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Indirect Effects and Context Dependency in Stream Fish Invasions

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Keywords: confounding effects | invasion drivers | invasion paradox | macroecology | nonnative richness | propagule pressure | regional variation

ABSTRACT

Aim: Invasion ecology is replete with a body of well-supported yet contradictory evidence for numerous invasion hypotheses, likely as a result of context dependency. Context dependency in invasion studies can arise in two ways: (1) *apparent*, when results differ between studies solely due to methodical differences, or (2) *mechanistic*, when results truly differ due to ecological processes. One form of apparent context dependency occurs when causally linked factors associated with invasion success (hereafter, *invasion drivers*) either mask or enhance each other's effect on invasion success. Mechanistic context dependency can occur when regional scale processes modify the influence of local scale invasion processes. Together, apparent and mechanistic context dependency likely give rise to conflicting support between invasion hypotheses via confounding effects of causally related invasion drivers and region-specific invasion processes.

Location: 2339 stream segments in two ecoregions of the United States.

Methods: Using local scale stream fish community data for two distinct ecoregions, we constructed identical path models to estimate the direct and indirect effects of invasion drivers on nonnative richness. We chose one variable to index invasion drivers from each of the following categories: propagule pressure, natural abiotic, anthropogenic abiotic and biotic factors.

Results: We found evidence of apparent context dependency through the presence of indirect effects, in which the effects of propagule pressure and biotic factors on nonnative richness were modulated by abiotic factors. The indirect effects of invasion drivers differed between both regions, providing evidence of mechanistic context dependency.

Main Conclusions: Apparent and mechanistic context dependency can lead to conflicting evidence between studies of invasion hypotheses. Accounting for indirect effects of invasion drivers is important in gaining a more general understanding of the invasion process. Furthermore, because indirect effects varied regionally, it is important to understand the large-scale processes that contextualise local invasion processes.

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1 | Introduction

Understanding the dominant drivers of species invasions remains an overarching goal of ecology (Early et al. 2016). The result is that invasion ecology is saturated with hypotheses seeking to explain invasion dynamics, including several frameworks attempting to unify these hypotheses (e.g., Blackburn et al. 2011; Enders et al. 2020). One such framework divides invasion drivers into three categories: propagule pressure (P), abiotic characteristics (A) and biotic characteristics (B) (Catford, Jansson, and Nilsson 2009). Propagule pressure is defined as the number and frequency of nonnative introductions in a given location or for a given taxon and is often considered the most important driver in the invasion process (Simberloff 2009). Abiotic factors can influence nonnative richness either positively or negatively by providing suitable or unsuitable environments for nonnative species, whether through natural habitat characteristics or anthropogenic habitat alterations (Davies et al. 2005; Dawson et al. 2017). Finally, biotic characteristics of communities can influence invasions through interspecific interactions such as competition, predatory/prey dynamics, mutualism and facilitation (Levine and Thomsen 2001). Understanding the relative roles of these factors in the invasion process remains an increasingly important goal among ecologists.

Many studies have focused on understanding the relative importance of invasion drivers among taxa and systems and have found compelling, yet conflicting, evidence due in large part to the context dependency of ecological processes (Fridley et al. 2007; Smith and Côté 2019; Tomasetto, Duncan, and Hulme 2019). Context dependency refers to occasions in which differences in ecological or methodological conditions cause observed ecological relationships to differ among similar studies, leading to the conclusion that ecological results are not generalisable across taxa, region, or study design (Brian and Catford 2023). One source of context dependency in invasion ecology arises from a statistical artefact in which the effect of one invasion driver is masked or enhanced by another, correlated, driver (i.e., apparent context dependency; Catford et al. 2022). When treated as independent of one another, these correlated invasion drivers can confound interpretation of invasion processes. For example, apparent context dependency often arises when estimating native-nonnative species richness relationships (NNRs), because the true effect of native richness is often masked by correlated abiotic variables that were not included in models (Fridley et al. 2007). To confront and account for apparent context dependency in the invasion process, it is important to consider causal effects among independent variables representing invasion hypotheses beyond simply screening for collinearity in regression analysis, as well as applying statistical methods that are robust to collinearity.

Invasion drivers do not act independently; they are hierarchical in nature, with interactive webs of direct and indirect effects (Figure 1; Beaury et al. 2020; Catford, Jansson, and Nilsson 2009; Comte, Grantham, and Ruhi 2021; Gurevitch

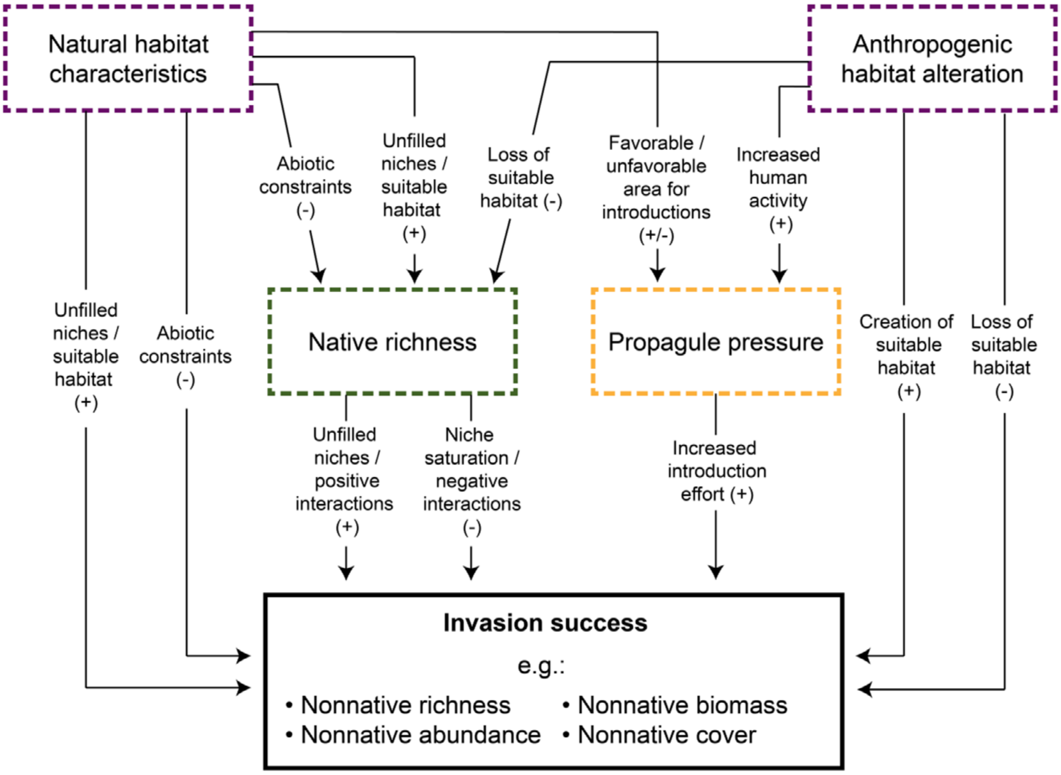

FIGURE 1 | A conceptual path diagram illustrating the hierarchical relationships between the PAB invasion drivers and invasion success. Dashed boxes represent invasion drivers, and the closed box represents measures of invasion success. Pathways indicate relationships between the drivers with descriptions of the relationships: (+) indicates one concept positively affects another and (−) indicates a negative effect. Concepts are colour-coded based on the category of the PAB invasion framework in which each concept is best aligned; propagule pressure with yellow, abiotic with purple and biotic with green.

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et al. 2011). If unaccounted for, the hierarchical structure of causally correlated invasion drivers can give rise to apparent context dependency among regionally constrained tests of invasion hypotheses. For example, in addition to the direct effects described above, abiotic characteristics can affect community invadedness (e.g., nonnative richness or dominance) *indirectly* by influencing native species diversity, and thus the potential for biotic interactions that may inhibit or promote the establishment of nonnative species (Figure 1; Byun, de Blois, and Brisson 2015; Davies et al. 2005; Levine and Thomsen 2001). Abiotic characteristics can also have indirect effects on community invadedness by modulating propagule pressure because some habitats are more favourable than others for human activities associated with the release of nonnative species, especially those that have been anthropogenically modified (Comte, Grantham, and Ruhi 2021; Davis and Darling 2017; Leprieur et al. 2008). Hierarchical causal relationships among invasion drivers can confound the interpretation of invasion drivers and make it difficult to draw causal inferences about invasion processes (Catford et al. 2022), especially when that relationship is being driven by an underlying driver that is not accounted for in the analyses (Fridley et al. 2007). Accordingly, a hierarchical approach is needed to better account for apparent context dependency among invasion drivers (Figure 1). The proposed hierarchical approach is intuitive and is built on the knowledge of other empirical studies that have addressed confounding factors in the invasion process (Evans, Warren, and Gaston 2005; Leprieur et al. 2008; Yiming, Zhengjun, and Duncan 2006).

Another potential source of empirical disparity in invasion ecology is mechanistic context dependency, whereby factors that vary across large spatial extents cause relationships between community invadedness and drivers to differ among regions, often as the result of cross-scale interactions (Brian and Catford 2023). Mechanistic context dependency is especially evident when comparing fine-scale, small-extent studies to one another, which often have well-supported but conflicting results that originated as a result of regional differences between study systems (Guo 2022; Smith and Côté 2019; Tomasetto, Duncan, and Hulme 2019). Large-extent analyses across multiple regions provide a means for addressing and quantifying interregional mechanistic context dependency. However, datasets that span large spatial extents are often collected from multiple sources and therefore are frequently coarsened to a coarse spatial grain size that may not always match the scale at which ecological mechanisms operate (Zipkin et al. 2021). Sacrificing spatial resolution to broaden spatial extent elucidates regional context dependency but is often achieved at the cost of scale-dependent inference (Dodds et al. 2021; Rastetter et al. 1992). As such, investigating invasion hypotheses at large, interregional extents with fine-resolution data can address mechanistic context dependency without sacrificing mechanistic understanding of invasion processes at appropriate spatial scales.

We hypothesise that both apparent and mechanistic context dependency can give rise to conflicting inference for key invasion hypotheses through (a) indirect effects among causally related independent variables representing PAB invasion drivers and (b) regional differences that cause the magnitude and direction of effects to differ in analyses (Catford et al. 2022). Using North American stream fishes as a model system, the objectives of this study were to (1) investigate apparent context dependency of invasion drivers by quantifying both direct and indirect effects of independent variables that represent invasion hypotheses on community invadedness; and (2) investigate mechanistic context dependency by examining how these effects vary among regions. It is important to emphasise that, unlike the vast majority of existing studies, our goal was not to focus on comparing the relative importance of invasion drivers in explaining community invadedness; this has been studied extensively across ecosystems and taxa (e.g., Anas and Mandrak 2021; Colangelo and Boggero 2017; Essl et al. 2019). Instead, we were interested in how the indirect effects of abiotic characteristics, split into natural habitat characteristics and anthropogenic habitat alterations, influence nonnative species richness by modulating native species richness and propagule pressure. We parsed out relationships among these mechanisms using path analysis applied to a fine-scale, continental-extent stream fish community dataset and conducted identical analyses in two ecologically distinct regions.

2 | Methods

2.1 | Study System

We tested our hypotheses using stream fish communities sampled at 2389 stream segments (COMIDs in the National Hydrography Dataset, version 2; McKay et al. 2012) in two ecologically distinct regions of the United States: the Rocky Mountains (1166 COMIDs) and Appalachian Forests (1223 COMIDs; Figure 2). The study regions were determined by consolidating similar level III ecoregions (Omernik and Griffith 2014). The Rocky Mountains study region was a compilation of the Northern, Middle and Southern Rockies level III ecoregions, and the Appalachian Forests was a compilation of the Blue Ridge, Ridge and Valley, Southwestern Appalachians and Central Appalachians level III ecoregions (Figure S1). A compilation of level III ecoregions provides more precise delineation of ecological processes than level II ecoregions while still offering sufficient gradients in key invasion drivers within regions and an adequate amount of stream fish community data. The two study regions were chosen as they are both upland systems from which comparisons can be drawn but have considerable biotic, climatic and biogeographic history differences that they present a strong contrast (Figure S2.3). Relative to the Appalachian Forests, the Rocky Mountain region is characterised by cooler summers and winters and less but more seasonally variable precipitation. The terrain consists of higher elevation mountains with forested landcover at lower elevations and alpine vegetation at higher elevations. In contrast to the Rocky Mountains, the Appalachian Forests region is characterised by a milder temperature regime with warmer summers and winters and greater precipitation. The terrain consists of highly eroded mountains, ridges, plateaus and valleys with forested landcover and mosaics of pastures, croplands and urban development (Wiken and Griffith 2011). Relative to the Rocky Mountains, the Appalachian Forests have much higher native freshwater fish species richness because they were not subjected to (a) the cyclical continental scale glaciation and embayment events during the Pleistocene and (b) major geological uplift events in recent

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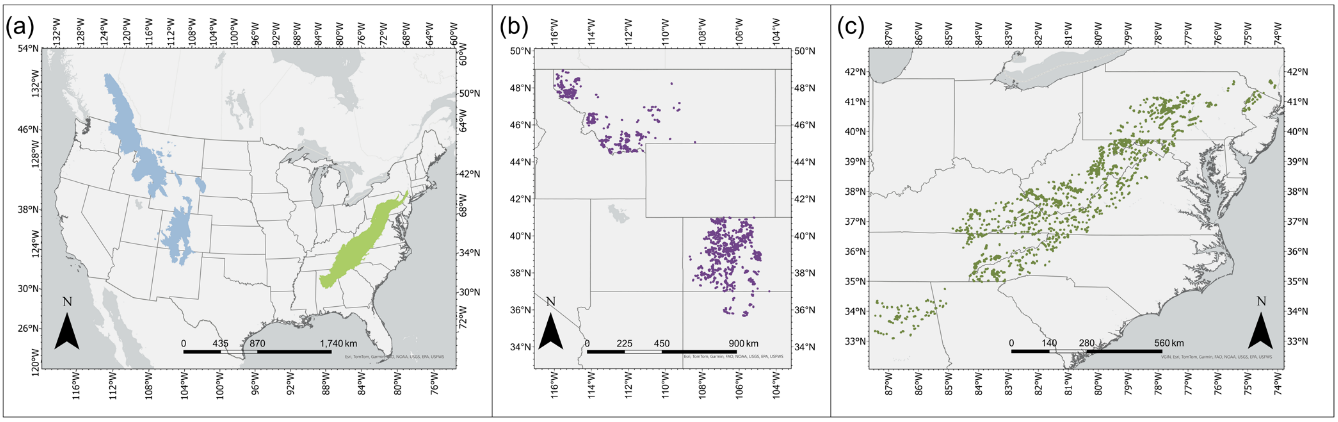

FIGURE 2 | Map of the two study regions (a). Shaded areas are colour-coded to represent the two study regions: Rocky Mountains (blue) and Appalachian Forests (green). Maps of the stream segments used as sites in the Rocky Mountains (b) and Appalachian Forests (c) regions. Points represent stream segments used in analysis for the Rocky Mountains ($n = 1166$) and Appalachian Forests ($n = 1223$) regions.

TABLE 1 | Variables used to represent each PAB invasion driver with descriptions and data source of each variable.

Variable	Invasion driver	Description	Source
Fishing demand	Propagule pressure (P)	Area-standardised sum of days that recreational fishing is in demand in a subwatershed (HUC12).	EPA EnviroAtlas (Pickard et al. 2015)
Habitat PC1	Natural habitat characteristics (A)	First axis of PCA using mean elevation (m), temperature (°C) and area (km^2) of upstream watershed.	EPA StreamCat (Hill et al. 2016)
Hydrological alteration index	Anthropogenic habitat alteration (A)	Measures the amount of hydrological alteration a stream segment is subjected to. Values range from 0 to 1, with 1 indicating the greatest alteration.	(McManamay et al. 2022)
Native species richness	Native biodiversity (B)	Number of native species in a stream segment. Nativity was determined at the subbasin scale (HUC8).	This study

evolutionary time that extirpated major freshwater fish lineages from western North America (Oberdorff et al. 2011).

2.2 | PAB Invasion Drivers

Each category of PAB invasion driver can be indexed by any number of independent variables. However, we emphasise that our goal was to investigate apparent and mechanistic context dependency in the invasion process and not to simply determine which factors affect nonnative richness, which has traditionally been the goal of large-extent analyses of invasion mechanisms. Therefore, to keep models parsimonious, we chose one variable to index each PAB category using a priori knowledge of known invasion drivers of stream fishes (Anas and Mandrak 2021; Comte, Grantham, and Ruhi 2021; Table 1; Figure S1).

Propagule pressure is difficult to measure due to the lack of records detailing the number and frequency of nonnative species introductions and is often indexed using proxies relating to anthropogenic activities (Simberloff 2009). This problem is particularly pervasive for freshwater fishes, as most introductions go largely undocumented (Hartman and Larson 2023). We represented propagule pressure in this study by using recreational fishing demand (Figure S1), as nonnative fishes are often introduced via means associated with recreational fishing, such as deliberate stocking of sportfishes or unintentional release of nongame fishes being used as bait (Hartman and Larson 2023; Rahel 2007). Recreational fishing demand was calculated from a model described in detail by Mazzotta et al. (2015). This model estimates the number of days recreational fishing is in demand in 30-m raster cells using information on angler travel distances, participant demographics and

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population distributions. Recreational fishing demand, summarised by area-standardised sum at the subwatershed level (12-digit hydrological unit code or HUC12 in the Watershed Boundary Dataset; Jones et al. 2022), was acquired from the US Environmental Protection Agency's (EPA) EnviroAtlas (Pickard et al. 2015). Recreational fishing demand estimates from this model have been used successfully to predict nonnative fish richness in previous studies (Comte, Grantham, and Ruhi 2021; Davis and Darling 2017; Peoples et al. 2020).

To simplify interpretation of our analyses and preserve degrees of freedom in path analysis, we used principal component analysis (PCA) to calculate a composite variable representing natural habitat characteristics, including elevation (Figure S1), mean temperature (Figure S1) and watershed area (Figure S1), all of which have been shown to influence riverine fish diversity (Griffiths, McGonigle, and Quinn 2014; Knouft and Page 2011; Oberdorff et al. 2011). This approach is ideal for including natural abiotic variables individually because it (a) captures multiple dimensions of critical habitat features in a single variable and (b) reduces the number of paths that must be estimated in path models, improving overall model fit without losing information. Elevation, mean temperature and watershed area data were obtained at the upstream watershed scale from the stream-catchment database (StreamCat; Hill et al. 2016). We performed PCA based on correlation matrices in each region using the *rda* function from the 'Vegan' package in R (Version: 2.5–7; Oksanen et al. 2020).

The first principal component (PC1) for both ecoregions explained a majority of the variation in the habitat variables (Rocky Mountains = 57.7% and Appalachian Forests = 47.8%), and therefore was used as the habitat composite variable. In both regions, high values of habitat PC1 were associated with higher elevation streams ($r = 0.92$ and 0.84 in the Rockies & Appalachians, respectively), which were characterised by lower temperature ($r = -0.93$ and -0.84, respectively) and smaller upstream watershed areas ($r = -0.12$ and -0.18, respectively). Conversely, low values on PC1 represented lower elevation, warmer streams with larger upstream watershed areas (Figure S2.3). The second principal component (PC2) also explained variation in the habitat variables (Rocky Mountains = 33.4% and Appalachian Forests = 33.0%; Figure S2.3), but only PC1 was selected to maintain parsimony in the path models. As only three variables were used in the PCA, the addition of the third component, which explained little variation in the original variables, was not considered.

We indexed anthropogenic habitat alterations using a metric of flow regime alteration (Figure S1). Natural stream flow regimes are an important determinant of fish diversity, as flow controls habitat complexity, connectivity and disturbance regimes (Poff et al. 1997). Therefore, the alteration of flow regimes represents a universal stressor in riverine ecosystems and facilitates the establishment of nonnative species through the creation of novel habitats and the reduction of native species (Olden et al. 2021). The hydrological alteration index was developed by McManamay et al. (2022) as a measure of flow alteration, ranging from 0 to 1, with values of 0 indicating no alteration and 1 indicating high alteration. Hydrological alteration, available at the stream segment resolution, is based on a comparison of expected and observed values of multiple hydrologic metrics describing the magnitude, frequency and duration of flow events from 7000 stream gauges that were subsequently extrapolated to the entire United States based on their association with a suite of natural and human disturbance variables (McManamay et al. 2022). Hydrological alteration is associated with and determined by other anthropogenic variables such as human population density, urbanisation, agriculture and dam density; therefore, the hydrological alteration index is a robust surrogate for overall degradation of riverine habitats (McManamay et al. 2022).

Nonnative species richness can be an estimate of community invadedness, and studying its drivers can lead to better understanding of invasion mechanisms (Guo and Ricklefs 2010). We calculated native and nonnative stream fish richness using a contemporary (2010–2022) stream fish community survey dataset (Figure S1). The dataset was compiled from stream fish community survey data from multiple state agencies across the conterminous United States (see Appendix S3). Stream fish community surveys used for this analysis were defined by a sampling event occurring at a specific location (*x*–*y* coordinate), on a specific date, with the goal of characterising the entire stream fish community composition. Surveys were matched with a stream segment (COMID) from the National Hydrology Dataset (NHD Plus version 2; McKay et al. 2012). Because a stream segment could have multiple surveys in the dataset, the most recent survey was selected for each stream segment. In some rare instances (~4% of sites in the dataset), multiple surveys were conducted on the same stream segment and date, in which we randomly selected one survey. Stream segments were then linked to level III ecoregions and were subset into the two study regions using the ecoregions defined in Appendix S1. In cases where stream segments fell between two ecoregions, that stream segment was removed from the dataset.

To ensure comparability between stream fish surveys, data were only included if they adhered to a strict set of criteria. First, we only included surveys collected using standardised electrofishing protocols so that local species richness from these surveys was represented uniformly among data sources (Bonar, Hubert, and Willis 2009). Second, to ensure that sampling protocols were as similar as possible among data sources, we only included 'wadeable' streams (*sensu* Barbour et al. 1999) with upstream watershed areas $< 300\,\mathrm{km}^2$; watershed area is a direct correlate of stream size (i.e., width and depth). Because their size and depth make stream fish community sampling increasingly difficult, larger streams require different sampling protocols that become increasingly divergent among data sources due to regional differences in stream morphology and species diversity. Third, community data were only included from stream segments that were classified as natural streams (NHD 'WaterType' = 'StreamRiver'; McKay et al. 2012); no artificial systems (e.g., reservoirs, ditches, canals) or lentic systems (e.g., ponds, lakes, palustrine wetlands) were included. After filtering, we had a total of 1116 and 1223 stream segments in the Rocky Mountains and Appalachian Forests, respectively.

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We defined native status at the subbasin watershed scale (HUC8s in the Watershed Boundary Dataset; Jones et al. 2022). This is the finest spatial scale at which stream fish native status can be determined in the United States (NatureServe 2010; U.S. Geological Survey 2019). This scale of native status delineation allows for a species to be native at some stream segments in an ecoregion but nonnative in other segments. This is important as these intra-regionally nonnative species are often underrepresented in analyses of nonnative richness (Hartman and Larson 2023; Vitule et al. 2019) but contribute inordinately to biotic homogenisation and representation of nonnative species in freshwater fish communities (Sommerwerk et al. 2017; Toussaint et al. 2016).

2.3 | Statistical Analyses

We created path models for both ecoregions to account for the direct and indirect effects of PAB invasion drivers on nonnative richness. For each region, we constructed a global path model (Figure 3) based on our conceptual hypotheses described above (Figure 1). We parameterised the path models and conducted path analysis using the *sem* function in the 'lavaan' package in R (Version: 0.6-15; Rosseel 2012). Prior to analyses, all variables were log-transformed to improve normality and standardised (mean zero-centred and divided by one standard deviation) to allow for direct comparisons of effect sizes. Maximum likelihood estimation with robust standard errors and a Satorra-Bentler scaled test statistic were used for model parametrisation. Global model fit was assessed based on *p*-values from global chi-squared tests, scaled root mean square error of approximation (RMSEA) and scaled comparative fit index (CFI). A global chi-squared test was used to determine if the expected and observed covariance matrices differ at $\alpha = 0.05$; models with $p \geq 0.05$ have adequate fit, which indicates that the hypothesised and observed variance–covariance matrices do not differ from each other (Hu and Bentler 1999). CFI is less sensitive to sample size than chi-square and compares the model fit to that of a baseline model in which there are no relationships between parameters. RMSEA measures fit based on how well the model approximates the data and prioritises parsimony in model structures. Adequate model fit is indicated by CFI ≥ 0.95 and RMSEA ≤ 0.06 (Hu and Bentler 1999). In cases where the global model did not have adequate fit, paths were removed starting with the smallest effect size until adequate model fit was achieved. Once model fit was achieved, no further alterations were made to the model. Therefore, it is possible for statistically nonsignificant pathways to exist in the final path model. This method of model pruning provided a standardised approach that allows comparison between the two regions and provides the most descriptive inference, given that the model has an appropriate fit. Finally, we calculated the indirect effects each PAB invasion driver had on nonnative richness as a derived quantity in the model by multiplying the parameter estimates for that entire pathway, allowing for the estimation of standard errors for indirect effects. The products for each pathway were summed to determine the total indirect effect of that driver on nonnative richness. The total effect of each PAB invasion driver was calculated by summing the direct and indirect effects (Shipley 2004).

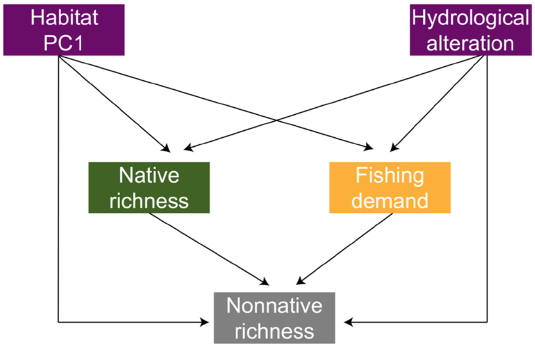

FIGURE 3 | Conceptual path diagram of the global path model. This path diagram represents the parameterizable relationships between the PAB invasion drivers and nonnative richness from the hypothesis in Figure 1. Arrows represent causal relationships between variables. Observed variables are represented with rectangles colour-coded based on the category of the PAB invasion framework. Propagule pressure is represented with yellow, abiotic factors with purple, biotic factors with green and the response variable with grey.

Covariances were estimated between habitat PC1 and hydrological alteration as well as between native richness and fishing demand. These covariances were indicated by the modification indices function from the 'lavaan' package in R (Version: 0.6-15; Rosseel 2012) as being necessary for model fit due to residual correlations. It is important to note the covariances do not represent a hypothesised causal relationship.

3 | Results

3.1 | Nonnative Richness

A total of 269 fish species were included in the analysis, with 100 being nonnative to at least one stream segment in the two study regions. The Rocky Mountains had 24 species that were nonnative to at least one HUC8 watershed and 11 species that were native to all watersheds in which they occurred. In contrast, the Appalachian Forests region had 85 species that were nonnative to at least one HUC8 watershed and 162 species that were native to all watersheds in which they occurred. In both regions, most stream segments contained nonnative species, with 66.7% of the segments in the Rocky Mountains and 64.4% of the segments in the Appalachian Forests having at least one nonnative fish species present. Nonnative richness was highly variable in both regions. Rocky Mountain stream segments had, on average, 1.02 [95% CI: 0.97, 1.08] nonnative species and Appalachian Forests segments had, on average, 1.34 [1.25, 1.42] nonnative species (Figure 3g.). The Rocky Mountains had on average 49.1% [46.7%, 51.4%] of a stream segment's species richness made up of nonnative species, and Appalachian Forests had, on average, 13.0% [12.2%, 13.8%] of segments' species richness made up of nonnative species.

With the exception of Brown Trout (*Salmo trutta*), most nonnative species were native to somewhere in North America (Appendix S4). While some nonnative species were native to regions on opposite sides of the continent, most nonnative species in our analyses were introduced from other watersheds within the region where they are native. For example, the Redbreast

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Sunfish (*Lepomis auritus*) is native to eastward-draining Atlantic Slope streams in the Appalachian Forests regions but is widely introduced in the westward-draining Tennessee River Basin in the same ecoregion. It is important to note that species occurring in a large number of stream segments in Appendix S4 are not necessarily the most widespread nonnative species in the region but simply occurred in the most stream segments we included, given our filtering criteria. The most common nonnative species were introduced via intentional stocking or bait bucket releases associated with recreational fishing (Peoples and Midway 2018).

3.2 | Path Analysis and Context Dependency

Model fit was achieved for both regions with minimal modification to global models. Neither global model exhibited acceptable fit in terms of global *p*-values from chi-squared tests, CFI or RMSEA as the models were saturated and model fit could not be assessed (see Appendix S5). However, the removal of only one pathway from each model was required for the models to become unsaturated and adequate fit to be achieved. The Rocky Mountains model achieved adequate fit ($p = 0.803$, $\mathrm{CFI} = 1.000$, $\mathrm{RMSEA} < 0.0001$) with the removal of the path with the smallest effect, which was the direct path between habitat PC1 and nonnative richness. Likewise, the Appalachian Forests model achieved adequate fit ($p = 0.849$, $\mathrm{CFI} = 1.000$, $\mathrm{RMSEA} < 0.0001$) with the removal of the path between hydrological alteration and native richness. A statistically nonsignificant path remained in the Rocky Mountains model between hydrological alteration and native richness, and all other paths were statistically significant.

We observed significant direct and indirect effects among invasion drivers and nonnative richness, illustrating how invasion drivers' cumulative direct and indirect effects may combine to obscure their overall effects to cause apparent context dependency (Figure 4). Habitat PC1, in which positive values indicate higher elevation and lower temperature and watershed area (Figure S2.3), had a significant positive indirect effect on nonnative richness in the Rocky Mountains ($\beta = 0.114 \pm 0.012$ SE) by decreasing native richness ($\beta = -0.379 \pm 0.027$) and increasing

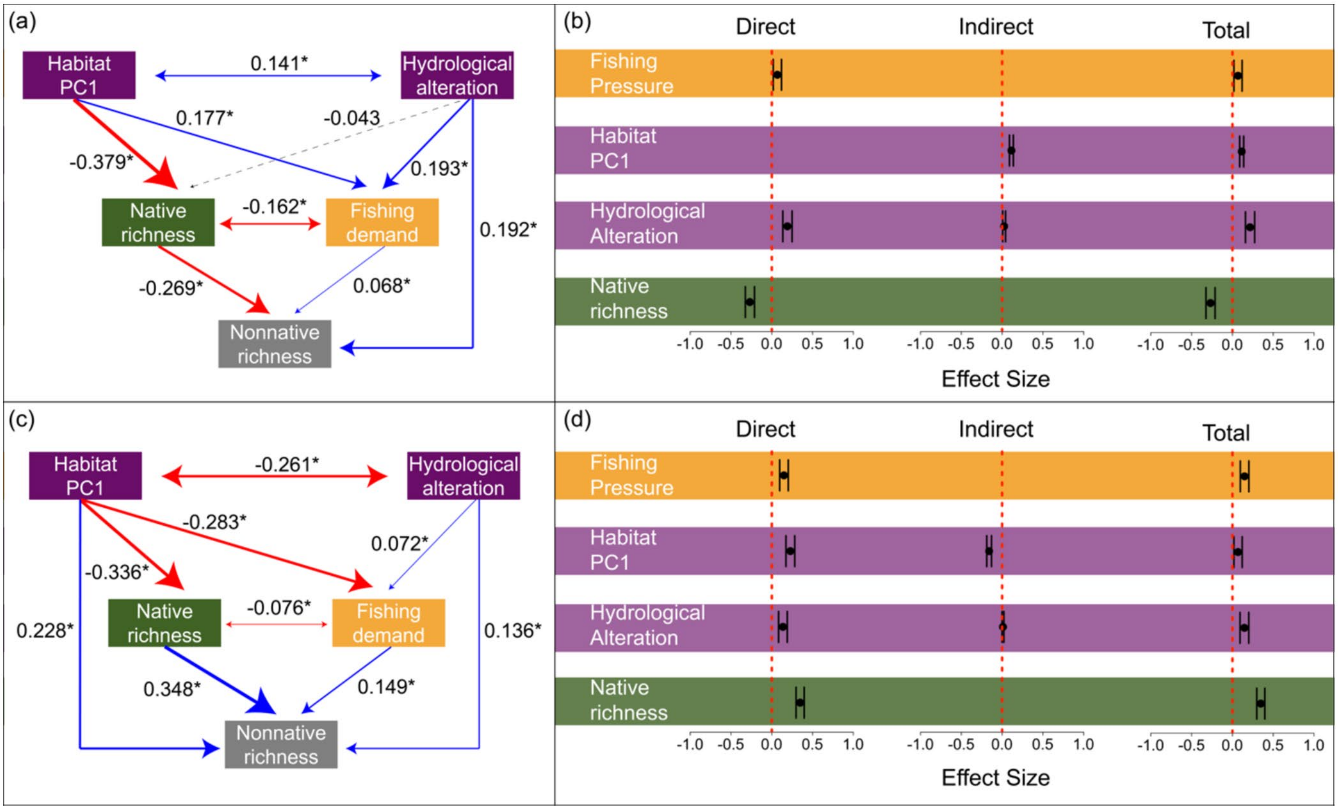

FIGURE 4 | Results of path analysis for both the Rocky Mountains (a) and Appalachian Forests (c) study regions. Observed variables are represented with rectangles colour-coded based on the category of the PAB invasion framework. Propagule pressure is represented with yellow, abiotic factors with purple, biotic factors with green and the response variable with grey. Double-sided arrows indicate covariances and single-sided arrows represent causal relationships. Arrows are scaled and labelled based on effect sizes. Larger arrows indicate larger effect sizes. Asterisks indicate statistical significance at $\alpha = 0.05$. Arrows are colour-coded based on direction of effect. Blue arrows indicate a positive relationship, red arrows indicate a negative relationship and grey dashed arrows indicate nonsignificant pathways. Forest plots (b; d) illustrate the direct, indirect and total effect sizes of each driver on nonnative richness. Direct effects are the effect a driver has on nonnative richness through a direct pathway; indirect effects are the sum of effects a driver has on nonnative richness through each of its indirect pathways; and total effects are the sum of all direct and indirect effects a driver has on nonnative richness. Each point represents the mean parameter estimate for each driver with arrows representing the 95% confidence intervals for that estimate. Confidence intervals that overlap with zero (red dashed line) indicate no significant effect. The absence of a point indicates that the corresponding pathways do not exist in the model.

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fishing demand ($\beta = 0.177 \pm 0.028$). In the Appalachian Forests, habitat PC1 had a significant negative indirect effect on nonnative richness ($\beta = 0.159 \pm 0.015$) by decreasing native richness ($\beta = -0.336 \pm 0.024$) and fishing demand ($\beta = -0.283 \pm 0.026$). This negative indirect effect offset the direct effect, leading to a weak positive total effect of habitat PC1 on nonnative richness in the Appalachian Forests ($\beta = 0.069 \pm 0.026$). The cumulatively weak total effect of habitat PC1 on nonnative richness would not have been evident had only direct effects been considered. Hydrological alteration had a significant positive indirect effect on nonnative richness ($\beta = 0.025 \pm 0.009$) by increasing fishing demand ($\beta = 0.193 \pm 0.029$) in the Rocky Mountains. In the Appalachian Forests, hydrological alteration increased nonnative richness indirectly ($\beta = 0.011 \pm 0.006$) by increasing fishing demand ($\beta = 0.072 \pm 0.035$), although this indirect effect was weak and only marginally statistically significant ($p = 0.059$). The indirect effects of hydrological alteration in both regions led to an increase in the positive total effect of hydrological alteration on nonnative richness (Rockies: $\beta = 0.216 \pm 0.029$; Appalachians: $\beta = 0.147 \pm 0.027$; Figure 4).

Interregional differences between path models provide evidence of mechanistic context dependency in the relative roles of PAB invasion drivers for determining the richness of nonnative stream fishes. The direction and magnitude of several relative effect sizes of each pathway often differed between study regions, with most notable interregional difference being in the direct pathway between native and nonnative richness (Figure 4). In both regions, the total effect size of native richness was among the largest of all drivers, but the native-nonnative richness relationship was negative in the Rocky Mountains ($\beta = -0.269 \pm 0.029$) and positive in the Appalachian Forests ($\beta = 0.348 \pm 0.025$). Patterns of fishing demand also differed between the two regions: High elevation, cold streams (high values of habitat PC1) had the most fishing demand in the Rocky Mountains ($\beta = 0.177 \pm 0.028$), but the opposite was observed in the Appalachian Forests ($\beta = -0.283 \pm 0.027$; Figure 4).

4 | Discussion

By estimating direct and indirect effects of PAB invasion drivers on nonnative stream fishes in two North American ecoregions, we found evidence of both apparent and mechanistic context dependency that would have masked inference produced by considering only direct or intraregional effects of invasion drivers. Our findings revealed an underlying hierarchical causal structure (sensu Shipley 2004) of invasion drivers in stream fish communities, suggesting that the effects of invasion drivers on nonnative species richness were modulated by abiotic factors from both natural and anthropogenic sources. By accounting for the underlying causal structure of invasion drivers, we offer a more detailed explanation of the processes leading to high nonnative richness. Furthermore, we found the causal structure differed between the two ecoregions, with some pathways showing opposing effects between regions, providing evidence of mechanistic context dependency in which ecological patterns are contextualised by regional-level processes (Brian and Catford 2023).

We found evidence for apparent context dependency through the presence of indirect pathways between invasion drivers and nonnative richness. Depending on the region, confounding effects of natural habitat characteristics on native richness and fishing demand either masked or overestimated the role that habitat characteristics play in affecting nonnative richness. For example, higher elevation, colder, smaller streams had higher nonnative richness in the Rocky Mountain region. However, the patterns of nonnative richness were not due to direct effects of these characteristics but to the increased fishing demand and lower native richness in those streams. Considering only the effects of habitat characteristics would miss these processes. These results corroborate studies from different systems and taxa that have illustrated how highly correlated invasion drivers can confound interpretation of invasion processes. For example, Evans, Warren, and Gaston (2005) found that species richness of nonnative birds was positively related to human population density, but this relationship diminished when energy availability was accounted for because of its correlation with human population density. Additionally, Yiming, Zhengjun, and Duncan (2006) found that a positive relationship between bullfrog invasion success and native frog species richness was confounded by the intensity of frog hunting by humans, which was higher in areas with high native richness. Accordingly, not accounting for confounding variables can contribute to apparent context dependency by providing misleading interpretations of the drivers of nonnative richness and mistakenly attributing variables as invasion drivers.

Many ecological studies use regression-based analyses that force researchers to remove or combine correlated variables to reduce collinearity. While correlation between variables does not always imply causation, it can be evidence of an underlying causal structure (Shipley 2004). Removing a variable from analysis due to collinearity without knowledge of the causal structure of those variables can cause misguided interpretations about the true roles of the variables that are excluded from analyses and can contribute to the body of studies with well-supported yet contradicting results (Catford et al. 2022). Explicitly hierarchical analytical approaches such as path analysis, Bayesian hierarchical models and recursive partitioning can reveal underlying causal structures of collinear relationships among variables and thus provide a more detailed understanding of invasion processes (Arhonditsis et al. 2006; Shipley 2004). Our analytical approach is not intended to malign non-hierarchical approaches but is instead intended to draw attention to the importance of potential underlying causal structures among correlated independent variables when interpreting and comparing results from invasion studies. Furthermore, because ours is an observational study, some of the relationships we quantified may still reflect unresolved causal structures, reflecting the inherent causal limitations of observational studies. Therefore, hierarchical approaches based on observational data, such as the framework proposed in this study, can be used to identify potential invasion mechanisms that can be tested using experimental approaches.

We also found evidence for mechanistic context dependency, in which the causal structures of invasion drivers differed in direction and magnitude between two regions in identical statistical models. While it was not surprising that the causal structures differed between regions, the presence of opposing directions of invasion driver effects illustrates how studies conducted in different regions may result in contradicting conclusions about the

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same invasion process. The primary difference between regions was in how natural habitat characteristics were associated with nonnative richness indirectly by modulating native richness and fishing demand. Higher elevation, colder, smaller streams had lower native richness in both regions; this is consistent with numerous analyses of freshwater fish diversity (Griffiths, McGonigle, and Quinn 2014). However, our results suggest that lower native richness affected nonnative richness differently between regions: high native richness inhibited nonnative richness in the Rocky Mountains but promoted it in the Appalachian Forests. The indirect effects of natural habitat characteristics on nonnative richness via fishing demand also differed between regions. In both regions, high fishing demand was related to high nonnative richness, consistent with studies across taxa relating propagule pressure to invasion success (Lonsdale 1999). However, this effect of fishing demand was modulated differently by habitat between the two regions: higher elevation, colder, smaller streams had the highest fishing demand in the Rocky Mountains but had the lowest fishing demand in the Appalachian Forests. The difference in fishing demand distribution between regions likely arises due to differences in regional species pools. Many native and nonnative species in the Rocky Mountains region are salmons and trouts (Salmonidae), which are highly sought-after game species that prefer colder, high-elevation streams (Knouft and Page 2011). Therefore, the prevalence of cold-water species may drive fishing demand into higher elevation, colder water streams in the Rocky Mountains. Alternatively, warmwater species, including black basses and sunfishes (Centrarchidae), drive greater fishing demand into lower elevation, warmer streams in the Appalachian Forests. The regionally varying patterns of invasion driver relationships illustrate that regional-level factors such as regional species pools and geophysiography can contextualise patterns in invasion drivers and lead to contradicting conclusions among invasion studies conducted across regions.

The opposing directions of the native-nonnative richness relationships (NNR) between our two study regions provide another example of mechanistic context dependency. Differing patterns of NNRs, often attributed to differences in spatial grain size among conflicting studies, have been referred to as the ‘invasion paradox’, wherein studies provide well-supported, yet conflicting evidence for the biotic resistance theory (Fridley et al. 2007; Tomasetto, Duncan, and Hulme 2019). However, we observed evidence both for and against biotic resistance at the same spatial scale with the same model structure, suggesting that the difference in NNRs may also result from spatially driven mechanistic context and not spatial scale alone (Beaury et al. 2020; Dos Santos, Hoeinghaus, and Gomes 2018; Smith and Côté 2019; Tomasetto, Duncan, and Hulme 2019). While it was outside of the scope of the study to determine what factors cause the causal structure to vary among regions, the two regions in our study exhibited biotic, abiotic and historical differences, and it was likely these differences played a role in modulating NNRs (Kominoski et al. 2018). Future studies should focus on determining what regional-level factors are influencing differences in invasion drivers to better compare and extrapolate studies across regional extents.

While regional differences have been found to contextualise NNRs, it is important to note that the conflicting NNRs found in this study could have arisen due to apparent context dependency via confounding relationships of unaccounted-for habitat characteristics (Beaury et al. 2020). The habitat characteristics used in the study are all strongly associated with local native fish diversity, yet unaccounted-for variables such as precipitation, landcover and terrain features may also be associated with both high native and nonnative fish diversity (Anas and Mandrak 2021; Griffiths, McGonigle, and Quinn 2014; Oberdorff et al. 2011). In addition, nonnative richness is often assumed to reflect the number of established nonnative species. However, the presence of a nonnative species in a survey does not necessarily reflect establishment, making it possible for a locality to have a mix of transient (introduced) and established species. As different invasion drivers affect different invasion stages (e.g., climate matching for establishment, species traits for spread, etc.; Blackburn et al. 2011; Pyšek et al. 2015), observing drivers across invasion stages may reveal further context dependency. The possibility of both apparent and mechanistic context dependency contributing to inconsistencies in NNRs suggests more work is needed to untangle the roles of apparent and mechanistic context dependencies in freshwater ecosystems.

While we did find regional-specific differences in causal structure among several pathways, we also found evidence of a common process in which anthropogenic habitat alteration affects nonnative richness. In both study regions, streams with highly modified flow regimes had greater nonnative richness than streams with natural flow regimes due to both direct and indirect effects. Alterations in flow regimes can directly benefit nonnative species through the creation of novel habitats and alterations of natural disturbance regimes (Comte, Grantham, and Ruhi 2021; Johnson, Olden, and Vander Zanden 2008; Olden et al. 2021). The relationship between altered flow regimes and nonnative stream fish richness mirrors a general pattern in invasion ecology in which habitat alteration is often linked to the success of nonnative species across taxa and ecosystem types (Dawson et al. 2017). In addition to the direct effects of flow alteration on nonnative richness, we found evidence for an indirect effect in which highly altered streams have greater fishing demand and therefore greater nonnative richness. Human activities such as recreational fishing are spatially structured nonrandomly across the landscape; freshwater systems in urban environments and with altered flow regimes, such as reservoirs, often have higher amounts of recreational fishing (Johnson, Olden, and Vander Zanden 2008). In addition, fishing demand is often higher in areas connected to urbanisation, which may have higher levels of flow alteration (Davis and Darling 2017; McManamay et al. 2022). Areas with higher amounts of human-mediated alterations and activities generally have higher propagule pressure due to the fact that human activity is the medium in which propagules are released into ecosystems (Simberloff 2009). Therefore, it is evident that habitat alteration has a twofold effect on nonnative richness: (1) altered habitats are more beneficial to nonnative species, and (2) these altered habitats are more likely to experience high introduction effort. While this pattern was similar between the two regions we studied, further research will be necessary to determine if it is universal across North American streams.

In this study we demonstrate how both apparent and mechanistic context dependency can contribute to a body of well-supported

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and contradicting invasion hypotheses. Apparent context dependency resulted from an underlying causal structure in invasion drivers that, when unaccounted for, could confound the interpretation of invasion drivers when only direct effects are estimated. Future studies should be aware that invasion drivers rarely act independently, and underlying causal structures may need to be considered when interpreting and comparing studies. Further, causal structures derived from observational studies can provide hypotheses for future experimental studies to confirm proposed invasion mechanisms. We also found evidence of mechanistic context dependency via regional differences in causal structures between the two study regions, implying that large-scale processes modulate invasion driver relationships (e.g., cross-scale interactions *sensu*; Soranno et al. 2014). Moving forward, identifying and accounting for sources of apparent and mechanistic context will be important for comparing empirical studies among regions and taxa.

Author Contributions

B.K.P., S.R.M., and J.D.O. secured funding for this work. W.K.A. conducted analyses, and all authors helped guide analyses. W.K.A. and B.K.P. conceived and developed the idea, and developed early manuscript drafts. W.K.A. and L.M.T. obtained and created the database. All authors contributed text to each draft of the manuscript.

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Disclosure

Any opinions, findings and conclusions or recommendations expressed in this material are those of the author(s) and do not necessarily reflect the views of the National Science Foundation.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data availability statementFish occurrences were obtained through data sharing agreements with governmental agencies. These data are not directly available for redistribution; however, data can be accessed through formal requests to the agencies listed in Appendix 1. Individuals with completed data requests may contact the corresponding author for harmonised versions of the data. Native fish distributions can be obtained by request to NatureServe (datasupport@natureserve.org) and the Nonindigenous Aquatic Species Database from the U.S. Geological Survey (https://nas.er.usgs.gov/taxgroup/fish/default.aspx). Level III ecoregion boundaries can be acquired from the Environmental Protection Agency's (EPA) Ecosystems Research website (https://www.epa.gov/eco-research/level-iii-and-iv-ecoregions-continental-united-states). Flowline data used to merge ecoregions with COMIDs can be found from the National Hydrography Databset Plus Version 2 (https://www.epa.gov/waterdata/get-nhdplus-national-hydrography-dataset-plus-data). Fishing demand from data is available at the EPA EnviroAtlas (https://www.epa.gov/enviroatlas), elevation, temperature and watershed area values are available from the EPA StreamCat dataset (https://www.epa.gov/national-aquatic-resource-surveys/streamcat-dataset), and HAI values can be obtained from McManamay et al. (2022; https://zenodo.org/record/5839011). Code for the data analysis can be found at https://zenodo.org/records/12101006. .

Peer Review

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Additional supporting information can be found online in the Supporting Information section.

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