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PERSPECTIVE

# Spatial Scale and the Underestimation of Stream Fish Community Invadedness

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## ABSTRACT

**Scale-Dependency of Native Status:** Classifying populations as native or nonnative requires well-defined range boundaries for species. While many studies define native status according to large biogeographic realms, natural dispersal barriers often limit species distributions at regional or smaller spatial extents. As such, native/nonnative definitions are inherently scale-dependent and estimates of community invadedness thus depend on the spatial resolution at which native status is defined. For example, nonnative species can be introduced among realms, among regions within realms, and among ecological provinces within regions (hereafter, simply "provinces"). By explicitly considering the scale-dependency of native/nonnative status definitions, we can more effectively compare results across studies, more comprehensively evaluate the degree of invasion levels, and more objectively communicate the native status of a species.

**Location:** 30,034 stream segments, conterminous United States.

**Time Period:** 2000–2023.

**Major Taxa Studied:** Freshwater fishes.

**Quantifying Fish Community Invadedness Across** US **Streams:** We illustrate the importance of scale-dependent native status definitions by quantifying nonnative species richness and relative abundance in stream fish communities across the United States, finding that provincially nonnative species are nearly four times as prevalent as extra-realm nonnative species, and represented approximately 10% of all individuals in average community surveys.

**Implications:** Unrealistically broad native status definitions underestimate community invadedness. Dismissing regionally and provincially nonnative species can have severe ecological consequences, including displacement and hybridisation with native species and the loss of unique communities through biotic homogenisation. These consequences may undermine efforts to maintain and protect distinct local biodiversity and conserve endemic species.

## 1 | Introduction

Species occurrences can only be characterised as nonnative at a location based on the spatial boundaries of their native distribution. Therefore, the field of invasion science is intrinsically based on spatial scale—the combination of spatial extent (size of the study area) and spatial resolution (size of the observational unit) (*sensu* Turner and Gardner 2001). Invasion research explicitly addressing spatial scale, particularly spatial resolution, has largely focused on the invasion paradox, wherein the observed processes that drive establishment success differ between studies conducted at small versus large spatial scales (Fridley et al. 2007). More specifically, previous research has sought to understand the sources of scale dependency in the invasion process (e.g., Davies et al. 2005; Peng et al. 2019; Tomasetto, Duncan, and Hulme 2019), and the potential for regional differences in invasion dynamics (Iannone III et al. 2015; Beaury et al. 2020; Comte, Grantham, and Ruhi 2021).

Concurrent to addressing issues of scale dependency, invasion scientists have long grappled with the need for clear and objective rules for defining the nonnative and invasive status of a species in a location (Richardson et al. 2000; Colautti and MacIsaac 2004; Pyšek et al. 2004; Jeschke et al. 2014; Soto et al. 2024). Spatial definitions of species' native range limits, and thus native status, have been variably expressed in the past. Examples of spatial units commonly used in native distributions include biogeographic realms (e.g., Blanchet et al. 2009), continents (Guo, Qian, and Zhang 2022), major world river basins (Tedesco et al. 2017), or national boundaries (e.g., Beaury et al. 2020). Yet, for many species, additional natural barriers exist within these broad spatial units that constrain species' native distributions, making it possible for a species to have both native and nonnative populations within the larger spatial unit (McKinney 2005; Nelufule et al. 2022). As such, a species occurrence classified as native at one spatial resolution (e.g., a nation) may be classified differently at a smaller resolution (e.g., an administrative unit). However, despite increased attention to scale dependency in the invasion process and efforts to establish clearer definitions in invasion science, the scale-dependent nature of species range limits and native status has received little consideration (Guo and Ricklefs 2010; Vitule et al. 2019; Nelufule et al. 2022).

Defining the native or nonnative status of species' populations—the most basic premise in invasion science—is inherently a hierarchical, scale-dependent process. All species have a native range that is spatially defined based on dispersal ability, natural barriers, and habitat requirements. Our ability to define the native range for a taxon is further constrained by dispersal ability, the availability of reliable historical occurrence records, and a clear understanding of its evolutionary and biogeographic history. Yet, given that all habitats are hierarchical in some way (e.g., Klijn and Udo de Haes 1994; Costello 2009; Omernik and Griffith 2014), and most species are globally rare and would therefore not have natural distributions that span entire continents or biogeographic realms (e.g., Enquist et al. 2019), logic dictates that the native range of most species should be spatially defined at sub-continental resolutions (e.g., only a specific set of ecoregions; Olson et al. 2001). Any species occurrences outside of that sub-continental native range would be considered nonnative. Overlooking the scale-dependency of native status has, in part, contributed to a rich literature of invasion science that is empirically well-supported, but also very contextual to the spatial definition used in assigning native/nonnative status. For example, Guo and Ricklefs (2010) demonstrated that not considering intranational plant introductions in mainland systems has resulted in the perception of islands being more susceptible to invasion than mainlands. Additionally, the spatial definition of native status is not always clearly specified in the literature (e.g., Dawson et al. 2017; Vitule et al. 2019), which can confound comparisons among studies.

The present study uses Nearctic freshwater fishes as a case study to support the perspective that different scale-based definitions of species native status can affect perceived levels of community invadedness. The consequences of our definitions extend beyond the basic science community to natural resource managers and the general public whose motivations and opinions, respectively, are shaped by species origins (Davis et al. 2011; Gbedomon, Salako, and Schlaepfer 2020). We contend that by explicitly considering the scale-dependency of native/nonnative status definitions, we can more effectively compare results across studies, more comprehensively evaluate the degree of invasion levels, and more objectively communicate the native status of a species to diverse audiences.

## 2 | Scale-Dependent Native Status in Freshwater Fishes

Freshwater fishes exemplify the phenomenon of scale-dependency in species' native status. Freshwater systems are organised into nested watersheds based on discrete geological and habitat boundaries that constrain natural fish dispersal and restrict native ranges (Fausch et al. 2002). Watersheds that are nearby in overland distance can be separated by great fluvial distances and major obstacles that inhibit natural freshwater fish movement (e.g., land, waterfalls, oceans; Tonkin et al. 2018). Accordingly, many adjacent watersheds in the conterminous United States (US) are separated by tens of thousands to several million years of unique evolutionary history. This restricted spatial structure, combined with continentally variable geologic history and biogeographic events, has resulted in a regionally unique freshwater fish fauna with discrete provincial boundaries (i.e., watersheds; Mayden 1988). Note that we use "provincial" and "province" ecologically, not politically, to refer to spatial units smaller than a region. Based on dispersal limitations, natural barriers, and the historical record, native status of freshwater fishes can be most narrowly defined at the provincial scale (HUC8: 8-digit hydrologic unit, $\bar{x} = 4621\,\text{km}^2$, Nature Serve 2020). River networks in the US are categorised into nested, increasingly smaller discrete units from major regional river drainages (HUC2: 2-digit hydrologic unit, Watershed Boundary Dataset, WBD; Jones et al. 2022) to interconfluent stream segments (COMID, National Hydrography Dataset; McKay et al. 2012). Thus, the native/nonnative status of an individual freshwater fish at a given location can be defined in increasingly larger incremental watershed units from the provincial scale (HUC8) out to the biogeographic realm scale (Figure 1). In other parts of the world, analogous scaling schemes have been developed at continental (e.g., Vogt et al. 2007; Kikoyo 2023) and global extents (Linke et al. 2019; Lehner et al. 2022).

Species occurrences considered native and nonnative depend on the spatial scale at which native status is classified (Figure 1). Thus, choosing a spatial definition of native status has direct effects on quantitative estimates of nonnative species richness and other measures of community invadedness (i.e., relative abundance of nonnative species) in ways that have the potential to fundamentally alter our perception of invasion levels. To demonstrate the scale-dependent native status of freshwater fishes in US stream segments, we focus on three specific spatial scales: biogeographic realm, regional, and provincial (Figure 1). Specifically, extra-realm nonnative species are those introduced from outside the focal realm—in this case, the Nearctic. Regionally nonnative species are those introduced from another region within the Nearctic realm (i.e., a different HUC2 regional watershed), and provincially nonnative species are those introduced from a watershed within the same region (i.e., a HUC8 outside the species' native range but within its native HUC2) (Figure 1). Although we treat these as discrete scales, we acknowledge that the concept of scale is continuous, and other spatial definitions may be more appropriate in other circumstances, especially for other taxa. Additionally, while our terminology is reflective of invasions, we are specifically referring to any freshwater fish outside of its spatially defined native range. Given the dispersal limitation of freshwater fishes, these introductions are known to be human-mediated. Some regionally and provincially nonnative fishes are known to have negative effects on native ecosystems; however, these nonnative fishes are chronically understudied and we do not assume that all of them are currently spreading or are harmful invaders (Cucherousset and Olden 2011; Hartman and Larson 2023).

Previous research in freshwater fishes has defined native status at spatial scales finer than the biogeographic realm, but few studies have explicitly considered multiple delineations simultaneously. Some common finer resolution spatial scale native

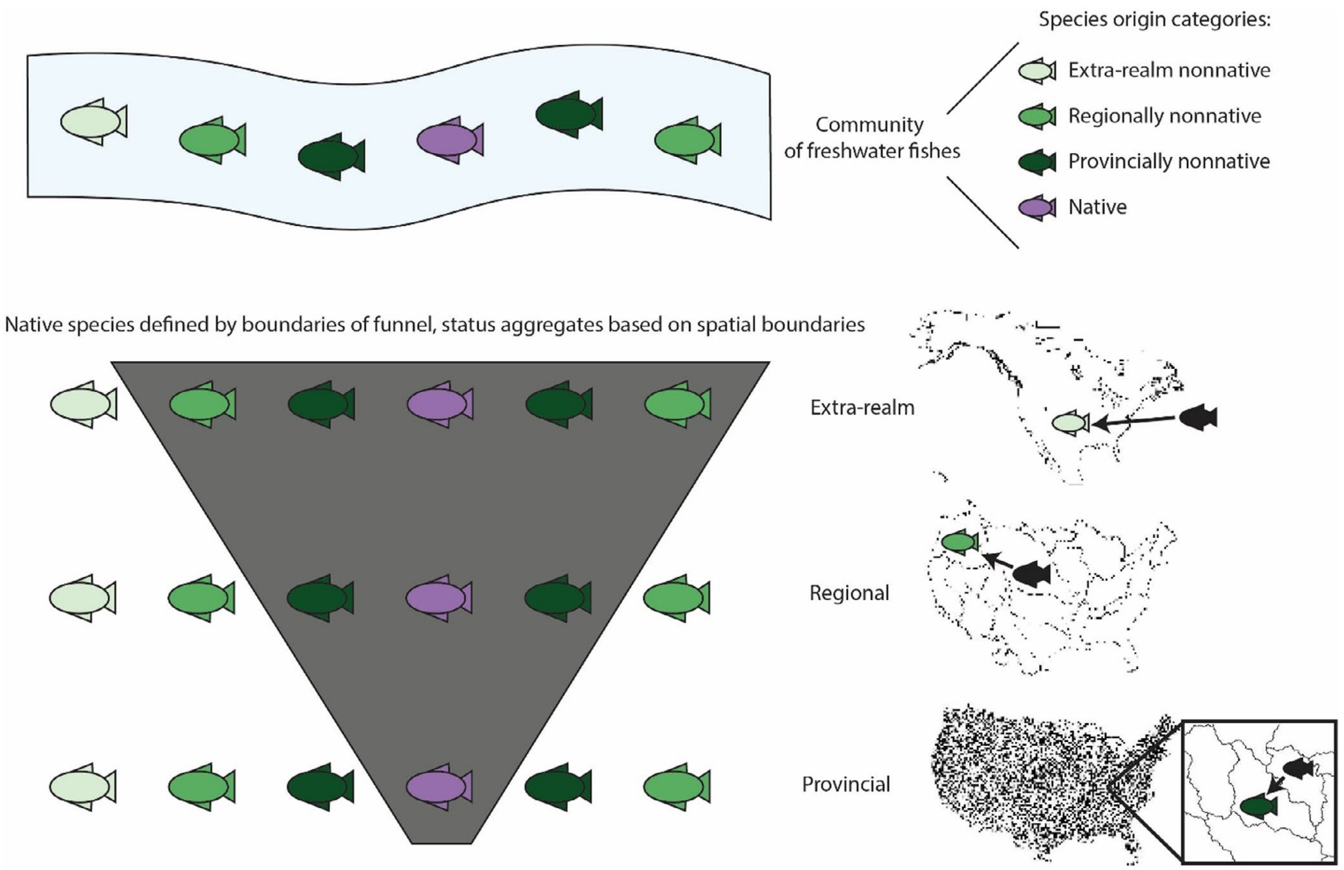


**FIGURE 1** | A freshwater fish community in the United States (US) is comprised of fish belonging to one of four species origin categories: *Extra-realm nonnative* fish (pale green) that have been introduced from outside the US, *regionally nonnative* fish (light green) that have been introduced from another region (HUC2) within the US, *provincially nonnative* fish (dark green) that have been introduced from another province (HUC8) within the same region, and *native* fish (purple) that are native to the province (HUC8) and all larger spatial units. Species status is typically aggregated into a dichotomy of native or nonnative. This aggregation can be visualised as a spatial "funnel" that filters fish considered native (inside the dark grey funnel) from those considered nonnative (outside the funnel). Therefore, when species status is aggregated based on biogeographic realm only the species with native ranges outside of the Nearctic realm are considered nonnative (nonnative = extra-realm nonnative; native = native + provincially nonnative + regionally nonnative). When aggregated by region, all species not native to the region are considered nonnative (nonnative = regionally nonnative + extra-realm nonnative; native = native + provincially nonnative), and when aggregated by province, all species not native to the province are considered nonnative (nonnative = provincially nonnative + regionally nonnative + extra-realm nonnative; native = native). Black fish indicate the native range before introduction.

status definitions include US state boundaries (Rahel 2000), watersheds associated with particular US states (e.g., Gido, Schaefer, and Pigg 2004; Marchetti et al. 2004; McKinney 2005; Kirk, Maitland, and Rahel 2020), "drainages" (Gido and Brown 1999), "river basins" (e.g., Olden, Kennard, and Pusey 2008; Liu et al. 2017; Sommerwerk et al. 2017; Tedesco et al. 2017), and our provincial (HUC8) definition. Studies using these narrower definitions of native status have contributed to our understanding of invasion patterns (Davis and Darling 2017; Anas and Mandrak 2021; Qian et al. 2023), drivers of nonnative richness (Guo and Olden 2014; Peoples et al. 2018), and biological homogenisation (Kirk, Maitland, and Rahel 2020; Peoples et al. 2020; Sleezer et al. 2021). While this foundational work has greatly contributed to our understanding of invasion patterns in freshwater fish, gaps remain in our understanding of how spatial precision in native status definitions changes the inferences we can make about nonnative success.

Using Nearctic freshwater fishes as a model system, our goal is to provide a detailed example of how specific spatial native status definitions change the observed prevalence of nonnative species in communities—a fundamental metric in invasion ecology. We use stream segment level data nested within a clearly defined watershed scaling scheme using explicit, reproducible spatial scale definitions of native status to demonstrate that specific spatial definitions of native status change the observed contribution of nonnative fishes to local $\alpha$-diversity (i.e., species richness, relative abundance) across the US.

## 3 | Quantifying Fish Community Invadedness Across US Streams

We illustrate changes in community invadedness with differing spatial definitions of native status by leveraging contemporary (2000–2023) stream fish community assemblage data from 30,034 local stream/river segments (COMIDs; McKay et al. 2012) spanning the US (Figure 2, Table S1). Unlike many assessments of nonnative species prevalence across the landscape (e.g., Castro et al. 2023), we specifically exclude elemental and incidental occurrences from targeted surveys (e.g., sport fish surveys). Instead, all data were collected using standardised electrofishing protocols designed to characterise local fish community structure (Meador, McIntyre, and Pollock 2003). These are based on protocols meant to monitor stream fish communities uniformly across the US (e.g., Barbour et al. 1999; Moulton et al. 2002). Although actual counts may not be comparable among data sources, richness and proportional representation of species are comparable. Each stream segment included in the assessment was represented by the single most recent survey, which meant that we could be confident that the communities in our assessment were made up of truly co-occurring species because they were all observed concurrently. It also was necessary to have data at the survey level to calculate meaningful relative abundance values. Thus, this large extent, fine-resolution dataset allowed us to directly assess levels of community invasion with real snapshots of community diversity and relative abundance, rather than summarised data representing the possible communities in a broad spatial unit.

Provincial native range maps are available for freshwater fishes in the US, and we combined native status information from the two main sources of this information to be the most conservative in our definition (NatureServe 2020; U.S. Geological Survey 2024). These maps were created using species occurrence data primarily from US state natural heritage programs, supplemented by the scientific literature, and reviewed by species experts (NatureServe 2020; U.S. Geological Survey 2024). They provide the very best available information on native distributions for freshwater fishes in the US and have been used to extensively in the literature both for determining native status of species occurrences and to provide data to represent historic fish communities (e.g., Anas and Mandrak 2021; Qian et al. 2023; Coulter et al. 2024; Silknetter et al. 2024). For each stream survey, we assessed levels of community invadedness using metrics of nonnative relative abundance (based on individual counts) and nonnative species richness (based on number of species). We first calculated the relative abundance (proportion of total

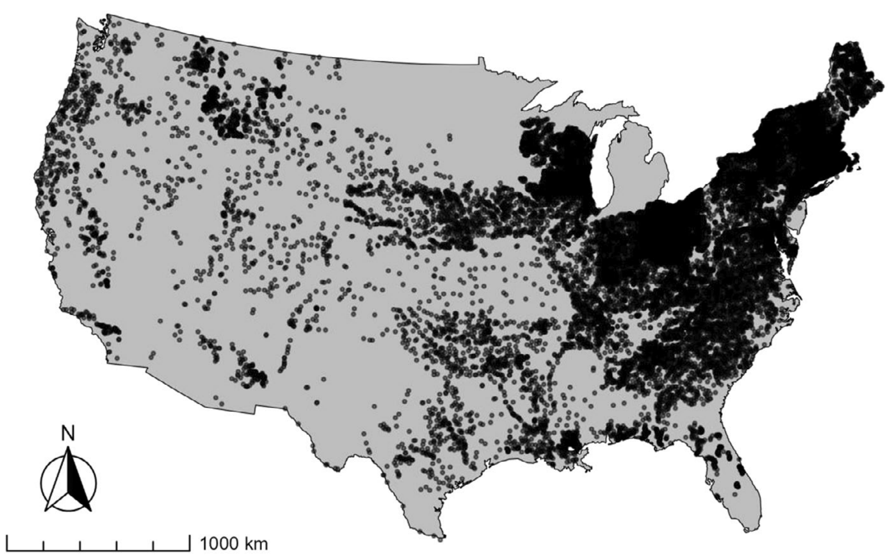


**FIGURE 2** | Map of stream fish community locations represented in the data evaluated. Each point corresponds to a stream segment (COMID) and the observations from the single most recent survey in that stream segment are presented here ($n = 30{,}034$).

individuals considered nonnative) and species richness of fishes in a community divided into each of the following four species origin categories: native fish (HUC8), provincially (HUC8) nonnative fish, regionally (HUC2) nonnative fish, and extra-realm nonnative fish (Figure 1). Based on those same spatial scales, we then aggregated these species origin categories into the simple classification dichotomy of native and nonnative. Extra-realm nonnative species are inherently nonnative at finer scales, but not necessarily vice versa. Thus, nonnative aggregation occurs upwardly from fine to coarse spatial scales. At the regional scale, for example, aggregate nonnative species would include those species with the regionally and extra-realm nonnative species origin categories (nonnative to HUC2 and above), while aggregate native species would include all species belonging to the native and provincially nonnative species origin categories. We differentiate between the two classification schemes by using species origin category to refer to the specific level at which a species becomes nonnative to a location and aggregate to refer to the classification into either native or nonnative at a particular spatial scale. To visualise how the different scale-dependent species origin categories influence perceived patterns of community invadedness across the landscape, we then conducted a hotspot analysis on average nonnative richness from stream segment communities summarised by province (HUC8). Spatial clumping of values was considered different than random using a Getis-Ord global *G* statistic with a threshold of $\alpha = 0.05$. Community invadedness was quantified using R version 4.3.0 (R Core Team 2021) and hotspot analyses were conducted using the packages 'spdep' version 1.3-3 (Bivand 2022) and 'sfdep' version 0.2.3 (Parry and Locke 2024).

## 4 | Spatial Dependency of Fish Community Invadedness

Based on species origin category, 2% of the 10.66 species observed in an average US stream fish community are categorised as extra-realm nonnative, and another 2% are regionally nonnative. Provincially nonnative species are more than twice as prevalent as either regionally or extra-realm nonnative species, making up 5% of the species in an average community (Figure 3a). When we assess levels of the species origin categories based on relative abundance, nearly 3% of individuals in an average stream community are not native to the Nearctic realm (extra-realm nonnative), another 3% of individuals are regionally nonnative, and nearly 4% of observed individuals are provincially nonnative (Figure 3b).

When we consider fish community invadedness in aggregate, 2.5% of individuals (1 in 40) and 2.3% of species (1 in 44) observed in an average stream survey in the US are not native to the Nearctic realm. The level of invasion increases with finer resolution aggregations of species status. When species status is aggregated at the regional scale, the prevalence of nonnative species in a single average stream survey approximately doubles to 5.5% of individuals (1 in 18) and 4.5% of species (1 in 22). Using the finest, provincial-scale aggregation the level of invadedness roughly doubles again; 9% of individuals and 9.7% of species in a single average survey are nonnative fishes. In other words, nearly one in every 10 fish observed in a given stream fish community survey in the US is nonnative (Figure 3c,d).

Species richness of the species origin categories was unevenly distributed across the US based on our hotspot analysis (Figure 4). Extra-realm nonnative fish species occur significantly more than expected by chance in the central United States and along the Mississippi River (Figure 4a). The most common fish species contributing to this pattern of extra-realm nonnative richness across provinces (Table S2) are carps (*Cyprinus carpio*, *Hypophthalmichthys spp.*, *Ctenopharyngodon idella*, and *Carassius auratus*) and Brown Trout (*Salmo trutta*). Regionally nonnative species are less prevalent in the central portion of the US than expected by chance and instead significant hotspots of regionally nonnative species were found in communities in the mid-Atlantic and western portions of the US (Figure 4b). Rainbow Trout (*Oncorhynchus mykiss*) and Brook Trout (*Salvelinus fontinalis*) are the most common species in provinces with more regionally nonnative species than expected (Table S3), likely due to the largely intentional cross-regional introductions of these sport fish species (Fausch 2008). Provincially nonnative species occur in numbers greater than expected by chance in the central portion of the US and especially in the Mid-Atlantic (Figure 4c). Species associated with angling are the most common fishes contributing significantly higher than expected levels of nonnative species (Table S4). These include species that are common targets of angling, such as sunfishes (*Lepomis* spp.), black basses (*Micropterus* spp.), and catfishes (*Ictalurus* spp. and *Pylodictus olivaris*). Other provincially nonnative species that occur in higher numbers than expected include those commonly used for bait or those that are easily transported inadvertently through hatchery stockings (e.g., many species of New World minnows, Leuciscidae).

Our evaluation of multiple detailed, reproducible spatial definitions of nonnative status based on biogeographic watershed boundaries using local community survey data demonstrates the fundamental consequences of these choices. When aggregated at the biogeographic realm, 1 in 4 fish communities (23%) were invaded, and invadedness increased to nearly 2 in 5 communities (35%) when species status was aggregated at the regional level. However, when aggregated at the provincial level, 52% of the stream segments we evaluated had at least one nonnative species—more than double the level using the biogeographic realm definition and well over the majority of streams in the US. Thus, we demonstrate a considerable underestimation of the prevalence of nonnative individuals and species in local fish communities when native status was classified with broad spatial definitions. This finding is reinforced by previous work demonstrating that the global hotspots of nonnative freshwater fishes dramatically changes when intra-nationally nonnative species are considered (Dawson et al. 2017; Vitule et al. 2019). Moving forward, it is clear that unambiguous, reproducible spatial definitions of native status at the finest resolution available should be standard in invasion science.

## 5 | Implications

Defining species occurrences as native or nonnative based on spatial definitions broader than the realities of species' natural distributions will cause an underestimation of community invasion. This may subsequently increase the potential for negative ecological and economic impacts of harmful, but overlooked, nonnative

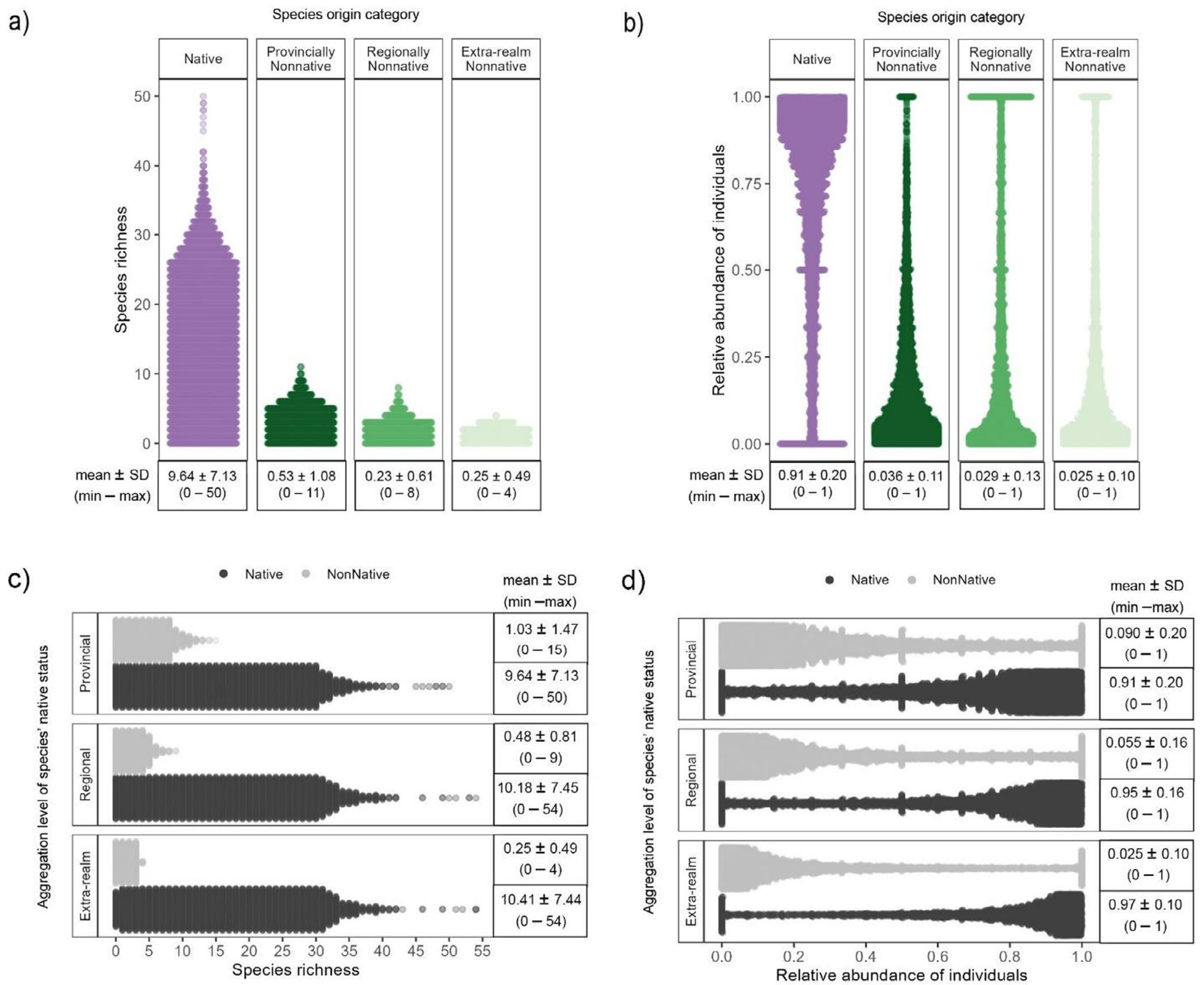


**FIGURE 3** | Native and nonnative species richness and relative abundance in freshwater fish communities of the United States visualised with beeswarm plots. Each fish in a community can be classified based on the finest spatial resolution (HUC8, HUC2, Neartic Realm) at which the species becomes nonnative as either native (HUC8), provincially (HUC8) nonnative, regionally nonnative (HUC2), or extra-realm nonnative (Figure 1). This is visualised for our fish communities of the US based on (a) species richness and (b) relative abundance. Typically, species status is presented for research as a dichotomy of native or nonnative based on the aggregation of species considered native or nonnative a specific spatial scale. We demonstrate how the choice of spatial scale for classification of spatially aggregated species status changes the level of community invadedness for (c) species richness and (d) relative abundance. Colours in (a) and (b) correspond to equivalent conditions in Figure 1. In (c) and (d), native fish are shown dark grey corresponding to the native "funnel" in Figure 1 and nonnative fish are shown in light grey.

species. The vast majority of Nearctic-native, but regionally- and provincially-nonnative freshwater fishes are understudied in their introduced range. Thus, very little is known about their impacts on native ecosystems (Hartman and Larson 2023). However, there is a growing body of evidence demonstrating that the introduction of these species can have severe consequences. For instance, regionally and provincially nonnative species are associated with the reduction of native species through displacement (e.g., Peterson, Fausch, and White 2004) and hybridisation (Muhlfeld et al. 2014), as well as the loss of unique communities through biotic homogenisation (Scott and Helfman 2001; McKinney 2005). Thus, the use of terminology like "native-alien," "native transplant," "native invader," or other similar nomenclature with contradictory verbiage obscures the potential and known threat posed by these species (reviewed in Nelufule et al. 2022; Soto et al. 2024). Furthermore, this terminology can be counterproductive to conservation efforts in public discourse because it casts these introductions in a favourable light. We discourage the use of blurred terminology that minimises potential threats of nonnative species, and instead encourage clear, unambiguous spatial definitions of native status in invasion science as much as possible, given species' life histories and native distributions.

Scale-dependent native status also carries implications for testing general theories of invasion ecology. Empirical support for major invasion hypotheses is based on variable spatial definitions of native status. However, the implications for how this variability contextualises our understanding of invasion theory remain unexplored. As an example, consider Darwin's naturalisation conundrum: It predicts that phylogenetic similarity between

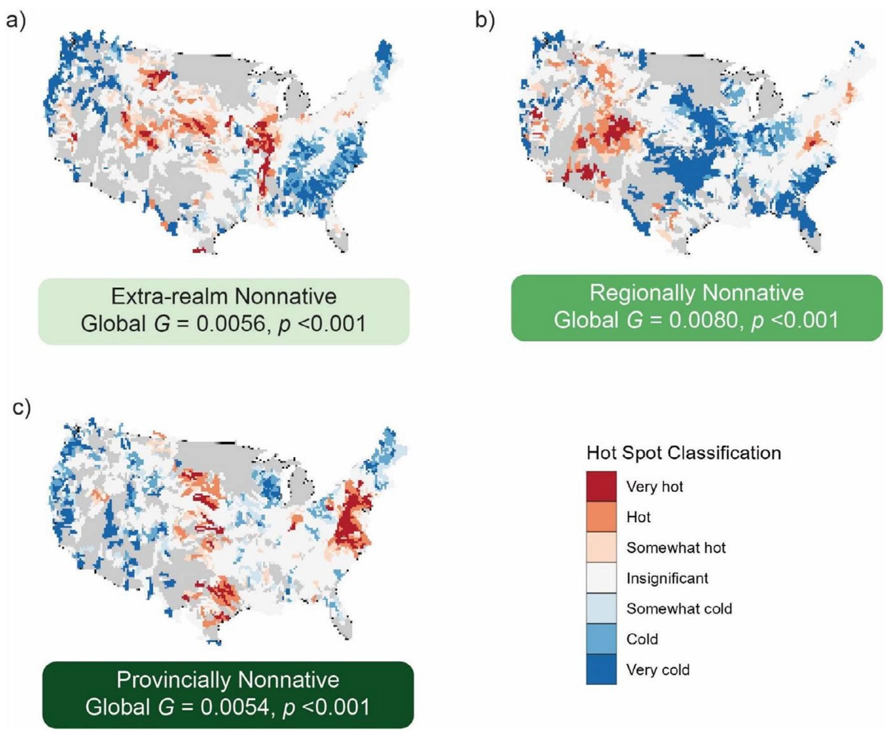


**FIGURE 4** | Results of hotspot analysis (local Getis-Ord Gi* test) for extra-realm nonnative (a), regionally nonnative (b), and provincially nonnative (c) species origin categories richness averaged from stream fish communities in the United States (US) by province (HUC8). Provinces are symbolised in a colour gradient based on whether observed nonnative species richness was statistically higher (red) or lower (blue) than expected at random. Values not different from random are symbolised in white.

native and nonnative species would either resist invasion because their similar traits would result in competitive exclusion of the nonnative species, or would promote invasion because phylogenetic similarity to native species suggests nonnative species are preadapted for survival in the new habitat (Darwin 1859; Diez et al. 2008). Clearly, the extent to which these predictions may be supported is directly spatially-dependent and based on both physical and phylogenetic distance between the invaded community and the native range of the species being introduced (Park et al. 2020). Evidence of Darwin's conundrum suggests that competition is more important at small scales and environmental filtering is more important at large scales (Park et al. 2020). For provincially nonnative species, the physical and phylogenetic distance to members of the recipient community will be much closer than extra-realm nonnative species (Strecker and Olden 2014). Thus, future work could investigate whether studies using smaller resolution native status support the competitive exclusion hypothesis (e.g., biotic resistance) and studies using larger resolution native status support the environmental filtering.

Another example of how scale-dependent native status may affect empirical support for invasion theory can be found in disturbance-based hypotheses, in which nonnative species are expected to thrive in disturbed habitats because they are tolerant generalists (Elton 1958; Hobbs and Huenneke 1992; Nordheimer and Jeschke 2018). Indeed, cosmopolitan extra-realm nonnative species may be tolerant of a larger range of conditions, making them more likely to be successful in a disturbed nonnative habitat (Bomford, Barry, and Lawrence 2010). However, more specialised, provincially nonnative species may be preadapted to a similar set of environmental conditions as the native species in a community, and thus, would be equally susceptible to negative effects from anthropogenic habitat disturbance. As such, empirical results using an extra-realm definition of native status may suggest that disturbance promotes invasion, while a provincial definition of native status may suggest that disturbed areas contain fewer species regardless of native status. A logical next step in this line of inquiry would be to empirically investigate how our understanding of these and other established invasion hypotheses (e.g., Barney and Whitlow 2008; Catford, Jansson, and Nilsson 2009; Blackburn et al. 2011) may change based on the spatially-varying definition of nonnative species status.

The finest possible spatial resolution of native status depends on the focal organism. We studied stream fishes specifically because they provide a system with clear, reproducible spatial delineations (watershed drainages), extensive species introductions, and fine resolution native range maps, allowing us to provide a tractable example of how our perception of invadedness can change based on native status definitions. While not all organisms have this level of spatial constraint or known introduction pathways, most species have native ranges that are smaller than an entire biogeographic realm. In these cases, introductions and spread within that realm can negatively impact native species and communities. For example, barred owls native to eastern US displace spotted owls in western US (Gutiérrez et al. 2007; Holm et al. 2016), and American bullfrogs native to eastern US negatively impact native frogs in western US (Snow and Witmer 2010; Yap et al. 2018). In terrestrial systems and for species that are less spatially constrained, establishing the appropriate spatial scale will be contingent on the availability of historic range data and the mobility of species across the landscape. Although other taxa may not have as clearly defined provincial native ranges as the freshwater fishes in our example, we join others in encouraging the use of the finest resolution native status definition available and appropriate in order to achieve the most robust understanding possible of invasion processes and potential impacts (Guo and Ricklefs 2010; Nelufule et al. 2022; Soto et al. 2024). Even if the most appropriate spatial definition is a broad one, we encourage researchers to clearly state it in their manuscripts to ensure that their work is reproducible and comparisons among studies are more meaningful.


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### Conflicts of Interest

The authors declare no conflicts of interest.

### Data Availability Statement

Fish occurrences were obtained through data sharing agreements with governmental agencies (Table S1). These data are not directly available for redistribution. However, summarised data files and code for the data analysis can be found at https://zenodo.org/doi/10.5281/zenodo.12797561. Native fish distributions can be obtained by request to NatureServe (datasupport@natureserve.org) and through the Nonindigenous Aquatic Species Database from the U.S. Geological Survey (https://nas.er.usgs.gov/taxgroup/fish/default.aspx).

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**Supporting Information**

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