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The architecture of river networks can drive the evolutionary dynamics of aquatic populations

Andréa T. Thomaz,[1,2] Mark R. Christie,[1,3,4] and L. Lacey Knowles[1]

[1]*Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, Michigan 48109*

[2]*E-mail: thomaz@umich.edu*

[3]*Department of Biological Science, Purdue University, West Lafayette, Indiana 47907*

[4]*Department of Forestry and Natural Resources, Purdue University, West Lafayette, Indiana 47907*

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It is widely recognized that physical landscapes can shape genetic variation within and between populations. However, it is not well understood how riverscapes, with their complex architectures, affect patterns of neutral genetic diversity. Using a spatially explicit agent-based modeling (ABM) approach, we evaluate the genetic consequences of dendritic river shapes on local population structure. We disentangle the relative contribution of specific river properties to observed patterns of genetic variation by evaluating how different branching architectures and downstream flow regimes affect the genetic structure of populations situated within river networks. Irrespective of the river length, our results illustrate that the extent of river branching, confluence position, and levels of asymmetric downstream migration dictate patterns of genetic variation in riverine populations. Comparisons between simple and highly branched rivers show a 20-fold increase in the overall genetic diversity and a sevenfold increase in the genetic differentiation between local populations. Given that most rivers have complex architectures, these results highlight the importance of incorporating riverscape information into evolutionary models of aquatic species and could help explain why riverine fishes represent a disproportionately large amount of global vertebrate diversity per unit of habitable area.

KEY WORDS: **Agent-based model (ABM), confluence position, dendritic shape, downstream migration, genetic structure, riverscapes.**

Understanding how the physical characteristics of an ecosystem affect patterns of genetic variation can enhance our ability to address a variety of evolutionary questions. River networks, for example, can have complex architectures that may drive patterns of neutral genetic variation among or within river basins (e.g., Burridge et al. 2008; Hopken et al. 2013; Paz-Vinas and Blanchet 2015; Thomaz et al. 2015). Yet, without knowing which factors contribute to population structure (e.g., the effects of the number of tributaries, river length, or differences in flow regime), it is not clear why genetic structure may differ across regions and/or taxa. Likewise, misleading inferences about putatively selected loci or purported genomic regions associated with local adaptation can result when an inappropriate null model is used to generate expected patterns of variation for neutral loci for tests of selection (Cruickshank and Hahn 2014; Lotterhos and Whitlock 2015; He and Knowles 2016). For example, outlier approaches for detecting selected loci are prone to errors if the differences between riverine systems and their terrestrial counterparts are not taken into account (Fourcade et al. 2013).

Here we take an agent-based modeling (ABM) approach to disentangle the relative contributions of different river properties to observed patterns of genetic variation. Specifically, we evaluate how the dendritic nature of river networks (e.g., different levels of branching and confluence position) and constraints on dispersal associated with downstream flow regimes affect the genetic diversity of localized populations within rivers, as well as genetic differentiation along river segments. The contribution of asymmetric migration in rivers (Morrissey and de Kerckhove

EVOLUTION
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2009; Paz-Vinas et al. 2013) and the role of connectivity (Labonne et al. 2008) at the metapopulation level (i.e., in the whole river) has previously been demonstrated to be an important factor for the maintenance of genetic variation, but how the interaction between these variables and other important river properties generates local population structure remains poorly understand. We also contrast riverscapes with open landscapes (e.g., terrestrial landscapes) from a local population perspective to highlight key river parameters for modeling expected patterns of genetic variation and differentiation. With the insights the simulations provide about the causal factors structuring genetic variation, we suggest particular mechanisms that might be worth pursuing as possible agents for explaining patterns of species diversity itself in these aquatic habitats. Specifically, we discuss how our findings could help explain why riverine freshwater fishes represent a disproportionate amount of freshwater fish diversity, and total fish diversity more generally, given that rivers represent a minute fraction of habitable aquatic area globally (Lundberg et al. 2000; Guinot and Cavin 2015).

Material and Methods

ABM IN RIVERS

To understand how different river shapes affect patterns of genetic diversity within local populations and genetic variation between local populations, we employed a spatial explicit forward-time agent-based model (ABM, see Christie and Knowles 2015). To test the effect of riverscape properties on population genetic structure, we measured both local genetic diversity within populations and genetic differentiation among populations along a riverscape after varying three explanatory variables: (1) the proportion of downstream migrants (from bidirectional to entirely asymmetrical migration from upstream to downstream), (2) river complexity (from linear to highly dendritic), and (3) the position of local populations within the riverscape (upstream and downstream populations, or confluence populations). We refer to upstream and downstream populations with respect to the direction of water flow, as well as those in the confluence (i.e., populations in which two river segments come together; Fig. 1). We also use river order as a measure of network complexity (also called "Horton–Strahler number"; Horton 1945; Strahler 1957), in which river order is defined as the number of upstream tributaries.

In the ABM, individuals and their genotypes are tracked through a river network in both space and time (i.e., per generation), in which each generation is characterized by reproduction, migration, mortality (as a function of user-defined carrying capacities), and mutation. Local population sizes were constrained by a carrying capacity (K) such that the total number of individuals in the entire network depended on the total number of local populations distributed throughout the network. Simulations were conducted with three different carrying capacities ($K = 100$, 200, and 1000) and numbers of offspring per individual ($n = 2$, 10, and 20). To consider the generalizability of the results on the contribution of river architecture when other factors vary (e.g., when fish are not evenly distributed throughout a river network), we also conducted simulations in which the population size varied systematically from large upstream populations to small downstream populations. We modeled asexual reproduction because sexual reproduction would introduce a species-specific behavioral component to the model (i.e., mate choice, maximum distance between mates, etc.) that would make it difficult to identify generalizations about how the properties of rivers contribute to genetic structure. Dispersal was modeled using a leptokurtic dispersal kernel with the package Fishmove in R (Radinger and Wolter 2013), which provides a taxon-specific probability distribution of dispersed individuals as a function of distance from the source population for a given set of environmental characteristics. The taxon characteristics chosen for these simulations corresponded to a small generalist fish (size = 60 mm standard length, caudal-fin aspect ratio = 1.5), with a dispersal probability of 0.095 under a lognormal distribution (i.e., dispersal in the Fishmove R package was set to river order three), in which the dispersal probability of individuals was integrated over a one-year period. We did not vary the dispersal kernel based on the location of the populations (i.e., different migration rates for different river sections; Fig. 1) because we did not want to confound the interpretation of network shape with migration rate. The total number of migrants per generation was calculated as a function of K, the dispersal kernel, and the distance between populations. Following the dispersal step in each generation, individuals were randomly removed (introducing an expected variance in reproductive success) from each local population according to the local population carrying capacity K. Lastly, a per locus mutation rate (10^{-6}) was applied under an infinite alleles model, prior to the start of a new generation.

For all simulations reported here, models were run for 500 generations with 30 independent replicates for each combination of river properties (i.e., direction of migration and level of river complexity). Models were run for 500 generations with a relatively high mutation rate to strike a balance between relevant timescales and a computational processing time, throughout which we tracked changes in the allele frequencies (see Text S1 for a detailed discussion on parameter settings). At the beginning of each simulation, 50 biallelic codominant SNPs were created in Hardy–Weinberg equilibrium and genotype frequencies were distributed equally throughout the populations.

The output from a single simulation consisted of multilocus genotypes for all individuals from every local population. We present the number of distinct multilocus genotypes per population (averaged across replicates) for the entire river, as well as the pairwise population F_{ST}'s calculated with the package

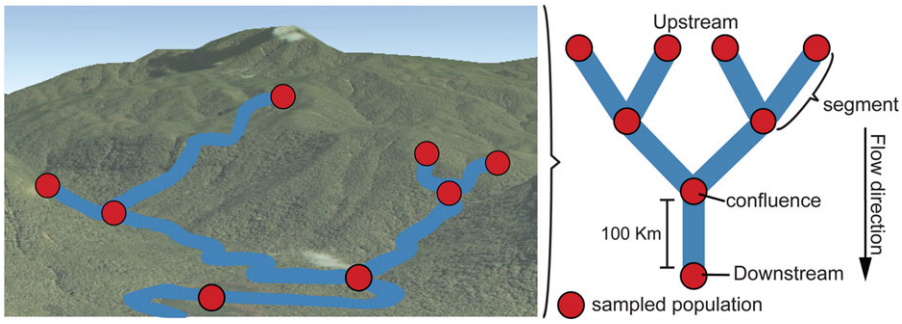

Figure 1. **Schema illustrating a hypothetical river network and the corresponding theoretical representation used in our model. In all simulations performed here, segments denote connection routes between local populations (circles), with populations equally spaced along the river. Migration was varied according flow direction from symmetric to completely asymmetric downstream (arrow).**

hierfstat in R (Goudet 2005). Patterns of genetic differentiation were visualized with a Principal Coordinate Analysis, PCoA, of the pairwise F_{ST} matrix using the function pcoa in the vegan package (Oksanen et al. 2013). For graphical illustration of patterns of genetic variation across populations, the first two axes of the PCoA were rescaled to range between 0 and 1 with a corresponding color score (Red Green Blue = RGB) that also ranged between 0 and 1. The first axis of the PCoA was represented by Red color variation and the second axis by the Green (Blue color variation was held constant at 0.8) such that the more dissimilar the colors are between two populations, the higher the F_{ST} value is between these populations. All models and analyses were performed with R version 3.1.2 (R Core Team, 2014).

LANDSCAPES VERSUS RIVERSCAPES

To assess how river networks differ from open landscapes (e.g., some terrestrial and marine environments), a hypothetical landscape scenario was generated to contrast with the results from the riverscapes. For this comparison, river networks and open landscapes each had 16 populations with identical numbers of individuals, with populations being separated by a constant segment length (67 km). Although the open landscape was organized as a 4×4 matrix, connected vertically and horizontally (Fig. 2A), the river network resembled a medium complexity river (branching = fourth-order river; Fig. 2B). For the river network, we used asymmetric migration because it is a more realistic migration in this environment (9:1 ratio for downstream:upstream migrants; see Morrissey and de Kerckhove 2009; Paz-Vinas et al. 2015). For the open landscape, we included two different migration scenarios: (1) asymmetric migration rate (9:1 ratio; see black arrows in Fig. 2A) and (2) symmetric migration in which the same number of individuals migrated between two populations. Thus, in the first set of comparisons the open landscape differed from the river network only by the number of connections between local populations whereas in the second set of comparisons we varied both the number of connections between local populations and the symmetry of migration (two factors that likely differ between terrestrial and riverine populations). Across all comparisons, the same total number of migrants was exchanged in each generation.

RIVERSCAPE ARCHITECTURES

To assess the effect of river architecture on the evolutionary dynamics of local populations we focused on three spatially important variables: (1) asymmetric migration, (2) the position of a confluence, and (3) the degree of branching (see Fig. 1). To assess the effect of asymmetric migration caused by downstream water flow on different river architectures, we compared two river networks: a low complexity river with a strictly linear shape, and a higher complexity river with a dendritic shape (branching = fourth-order river; Fig. 3). Both networks had 16 populations equally spaced, with constant total length of 1000 km (67 km per segment). For each river network, we varied the frequency of downstream migration from completely symmetric (0.5) to completely asymmetric downstream (1.0) in increments of 0.1. Even though the proportion of downstream migrants was varied, the total number of migrants was held constant. For example, if there were 100 total migrants and the migration was completely symmetric, then 50 individuals dispersed upstream and 50 individuals dispersed downstream. Conversely, if migration were completely asymmetric, then all 100 individuals would disperse downstream.

To evaluate how the location of the confluence with respect to other local populations influences the genetic pattern in river networks, we compared four networks with different confluence positions: no confluence, upstream confluence (e.g., those close to headwaters), confluence in the middle of the network, and downstream confluence populations (e.g., those close to river mouths; Fig. 4A–H). The total number of populations was kept constant to eight; total network size was set to 700 km (100 km per segment), and the frequency of asymmetric migration downstream to 0.9 among all scenarios.

Lastly, we created four river networks with differing levels of branching complexity that varied from very simple (i.e., a single confluence; second-order river) to highly branched (i.e., 15 confluences; fifth-order river). In this case the total number of

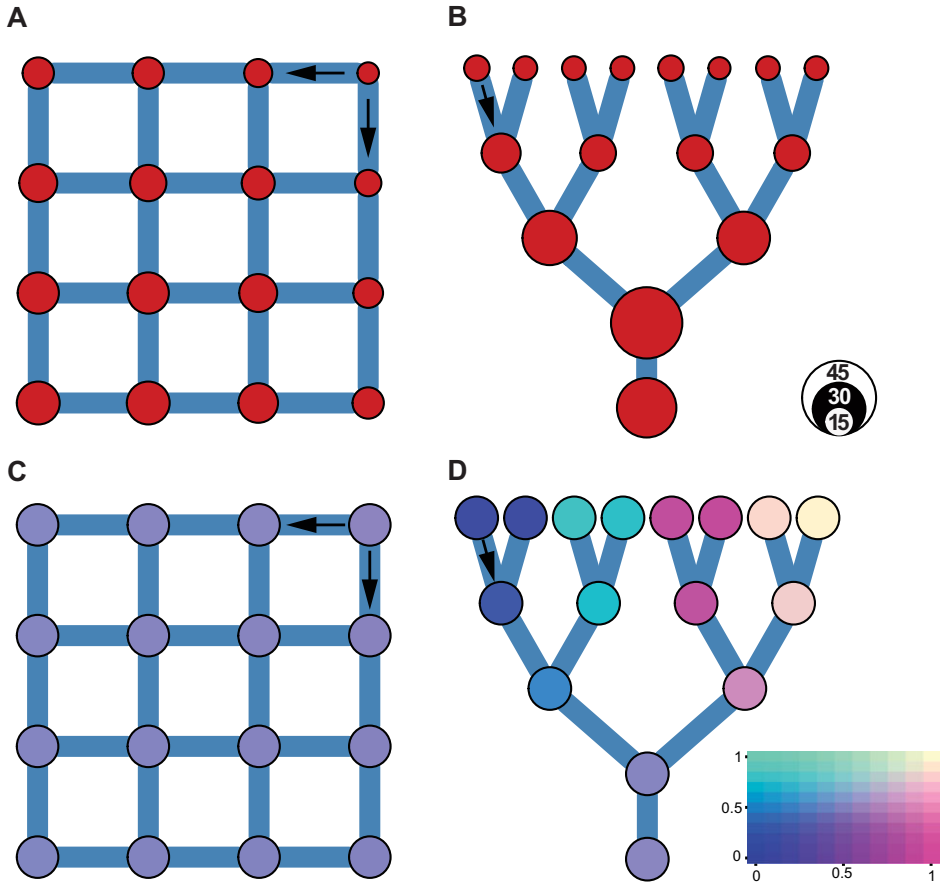

Figure 2. Genetic diversity (A and B) and genetic differentiation (C and D) for open landscapes (i.e., terrestrial) and river networks with asymmetric migration (black arrows indicate the direction of migration); all parameters were held constant between both scenarios (i.e., segment length, *K*, and number of offspring). Genetic diversity is demonstrated by red circle sizes indicating the number of distinct genotypes present in each population (see legend in B), whereas genetic differentiation is demonstrated by color in which more divergent differences in colors between two populations indicate higher pairwise F_{ST} values (legend in D illustrates position of local population in multivariate space). River networks have a distinctive distribution of genetic variation, with much greater genetic diversity found downstream of confluences and higher genetic differentiation between headwater populations.

populations (and thus the total number of individuals) varied as a function of the river complexity, ranging from four populations to 32 populations (Fig. 4I–P). Although the number of local populations varied, the results from this design were highly conservative because increasing the number of populations could only reduce the effects of genetic drift (see discussion). The total length of the network and the frequency of asymmetric migration downstream were kept constant (1000 km and 0.9, respectively).

Results

For all comparisons performed across different networks, the per population carrying capacity ($K = 100$, 200 and 1000) and number of offspring ($n = 2$, 10 and 20) did not qualitatively affect the genetic patterns observed (see Fig. S1). Varying the carrying capacity within the network (i.e., introducing heterogeneity in the system to represent a fish specialized to upstream environments) did not change the qualitative results (i.e., only the absolute standardized genetic diversity and amount of genetic differentiation differed; see Fig. S2). For these reasons, we report only the results for simulations with constant $K = 200$ and 10 offspring per individual per generation.

LANDSCAPES VERSUS RIVERSCAPES

We compared an open landscape with a branched river network to assess how river systems differ from less confined systems, such as certain terrestrial landscapes and marine environments. Based on levels of genetic diversity and differentiation among the populations, the genetic patterns associated with river networks differ quantitatively and qualitatively from open landscapes. Remarkably, genetic differentiation was an order of magnitude greater in the river network compared to the open landscape (river mean $F_{ST} = 0.06$ and open landscape mean $F_{ST} = 0.002$; Fig. 2C, D). The average genetic diversity per population across

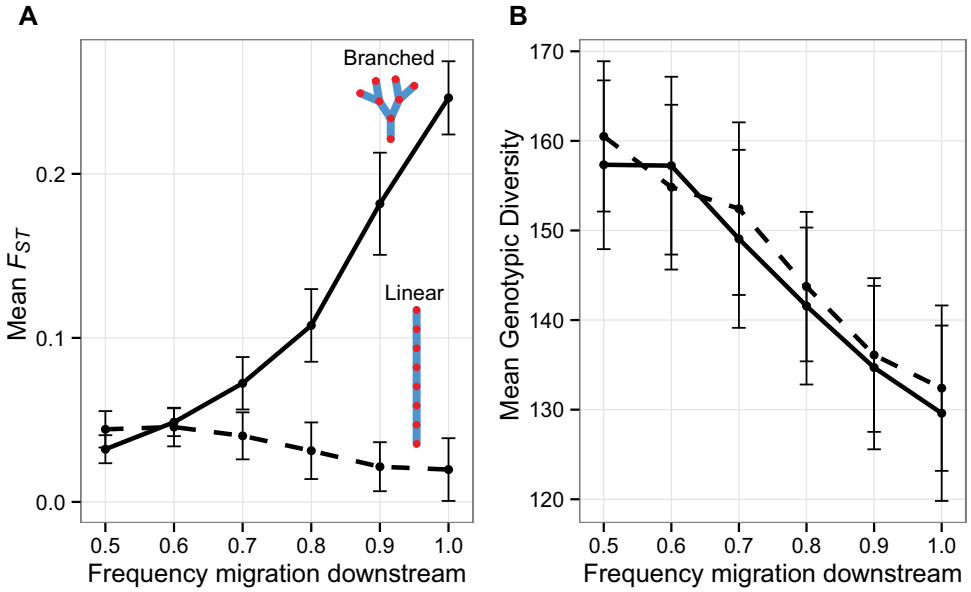

Figure 3. **Mean genetic differentiation (as measured by F_{ST}; A) and genetic diversity (i.e., number of genotypes; B) between a branched, fourth-order river network (solid line), and a strictly linear network (dashed line). The total number of migrants between two populations was kept constant, however, we varied the proportion of downstream migrants from symmetric (i.e., 0.5 translates to an equal percentage of migrants that dispersed upstream and downstream) to completely asymmetric downstream (i.e., 1.0 translates to 100 percent of migrants moved downstream). Genetic differentiation in networks with branched architecture increases with increases in the proportion of downstream migrants. However, there are no substantial changes in genetic differentiation in linear networks. Genetic diversity is lost in both networks when asymmetric migration increases towards downstream migration. This pattern is due to the more rapid loss of alleles associated with genetic drift when migration is asymmetric. Error bars represent one standard deviation.**

replicate simulation runs was the same in both systems (mean no. of genotypes = 21; Fig. 2A, C). However, at the population level, river networks have greater variance in genetic diversity among populations in comparison to the open landscapes (SD = 0.03 and 0.01, respectively). Note that the differences reported here are due solely to differences in connectivity between rivers and open landscapes because all other parameters were held constant.

At the population level, river networks accumulate higher genetic diversity at populations downstream of the confluence, with genetic diversity being on average three times smaller at the upstream populations (e.g., headwaters) in comparison to downstream populations (e.g., those at river mouth; Fig. 2B). In terms of genetic differentiation, river networks have the highest genetic differentiation between upstream populations than populations in open landscapes. For example, pairwise F_{ST} values between upstream populations are one order of magnitude larger in river networks (mean F_{ST} = 0.1) in comparison to two populations separated by the same distance in open landscapes (mean F_{ST} = 0.01) with asymmetric migration (see Fig. 2C, D). When we modify the migration directionality to be symmetric in the open landscape scenario (which is more realistic for landscapes in which individuals can move freely between two populations), there is even greater homogenization of the genetic diversity in the open landscape (Fig. S3).

RIVERSCAPE ARCHITECTURES

To evaluate the effect of asymmetric gene flow, we compared different migration patterns for both a linear network (i.e., low complexity; first-order river) with a heavily branched network (i.e, more complex; fourth-order river). All variables were kept constant except the proportion of downstream migration, which varied from completely symmetric (0.5) to completely asymmetric (1; downstream only). In the strictly linear network, increasing downstream migration did not affect mean genetic differentiation, whereas in the branched network, mean F_{ST} increased with increases in asymmetric migration (i.e., downstream migration), being more than eight times larger in completely asymmetric scenarios than in symmetric migration scenarios (symmetric mean F_{ST} = 0.03; asymmetric mean F_{ST} = 0.25; Fig. 3A). It is important to keep in mind that these differences were found after varying the proportion of downstream versus upstream migrants, but the total number of migrants was held constant across all tested scenarios.

In contrast, a similar pattern in genetic diversity is observed for both simple and complex river networks, independent of the river network complexity. Increasing asymmetric migration downstream reduces overall genetic diversity in both systems in which genetic diversity was calculated as the total number of unique genotypes in the entire river network (averaged across replicates; Fig. 3B). This effect is caused by the increasing rate

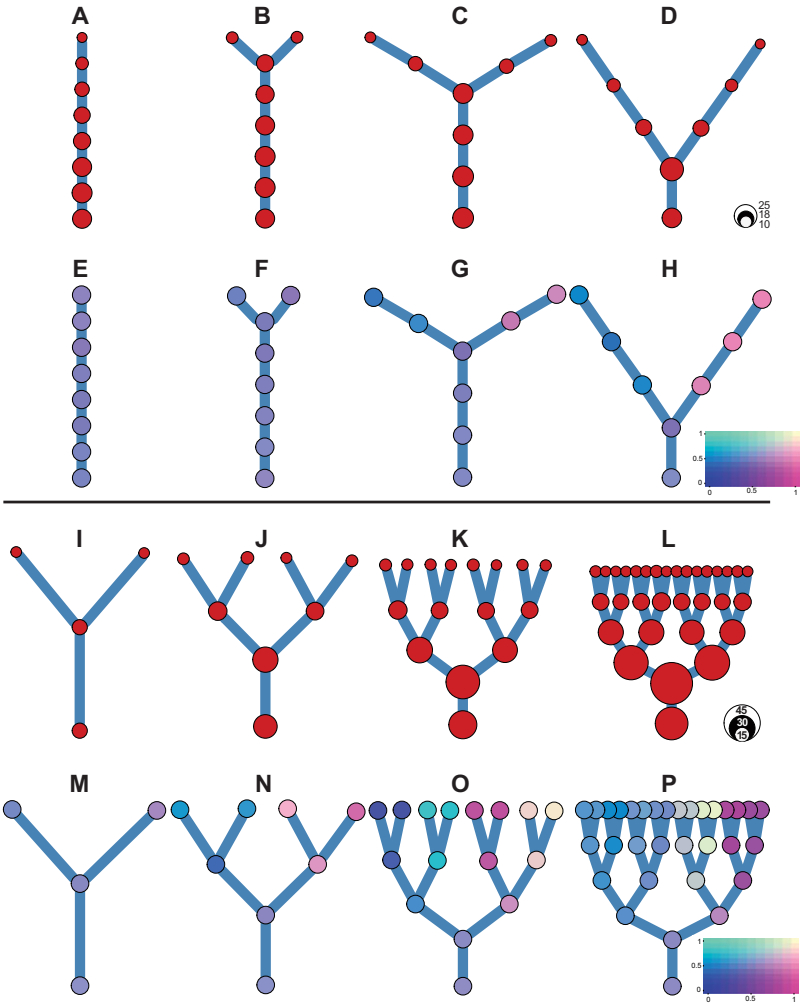

Figure 4. Comparison between different levels of river network complexity (i.e., confluence position and branching) in relation to genetic diversity (A–D; I–L) and genetic differentiation (E–H; M–P). Besides the network shape, all other variables were held constant (i.e., river total length, *K*, number of offspring, asymmetric migration rate, and dispersal kernel). Genetic diversity is demonstrated by red circle sizes indicating the number of unique genotypes present in each population (see legend in D and L), whereas genetic differentiation is demonstrated by color in which more divergent differences in colors between two populations indicate higher pairwise F_{ST} values (legend in H and P illustrates position of local population in multivariate space). The confluence (A–H) accumulates higher genetic diversity downstream its position, in comparison to tributaries that has less diversity. As the location of a confluence moves further downstream, greater genetic differences are observed between populations in the tributaries. In relation to the amount of branching (I–P), as river networks increase in complexity, higher heterogeneity among local populations is observed for both genetic diversity and genetic differentiation.

at which genetic diversity is lost in the upstream populations because, with higher asymmetric rates of migration, the effects of genetic drift are not mitigated by gene flow.

Varying the position of a confluence along a river network, while all other parameters were kept constant, demonstrates that the location of a river confluence with respect to other local populations influences both genetic diversity and genetic differentiation (Fig. 4A–H). In general, headwaters have a lower accumulation of genotypes than downstream populations (Fig. 4A–D). Importantly, populations located along the tributary rivers have lower genetic diversity, compared with populations located at a confluence. These patterns are observed because unique genotypes from different tributaries are mixed in populations positioned downstream of a confluence. For the results presented here, this pattern drives confluence populations to have an average of two times greater genetic diversity than upstream populations.

Genetic differentiation increases with the increase in length of the tributary rivers (confluence close to upstream populations: mean $F_{ST} = 0.003$ [SD = 0.005] and confluence close to downstream populations: mean $F_{ST} = 0.055$ [SD = 0.05]; Fig. 4E, H, respectively). For a confluence positioned further downstream, higher genetic differentiation accumulates in the

upstream populations, indicating that rivers with longer tributaries (Fig. 4G, H) will have higher genetic differentiation than rivers with linear shape and/or shorter tributaries (Fig. 4E, F).

To assess how increasing complexity can affect genetic patterns in river networks, we varied the number of branches in a network following a fractal shape (river order 2 to 5, Fig. 4I–P). Increasing the complexity of the river networks increases the overall genetic diversity and differentiation in these systems (second-order river: mean $F_{ST} = 0.008$ [SD = 0.007] and mean of 10 genotypes [SD = 2.2]; fifth-order river: mean $F_{ST} = 0.06$ [SD = 0.03] and mean of 278 genotypes [SD = 12.2]; Fig. 4I–P). Likewise, while the absolute level of genetic differentiation was affected by varying the population size in the river network (Fig. S2), the same qualitative patterns of differentiation compared to a linear network (Fig. 3A) persist. Genetic diversity increases substantially with increases in network complexity, but the diversity of upstream populations is uniformly low, regardless of the network complexity (Fig. 4I–L). On the other hand, downstream populations genetic diversity increases with each increase in river complexity (from a mean number of genotypes of 17 for second-order river to 35 in a fifth-order river). Interestingly, the downstream populations do not have the maximum genetic diversity; the local population with highest genetic diversity is the population positioned at the main confluence position (Fig. 4I–L). In contrast to genetic diversity, genetic differentiation is higher among upstream populations when complexity increases (mean F_{ST} among most distant headwaters: second-order river = 0.02 and fifth-order river = 0.1; Fig. 4M–P) and, in general, differentiation is diminished between downstream populations. For all simulations reported here, the total length of the river network was kept constant to 1000 km. As such, the distances between local populations were much greater in the less-branched network (333 km; Fig. 4I, M) versus the more-branched network (32 km; Fig. 4L, P).

Discussion

Half of all vertebrate species are fishes (33,629 of ~66,000; Eschmeyer and Fong 2015). Of this total, more than 40% of fishes live in fresh water, yet fresh water only accounts for 0.01% of all the water on earth. The high species diversity found among freshwater fishes is usually attributed to the comparatively high isolation of fishes found in different riverine basins (Lundberg et al. 2000; Guinot and Cavin 2015). Although this isolation leads to allopatric speciation without gene flow, the observed patterns of genetic differentiation presented by our ABM suggest that river properties may also be an important factor contributing to this high diversity of freshwater fishes, potentially leading to reproductive isolation within a river basin. For example, substantial isolation may be attained in the headwater populations, which can have little to no gene flow imposed by high levels of river branching and asymmetric migration downstream. Thus, the architecture of river networks alone may be an important factor in explaining the high species diversity observed in freshwater fishes.

In dendritic river systems, our results illustrate that greater levels of genetic differentiation occur with increases in network complexity (note that this effect is observed when total length is kept constant across river shapes). We also document that higher genetic diversity is observed in the downstream populations in comparison to the upstream populations. This result has been previously documented in observational studies. For example, in a comparative study in Great Plain fishes, higher haplotypic diversity was observed in branched systems in comparison to linear rivers across three different species (Osborne et al. 2014). Other empirical studies corroborate the accumulation of genetic diversity in populations located further towards the river mouth (for a summary see Fig. 6 in Morrissey and de Kerckhove 2009; Paz-Vinas et al. 2015). Furthermore, our results suggest that the population with highest genetic diversity is not necessarily the most downstream populations (e.g., those closest to a river mouth), but rather the population located in the main confluence of rivers (Crispo et al. 2006), suggesting that genetic diversity can decline between the confluence and populations located further downstream. From a conservation and management perspective, these reservoir populations may warrant additional protection, especially given that they may be subject to increased anthropogenic stresses (e.g., dams, upstream expansion by invasive species).

It is important to point out that the simulations presented here were modeled after a small, nonmigratory fish and the results would quantitatively and qualitatively vary depending on the vagility of the species (Labonne et al. 2008). For example, fishes that often migrate long distances could homogenize the genetic diversity within a river basin. Likewise, moderate to high genetic differentiation may still be maintained among local populations in species that exhibit high natal philopatry (e.g., anadromous salmonids; Whiteley et al. 2004), although river architecture per se may not be a factor of primary importance if reproduction is restricted to a particular river segment. Other potential caveats of our modeling approach were the equal population sizes and use of a constant dispersal kernel throughout the river network (i.e. dispersal patterns may vary along the length of a river network). Keeping these variables constant allowed us to isolate the effect of the river complexity. Adding additional parameters, such as decreased dispersal and smaller carrying capacities in populations located downstream, would only serve to increase genetic differentiation and decrease levels of gene flow in the upstream populations (e.g., in the headwaters of a river; see Fig. S2).

River architecture is just one factor that contributes to patterns of genetic variation and other geographic and/or ecological barriers (not considered in our simulations) within river networks could

be important (e.g., waterfalls, different geomorphology along a river, habitat heterogeneity). Moreover, such barriers have been demonstrated to increase genetic differentiation between populations (Crispo et al. 2006; Pearse et al. 2009; Waters et al. 2015). Our work does not discount the contribution of these other factors, but instead provides an important null model for expected patterns of differentiation that would arise from strictly neutral processes based on river architecture. This has important implications for partitioning the effects of geographic and ecological barriers, especially for comparisons among rivers or regions. For example, apparent differences in the effectiveness of a barrier due to differences in the degree of genetic differentiation among rivers might instead reflect differences in underlying river architectures. Likewise, differentiation that arises from river architecture should be taken into account for any inference about the role of adaptive divergence in isolating populations. Specifically, if genetic differentiation exceeds expectations based on genetic distance (one of the tests used to infer isolation by adaptation or ecology; Sexton et al. 2014), such differentiation might reflect the contribution due to river architecture rather than isolation arising from local adaption. For example, patterns ascribed to ecological divergence as inferred by F_{ST} outliers (i.e., adaptive divergence related to water color; Cooke et al. 2014) could be an artifact of the dendritic shape of the river. Here we show that by taking the river shape into consideration, a more strict and realistic assessment could be performed to test for ecological divergence, avoiding the false classification of neutral loci as having been under selection (Fourcade et al. 2013).

It is also important to note that the simulations performed here for identifying the impact of river shape are conservative by keeping the total river length constant across different levels of network complexity. For example, because the populations were positioned in each confluence, more complex networks contained local populations that were closer together in two-dimensional space (Fig. 4I–P). Yet, even with populations that were closer together, branched rivers had higher genetic differentiation than less-branched rivers despite higher amounts of gene flow between local populations. If we had kept segment length constant (and varied the total length of the river network; a less conservative approach), then the genetic differentiation would be even higher in complex river networks as there would be a concomitant decrease in gene flow between local populations. This has important implications for considering what factors might contribute to the low levels of genetic differentiation observed in marine fish populations distributed along coastline environments (Riginos and Nachman 2001; Bernardi et al. 2003; Knutsen et al. 2003; Palumbi 2003). In particular, our results imply that it is not simply the distance separating coastal marine fish populations, but also the linear environment imposed by coastlines itself, that contributes to patterns of genetic differentiation, based on the levels of gene flow between local populations observed in comparisons between linear and dendritic models in our simulations.

The genetic patterns obtained from our spatially explicit model demonstrate the importance of taking riverscape properties into consideration in population genetic and phylogeographic studies of aquatic populations. Our findings give clear evidence that the precise position of each local population can be an important variable to take into consideration when interpreting patterns of genetic variation within and between river basins (as opposed to averaging across populations within a river basin). Consequently, fully accounting for riverscape properties can generate realistic expectations of the genetic variation observed in these populations, which can be substantially different than open, more-connected landscapes (see also Paz-Vinas and Blanchet 2015). In general, our model results demonstrate that the architecture of river networks can explain the distribution and extent of genetic diversity found within aquatic populations (see also Della Croce et al. 2014 for how river architecture impacts in introgressive hybridization). Comparing these findings with empirical data and reconciling adaptive and neutral processes of diversity remain the next challenges for riverscape genetics.

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DATA ARCHIVING

All scripts and simulations are archived in Dryad Digital Repository under the doi: 10.5061/dryad.7rs2d.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Text 1. Discussion on parameter choice and, scalability and computation.

Figure S1. Comparison between different values of per population carrying capacity (K) and number of offspring.

Figure S2. Absolute and standardized genetic diversity, and genetic differentiation comparison between a river with constant carrying capacity (K) and varying K according the position of the population along the river.

Figure S3. Genetic diversity and differentiation comparison between open landscapes and riverine network with symmetric and asymmetric migration, respectively.