

Drivers and interrelationships among multiple dimensions of rarity for freshwater fishes

Xingli Giam and Julian D. Olden

X. Giam (<http://orcid.org/0000-0002-5239-9477>) (xgiam@utk.edu) and J. D. Olden, School of Aquatic and Fishery Sciences, Univ. of Washington, Seattle, WA, USA. Present address of XG: Dept of Ecology and Evolutionary Biology, The Univ. of Tennessee, Knoxville, TN, USA.

Species can be rare or common in three different dimensions: geographic range size, habitat breadth, and local abundance. Understanding drivers of rarity are not only fundamentally interesting; it is also pertinent for their conservation. We addressed this challenge by analyzing the rarity of 291 native freshwater fishes occurring in ca 3500 independent stream reaches that span a broad environmental gradient across continental USA. Using phylogenetic regression and path analysis, we examined the concordance among the three rarity dimensions, and identified possible mechanisms by which species life-history, habitat affinities, and biogeography drive variation in rarity. Weak double extinction jeopardies were driven by weakly positive correlations between habitat breadth and local abundance, and between habitat breadth and geographic range size. However, a triple extinction jeopardy was averted as local abundance and range size were not positively linked in our study. This is because large-river and lacustrine habitat use mediated a trade-off between local abundance and range size. Large rivers and lacustrine habitats represent important dispersal pathways and refugia that enabled fishes to acquire wide ranges; however, species using these habitats are less abundant overall because they are less adapted to small lotic channels, which comprise the majority of stream habitats in the US. Life-history traits were key in governing the relationship between abundance and range size as large-river and lacustrine habitat use were driven by body size, egg size, and parental care. Our analysis contributes novel insights into mechanisms that underlie multiple dimensions of rarity in freshwater fish and informs the prioritization of multiply rare species for conservation.

Species can be common or rare according to three major axes: local abundance, habitat breadth, and geographic range (Rabinowitz et al. 1981); and understanding why species differ in their rarity is interesting from both a fundamental and applied perspective (Gaston 1994, Angermeier 1995, Olden et al. 2010, Harnik et al. 2012). Species with low local abundance are more vulnerable to stochastic extirpations (Pimm et al. 1988, Gaston and McArdle 1993, Gaston and Blackburn 2000) whereas those with restricted geographic ranges are more susceptible to multiple threats such as habitat loss, human exploitation, and climate change (Gaston 1994, Gaston and Blackburn 2000). Highly specific habitat requirements further constrain the area occupied by a species within its geographic range, resulting in such species demonstrating less resilience to environmental changes (Nürnberg and Aberhan 2013). Identifying associations between the three axes of rarity and revealing their underlying mechanisms would help improve our understanding of species vulnerabilities to local and global extinction, and inform conservation strategies aimed at preventing such losses from occurring.

Mounting scientific evidence suggests an almost universal positive relationship between geographic range and local abundance for both plants and animals (Brown 1984,

Gotelli and Simberloff 1987, Poulin 1999, Gaston and Blackburn 2000, Blackburn et al. 2006). This relationship forms the basis of the 'double jeopardy' concept in which the co-occurrence of small geographic range and low local abundance predisposes a large number of species toward extinction (Rabinowitz et al. 1981, Lawton 1993, Gaston 1999). The mechanisms underlying this concept include sampling artefacts, niche (habitat) position, and niche (habitat) breadth (reviewed by Gaston and Blackburn 2000). If the observed covariance between geographic range and local abundance is driven by niche or habitat breadth (i.e. habitat breadth hypothesis; Brown 1984, Brown et al. 1995) it implies that species that are rare on one axis are also rare on the other two axes, resulting in a 'triple jeopardy' risk of extinction (Munday 2004).

Human activities have greatly impacted freshwater systems, and freshwater fishes – one of the most diverse vertebrate groups – are now also one of the most highly imperiled (Closs et al. 2016). Despite this, examination of double or triple extinction jeopardy has largely been focused on terrestrial and marine communities (Arita et al. 1990, Gaston et al. 1997, Munday 2004, Blackburn et al. 2006, Williams et al. 2009, Hobbs et al. 2010, Hughes et al. 2014), with little attention given to freshwater fishes.

Among North American suckers (Catostomidae) and sunfishes (Centrarchidae), for example, range size correlated positively with habitat breadth but not local abundance after accounting for phylogeny (Pyron 1999). An analysis of United States' fishes corroborated the double extinction jeopardy arising from restricted range size and habitat specificity but did not consider other axes of rarity and phylogeny (Pritt and Frimpong 2010). Further investigations that incorporate phylogenetic relationships among species from different families over broader spatial scales are required for a robust examination of both the patterns and drivers of the double or triple jeopardy phenomenon.

Species attributes (life-history strategies, ecological traits, phylogenetic heritability) and exogenous factors (environmental and biogeographic forces) are potential drivers of species rarity. Whether, and if so how, these drivers interact to influence the degree of inter-relationships between the different rarity axes remains uncertain. For example, species that are larger-bodied or at higher trophic levels may require larger geographic ranges to maintain minimum viable populations (Gaston and Blackburn 1996) owing to their higher energetic needs and home range size requirements (Swihart et al. 1988). Species that are larger may also disperse farther and more rapidly (Jenkins et al. 2007), thus enabling them to occupy a larger geographic range. At the same time, body size and trophic position may drive variation in local abundance (Brown et al. 2004). Assuming similar resource availability to species within the trophic guild, larger-bodied species are expected to be less locally abundant because they appropriate more energy per individual (Brown et al. 2004, White et al. 2007). Furthermore, lower available energy at higher trophic levels may limit the scope on local abundances (Marquet 2002, Brown et al. 2004). Given this array of relationships, species body size and/or trophic position can also cause the relatively uncommon negative correlation between range size and local abundance (Arita et al. 1990), especially in less productive habitats that are energy-limited.

Along with body size, reproductive traits such as seed or egg mass, use of potential dispersal habitats, occurrence in different biogeographic regions and climatic zones, and phylogeny have been demonstrated to correlate with rarity (Arita et al. 1990, Roy et al. 1994, Morin and Chuine 2006, Griffiths 2010, Blanchet et al. 2013, Di Marco and Santini 2015, Howard et al. 2015). For freshwater fishes, investigations into the drivers of species rarity are much less common and have primarily centered on range size. Maximum body size was positively correlated with range size in North American suckers but not sunfishes (Pyron 1999) and for the eastern *whipplei* clade of the North American minnow genus *Cyprinella* (Taylor and Gotelli 1994). By contrast, range size was neither directly correlated with body size nor phylogenetically conserved for Canadian fishes; instead, body and caudal fin morphology (hypothesized to confer greater dispersal ability, migration behavior, and use of lakes) were positively correlated with range size (Blanchet et al. 2013). Glaciation history and use of lakes but not body size associated with range extents in both North America and Europe albeit neither analysis accounted for the influence of shared phylogeny among species (Griffiths 2006, 2010). The role of other species traits such as parental care, egg size, and trophic position in driving range sizes of freshwater fish

remains largely unexplored, as are mechanisms underlying local abundance and habitat breadth. Further, the effect of ecosystem size (or equivalently, energy availability) on rarity pathways are poorly known. For example, we expect local abundance to decrease with increasing body size and/or trophic level in small, energy-limited streams but not in larger, more productive streams (Brown et al. 1995, White et al. 2007). We integrate results from previous studies and ecological theory to inform hypotheses regarding potential drivers of different rarity axes for freshwater fishes (Table 1).

Here, we test for the existence of double or triple extinction jeopardy and reveal the potential mechanisms underlying rarity associations for native freshwater fishes of the conterminous USA. Our study is the first to address the complex interplay between species traits and exogenous environmental and biogeographic factors in driving different dimensions of rarity within a single analytical framework that explicitly accounts for shared phylogeny among species. Using phylogenetic regression and path analytic models to evaluate hypothesized causal relationships (Table 1), we answered the following questions: 1) how are the different dimensions of rarity associated, 2) what are the direct and indirect pathways through which species attributes and exogenous factors influence different dimensions of rarity, 3) do pathways of rarity vary according to ecosystem size? With our analyses, we provide new insight into the ecological mechanisms that underlie survival in freshwater fish species.

Methods

Species community dataset

We used a database of fish communities occurring in 7846 stream localities across 1502 watersheds in the conterminous USA. This database consists of sites from survey programs performed by university researchers, state natural resource and environmental agencies, and US federal government agencies [e.g. National and Regional Environmental Monitoring and Assessment Program (EMAP and REMAP) and National Rivers and Streams Assessment (NRSA) by US Environmental Protection Agency (US EPA), National Water Quality Assessment Program (NAWQA) by United States Geological Survey] (see Giam and Olden 2016 for the full list of references). These surveys were designed to characterize the relative abundance of species in each community (US EPA 2009). To maximize comparability between sites sampled by different survey programs, we only included survey programs where electrofishing was the main method of sampling to minimize sampling gear bias. Backpack electrofishing was the common primary method of sampling for small wadeable streams whereas boat or raft electrofishing was used for deep and large rivers. The large majority of streams were sampled in summer during low-flow conditions to ensure comprehensive sampling of fish communities and to maximize personnel safety; this meant that assemblages are comparable and seasonal variation in flow conditions are unlikely to confound our findings. Sampling reach length generally increased with stream width, a standard protocol to accurately characterize fish communities in streams of

Table 1. Candidate predictors of response variables, predicted effects, and potential mechanisms. Predicted effects and potential mechanisms were developed from ecological theory and the literature: ^aJenkins et al. (2007), ^bGaston and Blackburn (1996), ^cBeamish (1978), ^dGriffiths (2010), ^eLuiz et al. (2013), ^fSwihart et al. (1988), ^gMinns (1995), ^hMarsh (1986), ⁱWinemiller and Rose (1992), ^jPaine (1990), ^kMatthews (1998), ^lGoodwin et al. (2005), ^mKnouft and Page (2003), ⁿBlanchet et al. (2013), ^oGregory and Gaston (2000), ^pHocutt and Wiley (1986), ^qGoetz et al. (2015), ^rBrown (1984), ^sHanski et al. (1993), ^tHartley (1998), ^uGaston and McArdle (1993), ^vPower (1987), ^wBrown et al. (1995), ^xWhite et al. (2007), ^yPage (1985), ^zLindeman (1942), ^{aa}Marquet (2002), ^{bb}Winemiller and Rose (1993), ^{cc}Mahon (1984), ^{dd}Oberdorff et al. (1993).

Predictors (organized by response)	Direction of effect and potential mechanism(s)
Range size	
Body size	(+) Larger body size is related to enhanced dispersal ability ^(a,b,c) , migratory behavior ^(d) , colonization ability ^(d,e) , and larger home ranges ^(f,g) .
Egg size	(-) Smaller egg size is positively associated with greater fecundity ^(h,i,j) , which increases probability of dispersal and recruitment to suitable habitats ⁽ⁱ⁾ . Among a small subset of darters (Percidae), range size was negatively correlated with egg size ⁽ⁱ⁾ .
Parental care	(-) Parental care (defined here as brood-guarding or livebearing) reduces the duration of independent passive dispersal. In teleost fishes, geographic ranges of livebearers are smaller than egg-laying species ^(l) .
Piscivory	(+) Holding body size constant, species at a higher trophic level have larger home ranges ^(f) .
Use of large rivers	(+) Large, high-order rivers connect different watersheds and act as dispersal corridors ^(m) . Large-river species are also more migratory ^(d) , which aids in dispersal and achieving larger range sizes ^(d,n) . (-) Ranges of large-river species may be restricted because large rivers form a minority of flowing waters in the US (habitat position hypothesis ^(o)).
Use of lacustrine habitats	(+) In northern USA, lakes are refugia during glacial periods that have facilitated recolonization via pro-glacial lakes as ice sheets retreated ^(d,n,p) . Fishes that occur in shallow lakes are tolerant of challenging physicochemical conditions ^(q) .
Western US	(-) The area west of the continental divide is smaller (and younger) than the east ^(p) , thus it may constrain species ranges to a greater degree than the latter.
Habitat breadth	(+) The ability to use a wider range of habitats allows species to increase their range more easily (habitat breadth hypothesis ^(o)).
Local abundance	(+) Species with higher local abundances achieve larger ranges owing to stochastic dispersal or distribution across the landscape ^(s,t) ; those with low local abundances may experience many local stochastic extinctions, leading to small ranges ^(u) .
Habitat breadth	
Body size	(+) Smaller species are restricted to small streams ^(m) . (-) In large-bodied species, greater space and energy requirements, as well as high predation risk from terrestrial predators ^(g,v,w) likely limit colonization of smaller channels. (Unimodal) these two mechanisms, acting in concert, may result in greater habitat breadth at intermediate body sizes.
Egg size	(+) Larger eggs increase chances of offspring survival ^(h,j) , allowing them to exploit different habitats. (-) Production of small but large numbers of eggs/offspring may allow colonization of multiple suitable habitats ⁽ⁱ⁾ .
Parental care	(+) Parental care increases the chance of offspring survival ^(k) , possibly across multiple habitats.
Piscivory	(-) Piscivores are limited to habitats with adequate prey fish biomass.
Use of lacustrine habitats	(+) Lacustrine species in North America are suggested to be less stenotopic than riverine species ^(d) . (-) Lacustrine species may be less adapted to lotic conditions characteristic of headwater to small river habitats thus restricting them to larger rivers and low water velocities.
Local abundance	
Body size	(-) In energy-limited environments (small streams) species abundance may decrease with body size ^(w,x) .
Egg size	(+) Larger eggs increase the chance of offspring survival ^(h,j) . In North American darters (family Percidae), larger eggs were positively associated with local densities ^(v) .
Parental care	(+) Parental care increases chances of offspring survival ^(k) , which may contribute to higher local abundance.
Piscivory	(-) Less energy is available to higher trophic levels ^(z) , limiting local abundances ^(aa) . As home range size increases with trophic position, local density is expected to decrease ^(f) .
Use of large rivers	(-) Small, low-order streams comprise the majority of streams in the United States ^(m) . Large-river species are therefore likely less abundant locally (habitat position hypothesis).
Use of lacustrine habitats	(-) Lacustrine species are likely less adapted to streams than lotic specialists (habitat position hypothesis ^(o)).
Habitat breadth	(+) The ability to use a variety of habitats allows fishes to achieve higher local abundances (habitat breadth hypothesis ^(o)).
Use of large rivers/use of lacustrine habitats	
Body size	(+) Greater habitat area and/or productivity in large rivers and lacustrine habitats allow colonization of larger-bodied species. Body size of fishes generally increases with stream size ^(d) .
Egg size	(-) Owing to high productivity and abundant planktonic food sources in many lentic waters ^(k) , having small (and many) eggs/larvae aids in offspring survival ^(bb) while having large (but few) eggs/larvae is not selectively advantageous ^(i,j) .
Parental care	(+) As lakes are temporally stable environments, species should invest more in parental care to increase juvenile survivorship ^(bb) . (-) Owing to high productivity and abundant food for larvae in large rivers and/or lakes, species could invest less in parental care ^(i,cc) .
Piscivory	(+) Abundance and richness of piscivorous species increases with stream size possibly owing to increased productivity and food availability ^(dd) .

different widths (Hauer and Lamberti 2007). All sites were located on natural stream reaches and at least 1 km apart.

Local abundance, geographic range size, and habitat breadth

In our calculation of local abundance, we excluded sites in which one or more nonnative or brackish/marine species were dominant in the assemblage (i.e. relative abundance of nonnative or brackish species greater than the reciprocal of species richness; Camargo 1993) to reduce the influence of nonnative species and marginal brackish habitats on our analysis. To maximize spatial independence of individual local abundance estimates, we ensured that every site was on a different stream reach, which was defined as ‘a contiguous piece of surface water with similar hydrological characteristics’ (USGS 2011). When multiple sites were on a single stream reach, we retained only the most recently sampled site. Overall, these filtering procedures resulted in a total of 5071 independent sites for further analyses.

We used these 5071 sites to derive a measure of local abundance for each native freshwater fish species minus those commonly stocked (i.e. species in the genera *Oncorhynchus*, *Salmo*, and *Salvelinus*) as their abundances many have been influenced by stocking. In the context of our study, the raw (or log-transformed) relative abundance RA_i ($= A_i / \sum A_i$), where A_i is the abundance of the i -th species) is not an appropriate measure of local abundance because it is sensitive to the total number of species and individuals present at a given site (Supplementary material Appendix 1). We therefore developed a measure of local abundance that accounts for variation in species richness and abundance among sites. At each given site, log-transformed relative abundances of

species are centered on its mean. This quantity, standardized log relative abundance (SRA_i) for the i -th of S species is expressed as,

$$SRA_i = \log(RA_i) - \sum_{i=1}^S \log(RA_i) / S \quad (1)$$

This centering procedure rendered relative abundance values comparable across sites and therefore aggregable for each species because mean SRA_i at each site is always 0. Importantly, it ensures that local abundance was not conflated with site richness and abundance during subsequent analyses of rarity (Supplementary material Appendix 1).

For each species occurring in at least 3 sites, we estimated the aggregated local abundance as the median SRA_i across the sites in which it occurs. Although we recognize that local abundance may be variable among sites, we quantified the central tendency of local abundance for each species so as to facilitate analyses at the species level. We analyzed sites with ≥ 2 species and 100 individuals ($n = 3471$ sites; Fig. 1); the former because relative abundances are only meaningful when multiple species are present, and the latter to improve the accuracy of our estimates.

Similar to the actual distribution of perennial stream reaches in the US, our dataset consists of more small, low-order sites than higher-order sites. Whereas 1st and 2nd order stream sites appear to be underrepresented in our dataset; many of these streams are likely to be non-fish bearing (e.g. low-order non-fish-bearing streams represent $\sim 65\%$ of the total stream length in western Washington; WDFW 2016). In general, our dataset is reflective of the size distribution of fish-bearing streams in the US. There was some variation in sampling intensity – the number of sampling sites relative to the number of perennial stream reaches – among regions (Supplementary material Appendix 2). Sampling intensity was highest in the Upper Mississippi, Arkansas-White-Red,

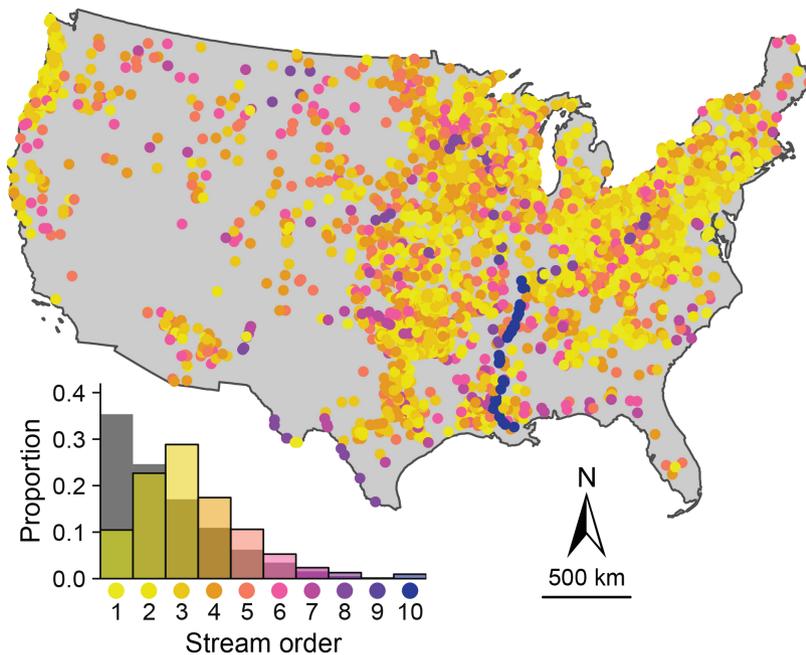


Figure 1. Map and distribution (inset) of sites of different stream orders in our dataset ($n = 3471$ sites with ≥ 2 species and 100 individuals). The grey histogram shows the actual distribution of the number of perennial stream reaches of different orders in the US (data from National Hydrology Dataset Plus ver. 2; McKay et al. 2012).

and Lower Colorado regions. However, variation in sampling intensity is unlikely to bias our analyses because there is no evidence to suggest that fish communities in these regions are structured differently from other regions (Giam and Olden 2016) and that all sampling intensity values were within the range of normal variability (i.e. 2 standard deviations from the mean).

We calculated the geographic range size of each species in our assemblage dataset as the total area (in km²) of watersheds to which the species is native historically. The nativity status of a species was assigned based on native range maps produced by NatureServe (2010) and non-native species occurrences collated by the USGS Nonindigenous Aquatic Species Program (<www.nas.er.usgs.gov>). Species whose US ranges are at the northern or southern limits of their global ranges were excluded from our analysis because their ranges are likely constrained by biogeography and/or climate, and because local abundances at range edges may be atypical (Brown 1984, Lawton 1993, Gaston and Blackburn 2000). To do this, we conservatively removed species whose Canadian range size exceeds its US range size (Canadian ranges from Mims et al. 2010). As detailed range maps for Central American species were not available for quantitative filtering, we excluded species whose range centers appear to lie outside of the US (i.e. *Astyanax mexicanus* and *Herichthys cyanoguttatus*, based on Miller et al. 2005).

We defined the habitat breadth of a species by their affinities to different aquatic habitat types, substrate categories, and water flow velocities. Species were assigned to one or more of 6 aquatic habitat types (i.e. springs, headwaters, creeks, small rivers, medium rivers, large rivers), 5 substrate categories (i.e. fine, coarse, rocky, vegetation, and organic debris/detritus), and 3 water velocities (i.e. slow, medium, and fast). We used a single primary source for each of the aquatic habitats and altitudinal category assignments so as to maximize comparability across species. Aquatic habitat assignments were primarily based on Page and Burr (2011) following Griffiths (2010), and substrate and water velocity category assignments were primarily retrieved from FishTraits (<www.fishtraits.info>; Frimpong and Angermeier 2009). For a small subset of species (n = 7) for which data were not available from the primary sources, we used species accounts from fish catalogues (e.g., Etnier and Starnes 1993), online databases (e.g. California Fish Website; <www.calfish.ucdavis.edu>) and the IUCN Red List (<www.iucnredlist.org>). We summed the number of aquatic habitats,

substrate categories, and flow velocities separately for each species, scaled individual scores to a range of 0–1 and then averaged to form the overall habitat breadth score (modified from Pritt and Frimpong 2010). Habitat breadth can also be quantified via specialization indices based on our actual abundance/occurrence data (Julliard et al. 2006, Devictor et al. 2008); however, this strategy was not appropriate for our study as it introduces circularity in our analyses.

Species life-history and ecological traits, habitat affinities, and biogeography

From the literature, we collated data on nine species variables hypothesized to play a role in driving the three dimensions of rarity (Table 2). Five life-history traits, body size (BS), age at maturation (MAT), log-transformed fecundity (FEC), egg size (EGG), parental care (PC), and one ecological trait, piscivory (PISC), were compiled using a multi-tiered, comprehensive data collection procedure from a wide range of published literature including regional/state fish catalogues, state agency reports, scientific journal papers, graduate dissertations, and reputable electronic databases (see Mims et al. 2010 for details). Body size was highly correlated with age of maturity and fecundity (Pearson $r > 0.7$); we therefore retained body size for analysis while excluding the latter two collinear variables (Dormann et al. 2013).

Two variables describe species affinities toward habitats that represent possible dispersal routes: the use of large rivers (LG) and the use of lacustrine habitats (LAC). LG and LAC were primarily assigned from Page and Burr (2011); gaps (n = 3 species) were filled in with data from a state fish catalogue (Etnier and Starnes 1993) and the IUCN Red List. The last trait relates to differences in zoogeographic history among species (WEST): species were classified as belonging to the eastern or western biogeographic zones (defined respectively as the continental area east and west of the Continental Divide; Smith 1981) based on their native ranges.

Species phylogeny

To account for the effects of shared phylogeny (lack of non-independence) among species, we used a recent time-calibrated molecular phylogeny for 7822 extant ray-finned fishes (Actinopterygii) (Rabosky et al. 2013) pruned to the

Table 2. Species traits considered as potential drivers of rarity. ^aDefinition of large rivers follows Page and Burr (2011).

Traits (code)	Variable type and description	Mean (range)
1. Body size (BS)	Continuous: log-transformed maximum body length (in mm)	5.13 (3.56–8.02)
2. Age at maturation (AGE)	Continuous: age of female (secondarily male) maturation (in years)	2.15 (0.10–22.50)
3. Fecundity (FEC)	Continuous: log-transformed number of eggs produced over the breeding season per female	7.39 (2.14–14.63)
4. Egg size (EGG)	Continuous: diameter of mature ovarian oocytes (in mm)	1.59 (0.16–4.35)
5. Parental care (PC)	Binary: livebearer or egg-guarder (yes vs no)	yes: 91; no: 200
6. Piscivory (PISC)	Binary: Piscivore as adult (yes vs no)	yes: 40; no: 251
7. Use of large rivers (LG)	Binary: occurrence in large rivers (yes vs no); large rivers defined as > 50 m wide ^a	yes: 108; no: 183
8. Use of lacustrine habitats (LAC)	Binary: occurrence in lakes (yes vs no)	yes: 105; no: 186
9. Western biogeographic zones (WEST)	Binary: native to west of the Continental Divide (yes vs no)	yes: 26; no: 265

number of species in our dataset (Supplementary material Appendix 3).

Data analyses

To evaluate the potential for double or triple extinction jeopardy owing to the concordance between different dimensions of rarity, we used phylogenetic generalized least squares regression (PGLS) to examine pairwise correlations between log-transformed range size, habitat breadth, and local abundance. PGLS accounts for phylogenetic non-independence between related species by estimating predictor coefficients and the phylogenetic signal (through Pagel's λ ; Pagel 1999) in the residuals simultaneously (Revell 2010, Symonds and Blomberg 2014).

We took a three-step approach to analyze the drivers of and interrelationships between different rarity dimensions for these species. First, we set up a preliminary path model describing how species traits potentially drive variation in the three measures of rarity based on previous findings in the literature and logical predictions based on life-history theory (Fig. 2, Table 1). Life-history traits likely coevolved as a result of allometric and energetic tradeoffs (Winemiller and Rose 1992, Mims et al. 2010); we therefore specified bidirectional correlations among life-history traits in our path model. We also specified a bidirectional correlation between use of large rivers and use of lacustrine habitats because of their habitat similarities.

Second, we identified pertinent drivers of each endogenous (response) variable via standard model selection procedures. The continuous endogenous variables, local abundance, habitat breadth, and \log_{10} -transformed range size were modeled using PGLS. Because PGLS models were fit using maximum likelihood, we used all-subsets AIC_c

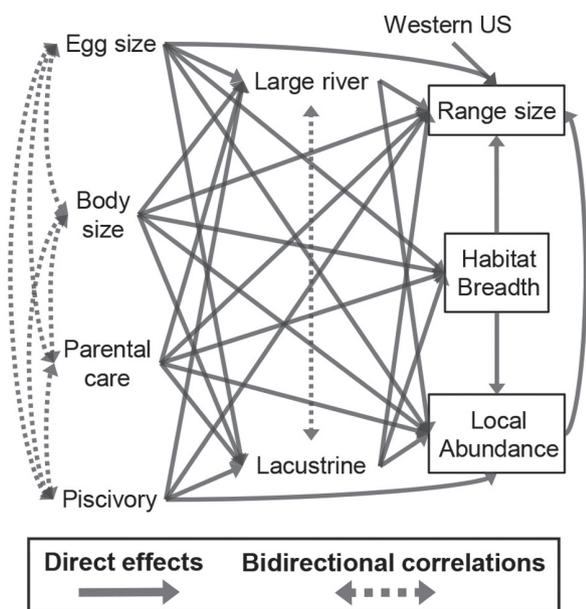


Figure 2. Full candidate path model describing potential direct effects and bidirectional correlations among life-history traits, ecological traits, biogeography, and three dimensions of rarity. Potential underlying mechanisms of direct effects are presented in Table 1.

model selection (Burnham and Anderson 2002) to identify the top-ranked model for statistical inference. The 2 other endogenous variables, use of large rivers and use of lacustrine habitats, were binary. They were hence modeled by phylogenetic logistic regression (PLR) that estimates both predictor coefficients and a measure of residual phylogenetic dependence (α) for binary response variables by maximizing penalized log-likelihood (Ives and Garland 2010). Because AIC_c model selection is not appropriate for models fitted by maximum penalized likelihood, we performed backward selection starting from the full model with a p-to-exit value of 0.1. This threshold roughly corresponds to the p-values of the variables chosen in the top AIC_c -ranked PGLS models. The variance explained by each top-ranked model was estimated with Cox–Snell R^2 (for continuous variables) and Nagelkerke's R^2 (for binary variables). Variable importance was evaluated using p-values derived from t -statistics in models with no quadratic variables (Cade 2015). For models in which quadratic relationships were present, we used p-values from likelihood-ratio tests after excluding each predictor from the top-ranked model (Favre et al. 2008).

Last, we combined top-ranked PGLS and PLS models to construct the final path model. We tested whether this model was consistent with our data using a d-separation (d-sep) test (Shipley 2016). The d-sep test examines the validity of conditional independence statements implicit in a given causal path model. For a set of k conditional independence statements, we can perform an appropriate statistical test and obtain a p-value for each statement. The composite validity of all k independence statements can be tested by combining the p-values into a C statistic and testing it against a χ^2 distribution with $2k$ degrees of freedom. The C statistic is calculated as,

$$C = -2 \sum_{j=1}^k \ln(p_j) \quad (2)$$

where p_j is the p-value of the j -th conditional independence statement.

We performed two separate analyses. The first analysis involves examining drivers of rarity among species present in all sites in our dataset ($n = 291$ species in 3471 sites). The second analysis compares drivers of rarity among all species occurring in small (i.e. 1st–3rd order) streams ($n = 218$ species in 2151 sites) vs all species occurring in medium-to-large (≥ 4 th order) streams ($n = 252$ species in 1320 sites). We followed Vannote et al. (1980) in using stream order to define small vs medium-large streams. In the second analysis, local abundance for each species was estimated from small and medium-to-large stream sites separately. We performed the second analysis to examine the hypothesis that energy and/or space limitations drive a negative association between body size and local abundance in small streams but not in medium-to-large streams.

We used the 'phylolm' package (Ho and Ane 2014) to fit PGLS and PLR models in the R statistical environment ver. 3.3.1 (R Core Team).

Results

Local abundance and geographic range size of fishes were not correlated ($n = 291$ species, $p = 0.13$; Fig. 3a). Habitat

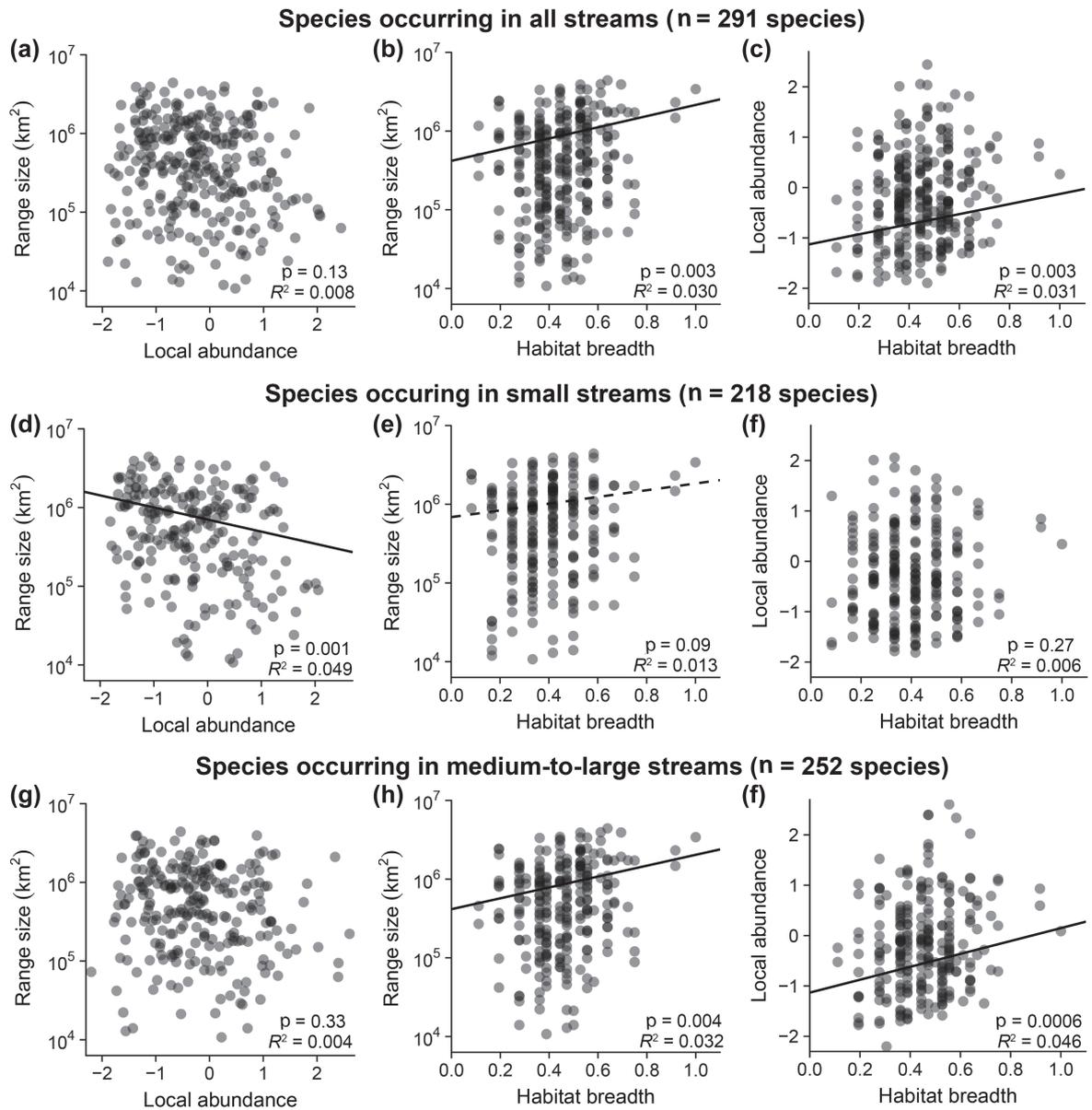


Figure 3. Relationships between range size, habitat breadth, and local abundance among (a, b, c) all species, (d, e, f) species in small (1st–3rd order) streams, and (g, h, i) species in larger (≥ 4 th order) streams. Significant relationships inferred from phylogenetic generalized least squares (PGLS) models are plotted (solid lines: $p < 0.05$; dashed lines: $0.05 \leq p < 0.10$).

breadth, however, had weak positive correlations with both range size ($p = 0.003$, $R^2 = 0.030$) and local abundance ($p = 0.003$, $R^2 = 0.031$) (Fig. 3b, c). Local abundance of fishes in small (1st–3rd order) streams was negatively correlated with range size ($n = 218$ species, $p = 0.001$, $R^2 = 0.049$; Fig. 3d). Among fishes present in small streams, habitat breadth remained weakly positively correlated with range size ($p = 0.09$, $R^2 = 0.013$) but not with local abundance ($p = 0.27$) (Fig. 3e, f). Rarity correlations among fishes ($n = 252$ species) present in medium-to-large (≥ 4 th order) streams were similar to those among fishes present in all sites (Fig. 3g, h, i).

The top model predicting local abundance across all sites (as well as in medium-to-large streams) comprised the following predictors (in decreasing order of importance): habitat breadth, use of lacustrine systems, and use of large rivers

($R^2 = 0.08$ – 0.09). Local abundance increased with habitat breadth whereas species known to use lacustrine systems and large rivers demonstrated lower abundances. In small streams, species that use lacustrine habitats and large rivers, as well as those with larger bodies, smaller eggs, lacking parental care (i.e. non-bearers or non-guarders), and lower habitat breadth tended to have lower abundances ($R^2 = 0.17$) (Table 3).

Habitat breadth was highest at intermediate body sizes and in lacustrine species among all fishes in our dataset ($R^2 = 0.05$) as well as among fishes occurring in medium-to-large streams ($R^2 = 0.05$). The unimodal habitat breadth-body size relationship was also present but lake use was excluded from the top model among fishes occurring in small streams ($R^2 = 0.02$; Table 4).

Use of lacustrine habitats, body size, biogeography, habitat breadth, egg size, use of large rivers, and parental care were

Table 3. Top-ranked PGLS models predicting local abundance of fishes occurring in all streams, small (1st–3rd order) streams, and medium-to-large (≥ 4 th order) streams. Predictors are arranged in order of importance based on their p-values, which are derived from $|t|$ statistics.

Predictors	Coefficient	$ t $	p-value
All streams ($R^2 = 0.09$; $\lambda = 0.66$)			
1. Habitat breadth	1.14	3.53	4.7×10^{-4}
2. Use of lacustrine habitats	-0.32	3.11	0.002
3. Use of large rivers	-0.22	2.12	0.035
Small streams ($R^2 = 0.17$; $\lambda = 0.68$)			
1. Use of lacustrine habitats	-0.30	2.48	0.014
2. Use of large rivers	-0.31	2.45	0.015
3. Body size	-0.22	2.23	0.026
4. Egg size	0.21	1.97	0.050
5. Parental care	0.25	1.66	0.098
6. Habitat breadth	0.51	1.56	0.121
Medium-to-large streams ($R^2 = 0.08$; $\lambda = 0.60$)			
1. Habitat breadth	1.38	3.80	1.8×10^{-4}
2. Use of lacustrine habitats	-0.28	2.37	0.019
3. Use of large rivers	-0.19	1.65	0.101

(in decreasing order) important predictors of range size among all fishes ($R^2 = 0.38$). These same variables were predictive of range size for fishes occurring in medium-to-large streams ($R^2 = 0.38$). Among fishes present in small streams, the top model included all of the above predictors except parental care ($R^2 = 0.36$). Range size was positively correlated with use of lacustrine habitats, body size, use of large rivers, and habitat breadth, and negatively correlated with egg size. In addition, species native to western US had smaller ranges than those found east of the continental divide (Table 5).

The residual phylogenetic signal was stronger in local abundance models ($\lambda = 0.60$ – 0.68) than in habitat breadth ($\lambda = 0.15$ – 0.18) and geographic range ($\lambda = 0.06$ – 0.14) models. Model rankings for all three rarity dimensions are presented in Supplementary material Appendix 4.

Life-history traits were important correlates of large river and lacustrine habitat usage by fishes. Species that use large rivers and lacustrine habitats tend to be larger, and have smaller eggs. In addition, among all species in our dataset, and among species occurring in medium-to-large streams, lacustrine species were more likely to exhibit parental care than non-lacustrine species (Supplementary material, Appendix 5).

Based on the results of PGLS and PLS modelling, we constructed a final path model describing direct effects between life-history traits, habitat affinities, and the three dimensions

Table 4. Top-ranked PGLS models predicting habitat breadth of fishes occurring in all streams, small (1st–3rd order) streams, and medium-to-large (≥ 4 th order streams). Predictors are arranged in order of importance based on the p-values of likelihood-ratio (LR) tests after excluding the predictor from the top-ranked model.

Predictors	Coefficient	LR	LR p-value
All streams ($R^2 = 0.05$; $\lambda = 0.17$)			
1. Body size + Body size ²	0.35, -0.03	12.80	0.002
2. Use of lacustrine habitats	0.03	3.35	0.067
Small streams ($R^2 = 0.02$; $\lambda = 0.18$)			
1. Body size + Body size ²	0.33, -0.03	5.22	0.073
Medium-to-large streams ($R^2 = 0.05$; $\lambda = 0.15$)			
1. Body size + Body size ²	0.33, -0.03	10.52	0.005
2. Use of lacustrine habitats	0.03	2.65	0.103

Table 5. Top-ranked PGLS models predicting geographic range size of fishes occurring in all streams, small (1st–3rd order) streams, and medium-to-large (≥ 4 th order streams). Predictors are arranged in order of importance based on their p-values, which are derived from $|t|$ statistics.

Predictors	Coefficient	$ t $	p-value
All streams ($R^2 = 0.38$; $\lambda = 0.07$)			
1. Use of lacustrine habitats	0.42	6.23	1.7×10^{-9}
2. Body size	0.20	4.53	8.8×10^{-6}
3. Western US	-0.43	4.44	1.3×10^{-5}
4. Habitat breadth	0.62	3.06	0.002
5. Egg size	-0.14	3.06	0.002
6. Use of large rivers	0.18	2.65	0.009
7. Parental care	0.11	1.65	0.100
Small streams ($R^2 = 0.36$; $\lambda = 0.14$)			
1. Use of lacustrine habitats	0.43	5.46	1.3×10^{-7}
2. Body size	0.21	3.87	1.4×10^{-4}
3. Western US	-0.43	3.20	0.002
4. Use of large rivers	0.18	2.39	0.018
5. Egg size	-0.12	2.01	0.046
6. Habitat breadth	0.40	1.84	0.067
Medium-to-large streams ($R^2 = 0.38$; $\lambda = 0.06$)			
1. Use of lacustrine habitats	0.37	5.43	1.3×10^{-7}
2. Western US	-0.45	4.56	7.9×10^{-6}
3. Body size	0.18	4.18	4.1×10^{-5}
4. Egg size	-0.15	3.26	0.001
5. Habitat breadth	0.65	3.21	0.001
6. Parental care	0.15	2.23	0.026
7. Use of large rivers	0.14	2.05	0.041

of rarity for all species in our dataset (Fig. 4) as well as for species present in small and medium-to-large streams (Fig. 5). The d-sep test indicated that the path models were consistent with the data (all fishes: $C = 36.8$, 46 df, $p = 0.83$; fishes in small streams: $C = 52.1$, 46 df, $p = 0.25$; fishes in medium-to-large streams: $C = 33.8$, 46 df, $p = 0.91$) (Supplementary material Appendix 6). Our models confirm that life-history traits demonstrate strong direct correlations with all rarity dimensions as well as displaying indirect associations via habitat affinities. For example, large body size and small egg size were direct drivers of species occupancy of large rivers and utilization of lake ecosystems, which in turn contributed to broader range size but decreased local abundances. After accounting for indirect pathways, large body size and small egg size persisted as direct correlates of range size but not local abundance. Body size was a direct negative driver of local abundance among species occurring in small streams but not medium-to-large streams.

Discussion

Positive correlations between habitat breadth and local abundance, and between habitat breadth and geographic range size, indicate weak double extinction jeopardies in US freshwater fishes. However, local abundance and range size were not positively linked in our study, suggesting that a triple extinction jeopardy for US freshwater fishes may be averted. This result is inconsistent with the habitat breadth hypothesis (Brown 1984, Brown et al. 1995), which posits that positive associations between habitat breadth and local abundance, and between habitat breadth and geographic range size, explain the commonly observed correlation between local abundance and range size in terrestrial species.

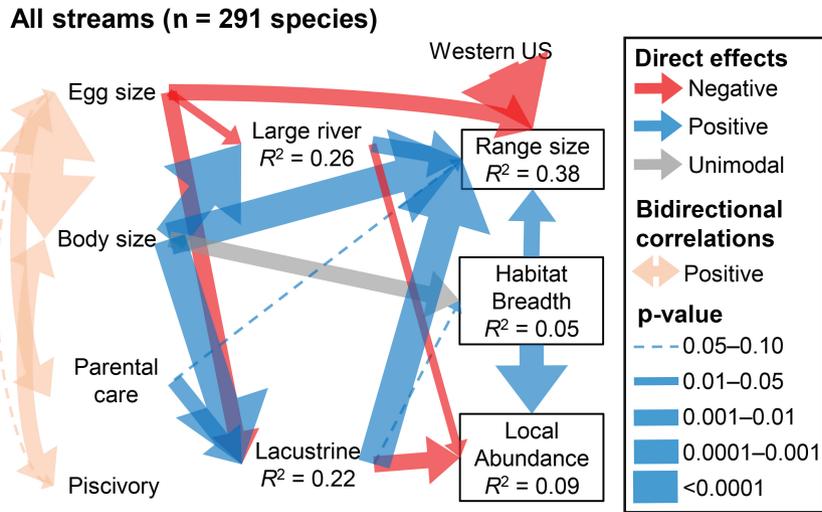


Figure 4. Final path model describing direct effects and bidirectional correlations among life-history traits, habitat affinities, and the three dimensions of rarity among fishes found in all streams. Width of arrows represents the strength of direct effects and bidirectional correlations. To improve clarity, the bidirectional correlation between use of large rivers and use of lacustrine habitats was omitted ($p < 0.0001$).

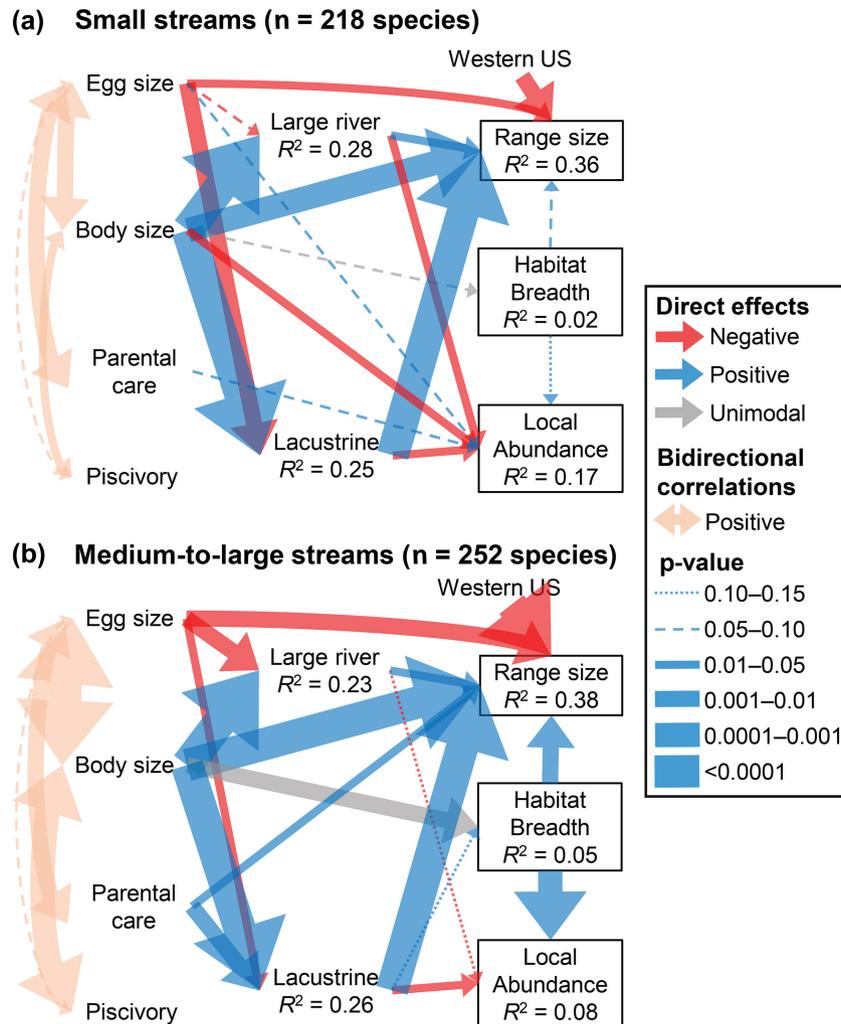


Figure 5. Comparison between final path models of rarity among (a) fishes found in small (1st–3rd order) streams and (b) fishes found in medium-to-large (≥ 4 th order) streams. Width of arrows represents the strength of direct effects and bidirectional correlations. To improve clarity, the bidirectional correlation between use of large rivers and use of lacustrine habitats was omitted ($p = 0.003$ in small streams and $p = 0.043$ in medium-to-large streams).

Why then were local abundance and range size not positively correlated despite their respective positive associations with habitat breadth? Our analysis suggests that habitat affinities of species, driven by life-history, invoke a trade-off between local abundance and range size. Species that use large rivers and lacustrine habitats had larger range sizes but lower local abundances than species that do not use these habitats. The positive relationship between lacustrine habitat use and range size had previously been observed in North American and Canadian fishes; it is hypothesized that lacustrine species were able to seek refuge in non-glaciated lakes during the last glacial maxima and recolonize northward as glacial sheets retreated (Griffiths 2010, Blanchet et al. 2013). Our analysis, which excluded species with a substantial part (> 50%) of their ranges in Canada, suggests that the use of lakes as refuges or dispersal pathways extends beyond northern species in the last glacial maxima. Further, fishes occurring in shallow lakes are highly tolerant of physicochemical stressors such as low dissolved oxygen, high turbidity, and extreme water temperatures (Goetz et al. 2015); these traits likely aided their dispersal and establishment over larger geographic areas.

Large main-stem rivers were likely efficient dispersal corridors for freshwater fish as they connect different watersheds (Knouft and Page 2003). For headwater or small stream fishes that are not able to use main-stem habitats, opportunities for dispersal across watersheds are limited to river capture events (Griffiths 2010). Moreover, large-river species tend to be more migratory compared to headwater and small stream species (Griffiths 2010); the ability to migrate over long distances allows the former to more readily establish larger geographic ranges.

In contrast to the positive correlation with range size, the use of large rivers and lacustrine habitats were negatively associated with local abundance. As environmental conditions of large rivers and lacustrine habitats are very different from smaller streams (Matthews 1998), species that use larger rivers and lacustrine environments may not be as well adapted to lotic conditions and therefore achieve lower relative densities in small streams. This, combined with the preponderance of small, low-order channels over large, high-order rivers in our dataset and the US in general (Fig. 1; Knouft and Page 2003), was most likely responsible for the overall lower local abundance of large river and lacustrine species.

Life-history traits were responsible for much of the variation observed in local abundance and range size. Body size, egg size, and parental care were important direct correlates of large river and lacustrine habitat usage by species, which in turn was associated with variation in local abundance and range size. Species with larger body size and smaller eggs tended to use large rivers and lacustrine habitats. The greater availability of space and food sources in productive large rivers and lakes likely allowed colonization of larger-bodied fishes when compared to small headwater streams. Size-specific predation risk – where small body sizes are selected in small, shallow streams to deter terrestrial predation and large body sizes are selected in large, deep streams to minimize piscivory – potentially contributed to the positive correlation between body size and channel size (Power 1987, Schlosser 1991). Lakes and large rivers are prey-rich environments for fish larvae owing to their high planktonic

productivity (Matthews 1998, Wetzel 2001); in such environments, the production of many small eggs and larvae maximizes fish survival as opposed to having large but few eggs (Winemiller and Rose 1992, 1993). Last, lacustrine environments, owing to its temporal stability, likely favor species that maximizes juvenile survivorship through increased parental care (Winemiller and Rose 1992).

Besides acting via habitat affinities, our results suggest that some life-history traits directly help define range size. Fishes with larger body sizes and smaller eggs tended to have large geographic range sizes. Body size is positively associated with dispersal ability (Jenkins et al. 2007) as large fishes swim faster and more efficiently (Beamish 1978, 1980). Consequently, larger fishes are better equipped to perform long-distance migrations (Mahon 1984, Griffiths 2010) and to colonize and persist in new habitats (Griffiths 2010, Luiz et al. 2013). To meet energetic demands, larger-bodied fishes also require larger home ranges (Swihart 1988, Minns 1995), which likely contributes to their ability to acquire larger geographic ranges. Having small (and many) eggs increases the probability that at least some offspring would successfully disperse and recruit to new suitable habitats (Winemiller and Rose 1992) thus potentially enabling fishes to acquire larger ranges. Some cyprinids have small eggs that are pelagic (passively dispersed by stream flow) (Perkin and Gido 2011), which likely increases dispersal distance of offspring, and therefore range size, compared to larger, more adhesive eggs.

Biogeography and habitat breadth were the other direct effects on range size and local abundance. Consistent with our a priori predictions, western US fishes had smaller range sizes, likely owing to the smaller land area in western US and/or their relatively younger evolutionary age (Hodges and Belwood 2015). Holding all other factors constant, the ability to use a wide range of habitats allowed fishes to achieve both higher local abundances and larger range sizes, which provided support for a module of the niche (habitat) breadth model proposed by Brown (1984) and Brown et al. (1995). Habitat breadth was highest at intermediate body sizes. As discussed above, body size is positively correlated with stream size owing to resource limitation and/or size-specific predator risk (Power 1987, Schlosser 1991); it therefore follows that intermediate body sizes are likely to use a wider range of habitats than either extreme.

Our analysis of fishes occurring in small vs medium-to-large streams indicates rarity pathways vary with ecosystem size. Specifically, it supports our hypothesis that local abundance is limited by body size in small but not large streams. This indicates that biotic communities in small streams are energy-limited, likely a result of their low productivity owing to extensive riparian cover and lower habitat volume (Vannote et al. 1980). In addition, we found that local abundance increased with egg size in small streams only. This is a likely consequence of the limited availability of planktonic prey for fish larvae in small streams; larger eggs produce larger larvae, which increases survival probabilities in prey-poor environments (Marsh 1986, Winemiller and Rose 1993). Last, direct links from habitat breadth to range size and local abundance were weaker among fishes occurring in small streams than those present in medium-to-large streams. The weakening of the habitat breadth-range size effect indicates that this effect

primarily acted on fishes occurring in larger channels (stream orders ≥ 4), consistent with the notion that larger channels are important for fish dispersal to different habitats (Knouft and Page 2003). In small streams, local abundance was only weakly associated with habitat breadth probably because the former was calculated over small streams whereas habitat breadth represented the range of all habitats used. Taken together, these key differences underlie a negative, albeit weak, association between local abundance and range size among fishes in small streams.

Our models explained a greater proportion of the variation in species range size ($R^2 = 0.36\text{--}0.38$) than local abundance ($R^2 = 0.08\text{--}0.17$) or habitat breadth ($R^2 = 0.02\text{--}0.05$). These effect sizes can be interpreted as large, medium, and small, respectively (Cohen 1988). Residuals of local abundance models showed higher phylogenetic dependence than habitat breadth or range size models. This suggests that after accounting for traits examined in our study, local abundance may be phylogenetically conserved and/or driven by other traits that exhibit a phylogenetic signal. The lack of phylogenetic inertia in range size residuals might be explained by dominance of peripheral speciation events in which a widespread species gives rise to one or more small-ranged species along its geographic range limits, resulting in a large difference in range size between closely related species (Hodges and Belwood 2015), e.g. *Cottus bairdii* and *C. caeruleomentumum* (Kinziger et al. 2000); *Etheostoma parvipinne* and *E. phytophilum* (Near et al. 2011). Habitat breadth appears to be phylogenetically labile and weakly predicted by a single trait, body size. This indicates that habitat breadth is an evolutionarily malleable trait, consistent with the finding that niche shifts and evolutionary time are largely decoupled in European birds (Pearman 2014). Future studies that aim to uncover correlates of habitat breadth should examine traits that tend to be more phylogenetically labile such as behavior (Blomberg 2003), morphology (Sternberg and Kennard 2014) and/or fine-scale trophic niche (Pearman 2014).

Overall, our results indicate that neither the habitat breadth hypothesis (Brown 1984, Brown et al. 1995) nor the habitat position hypothesis (Gaston and Blackburn 2000, Gregory and Gaston 2000) could adequately explain the relationship between local abundance and range size in US freshwater fishes. Habitat breadth was positively associated with both local abundance and range size; however, these associations did not drive a positive relationship between the latter two variables. The habitat position hypothesis posits that the proportional rarity of niches or habitats drives a positive association between local abundance and range size; species adapted to the most common niche or habitat are likely to achieve greater local abundance as well as larger ranges because these habitats are simply more available for species to exploit. We found support for the effect of habitat position on local abundance but not range size. Large rivers, which comprise the minority of stream length in the US, and lakes, whose habitat conditions differ greatly from flowing streams, support stream fish species with the largest ranges because they represent an efficient dispersal pathway or a refuge from adverse environmental changes. These observed model departures stress a key difference between terrestrial communities, from which these models were largely developed, and freshwater stream communities:

dispersal of stream biota is strongly dependent on its position in the stream network and refuge use.

As with all macroecological studies, important caveats to the findings must be considered. First, whereas range size and habitat breadth were defined based on their original ranges and habitats, local abundance was calculated based on contemporary (past two decades) assemblages that are likely exposed to varying levels of anthropogenic threats. We attempted to minimize the influence of human impact on our analyses by examining only stream assemblages while excluding those found in ditches or canals and those in which non-native species were dominant. We acknowledge that while human impacts may still have some, albeit reduced, effect on our analysis, we contend that it is unlikely to confound our conclusions because local abundance was calculated by taking the median value across multiple sites with potentially different levels of human disturbance and that phylogenetic constraints on tolerance (Matthews 1998) were accounted for in our analysis. Second, by taking the median value across sites as the point estimate of local abundance for each species, we were not able to explicitly incorporate the variation in local abundance among sites. Although our approach was reasonable given that our goal was to elucidate species-level relationships between rarity axes and their potential drivers, among-site variation in local abundance remains poorly understood and should be explored in future studies.

In conclusion, our study builds upon existing studies of range size correlates (Taylor and Gotelli 1994, Pyron 1999, Griffiths 2006, 2010, Blanchet et al. 2013) by identifying potential mechanisms by which species life-history, ecology, and biogeography affect not just range size but also inter-relationships between different dimensions of rarity in US freshwater fishes. Body size, the use of lacustrine habitats, and the use of large rivers were strong predictors of rarity; as information on these traits are relatively easy to obtain, they could be used to inform extinction risk and conservation planning in regions such as the Neotropics and SE Asia where threats are intense and fish conservation needs are high (Giam et al. 2012, Frederico et al. 2016). Finally, although US fishes as a whole does not appear to be affected by strong concordance among different rarity dimensions, it is still important to focus on the species that are in double or triple jeopardy. Using the methodology developed here, future studies can identify priority regions that are disproportionately rich in species which are rare in multiple axes to inform conservation policy and planning.

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Supplementary material (Appendix ECOG-02946 at <www.ecogeography.org/appendix/ecog-02946>). Appendix 1–6.