depth to length) and swim factor (the ratio of caudal peduncle depth to caudal fin height). These were calculated by hand-measuring standardized photographs from ichthyology textbooks (Jenkins & Burkhead, 1994; Table 1).

2.3 | Analyses

To identify causal structure in relationships among species traits, human use, native range size and establishment/spread success, we first developed a hierarchical conceptual hypothesis (Figure 2). We hypothesized that variables indexing invasion success are affected directly by human use, native range size and species traits. In addition to direct effects of traits, we hypothesized that traits affect establishment success indirectly by affecting native range size and introduction effort. We further hypothesized that native range size also affects establishment success indirectly by affecting introduction effort (Maurel et al., 2016; Peoples & Goforth, 2017a,b; Pyšek et al., 2015).

TABL	E 1	Ľ	Variables usec	l to mode	l establishmen	t and sprea	d of 27	'2 stream	fish specie	es in 29	7 watershe	eds in the o	eastern	United	States
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Variable	Definition	Source		
Establishment (response)	Whether or not a species was detected in a watershed outside its native range	NatureServe 2010, contem- porary sampling data set		
Spread (response)	Number of watersheds in which a species established outside its native range			
Fishing	Number of abstracts from the ASFA database returned from searching each species' scientific name and "fishing"	Aquatic Science and Fisheries Abstracts (ASFA) database		
Aquaculture	Number of abstracts from the ASFA database returned from searching each species' scientific name and "aquaculture"			
Native range size	Area of native range (km²)	FishTraits Database (Frimpong		
Maximum total length	Maximum reported total length (cm)	& Angermeier, 2009)		
Maximum fecundity	Maximum reported fecundity			
Age at maturity	Mean, median or modal age ate maturity for females (years)			
Maximum lifespan	Longevity based on life in the wild (years)			
Temperature range	Maximum minus minimum temperature; calculated as 30-year average minimum January temperature at range centroid (°C)			
Serial spawning	Presence/absence of producing two or more egg clutches per year			
Diet breadth	Sum of presence/absence of feeding on nine trophic categories (see Frimpong & Angermeier, 2009)			
Swim factor	Ratio of caudal peduncle depth and caudal fin height	Hand-measured		
Shape factor	Ratio of body depth to total length	Hand-measured		



FIGURE 2 Conceptual path diagram depicting direct and indirect effects of traits and native range size (green), and human use indices (blue) on metrics indexing stream fish invasions (e.g., establishment or spread, orange). Arrows indicate hypothesized causal relationships [Colour figure can be viewed at wileyonlinelibrary.com]

We used piecewise path analysis (PPA) to quantitatively assess our conceptual hypothesis. Path analysis is ideal for testing complex causal hypotheses because it allows for estimation of both direct and indirect effects of explanatory variables, and allows for hierarchical nested structure, random effects and non-Gaussian response variables. Path analysis is a correlative approach, and of course cannot directly infer causation. However, path models do imply an underlying causal structure. (Shipley, 2009). Path analysis involves two levels of estimation: (1) effect sizes in submodels (i.e., paths) and (2) whole-model fit (overall fit of all paths). Direct effects represent standardized regression coefficients, and indirect effects are calculated by summing the products of all paths leading from one variable to the terminal response variable.

Prior to analyses, explanatory variables were scaled and centered to mean = 0 and variance = 1. For each terminal response variable, we then fit a "global" PPA including all hypothesized paths. This consisted of fitting a series of linear or generalized linear mixed models for each dependent variable as submodels (i.e., receiving an arrow in Figure 2) within a whole-model. Establishment was modelled as a binomial random variable, and spread was modelled as a Poisson random variable. Because fishing and aquaculture were highly correlated (r = .86), we included only fishing in models. We included family as a random effect to account for phylogenetic non-independence among species. While this approach is not as resolute as eigenvectorbased methods on phylogenetic distance matrices (Diniz-Filho, de Sant'Ana, & Bini, 1998), it is satisfactory at this phylogenetic scale (sensu Marczak, Thompson, & Richardson, 2007; Mahoney et al., 2015). We sought a parsimonious model in which (1) all paths were statistically significant with 95% confidence and (2) the whole-model fit the data well, as indicated by $p \ge .05$ on the global goodness-offit test (Fisher's C statistic). In this case, $p \ge .05$ indicates that the observed (fitted model) and expected (specified in model syntax) covariance matrices do not differ significantly, indicating acceptable whole-model fit. After fitting the global model, we then removed non-significant (p > .05) paths in a stepwise manner (beginning with

the smallest effect size, β) until either all paths were statistically significant or their removal caused reduced overall model fit. Changes in model fit associated with removing non-significant paths were assessed based on Akaike's information criterion, adjusted for sample sizes (AICc); increased AICc indicates reductions in model fit/precision, given the number of paths (Shipley, 2013). PPA was conducted using the *piecewiseSEM* package (Lefcheck, 2016) in R version 3.3.2 (R Development Core Team, 2018).

3 | RESULTS

We analysed 272 species representing 23 families. Of those, 68% (184 species) were established outside their native range, but 20% (38 species) of established non-natives had colonized only one watershed. However, many species had large non-native ranges; 25 species were established in at least 20 non-native watersheds, and six species were established in over 100 watersheds. These include Brown Trout *Salmo trutta* (146), Green Sunfish *Lepomis cyanellus* (140), Bluegill *L. macrochirus* (135), Rainbow Trout *Oncorhynchus mykiss* (134), Smallmouth Bass *Micropterus dolomieu* (124) and Largemouth Bass *M. salmoides* (119).

The species we analysed represented a linear continuum of life history traits. The first principal coordinate eigenvector explained 78% of the variation in the four life history traits; the next strongest eigenvector captured only 5% of the variation, and the remaining variation was negligible. We thus retained only the first eigenvector. This variable was positively correlated with all life history variables: maximum total length, maximum lifespan, age at maturity and maximum fecundity (r = .77, .71, .62, and .42, respectively). Thus, ranging from lowest to highest eigenvector values, species grow larger, live longer, mature later and produce more eggs. This represents a general shift away from the opportunistic endpoint of the trilateral life history continuum (Winemiller, 2005; Winemiller & Rose, 1992).

Piecewise path analysis revealed both direct and indirect effects of factors affecting establishment and non-native range size of stream fishes. Whole-model tests revealed good fit for both *establishment* (C = 2.67, p = .67) and *spread* (C = 5.19, p = .59). We retained a few paths with p > .05 because removing them decreased model fit. As expected, traits had few direct effects on *establishment* and *spread*, all of which were smaller than the direct effects of *native range size* and/or *fishing*. *Native range size* had the strongest direct effects on both *establishment* and *spread* of non-native stream fishes. *Fishing* also had a strong direct effect on *spread*, but had no significant effect on *establishment*. However, both *fishing* and *native range size* were directly influenced by species traits (Figure 3).

Species traits had significant direct and indirect effects on both *establishment* and *spread*. Traits played a more direct role in determining whether or not a species would become established outside its native range, with significant effects of *diet breadth* and *life history* on *establishment*. *Temperature range*, *diet breadth* and *serial spawning* also indirectly affected *establishment* by directly affecting *native range size* (Figure 3a). Traits played a more indirect role at



FIGURE 3 Direct and indirect effects of functional traits and native range size (green), and human use indices (blue) on metrics indexing stream fish introductions (orange). Numbers indicate standardized effect sizes (β) ±standard error; arrow widths indicate effect sizes [Colour figure can be viewed at wileyonlinelibrary.com]

determining the number of watersheds in which species established; serial spawning and life history had significant, but weak direct effects on spread. However, serial spawning, diet breadth, life history and temperature range all had appreciable indirect effects on spread by directly affecting fishing and native range size (Figure 3b). In fact, the indirect effects of most significant traits (excluding diet breadth) were comparable to the direct effect of fishing (Table 2).

4 | DISCUSSION

Our analyses suggest a complex causal structure underlies establishment and spread of non-native stream fishes in the eastern United States. Our results suggest that functional traits may give some species an advantage for establishing outside of their native range, and that humans also play an important role at spreading those species once they have become established. Likewise, species with large native ranges are more likely to establish in numerous watersheds outside their native range, and species with larger native ranges are more likely to be pursued for fishing. However, selection for human use was non-random, being significantly affected by traits.

By far, the most influential variable in our analysis was *native range size*. Native range size has been shown to directly influence indices of invasiveness for numerous taxa (Allen et al., 2013; González-Suárez, Bacher, & Jeschke, 2015), including fishes **TABLE 2** Cumulative direct and indirect effects of species traitson establishment and spread (number of established watersheds) of272 stream fishes in the eastern United States

Terminal response variable	Trait variable	Cumulative effect
Establishment	Diet breadth	0.70
Establishment	Life history	0.49
Establishment	Serial spawning	0.21
Establishment	Temperature range	0.56
Number of established watersheds	Diet breadth	0.34
Number of established watersheds	Life history	0.48
Number of established watersheds	Serial spawning	0.45
Number of established watersheds	Temperature range	0.50

(Marchetti et al., 2004; Ribeiro, Elvira, Collares-Pereira, & Moyle, 2008; Sommerwerk, Wolter, Freyhof, & Tockner, 2017). However, emerging evidence suggests that native range size itself does not

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make species better invaders, but is instead a representation of the traits that make a species successful. Native range size can represent a variety of adaptive traits, such as habitat or trophic generalism (Dawson, Rohr, van Kleunen, & Fischer, 2012; González-Suárez et al., 2015), or trait diversity/plasticity (Richardson & Pyšek, 2006). In this case, we found stream fishes that spawn more frequently per season and have broader diets and thermal tolerances, result in larger native range sizes, and in turn colonize more watersheds outside their native range size—for example, parthenogenesis and fecundity in invasive herpetofauna (Peoples & Goforth, 2017b), winter hardiness in invasive ornamental plants in Germany (Maurel et al., 2016) and temperature range in invasive vertebrates between North American and Europe (Peoples & Goforth, 2017a). Success in the native range may be a good predictor of success in the non-native range.

As a surrogate for propagule pressure, human use for fishing played an important role in determining the number of non-native watersheds in which a species would establish, but not in establishment itself. Recreational fishing is a major driver of species introductions (Davis & Darling, 2017), whether by direct stocking for angling (Clavero & Garcia-Berthou, 2006; Dextrase & Mandrak, 2006), bait-bucket introductions (Kilian et al., 2012) or secondary transport (Clarke Murray, Pakhomov, & Therriault, 2011; Drake & Mandrak, 2014). Many of the most prolific non-natives in our system were heavily associated with fishing use-for example, Brown Trout Salmo trutta (146 watersheds, 1,174 abstracts), Largemouth Bass Micropterus salmoides (119 watersheds, 525 abstracts) and Channel Catfish Ictalurus punctatus (62 watersheds, 253 abstracts). The traits driving fishing pressure certainly characterize these species: large body size, later age at maturation, higher fecundity and longer lifespan.

However, sportfishes make up a relatively low proportion of the overall North American freshwater diversity (nearly 900 species), and this was reflected in their contribution to the diversity of established non-natives. Most established species were smaller-bodied non-game minnows (Cyprinidae) and darters (Etheostoma and Percina spp.) that are not cultured for the commercial bait industry (excluding Golden Shiner Notimegonus crysoleucas and Fathead Minnow Pimephales promelas). Of the 184 established non-natives, 70% (129 species) had fewer than 10 abstracts associated with "fishing," and many of those were incidental mentions; 27% (50 species) of those had human use values of zero. These results reflect the character of introduction pathways and spread in our study system. Most stream fish introductions in the eastern United States come mostly from interbasin transfers by anglers who have harvested and released bait fishes from nearby watersheds, and not from the commercial bait industry. However, our results suggest these species are less likely to colonize many watersheds where they are not native because they do not have the traits humans find desirable for fishing.

In addition to the significant indirect effects described in the preceding paragraphs, a few traits also had significant direct effects. Most notably, life history strategy was a significant direct predictor of both establishment and spread. Our results suggest species of nearly any life history strategy can become established (sensu Olden et al., 2006), but some traits can favour establishment. On the surface, these results seem to contradict our finding that most established non-natives were small-bodied non-game species. Accordingly, we conducted a post hoc analysis using mixed effects models, with family identity as a random effect, comparing the four life history variables between established and non-established species only for non-game species. This allowed us to further explore the potential that a few large game species contributed to the significant direct effect of life history strategy on establishment. Compared to species that had not established outside their native range, we found established non-game fishes had greater maximum total length (25.6 \pm 7.7 vs. 12.3 \pm 3.7 cm, p < .0001), age at maturation $(1.9 \pm 0.3 \text{ vs.} 1.5 \pm 0.3 \text{ years}, p = .0058)$, fecundity (24,356 ± 13,226) vs. $1,675 \pm 658$ eggs, *p* < .0001) and maximum lifespan (5.6 ± 0.6 vs. 3.6 ± 0.3); error bounds represent standard deviations. These results suggest that despite their correlation with human use, certain life history traits indeed favour establishment of freshwater fishes. These results are very similar to those of Liu et al. (2017), who found invasiveness of freshwater fishes is positively affected by body size, longevity, age/size at maturation and fecundity. Other studies have observed positive effects of adult body size (Ribeiro et al., 2008) and fecundity (Drake, 2007; Howeth et al., 2015) on fish invasiveness.

We also observed a significant direct effect of serial spawning—a reproductive condition in which a species can produce multiple clutches per year. In general, evidence from numerous systems is converging to demonstrate that overall reproductive allocation is a key contributor to invasiveness of freshwater fishes. Similarly to Marchetti et al. (2004), we found that diet breadth contributed directly to establishment, but not spread of non-native species. The benefits of trophic generalism during the establishment phase are straightforward: species with broader diets are less likely to encounter resource scarcity during the critical establishment phase when extirpation is more likely. Several other studies have found trophic status as a key predictor of freshwater fish invasions (Howeth et al., 2015; McKnight et al., 2017).

Quantifying the indirect effects of species traits at sequential phases of the invasion process is necessary for gaining a holistic understanding of how invasions function (Maurel et al., 2016; Peoples & Goforth, 2017a,b; Pyšek et al., 2015). Accounting for the hierarchical structure among potential mechanisms in this system revealed that the two most important drivers of non-native species spread (native range size and fishing pressure) are non-random, being structured by species traits. In contrast, a more traditional "direct effects" approach would have yielded different conclusions about the role of traits. We encourage more studies to consider trait–environment interactions, or to quantify both direct and indirect effects of invasion mechanisms (sensu Catford et al., 2009) to identify hierarchical structure among other taxa and systems.

It is also important to recognize the scale-dependent definition of native status. Among the 184 non-native species in our study area, only four were native to a continent other than North America, and seven were native to a part of North America outside the focal area (e.g., the Pacific or western Gulf of Mexico basins). Thus, the vast majority of non-natives were either transplanted from nearby watersheds by humans or potentially colonized from connected but distant watersheds (Scott & Helfman, 2001). Newly available data sets and tools have enabled numerous macroscale invasion analyses that have greatly expanded our knowledge of how invasions function in stream ecosystems (Davis & Darling, 2017; Dawson et al., 2017; Fitzgerald, Tobler, & Winemiller, 2016; Guo & Olden, 2014), but have only considered a continental-scale definition of native status. This approach is certainly insightful, as modelling introduction and spread of purely exotic species describe invasions of species that lack a coevolutionary history with the native community (Fridley & Sax, 2014; Shea & Chesson, 2002). One interesting hypothesis is that different mechanisms drive introduction and spread dynamics in exotic versus "native" invaders (Leprieur, Olden, Lek, & Brosse, 2009), although other studies of stream fishes suggest otherwise (Sax et al., 2007; Stewart et al., 2016). Regardless, we argue that a rigid, continental-scale view of native status may underestimate the presence, richness or proportions of potentially harmful non-native species in freshwater systems. Analyses considering cross-scale changes in native status may lead to further insights into how invasion mechanisms operate and interact (Buckwalter, Frimpong, Angermeier, & Barney, 2017; Peoples et al., 2017).

Emerging macrosystems approaches are enabling an understanding of species invasions at an unprecedented scale and extent. Like many such studies, ours could be improved in some ways. Firstly, because stream fishes are relatively understudied/ monitored, we have no estimate of introduction effort and thus cannot distinguish successful from failed introduced species. We know which species established, but we do not know which were introduced unsuccessfully; future studies incorporating introduction effort will be particularly useful for improved risk assessment (Howeth et al., 2015; Keller et al., 2011). Along the same line, we were not able to incorporate abiotic mechanisms into analyses-a key component of invasion drivers (Catford et al., 2009). This stems primarily from the fact that we modelled species, and not invasions themselves, as observational units. While species-level analyses are insightful, they are not accomodating to location-level variables (sensu Barney & Whitlow, 2008). Finally, although useful for understanding drivers of establishment and spread, neither of these variables equate directly to ecosystem impact; this issue is shared among most macroscale invasion analyses (Fei, Guo, & Potter, 2016). We do not assume our metrics of establishment and spread correlate directly to ecological impacts, although four of the most widespread non-native species from our data set are all represented among the world's "worst" invasive species (Lowe, Browne, Boudjelas, & De Poorter, 2000). Moving beyond analysing establishment and spread, towards measurable estimates of ecosystem impact, will be an important next step in invasion macroecology.

By volume, streams and their fauna represent one of the most biologically diverse ecosystems on earth, but also one of the most imperiled (Jelks et al., 2008). Understanding how species traits, propagule pressure and abiotic factors control biological invasions **Diversity** and **Distributions**

will better enable ecologists to predict and prevent future invasions. Quantifying both direct and indirect effects of these factors will lead to a better overall understanding of the invasion process.

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DATA ACCESSIBILITY

Summarized fish distribution data (response variables) and propagule pressure indices used for modelling are included in Appendix S2. Species trait data are available from Frimpong and Angermeier (2009).

ORCID

Brandon K. Peoples D http://orcid.org/0000-0002-3954-4908 Stephen R. Midway D http://orcid.org/0000-0003-0162-1995

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BIOSKETCHES

Brandon Peoples is an Assistant Professor in the Department of Forestry and Environmental Conservation at Clemson University; his research focuses on functional, cross-scale approaches to fluvial fish ecology and conservation.

Stephen Midway is an Assistant Professor in the Department of Oceanography and Coastal Sciences at Louisiana State University. His research team addresses species and ecosystemlevel questions of fishes inhabiting headwater streams to coastal and offshore habitats.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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