

Differential saturation of Pacific Northwest and Southeast (USA) fish assemblages

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Abstract – Plots of local versus regional richness have been used to test whether assemblages are ‘saturated’ with species. However, the validity of these tests is limited by scale-dependence and arbitrarily defined sampling units, statistical autocorrelation between local and regional richness data, and the confounding effects of propagule pressure. In this study, local versus regional richness plots were used to test the saturation hypothesis for Pacific Northwest and Southeast (USA) fish assemblages, taking care to account for each of the above problems. Specifically, longitudinal river zones were used to ensure that the regional sampling units were not scale-dependent or biologically arbitrary. A log-ratio transformation was used to remove autocorrelation from the local and regional richness data. And a comprehensive fish stocking database was used to account for propagule pressure. Results suggest that the Pacific Northwest fish assemblages, which have low native richness, are not saturated, but the species-rich Southeast assemblages are at or approaching saturation.

Key words: local versus regional richness; regional species pool; non-native species; propagule pressure; longitudinal zonation

Introduction

Nonnative fishes are rapidly becoming established in U.S. freshwaters (Mitchell & Knouft 2009). So far, nonnative fish invasions have tended to outpace native extirpations in the United States, and the net effect has been one of homogenisation; overall richness has increased while differences between fish assemblages have decreased (Rahel 2000). But nonnative invasions have not occurred at equal rates throughout the United States. They are most common in the west, where native fish richness is relatively low (Schade & Bonar 2005). In the east, where native fish richness is higher, nonnative invasions are less prevalent (Gido & Brown 1999).

Noting that numbers of native and nonnative fish species are often inversely correlated within a given system (see Ross 1991; Gido & Brown 1999), some researchers have suggested that biotic resistance may be a key determinant of invasion success (e.g., Tonn et al. 1990; Angermeier & Winston 1998). The underlying assumption is that all else being equal,

interspecific competition for limiting resources should be more intense in systems with many resident, native species than in systems with few native species (Kennedy et al. 2002). In this way, nonnative species are more likely to survive and become established in species-poor systems. By the same logic, richness may increase over time until a system reaches its carrying capacity and becomes effectively ‘saturated’ with species (Case 1990).

Local versus regional richness (LRR) plots are simple tools that have been used to test the saturation hypothesis for a variety of freshwater fish assemblages (e.g., Angermeier & Winston 1998; Oberdorff et al. 1998). LRR plots model average local richness (dependent variable) as a function of the total richness within a larger region (independent variable). By convention, an asymptotic or curvilinear LRR model indicates that local richness is constrained by locally realised processes, such as interspecific competition, and that local assemblages are saturated. Alternatively, a linear LRR model suggests that local communities may be

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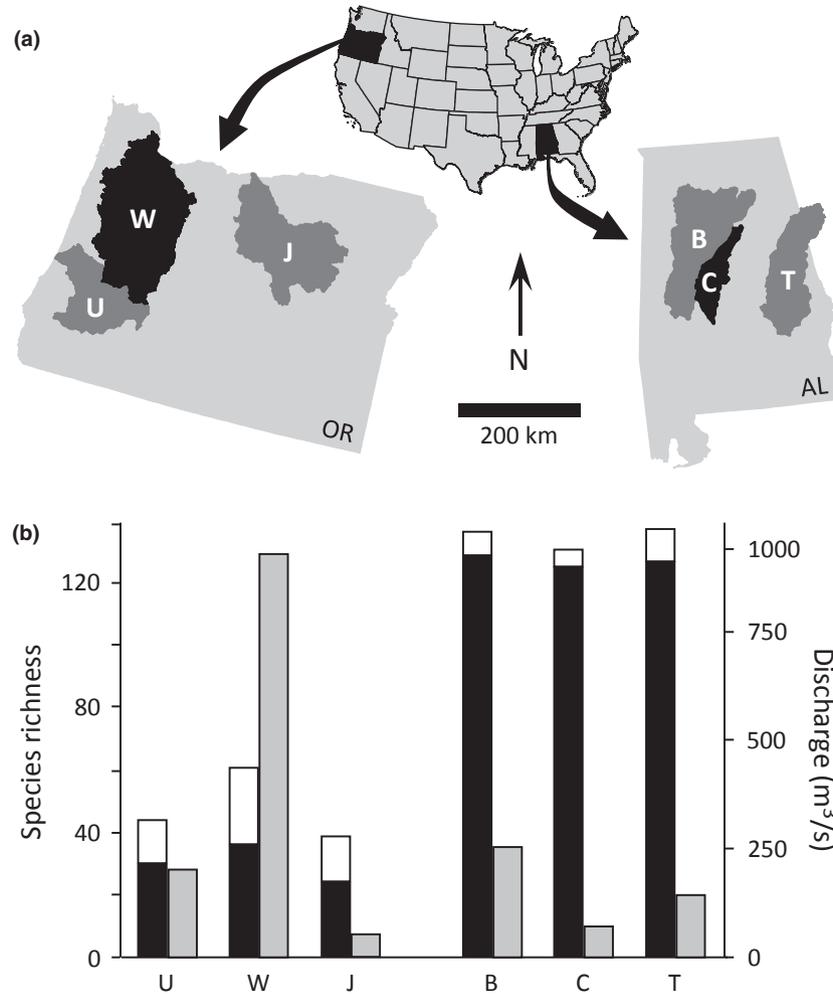


Fig. 1. (a) Map of the six study basins, in the states of Oregon (OR) and Alabama (AL). North-west rivers include the Umpqua (U; basin area = 12,133 km²), Willamette (W; area = 29,728 km²) and John Day (J; area = 20,980 km²). South-east rivers include the Black Warrior (B; area = 16,252 km²), Cahaba (C; area = 4,730 km²) and Tallapoosa (T; area = 12,108 km²). The OR and AL maps are plotted at a common scale. (b) Fish species richness and discharge in each river basin. Numbers of native and nonnative species in each basin are illustrated by black and white bars, respectively. Grey bars show mean annual discharge near the mouth of each river. Richness data were obtained from Boschung & Mayden (2004), McGarvey & Hughes (2008) and McGarvey and Ward (2008). Discharge data were obtained from the U.S. Geological Survey (<http://water.usgs.gov/>).

random subsets of a larger pool of potential colonists – the regional species pool (RSP) – and are therefore unsaturated (Cornell 1999).

Unfortunately, traditional LRR models are limited by several conceptual and statistical problems, three of which are addressed here. First, LRR results are often scale-dependent and prone to bias when biologically arbitrary definitions of local and/or regional assemblages are used (Srivastava 1999; Loreau 2000). Investigators must therefore use explicit, biologically defensible criteria to delineate local and regional assemblages (see ‘Estimating regional and local richness’ below). Second, standard regression methods should not be used to analyse the LRR relationship because local and regional richness are autocorrelated; by definition, local richness will always be less than or equal to regional richness

(Cresswell et al. 1995). A statistical tool to remove this autocorrelation is therefore needed (see Szava-Kovats et al. 2012). Third, low numbers of nonnative species may reflect biotic resistance or saturation, but they may also be artefacts of low propagule pressure. On average, nonnative species are more likely to become established in systems where many nonnative individuals are introduced or where repetitive nonnative introductions, such as stocking events, occur (i.e., where propagule pressure is high; Marchetti et al. 2004; Leprieur et al. 2008). Thus, one should not infer that a given assemblage is saturated and therefore resistant to invasion without first verifying that it has been exposed to a moderate to high level of propagule pressure (Gido & Brown 1999). Low propagule pressure weakens support for the saturation hypothesis.

In this study, I use improved LRR methods to address each of the above problems and test the saturation hypothesis for fish assemblages in Pacific Northwest and Southeast U.S. rivers. I begin by using longitudinal river zones, which are characterised by co-occurring species within relatively homogenous environments, to estimate regional richness (see 'Estimating regional and local richness' below). Next, I use the log-ratio transformation of Szava-Kovats et al. (2012) to account for autocorrelation in the local and regional richness data, thereby ensuring that the LRR results are statistically valid. I then use a national fish stocking database (Halverson 2008) to assess whether the LRR results may be artefacts of differential propagule pressure. Northwest and Southeast rivers were chosen because they exhibit a strong gradient in fish diversity, with higher native richness in Southeast rivers, and this gradient reflects the disparate environmental histories of the two biogeographical regions. Southeast U.S. rivers are relatively stable environments with low historical extinction rates, while Northwest U.S. rivers are historically unstable environments where numerous extinctions have occurred (Smith 1981; Moyle & Herbold 1987). I therefore hypothesised that the Southeast fish assemblages are at or near saturation, while the Northwest fish assemblages are not.

Material and methods

Study sites

Three Pacific Northwest (Umpqua, Willamette and John Day) and three Southeast (Black Warrior, Cahaba and Tallapoosa) rivers were included in this study (Fig. 1a). These rivers were chosen because they reflect the interregional trend in fish richness described above: the Northwest rivers have low native fish richness and high nonnative richness, while the Southeast rivers have high native fish richness and low nonnative richness (Fig. 1b). Notably, this disparity in native richness is not a simple effect of river size. The relatively depauperate Northwest rivers are comparable to or larger than the more diverse Southeast rivers, both in terms of total basin area and river discharge (Fig. 1b). Thus, the interregional differences cannot be attributed to a simple species-area or species-discharge effect.

Estimating regional and local richness

The first step that must be undertaken in an LRR study is to characterise the RSP in a biologically meaningful way. By definition, the RSP should

include only those species that are physically capable of migrating to and surviving in a typical locality within a given region, or would be in the absence of interspecific competition and predation (Srivastava 1999). Fish studies have often used geographical units such as river basins, physiographical provinces or lakes as RSPs (e.g., Griffiths 1997; Angermeier & Winston 1998). However, these units will overestimate the true size of the RSP if they combine species that have disparate habitat requirements or are otherwise unlikely to co-occur. For instance, a distinct longitudinal gradient in fish species' distributions and turnover was reported by Li et al. (1987; see their Fig. 24.2) for Pacific Northwest rivers. Strong gradients and discontinuities, such as high species turnover at the fall line, also exist in Southeast rivers (e.g., Mettee et al. 1996). LRR studies that use large river basins as RSPs without accounting for species' turnover within basins may therefore overestimate the true size of the RSP.

Longitudinal zones can potentially solve this problem. When examined at large spatial scales, such as complete river basins, many riverine fish assemblages can be divided into a series of adjacent, zonal subassemblages (Huet 1959; Hawkes 1975). Zonal structure is quantified using multivariate ordinations or clustering algorithms to locate longitudinal discontinuities in assemblage structure (McGarvey & Ward 2008). Adjacent locations that exhibit high turnover in species composition are indicative of zone boundaries, while locations between zone boundaries have comparatively similar assemblage structure. Longitudinal zones typically range from 10 to 100 km in length (e.g., Balon & Stewart 1983) and are often congruent with longitudinal transitions in physical habitat variables, such as water temperature and substrate composition (Hawkes 1975; Stutzner & Borchardt 1992; Lamouroux et al. 2002). Thus, longitudinal zones consist of species that co-occur within relatively uniform environments.

Similar zonation patterns have been described in each of the six rivers considered here. Using extensive fish assemblage data and common statistical methods, McGarvey & Hughes (2008) and McGarvey & Ward (2008) detected 'upper', 'middle' and 'lower' zones in each of the Pacific Northwest and Southeast rivers. In each river, the succession from upper to middle to lower fish zones coincided with a transition from small, cool, high-gradient environments with few resident species to large, warm, low-gradient habitats with comparatively rich, mixed fish assemblages. Zones were also of similar size among biogeographical regions. For example, mean wetted channel widths were, respectively, 11, 42 and 106 m in the upper, middle and lower zones of the Northwest rivers and 8, 38 and 99 m in the upper,

middle and lower zones of the Southeast rivers. Upper zone fish assemblages were composed primarily of sculpins (*Cottus* sp.) and cutthroat trout (*Oncorhynchus clarki*) in the Northwest rivers and small-bodied minnows (e.g., *Cyprinella* sp. and *Notropis* sp.), sunfishes (*Lepomis* sp.) and darters (*Etheostoma* sp.) in the Southeast rivers. Lower-zone fishes in the Northwest rivers included large-bodied species such as white sturgeon (*Acipenser transmontanus*), largescale sucker (*Catostomus macrocheilus*) and northern pikeminnow (*Ptychocheilus oregonensis*), in addition to small Cyprinids (e.g., *Acrocheilus alutaceus*, *Richardsonius balteatus* and *Rhinichthys* sp.) and a large number of nonnative sunfishes (*Micropterus dolomieu* and *Lepomis* sp.) and catfishes (*Ictalurus punctatus* and *Ameiurus* sp.). Characteristic species in the lower zones of the Southeast rivers included bowfin (*Amia calva*), paddlefish (*Polyodon spathula*), large suckers (e.g., *Carpionodes* sp. and *Moxostoma* sp.), Centrarchids (*Micropterus* sp., *Lepomis* sp. and *Pomoxis* sp.), Esocids (*Esox americanus* and *E. niger*), catfishes (*Pylodictis olivaris*, *Ameiurus* sp. and *Ictalurus* sp.), gars (*Lepisosteus* sp.), temperate basses (*Morone* sp.), freshwater drum (*Aplodinotus grunniens*) and Clupeids (*Alosa* sp. and *Dorosoma* sp.), in addition to many Cyprinids (e.g., *Cyprinella* sp. and *Notropis* sp.) and Percids (*Sander vitreus*, *Ammocrypta* sp., *Etheostoma* sp. and *Percina* sp.). Complete descriptions of the zonal fish assemblages and all data sources are provided in McGarvey & Hughes (2008) and McGarvey & Ward (2008).

In each of the Northwest and Southeast rivers, longitudinal zones satisfied the functional RSP criteria – species with overlapping distributions that could potentially co-occur at a given locality (Srivastava 1999) – better than complete river basins. In other systems, the use of complete river basins as RSPs has been justified. For example, Matthews & Robison (1998) used small, headwater drainage basins within the Ozark and Ouachita highlands (Arkansas) as RSPs, noting that these basins contained high-gradient, clear-water habitats that flowed into and were bounded by low-gradient, turbid rivers; fishes within the highland streams were free to move throughout them but were unlikely to enter turbid rivers further downstream. However, using complete river basins as RSPs in the Northwest and Southeast rivers would have pooled many species with disjunct ranges, thereby inflating the sizes of the RSPs. I therefore used longitudinal zones as RSPs and, in each zone, estimated regional richness as the sum of all species known to occur within the zone.

To estimate local richness, I began with the local fish assemblage definition of Matthews (1998, p. 2): ‘fish that occur together in a single place, such that

they have at least a reasonable opportunity for daily contact with each other’. By this definition, I assumed that conventional field samples could be used as indicators of local fish assemblage structure and richness. Specifically, I used field samples from the U.S. Environmental Protection Agency’s Environmental Monitoring and Assessment Program and the Alabama Geological Survey to characterise local fish assemblage structure in the Northwest and Southeast rivers, respectively. Fish sampling methods used in each of these programmes were standardised by habitat type: single-pass backpack electrofishing was used in shallow, wadeable habitats and boat electrofishing was used in nonwadeable habitats. Sampling effort was also similar among sites and biogeographical regions, with most sampling events lasting between 45 and 90 min (total electrofishing time) and encompassing $\sim 40\times$ the mean channel width (see McGarvey & Hughes (2008), McGarvey & Ward (2008) and references therein). Additionally, *post hoc* data analysis tools, such as species accumulation curves, were used to verify that the standardised field samples provided reliable, asymptotic estimates of local richness. For instance, Reynolds et al. (2003) and Paller (1995) showed that standardised field protocols consistently captured $\geq 90\%$ of all fish species that were locally present in Northwest and Southeast streams, respectively. For these reasons, I was confident that the standardised field samples could be used to identify fishes that potentially interact on a daily, real-time basis (i.e., to define local assemblages).

Local richness was then estimated within each longitudinal zone, or RSP, by calculating the mean richness of 10 randomly selected field samples. This resulted in nine LRR data points (3 zones \times 3 rivers) in each of the two biogeographical regions. Multiple field samples were combined into a single local richness average to avoid pseudoreplication; individual samples collected within a common RSP are spatially correlated and will therefore introduce a source of bias when treated as independent replicates in regression analyses (Srivastava 1999). By averaging field samples, I was able to incorporate some of the among-sample variability in my LRR analyses without introducing spatial bias. Error bars (± 1 standard deviation) were also included in the LRR plots as measures of among-sample variability.

Log-ratio transformation

The original LRR method used ordinary least squares regression of untransformed data to first test whether a significant linear relationship existed between local and regional richness and then to test whether a quadratic term significantly improved the fit of the model

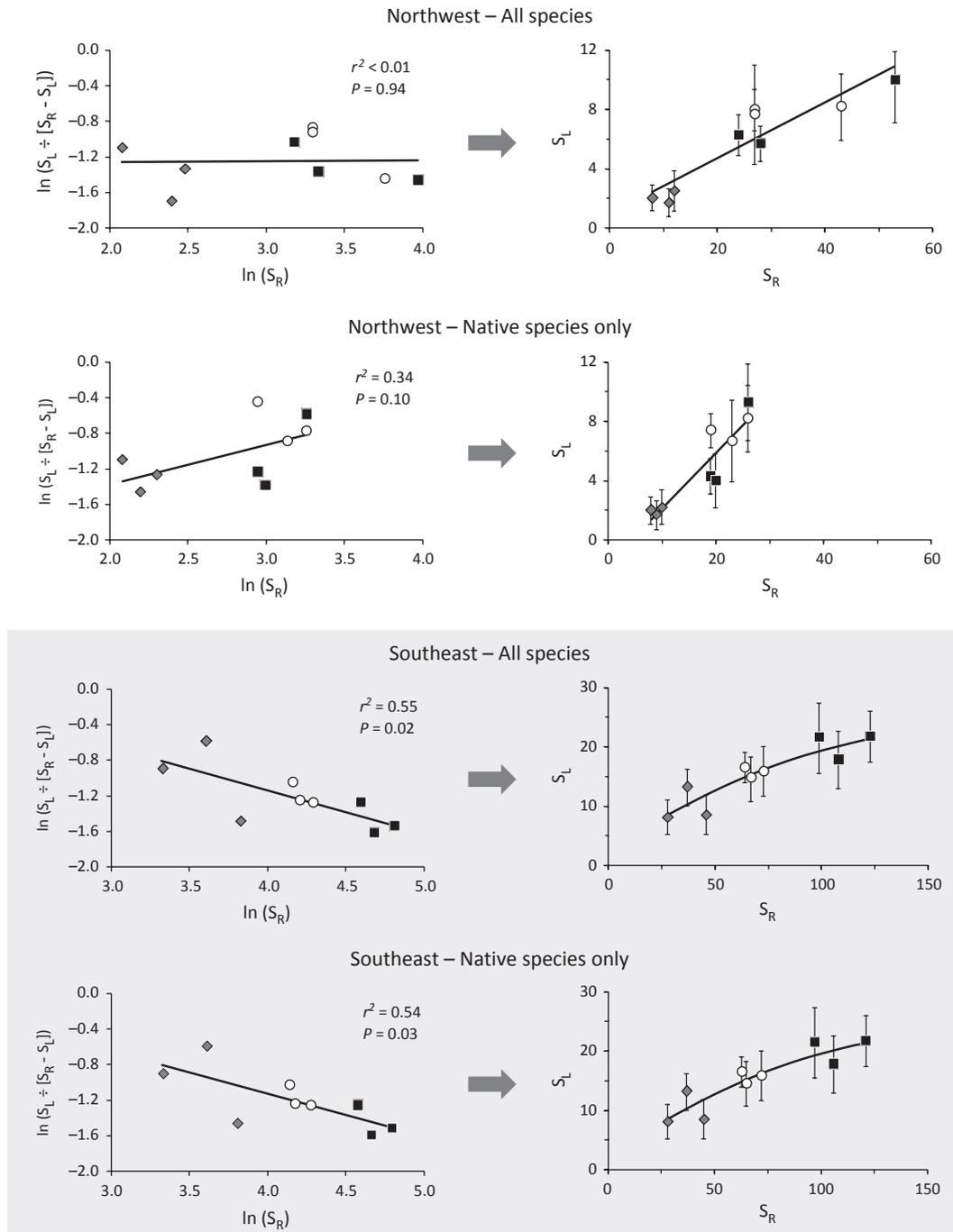


Fig. 2. Local (S_L) versus regional richness (S_R) plots for Northwest and Southeast rivers. Plots are shown for complete species lists ('All species') and for species lists that did not include nonnative fishes ('Native species only'). Log-ratio-transformed S_L and S_R data are shown on the left, and the untransformed arithmetic data are shown on the right. Each data point reflects a discrete longitudinal zone or regional species pool. Upper, middle and lower zones are indicated by grey diamonds, white circles, and black squares, respectively. S_L estimates are the mean averages of 10 randomly selected field samples within each zone; vertical error bars are ± 1 standard deviation in local richness.

(i.e., whether the relationship was asymptotic; Cornell 1999). However, this method was biased because untransformed local and regional richness data are autocorrelated. Local richness is always a subset of, and therefore less than or equal to, regional richness. This autocorrelation ensures that the resulting LRR relationship will be constrained to a 'wedge-shaped'

area in arithmetic space (i.e., the area below the 1:1 line in LRR plots), thereby invalidating ordinary regression results (Cresswell et al. 1995).

Szava-Kovats et al. (2012) solved this problem with a log-ratio transformation. They first partitioned regional richness into two additive components: α -diversity (local richness) and β -diversity (regional –

local richness). Next, they used an additive log-ratio transformation to generate the unconstrained, statistically independent function $y = \ln(\alpha\text{-diversity}/\beta\text{-diversity})$. Finally, they plotted y against the natural log of regional richness and used least squares regression to model the relationship. This allowed them to determine whether local richness was a relative, rather than absolute, function of regional richness. Significantly negative slopes provided unbiased evidence of asymptotic LRR relationships (in arithmetic space) while nonsignificant or zero-slope models were indicative of linear, unsaturated LRR relationships (see Fig. 1 in Szava-Kovats et al. 2012). I used this method to perform unbiased LRR tests for the Pacific Northwest and Southeast fish data.

Propagule pressure

Large numbers of nonnative species may create the impression that abundant, unoccupied niche space is available within a given system and that native assemblages are unsaturated. Alternatively, low numbers of nonnative species suggests that little unoccupied niche space is available and that native assemblages are saturated. But a valid test of the saturation hypothesis cannot be performed without first accounting for propagule pressure; one cannot prove that an assemblage is invasion resistant without first documenting that invasions have in fact been attempted (see Introduction; Gido & Brown 1999).

I used the fish stocking data of Halverson (2008) as an index of propagule pressure in Pacific Northwest and Southeast rivers. Halverson (2008) compiled all stocking efforts by state and federal

agencies in 2004, including total numbers of individuals and total biomasses stocked, and summarised these data by species and region (western, southern, north central, and north-eastern states). By comparing the numbers and biomasses of fishes stocked in western and southern states, I tested whether propagule pressure differs between the two biogeographical regions. These results were then combined with the LRR test results to assess the overall strength of evidence for the saturation hypothesis. If the LRR test results indicate saturation and the stocking data indicate high propagule pressure, support for the saturation hypothesis is increased. However, if the LRR results reflect saturation but the stocking data do not indicate high propagule pressure, support for the saturation hypothesis is weakened.

Results

When the log-ratio transformed LRR data were plotted for Pacific Northwest fishes, I observed little or no evidence of a significant relationship, negative or otherwise ($P \geq 0.10$; Fig. 2 upper panel). This was the case when all species were included in the LRR analyses and when only native species were included. Accordingly, the untransformed LRR plots (i.e., local and regional richness plotted in arithmetic space) were linear, rather than asymptotic, and provided no evidence for the saturation hypothesis. However, the LRR analyses did suggest that the Southeast fish assemblages may be at or approaching saturation. Both the all-species data set and the native-species-only data set exhibited significant, negative relationships when the log-ratio transformation was applied to the LRR data (Fig. 2 lower panel). The corresponding arithmetic LRR plots therefore exhibited significant curvature for Southeast fishes.

When all species were considered, fish stocking effort in the western United States exceeded that in the southern United States by an approximately 4:1 margin, both in terms of total numbers of individuals and total biomass (Table 1). However, these figures were potentially misleading because many of these fishes were native to the systems they were stocked in and should not be included in indices of nonnative propagule pressure. For example, ~50% of the fishes stocked in the western United States were native salmon, and ~70% of the fishes stocked in the southern United States were native sunfishes (Halverson 2008). When the stocking effort data were limited to nonnative species that are known to occur in at least one of the six study rivers (Fig. 1a), the number of individuals stocked in the western United States still exceeded the number stocked in the southern United States, but the total biomass of stocked fishes was greater in the southern United States (Table 1).

Table 1. Total numbers ($\times 1000$ individuals) and biomasses ($\times 1000$ kg) of fishes stocked in Western and Southern U.S. states in 2004.

	Western states [†]		Southern states [‡]	
	Number	Biomass	Number	Biomass
All species	424,820	10,805	111,767	2,684
Non-native species within study rivers	85,582	310	13,344	1,742
Without walleye	6576	288	–	–

[†]All species' data are inclusive of all stocked fishes. [‡]Non-native species within study rivers data are specific to non-native fishes that are stocked in the Pacific Northwest study basins (Umpqua, Willamette John Day) or the Southeast study basins (Black Warrior, Cahaba, Tallapoosa). Adjusted 'without walleye' numbers are not shown for the Southern states because walleye are native to the three Southeast rivers. All stocking data are from Halverson (2008).

[†]Western states include Oregon, Washington, Alaska, California, Nevada, Arizona, New Mexico, Utah, Colorado, Wyoming, Idaho, Montana, and Hawaii.

[‡]Southern states include Alabama, Mississippi, Louisiana, Texas, Oklahoma, Arkansas, Florida, Georgia, South Carolina, North Carolina, Tennessee, Virginia, West Virginia, Kentucky, and Maryland.

Furthermore, walleye (*S. vitreus*) comprised >90% of the remaining stocking effort in the western United States. But of the three Pacific Northwest rivers included in this study, walleye are only known to occur in the lower zone of the Willamette River, and they are generally rare within this zone (see McGarvey & Hughes 2008). When walleye were removed from the western stocking data, both the numbers and biomasses of stocked nonnative fishes were greater in the southern United States than in the western United States. Thus, the data of Halverson (2008) suggest that nonnative propagule pressure is not greater in Pacific Northwest rivers than in Southeast rivers. This in turn supports the hypothesis that Northwest rivers, which contain many nonnative fishes, are not saturated while Southeast rivers, which contain relatively few nonnative fishes, are at or near saturation.

Discussion

This study is, to my knowledge, the first to use LRR plots to test for differential saturation of riverine fish assemblages in two distinct biogeographical regions (but see Tonn et al. 1990 and Griffiths 1997 for lacustrine comparisons). LRR plots revealed no evidence of saturation within Pacific Northwest fish assemblages, but did support the saturation hypothesis for Southeast fish assemblages (Fig. 2). Moreover, these results were robust to methodological problems associated with previous LRR studies. The regional richness estimates, which were derived from longitudinal river zones, and the local richness estimates, which were derived from standardised field samples, were based on explicit biological criteria and did not require the use of arbitrary spatial units (Srivastava 1999; Loreau 2000). The log-ratio transformation of Szava-Kovats et al. (2012) corrected for statistical autocorrelation between local and regional richness (Cresswell et al. 1995). And the fish stocking data of Halverson (2008) supported the LRR results by indicating that nonnative propagule pressure is at least as strong in the Southeast rivers as the Northwest rivers (Table 1).

The differential saturation results are intuitive when placed in a historical context. Since the Pleistocene (<2 mya), Pacific Northwest fishes have endured multiple catastrophic disturbances. Massive floods, caused by the failure of glacial dams, have inundated and scoured the landscape, while faulting, uplift and volcanism continue to degrade basin divides and alter the directionality and connectivity of stream networks (Smith 1981; Minckley et al. 1986). These disturbances are thought to have prevented Pacific Northwest fish assemblages from achieving equilibrium (Smith 1981; Li et al. 1987) and are therefore a parsimonious explanation for their apparent lack of saturation, as saturation is not expected within

nonequilibrium systems (Wiens 1984; Mouquet et al. 2003). Southeast rivers have, however, been comparatively stable environments with low extinction rates since the late Miocene (~5 mya; Smith 1981; Swift et al. 1986). Thus, Southeast fish assemblages should be closer to equilibrium and/or saturation than Northwest assemblages (Wiens 1984; Moyle & Herbold 1987). Interestingly, this historical interpretation of the LRR results is consistent with the study of Mouquet et al. (2003). They used niche colonisation simulations to test whether historical assembly time and environmental stability have predictable effects on LRR relationship. At intermediate stages of development, when environmental stability was relatively low, their simulations predicted a linear LRR relationship. Over longer time horizons, however, environmental stability increased and the predicted LRR relationship became asymptotic.

Species' characteristics within the Northwest and Southeast rivers were also consistent with Moyle & Herbold's (1987) predictions for western and eastern U.S. fish assemblages. The Northwest assemblages include many large, long-lived (2+ years) species with high fecundity, long reproductive spans and large home ranges or strong migratory tendencies (e.g., largescale sucker and northern pikeminnow), while the Southeast assemblages include a greater proportion of small-bodied, short-lived species with comparatively low fecundity, short reproductive spans and small home ranges or weak migratory tendencies (e.g., *Etheostoma* sp. and *Notropis* sp.). This general agreement with the predicted, interregional trends in species' morphologies and life histories (Moyle & Herbold 1987) suggests that the observed LRR patterns may be broadly representative of Northwest and Southeast fish assemblages.

These results also have implications for the conservation and management of North American freshwater fishes. Ecological theory predicts that saturated assemblages are regulated by deterministic processes at local scales, such as interspecific competition, while unsaturated assemblages are governed by regional-scale processes, such as immigration and extinction (Cornell 1999). Accordingly, if Southeast fish assemblages are truly saturated, effective conservation plans will need to protect limiting resources, such as habitat and food, on a per-species basis. Failure to do so may tip the balance in favour of an interspecific competitor (Wiens 1984; Matthews 1998). But the unsaturated Northwest fish assemblages should benefit more from strategies that facilitate landscape-scale movement (Cornell 1999). For instance, many Northwest fishes are migratory or exhibit metapopulation structure (e.g., Cooper & Mangel 1999). Policies that facilitate upstream-downstream movement, perhaps via enhanced dam

passage, might therefore be more effective than local, in-stream habitat improvements.

One limitation of this study is the relatively small sample size. Nine paired local and regional richness estimates were included in each LRR plot. These data were sufficient to test for an overall LRR relationship in each biogeographical region, but not to test for secondary influences, such as zone (i.e., habitat) type. This is important because the LRR plots indicate a strong zone effect in the Southeast rivers. In both the all-species and the native-species-only LRR plots, the asymptotic LRR relationship (arithmetic data) was a clear function of among-zone (i.e., upper → middle → lower zone) increases in local and regional richness (Fig. 2 lower panel). Within zones, there was no evidence of a significant LRR relationship, asymptotic or otherwise; zones were tightly clustered in the Southeast LRR plots with little vertical (local richness) or horizontal (regional richness) variation. Zone effects were less apparent in the Northwest rivers; local and regional richness were lowest in the upper zones, but richness levels were comparable in the middle and upper zones (Fig. 2 upper panel). Resolving the effects of zone type will require additional data from rivers in each biogeographical region. However, tests for zone effects on the LRR relationship will not change the fundamental conclusion of this study: the ratio of local:regional richness is nearly constant (linear LRR relationship) in Northwest rivers, but it decreases in a predictable manner (asymptotic LRR relationship) as one moves downstream in the Southeast rivers.

The observed LRR relationships could also be influenced by species' characteristics that have little to do with direct, interspecific interactions. A fundamental assumption of the LRR method is that all species within a given RSP are functionally or ecologically equivalent and therefore equally likely to occur at any given locality (Srivastava 1999). If this assumption is violated, LRR patterns may be misleading. For example, if fishes in the Southeast are, on average, less mobile than fishes in the Northwest, then it is less likely a given Southeast species will be sampled and included in a local richness estimate, regardless of interspecific competition. Thus, a relatively low number of co-occurring species at a given locality may reflect competitive exclusion of some species within the RSP, but it may also reflect the specialised, noninteractive habitat requirements of species with limited vagility. This is a particular concern because, as noted above, migratory behaviours and large home ranges are more common among Northwest than Southeast fishes (see Moyle & Herbold 1987). A natural next step would therefore be to partition the local and regional richness data into groups of species with comparable vagilities. Similarly, LRR plots that focus

on specific functional groups, such as large piscivores or benthic insectivores (i.e., species that are most likely to compete), could enhance the current results (Matthews & Robison 1998).

A third caveat of the differential saturation conclusion is the fact that native eastern, warm-water fishes, such as smallmouth bass (*M. dolomieu*), often thrive when introduced to impounded systems in the west. But native western, cold-water fishes, such as rainbow trout (*Oncorhynchus mykiss*), are less likely to encounter suitable habitats in eastern rivers (Gido & Brown 1999). This makes it difficult to determine whether the success of nonnative fishes in Pacific Northwest rivers is because of a lack of biotic resistance *per se* or because of a selective advantage created by warm-water, lentic impoundments (Marchetti et al. 2004). For the moment, I suggest that the nonnative trends shown here are not an acute effect of impoundments because none of the Northwest fish samples was collected in reservoirs (see McGarvey & Hughes 2008). A systematic method to remove the confounding effects of impoundments (or other habitat alterations) would, however, greatly benefit studies of fish assemblage saturation.

The propagule pressure results should also be interpreted with caution. Halverson (2008) summarised the fish stocking data by large geographical regions (groups of 10–15 states) and did not provide stocking data for individual states or major river basins. It was therefore necessary to assume that the summarised western and southern stocking data were broadly representative of the subunits that they encompassed or that stocking effort was equally distributed within geographical regions. If this assumption was not valid and stocking trends in the six study rivers deviated from the broader regional trends, the assertion that the differential numbers of nonnative fishes in Pacific Northwest and Southeast rivers are not an artefact of propagule pressure may be incorrect. I also assumed that the 2004 stocking data of Halverson (2008) were representative of historical trends and that the deliberate stocking activities of state and federal agencies were the primary sources of nonnative propagule pressure. Clearly, a more precise assessment of propagule pressure should be a priority in future research. But few studies have measured propagule pressure directly, and I submit that the current analysis is a useful starting point.

Additional lines of evidence are now needed to corroborate or refute the differential saturation results. For example, the hypothesis that Southeast fish assemblages are saturated and therefore governed by interactive processes, while Pacific Northwest fish assemblages are not, could be tested directly with *in situ* competition experiments. But without a broader context to place those experiments in, it may

be difficult to distinguish meaningful patterns from idiosyncratic results (Matthews 1998). The differential saturation results shown in Fig. 2 provide this broader context and can serve as the foundation of a more comprehensive effort to determine whether upper limits to the richness of freshwater fish assemblages do, in fact, exist.

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References

- Angermeier, P.L. & Winston, M.R. 1998. Local vs. regional influences on local diversity in stream fish communities of Virginia. *Ecology* 79: 911–927.
- Balon, E.K. & Stewart, D.J. 1983. Fish assemblages in a river with unusual gradient (Luongo, Africa – Zaire system), reflections on river zonation, and description of another new species. *Environmental Biology of Fishes* 9: 225–252.
- Boschung, H.T.J. & Mayden, R.L. 2004. *Fishes of Alabama*. Washington, DC: Smithsonian Books.
- Case, T.J. 1990. Invasion resistance arises in strongly interacting species-rich model competition communities. *Proceedings of the National Academy of Sciences of USA* 87: 9610–9614.
- Cooper, A.B. & Mangel, M. 1999. The dangers of ignoring metapopulation structure for the conservation of salmonids. *Fishery Bulletin* 97: 213–226.
- Cornell, H.V. 1999. Unsaturation and regional influences on species richness in ecological communities: a review of the evidence. *Ecoscience* 6: 303–315.
- Cresswell, J.E., Vidal-Martinez, V.M. & Crichton, N.J. 1995. The investigation of saturation in the species richness of communities: some comments on methodology. *Oikos* 72: 301–304.
- Gido, K.B. & Brown, J.H. 1999. Invasion of North American drainages by alien fish species. *Freshwater Biology* 42: 387–399.
- Griffiths, D. 1997. Local and regional species richness in North American lacustrine fish. *Journal of Animal Ecology* 66: 49–56.
- Halverson, M.A. 2008. Stocking trends: a quantitative review of governmental fish stocking in the United States, 1931 to 2004. *Fisheries* 33: 69–75.
- Hawkes, H.A. 1975. River zonation and classification. In: Whitton, B.A., ed. *River ecology*. Berkeley, CA: University of California Press, pp. 312–374.
- Huet, M. 1959. Profiles and biology of Western European streams as related to fish management. *Transactions of the American Fisheries Society* 88: 155–163.
- Kennedy, T.A., Naeem, S., Howe, K.M., Knops, J.M.H., Tilman, D. & Reich, P. 2002. Biodiversity as a barrier to ecological invasion. *Nature* 417: 636–638.
- Lamouroux, N., Poff, N.L. & Angermeier, P.L. 2002. Intercontinental convergence of stream fish community traits along geomorphic and hydraulic gradients. *Ecology* 83: 1792–1807.
- Leprieur, F., Beauchard, O., Blanchet, S., Oberdorff, T. & Brosse, S. 2008. Fish invasions in the world's river systems: when natural processes are blurred by human activities. *PLoS Biology* 6: e28.
- Li, H.W., Schreck, C.B., Bond, C.E. & Rexstad, E. 1987. Factors influencing changes in fish assemblages of Pacific Northwest streams. In: Matthews, W.J. & Heins, D.C., eds. *Community and evolutionary ecology of North American stream fishes*. Norman, OK: University of Oklahoma Press, pp. 193–202.
- Loreau, M. 2000. Are communities saturated? On the relationship between alpha, beta and gamma diversity. *Ecology Letters* 3: 73–76.
- Marchetti, M.P., Moyle, P.B. & Levine, R. 2004. Alien fishes in California watersheds: characteristics of successful and failed invaders. *Ecological Applications* 14: 587–596.
- Matthews, W.J. 1998. *Patterns in freshwater fish ecology*. New York: Chapman and Hall.
- Matthews, W.J. & Robison, H.W. 1998. Influence of drainage connectivity, drainage area and regional species richness on fishes of the Interior Highlands in Arkansas. *The American Midland Naturalist* 139: 1–19.
- McGarvey, D.J. & Hughes, R.M. 2008. Longitudinal zonation of Pacific Northwest (U.S.A.) fish assemblages and the species-discharge relationship. *Copeia* 2008: 311–321.
- McGarvey, D.J. & Ward, G.M. 2008. Scale dependence in the species-discharge relationship for fishes of the southeastern U.S.A. *Freshwater Biology* 53: 2206–2219.
- Mettee, M.F., O'Neil, P.E. & Pierson, J.M. 1996. *Fishes of Alabama and the mobile basin*. Birmingham, AL: Oxmoor House.
- Minckley, W.L., Hendrickson, D.A. & Bond, C.E. 1986. Geography of western North American freshwater fishes: description and relationships to intracontinental tectonism. In: Hocutt, C.H. & Wiley, E.O., eds. *The zoogeography of North American freshwater fishes*. New York: John Wiley and Sons, pp. 519–613.
- Mitchell, A. & Knouft, J. 2009. Non-native fishes and native species diversity in freshwater fish assemblages across the United States. *Biological Invasions* 11: 1441–1450.
- Mouquet, N., Munguia, P., Kneitel, J.M. & Miller, T.E. 2003. Community assembly time and the relationship between local and regional species richness. *Oikos* 103: 618–626.
- Moyle, P.B. & Herbold, B. 1987. Life-history patterns and community structure in stream fishes of western North America: comparisons with eastern North America and Europe. In: Matthews, W.J. & Heins, D.C., eds. *Community and evolutionary ecology of North American Stream fishes*. Norman, OK: University of Oklahoma Press, pp. 25–32.
- Oberdorff, T., Hugué, B., Compin, A. & Belkessam, D. 1998. Non-interactive fish communities in the coastal

- streams of north-western France. *Journal of Animal Ecology* 67: 472–484.
- Paller, M.H. 1995. Relationships among number of fish species sampled, reach length surveyed, and sampling effort in South Carolina Coastal Plain streams. *North American Journal of Fisheries Management* 15: 110–120.
- Rahel, F.J. 2000. Homogenization of fish faunas across the United States. *Science* 288: 854–856.
- Reynolds, L., Herlihy, A.T., Kaufmann, P.R., Gregory, S.V. & Hughes, R.M. 2003. Electrofishing effort requirements for assessing species richness and biotic integrity in western Oregon streams. *North American Journal of Fisheries Management* 23: 450–461.
- Ross, S.T. 1991. Mechanisms structuring stream fish assemblages: are there lessons from introduced species? *Environmental Biology of Fishes* 30: 359–368.
- Schade, C.B. & Bonar, S.A. 2005. Distribution and abundance of nonnative fishes in streams of the western United States. *North American Journal of Fisheries Management* 25: 1386–1394.
- Smith, G.R. 1981. Late Cenozoic freshwater fishes of North America. *Annual Review of Ecology and Systematics* 12: 163–193.
- Srivastava, D.S. 1999. Using local-regional richness plots to test for species saturation: pitfalls and potentials. *Journal of Animal Ecology* 68: 1–16.
- Statzner, B. & Borchardt, D. 1992. Longitudinal patterns and processes along streams: modeling ecological responses to physical gradients. In: Giller, P.S., Hildrew, A.G. & Raffaelli, D.G., eds. *Aquatic ecology: scale, pattern, and process*. Oxford: Blackwell Scientific Publications, pp. 113–140.
- Swift, C.C., Gilbert, C.R., Bortone, S.A., Burgess, G.H. & Yerger, R.W. 1986. Zoogeography of the freshwater fishes of the Southeastern United States: Savannah River to Lake Pontchartrain. In: Hocutt, C.H. & Wiley, E.O., eds. *The zoogeography of North American Freshwater fishes*. New York: John Wiley and Sons, pp. 213–265.
- Szava-Kovats, R.C., Zobel, M. & Pärtel, M. 2012. The local-regional species richness relationship: new perspectives on the null-hypothesis. *Oikos* 121: 321–326.
- Tonn, W.M., Magnuson, J.J., Rask, M. & Toivonen, J. 1990. Intercontinental comparison of small-lake fish assemblages: the balance between local and regional processes. *The American Naturalist* 136: 345–375.
- Wiens, J.A. 1984. On understanding a non-equilibrium world: myth and reality in community patterns and processes. In: Strong, D.R., Simberloff, D., Abele, L.G. & Thistle, A.B., eds. *Ecological communities: conceptual issues and the evidence*. Princeton, NJ: Princeton University Press, pp. 439–457.