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Functional Trait Variability of Native Fish Communities Across Fragmented River Landscapes

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Abstract: River fragmentation due to dams, weirs, and culverts is one of the major threats to freshwater fish, but its impacts on the functional composition of native fish assemblages are poorly characterized with regard to restoration planning. In this study, looked into how functional trait variability in native fish communities varies depending on the degree of river fragmentation using a simulation experiment based on traits. A set of 60 native fish species, which were described by seven life history, morphology, and ecology traits, was used to create 36 river segments, which belonged to four fragmentation categories ranging from free flowing to highly fragmented based on the connectivity index estimated from the barrier density. The ability of species to survive in each segment depended on the particular functional traits, such as migration, rheophily, large body size, and parental care. Calculated richness, functional richness, functional dispersion, standardized effect sizes compared to null communities, and community-weighted trait averages. Species richness decreased by 28%, and functional richness reduced by 30% from free-flowing to highly fragmented sites ($R^2 = 0.82$ and 0.62, $p < 0.001$), while the proportion of migrating species abundance reduced by about one-third. On the other hand, functional dispersion was unchanged ($R^2 < 0.01$, $p = 0.80$) due to the fact that abundant non-migrating species concealed the loss of rare trait combinations. The deviation from random assembly occurred only in moderately fragmented sites. This proves that single dispersion measures tend to underestimate functional degradation, and multifaceted traits combined with connectivity measures have to be considered in bioassessment and barrier management.

Keywords: River Fragmentation; Functional Diversity; Native Fish; Connectivity; Migratory Fish; Bio-Assessment; Ecosystem Restoration.

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I. Introduction

Rivers occupy a tiny proportion of the Earth's surface yet harbor an overwhelming proportion of the world's freshwater biodiversity; fishes are one of the most biodiverse groups in rivers and also one of the most vulnerable vertebrate groups. Longitudinal connectivity is a fundamental requirement for the diversity of fishes, as they use different sections of the river for various activities throughout the year. This connectivity is extremely uncommon today. According to a study that mapped all the rivers globally, less than one-third of the 1,000 km-long rivers on Earth remain unobstructed through their full course, while the rest are obstructed by dams, reservoirs, and other structures (Grill et al., 2019). Fragmentation interacts with other pressures such as flow regulation, habitat modification, pollution, alien species, and climate change, and has emerged as one of the consistent threats that have continued to threaten freshwater biodiversity for the past few decades (Reid et al., 2019). Global assessments of current and planned dams have revealed that the existing dams fragment the geographical distribution of many freshwater fishes, and future development of hydropower will fragment even more species (Barbarossa et al., 2020).

The problem for those managing aquatic ecosystems is that fragmentation is simple to quantify but difficult to biologically understand. Fragmentation barriers vary in height, passage, age, operating status, and network placement, while fishes vary in their ability to pass them. The measurement of hydrological connectivity for riverine fishes is therefore still problematic, with different metrics leading to different barrier rankings (Fullerton et al., 2010). Indices of longitudinal connectivity that consider both passage of and isolation by fragmentation barriers have been developed as an attempt to overcome this difficulty (Cote et al., 2009). These indices characterize the physical template but do not provide biological insight into what biological processes are being disrupted by decreasing connectivity. While species richness is the

most popular response variable used, it treats all species as equivalent and cannot demonstrate whether or not any of the species lost play specific roles in migration, energy flow, or nutrient transfer.

These methods represent a solution to closing such gaps. The concept of landscape being used as a filter that only allows species with adequate traits to survive in an area is one way through which the prediction of changes in communities as a result of changes in the environment in streams becomes possible (Poff, 1997). Fishes exhibit different life histories based on recognizable strategies involving trade-offs between fecundity, growth, and the timing of reproduction. This makes it possible to separate opportunistic, periodic, and equilibrium strategies among North American fishes (Winemiller & Rose, 1992). Life history strategies vary depending on the hydrologic regime, and changes in assemblages occur based on the alteration of flows towards certain life history types (Mims & Olden, 2012). In general, functional traits help detect the response of the community to disturbances through measures of diversity of function and not just taxonomy (Mouillot et al., 2013). Functional methods have greatly advanced in the study of fish ecology, and current major issues involve the selection of traits, indices, and their interpretation (Villéger et al., 2017).

However, little research has been done on how several aspects of functional diversity respond to the gradient of river fragmentation at once, and even less on how various measures such as volume, dispersion, and trait-based measures compare. This is significant because in bio-assessment, one index is preferred because of its simplicity, but in reality, various indices respond to various changes in the community.

This study helps fill this gap with a transparent and trait-based experiment built on the filtering theory. Specifically, the purpose of this research was to examine how functional richness, functional dispersion, and community-weighted mean trait values change along the gradient of connectivity of native fish assemblages, and whether these assemblages deviate from random assembly expectations under various levels of habitat fragmentation. It was assumed that (i) species richness and functional richness would decrease with lower levels of connectivity, (ii) migratory, rheophilic, and large-sized species would be overrepresented in losses, and (iii) functional dispersion would be less affected compared to functional richness as it takes into account species abundance.

II. Materials and Methods

2.1 Study Design and Rationale

The experiment involves forming virtual communities of native fishes in river reaches differing in their degree of connectivity. Fish communities were studied in the field, and all values provided in the study are outputs of the model. There are three arguments for choosing a certain design. Firstly, it enables varying the level of connectivity while keeping other factors (water quality, habitat type, introduction of non-native fishes) constant, which is very rare in natural basins. Secondly, it provides a clear understanding of assumptions under trait filtering, which can then be criticized and improved. Thirdly, it provides predictions for areas where trait data and barrier distribution are insufficient. The structure of the model is based on the landscape-filter concept and life-history theory; thus, conclusions drawn from the study should be seen as conditional upon these theories and not empirical values.

2.2 Regional Species Pool and Functional Traits

Regional pool of 60 species of native fish, consisting of 29 resident species, 22 potamodromous species that make migrations in freshwater, and 9 diadromous species that make migrations from freshwater to saltwater. All species had 7 trait values that were usually used in studying stream fishes: maximal body length (natural logarithm of millimeters), fecundity (natural logarithm of egg number), age at maturation (years), migration type (0 – resident, 1 - potamodromous, 2 – diadromous), trophic level (from 2.0 to 4.5), parental care (0 – absence, 1 – presence), and rheophily index (from 0 to 1), characterizing dependence on running water. Trait values were sampled from distributions and correlations reflecting the known trade-offs in fish life history: bigger body size correlates with high fecundity and late maturation; migratory species tend to be bigger; parental care is common for low fecundity species.

All traits were standardized to have mean zero and variance one, and ordinated through principal component analysis. The first four components captured 83.0% of trait variability (35.5%, 22.1%, 14.6% and 10.7%, respectively) and served as the functional space within which further calculations were performed, according to the multidimensional model for functional diversity indices (Villéger et al., 2008). The first component described the continuum between small, early maturing resident species and large, late maturing migratory species.

2.3 River Landscape and Connectivity Gradient

Thirty-six river segments were created, nine per fragmentation class of free-flowing, weakly fragmented, moderately fragmented, and strongly fragmented rivers. Barrier density (number of barriers per 100 km) varied randomly in the ranges of 0 to 0.4, 0.5 to 1.5, 1.8 to 3.5 and 4.0 to 8.0, respectively. The connectivity index (CI) on the scale of 0 to 100 was calculated from the barrier density according to the formula $CI = 100 \times \exp(-0.32 \times \text{density})$ with a normally distributed error term (standard deviation 2.5) and constrained within 3 to 100. This equation is consistent with a longitudinal connectivity index, where each new barrier results in an additional decrease in the proportion of the river network available for fish, and generates a very strong negative association with barrier density ($r = -0.95$) (Cote et al., 2009).

2.4 Assemblage Model

The probability of survival of each species was computed using a logistic function of the intensity of fragmentation and the species' trait set, including random variation (standard deviation of 0.5 on the logit scale) accounting for local effects that have not been quantified. Migration, rheophilism, and large body size were the traits associated with highest sensitivity to fragmentation, as expected from the idea that migration and flowing water habitat are the requirements filtered out first (Poff, 1997; Mims & Olden, 2012). Parental care and lower fecundity compensated somewhat for this penalty, in accordance with the increased robustness of equilibrium strategy in isolated areas (Winemiller & Rose, 1992). Abundances of the species were drawn from a lognormal distribution, and the residents were given additional abundance as compensation for fragmentation as a result of release from competition and predation. Each assemblage had to maintain at least five species. All reaches used the same parameter values of the model so that any difference between reaches depended only on connectivity.

2.5 Diversity Metrics

Species richness, functional richness (FRic), functional dispersion (FDis), and community-weighted means of body size, the proportion of abundance from migratory species, and the proportion of abundance from species with parental care were all calculated for each reach. Species richness was simply the number of species in each reach. Functional richness was the volume of the convex hull formed by the set of species present in the first three ordination axes, as a ratio of the volume of the convex hull formed by the regional pool (Villéger et al., 2008). The measure of functional dispersion was the mean distance of each species from the center of mass of the assemblage in four-axis space (Laliberté & Legendre, 2010). In order to test if the observed measure of functional dispersion is significantly greater than that expected from a random assemblage, the standardized effect size (SES) was calculated as the difference between observed FDis and the mean of 499 null assemblages divided by the standard deviation of the null distribution.

2.6 Statistical Analysis

For each of the response variables, its association with the connectivity index was examined using ordinary least squares regression and the Spearman rank correlation. The differences in fragmentation classes were analyzed using one-way analysis of variance, whereas the means of SES for each of the classes were compared to zero using a one-sample t-test. Significance level was $\alpha = 0.05$. All computations were done using the Python 3 programming language along with NumPy and SciPy packages, where the same random seed was used in order to allow for exact reproduction of all results. Due to the simulation of the data, p-values should be interpreted as evidence for the consistency of the modeled response variable.

III. Results

Mean values of the response variables for each fragmentation category are presented in table 1, while their association with the connectivity index is presented in figure 1.

Table 1: Mean ± SD of Connectivity, Richness, and Functional Metrics by Fragmentation Class (n = 9 Reaches Per Class), with Regression Results Against the Connectivity Index (CI) Across All 36 Reaches

Class	CI	Richness	FRic	FDis	SES-FDis	Migratory Share
Free-Flowing	92.4 ± 4.3	49.6 ± 1.9	0.89 ± 0.07	2.22 ± 0.09	−0.34 ± 0.68	0.42 ± 0.09
Weak	68.5 ± 3.8	45.4 ± 2.5	0.80 ± 0.09	2.18 ± 0.20	−0.58 ± 1.27	0.41 ± 0.08
Moderate	46.7 ± 7.3	40.9 ± 2.5	0.72 ± 0.06	2.08 ± 0.21	−1.15 ± 1.33	0.33 ± 0.08
Strong	16.1 ± 9.1	35.7 ± 3.6	0.62 ± 0.08	2.22 ± 0.16	−0.12 ± 0.96	0.28 ± 0.07
R^2 vs CI	–	0.82***	0.62***	<0.01 ns	<0.01 ns	0.32***
ANOVA F (3, 32)	–	44.8***	19.0***	1.34 ns	1.50 ns	6.35**

Class = fragmentation class (weak = weakly, moderate = moderately, strong = strongly fragmented). FRic = functional richness; FDis = functional dispersion; SES-FDis = standardized effect size of FDis against 499 null assemblages; Migratory share = proportion of abundance contributed by migratory species. ** $p < 0.01$; *** $p < 0.001$; ns = not significant.

3.1 Connectivity Gradient and Species Richness

The connectivity index varied from 92.4 for freely flowing stretches to 68.5, 46.7 and 16.1 for weakly, moderately, and strongly fragmented stretches, respectively (Table 1). Species richness followed a similar pattern, varying from 49.6 in freely flowing stretches to 35.7 in strongly fragmented stretches, representing a 28% reduction. Species richness was found to be highly and positively associated with the connectivity index (slope = 0.18 species per index unit, $R^2 = 0.82$, $p < 0.001$; Spearman's $\rho = 0.91$), and showed significant differences between classes ($F(3, 32) = 44.8$, $p < 0.001$).

3.2 Functional Richness and Functional Dispersion

There was a decrease in functional richness from 0.89 for free-flowing sites to 0.62 for highly fragmented sites, corresponding to a drop of 30% in the occupancy of the regional trait space. This was a significant trend along the gradient in connectivity (slope = 0.0034 for each index increment, $R^2 = 0.62$, $p < 0.001$; $\rho = 0.79$) and within classes ($F(3, 32) = 19.0$, $p < 0.001$; figure 1a). The reduction in functional richness thus was marginally greater in relative size compared to the reduction in species richness, suggesting the lost species had peripheral roles in the trait space and were not redundant with the other species.

However, functional dispersion showed another pattern. FDis mean values ranged narrowly between 2.08 and 2.22 for all fish classes, and were not correlated with the connectivity index ($R^2 < 0.01$, $p = 0.80$; $\rho = 0.05$), nor were there any significant differences in FDis among classes ($F(3, 32) = 1.34$, $p = 0.28$). Standardized effect size of FDis was also not affected by the connectivity level ($R^2 < 0.01$, $p = 0.86$; $F(3, 32) = 1.50$, $p = 0.23$). Mean SES for FDis was negative for all fish classes, implying trait clustering tendency; however, it was significantly different from zero only in moderately fragmented reaches (mean = -1.15; $t(8) = -2.61$, $p = 0.031$). For free-flowing, weakly and strongly fragmented reaches, observed FDis did not differ significantly from random distribution.

3.3 Trait-specific responses

The proportion of abundance in migratory species fell from 0.42 in free-flowing river sections to 0.28 in strongly fragmented sections, a decline of nearly one third (slope = 0.0019 per index unit, $R^2 = 0.32$, $p < 0.001$; $F(3, 32) = 6.35$, $p = 0.002$; figure 1b). In turn, the community weighted body size mean remained insignificant throughout the gradient ($R^2 = 0.04$, $p = 0.25$), while the proportion of abundance represented

by species with parental care increased weakly and insignificantly with fragmentation ($R^2 = 0.04$, $p = 0.22$). Thus, migration was the most pronounced trait along the connectivity gradient on the whole community scale, while effects of body size and parental care could be observed only in the species composition.

Together, these results show a response that is both consistent and selective. Taxonomic and volumetric variables decreased consistently along the gradient of connectivity, the abundance of migrants decreased by about one-third, and the dispersion weighted by abundance remained constant. Thus, the gradient influenced the combination of traits much more than the dispersion of dominant taxa within the functional space. Variation in the reaches within each category of fragmentation was rather modest, with standard deviation of the functional richness ranging from 0.06 to 0.09.

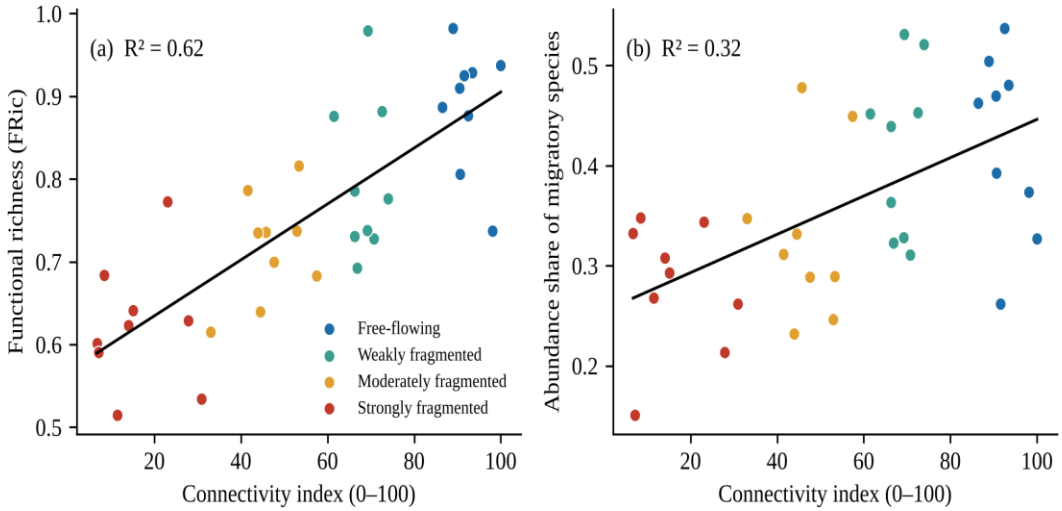


Figure 1: Relationships between the Connectivity Index and (a) Functional Richness (FRic) and (b) The Abundance Share of Migratory Species Across 36 Simulated River Reaches. Colours Indicate Fragmentation Class; Lines are Ordinary Least-Squares Fits

IV. Discussion

4.1 Fragmentation Effects on Species and Functional Richness

Results show that fragmentation leads to decreased species richness and functional richness, where the latter suffers relatively larger decreases. Fragmented reaches had about 28% fewer species and 30% fewer functional richness compared with reaches without fragmentation. This result implies that fragmentation eliminates species belonging to different functional groups especially those relying on connectivity of habitat. This trend has been observed in studies focusing on damming and loss of species in freshwater (Grill et al., 2019; Reid et al., 2019; Barbarossa et al., 2020). While highly fragmented reaches contained more than 35 out of the initial 60 species, the decreased functional space implies that counting species might not be enough to quantify ecological destruction.

4.2 Functional Dispersion and Community-Level Responses

Functional dispersion was fairly constant even though there were decreases in functional richness, suggesting that different functional diversity metrics are measuring different ecological processes. Functional richness is the measure of how much space in trait space is covered by the species, while functional dispersion refers to the amount of abundance-weighted spread of traits away from the center point of the community. The elimination of rare migratory species, for example, may decrease functional richness but not change dispersion if other species become more abundant. These results show the drawbacks of depending on one single measure of functional diversity (Mouillot et al., 2013;

Villéger et al., 2017; Laliberté & Legendre, 2010). Trait clustering was also detected in moderately fragmented reaches, while free-flowing reaches and highly fragmented reaches deviated less than expected from random.

4.3 Migratory Traits and Ecological Filtering

Migration proved to be the most indicative functional trait linked to connectivity loss. Habitat fragmentation reduces movements between feeding, spawning, and refuge sites, thereby impacting migratory taxa more (Poff, 1997). Such results are in accordance with ecological filtering and life-history theory, which links the need for movement, body size, reproduction, and habitat accessibility (Winemiller & Rose, 1992). Earlier work has already shown that hydrological modifications have an effect on fish community structure through changes in life-history structure (Mims & Olden, 2012). While body size and parental care were less responsive than other traits, they can potentially play an important role in species survival.

4.4 Connectivity Measurement and Functional Interpretation

Connectivity metrics have a strong impact on the understanding of functional biodiversity responses. The number of barriers does not take into account the difference in the locations, passability of barriers, and available lengths of the rivers. Network metrics better reflect habitat connectivity than simple barrier counts do (Fullerton et al., 2010; Cote et al., 2009). In the current simulation, the connectivity index was similar to barrier density, and consequently similar correlations were obtained for both metrics and functional diversity. Nevertheless, real-life river networks have barriers with very different ecological implications. Functional richness needs to be considered within the context of the regional species pool, and functional dispersion and community-weighted traits represent local community properties.

4.5 Conservation and Restoration Implications

The findings justify the inclusion of species richness, functional richness and migration trait indicators in bioassessments for freshwater ecosystems. This kind of combination helps to reveal ecological degradation which might not be identified by regular species abundance measurements. Barrier management must focus on barriers having significant isolation effect on habitats, taking into account their location, permeability and influence on migratory routes (Fullerton et al., 2010; Cote et al., 2009). The restoration efforts have to be judged by functional group restoration instead of just species recovery. Scenario analysis could also be used for evaluating the benefits gained from barriers dismantling and connectivity improvement (Grill et al., 2019; Reid et al., 2019).

4.6 Study Limitations and Future Research

The main limitation concerns the simulation-based modeling, wherein ecological filtering, species traits, and connectivity interactions have been predetermined. Thus, the predictions about the biodiversity loss will necessarily depend on the modeling assumptions and cannot be treated as an effect observed in nature. The other limitations concern such factors as water quality, climate fluctuations, fishing activity, invasions of alien species, and the structure of the river network. Future work needs to test the presented findings in the field studies by means of environmental DNA analysis, the use of trait databases, and barriers mapping. Further work needs to consider directional connectivity, recolonization by species, climate interactions, and restoration efficiency.

V. Conclusion

Native fish community functional traits were significantly and asymmetrically influenced by the fragmentation of rivers in this simulated analysis. As the connectivity index decreased, there was a gradual decrease in both species richness and functional richness, each dropping to around 72% of the levels of unfragmented rivers, as well as a decline in the proportion of migratory fish of about one-third. However, functional dispersion was not associated with connectivity levels, and deviations from random assembly

occurred only at moderate fragmentation. These findings demonstrate the selective removal of trait combinations through fragmentation, beginning with migratory, rheophilic, and large-bodied species, while the abundance-weighted functional dispersion of the residual community may be artificially high. Three main messages emerge for aquatic ecosystem managers. Firstly, bio-assessment programs need to combine richness with a volume-based metric and trait-specific metrics, rather than just a single measure of dispersal index. Secondly, connectivity metrics that consider the barrier location and passability are good predictors of functional loss and allow ranking of barriers for potential removal, rerouting, or modifications. Finally, restoration success will have to be assessed based on recovery of missing functional traits groups, in particular migration guilds, and not only the number of species restored. This model certainly has limitations, as it uses simulated assemblages and filtering rules based on assumptions of life-history theory, and it does not consider habitat quality, invasive species, or climate impacts. Thus, field application using standardized inventories of functional traits and barriers is the logical next step. In the meantime, this approach allows for exploration of different restoration scenarios and monitoring of functional loss in an easily reproducible way.

Data availability: All the data used in this experiment have been created using simulation. The parameters of the simulation, random seed, and analysis procedures are completely explained in Section 2.

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