

**RIVER PERMEABILITY PREDICTS POPULATION STRUCTURE IN BIRDS**

by

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A thesis submitted in partial fulfillment  
of the requirements for the degree of  
Master of Science in Environment and Sustainability

The University of Michigan

April 2022

Thesis Committee

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## **Abstract**

Intra-specific population genetic differentiation is an important predictor of speciation. Understanding how geographic barriers impact the cohesion of populations is therefore critical in explaining diversification. However, quantifying barrier permeability at broad scales is difficult, as permeability is determined by a host of factors including the attributes of the barrier, ecological constraints on dispersal, and species-level differences in dispersal ability; as a result, large scale comparative empirical studies that examine the relationship between barrier permeability and population divergence are limited. We test whether river and mountain permeability predict intra-specific genetic divergence for 30 species of birds spanning 17 families across both passerines (90%) and non-passerines (10%). Using 141 cross-barrier populations, we model mitochondrial divergence as a function of barrier permeability (river width, and least-cost-distance across mountains), dispersal ability, average population size, diet, habitat, and territoriality. Surprisingly, we find no relationship between dispersal ability and divergence, and no evidence that dispersal ability mediates the effects of barrier permeability on divergence. Similarly, we find no evidence of a strong role for any of our ecological variables on divergence. Variation in mountain permeability does not predict differentiation, suggesting mountains can largely be considered similar in their effects on population genetic structure. We do find that variation in river permeability predicts genetic differentiation, suggesting that rivers vary in their impacts on gene flow, and that width may be a good indicator of river permeability despite its dynamic nature.

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## **Introduction**

Understanding the variation of diversification rates across lineages remains a fundamental goal of evolutionary biology. In birds, allopatric speciation is likely the main engine of diversification (Barraclough & Vogler, 2000; Phillimore et al., 2008), and rates of population divergence are broadly correlated with speciation rates, suggesting that the drivers of population genetic divergence are also associated with diversification (Harvey et al., 2017). The importance of population divergence has long been appreciated, and as a result, the drivers are well known, with natural selection (Price, 1998), ecological opportunity (Wellborn & Langerhans, 2015), geological dynamism (Hoorn et al., 2010; Qu et al., 2011), and dispersal ability (Claramunt et al., 2012; Weeks & Claramunt, 2014) all known to play critical roles in facilitating or inhibiting population divergence. To date, however, comparative empirical analyses of the impacts of variation in barrier permeability on population-level divergence have been limited.

The importance of major geographic barriers in driving speciation is widely recognized in birds. For rivers, the riverine barrier hypothesis suggests that large rivers act as geographical barriers to gene flow (Wallace, 1854). This hypothesis has extensive empirical support in birds (Ribas et al., 2012; Smith et al., 2014; Voelker et al., 2013), and the role of rivers in structuring bird diversity in diversity hotspots has been apparent for decades (Cracraft, 1985; Cracraft & Prum, 1988; Oliveira et al., 2017; Voelker et al., 2013). Similarly, mountains are important barriers to gene flow and can also promote genetic differentiation (Davies et al., 2007; Fjeldså et al., 2012; Machado et al., 2018).

Better understanding the effects of rivers and mountains on the degree of genetic differentiation between cross-barrier populations may provide further insights on the origins of speciation. However, the permeability of rivers is expected to be highly variable given that their

width, shape, and location change over time (Harvey et al., 2017; Willett et al., 2014). Each of these types of variation are likely to impact their effect on gene flow across the river, complicating efforts to understand the historical influences of river barriers on divergence (Hayes & Sewlal, 2004; Naka & Brumfield, 2018). High-altitude mountain systems have also been acknowledged to shape patterns of biodiversity through isolation (Moritz et al., 2000), and many global diversity hot spots are in montane regions (Kohler et al., 2010). However, population connectivity across mountains is complex, with important effects of small-scale topographic features (Winger & Bates, 2015) and large-scale variation on the impacts of mountain characteristics on gene flow (Janzen, 1967).

To study the effects of these major geographic barriers on the structuring of avian populations, we use river width and least-cost-distance as metrics of permeability. Although river permeability is difficult to capture in a single metric due to its dynamic nature, evidence suggests river width to be predictive of bird distributions and population structure (Hayes & Sewlal, 2004; Smith et al., 2014). Due to the difficulty in determining which part of a river's width was most relevant in affecting each cross-barrier population's genetic structure, we created a metric of permeability based on the relative location of each half of a population pair. For mountain barriers, we focused on the relationship between topography-driven isolation (Igea & Tanentzap, 2021; Steinbauer et al., 2016). Following White's (2016) method, we calculated least-cost distance between mountain-separated populations over an elevational raster.

While barrier permeability is expected to impact rates of gene flow, the extent to which any major barrier limits dispersal is determined by a species' vagility (Tobias et al., 2020). However, current methods of quantifying dispersal are expensive, time-consuming, and infeasible to implement at a broad scale. To overcome this challenge, ornithologists have relied

on the physics of flight to develop morphological predictors of flight capacity. A critical determinant of the efficiency of long distance flight is the aspect ratio of bird wings, with higher aspect ratio wings resulting in more efficient long distance flight (Norberg, 1995). A related index, the hand-wing index (HWI), is similarly associated with flight efficiency and can be measured on museum specimens. HWI is correlated with natal dispersal distance and has been used in a wide range of macroevolutionary studies exploring the effects of dispersal on diversification (Chua et al., 2017; Claramunt et al., 2012; Weeks & Claramunt, 2014; Sheard et al. 2020). While dispersal has long been thought to impact rates of population divergence and speciation, it has also been hypothesized that the relationship between dispersal capacity and barrier permeability may mediate this relationship (Weeks and Claramunt, 2014). When dispersal capacity is high relative to landscape connectivity, dispersal is thought to inhibit divergence, while in systems with low dispersal abilities relative to connectivity, dispersal might be predicted to increase rates of divergence as a result of increased colonization of new areas (Weeks and Claramunt 2014).

To assess the interactive effects of avian dispersal ability with our two categories of major barriers, we gathered genetic data and geographic coordinates from published studies that evaluated differentiation in areas that were delineated by mountains or rivers. Specimens sampled across rivers are grouped into populations using areas of endemism as sampling units, while the population classification of specimens sampled across mountains are defined by the side of the mountain on which they are found. For a proxy of dispersal ability, HWI measurements were obtained through the comprehensive dataset from (Sheard et al., 2020). Using these data, we test the hypotheses that river and mountain permeability predict differences in GST, with more permeable barriers resulting in higher rates of gene exchange and lower rates

of population divergence. We also test the hypotheses that the permeability of river and mountain barriers is contingent on HWI, as barrier permeability will restrict gene flow more in species with low dispersal abilities.

## **Methods**

### ***Literature review***

To identify papers containing mitochondrial DNA data for cross-barrier bird populations, we conducted a systematic review of the literature on Google Scholar using the key search terms “comparative phylogeography birds mitochondria”. Of the papers returned from 2011 to 2016, we reviewed the top 200 per year to identify all papers meeting our criteria of having at least one species with mitochondrial DNA data sampled across a geographic or biogeographic barrier. Papers that used either the cytochrome b (Cytb) or NADH dehydrogenase 2 (ND2) genes were read in detail to see if they sampled across one of two major barrier types: mountains and rivers. Papers that met these criteria and had accessioned specimen data in GenBank were added to a preliminary dataset. For each taxon, all specimens were then plotted in ArcGIS Pro 2.8.0 and assigned to population pairs depending on their locations relative to major river or mountain barriers. Specimens in the Amazon basin were also sampled based on their locations within Amazonian areas of endemism, following Silva et al. (2017).

### ***Calculating population differentiation***

We obtained the Cytb or ND2 gene sequences for all specimens using R package ape (Paradis & Schliep, 2019) and grouped them into cross-barrier population pairs. For each pair of populations, sequences were then converted into DNASTringSet objects using the R package

Biostrings (Pagès et al., 2021) and aligned using the ClustalW algorithm (Thompson et al., 1994) as implemented through R package msa (Bodenhofer et al., 2015). The resultant 141 sets of multiple sequence alignments were written into aligned FASTA files using the bios2mds package (Pelé et al., 2012). Each of our aligned FASTA files was loaded into DnaSP 6 (Rozas et al., 2017) where we assigned individuals to populations and calculated population differentiation using GST (Nei, 1982).

### *Quantifying barrier permeability*

For rivers, populations were defined as all specimens occurring within the same area of endemism (Silva et al., 2017) To calculate river width for each population pair, we drew a line connecting the centroids of the sampling localities of each population on either side of the river and estimated the width of the river where it was crossed by this line. To obtain estimates of river width, we downloaded 30-meter spatial resolution rasters from the Global River Widths from Landsat Database (Allen & Pavelsky, 2018) and subset them to tiles which contained the rivers separating our populations. We created river network mosaics from these rasters using ArcGIS Pro 2.8.0 and exported extracted rivers as shapefiles per cross-river population pair. To prepare these river polygons for analysis, we stripped them down into simpler structures by converting them into valid geometry objects using the sf package (Pebesma et al., 2021). Line objects were created to link each population-pair using the sp package (Pebesma et al., 2021), and the widths of the intersections between lines and river objects were considered the estimate of river permeability.

For mountains, populations were defined based on the side of a mountain where they occurred. Similar to the river barrier populations, we used the geographic coordinates of the



specimens from each population to identify a central point of the population. For each of our cross-mountain population pairs, a measure of least cost path was used as a proxy for mountain barrier effects. These least cost paths are the routes with the least accumulated elevational cost between two points. Following White (2016), an elevational raster from WorldClim 2 (Fick & Hijmans, 2017) with a spatial resolution of 30 arc-seconds was used to represent the cost per pixel of mountain barriers separating our cross-mountain centroids. The `gdistance` package (van Etten, 2017) in R was used to calculate the least cost path between each centroid pair. Using the WorldClim 2 elevational raster, we created a transition object based on Moore's neighborhood, which consisted of the eight pixels surrounding a target pixel. A geographic correction was then applied to each transition object to account for both the large extent of each mountain barrier and our use of Moore's neighborhood. We then calculated our least cost distance based on Dijkstra's algorithm, which uses an iterative process to accumulate the minimum amount of elevational resistance between centroids (Dijkstra, 1959).

### ***Morphological and ecological predictors***

We extracted HWI, average population size, diet classification, habitat classification, and territoriality from a comprehensive dataset for all birds (Sheard et al., 2020). Population size was averaged between specimens sampled on both sides of a barrier. We control for the impacts of ecology by including diet, habitat, and territoriality in our models. Diet classifications were assigned depending on the primary food types eaten per species and categorized as frugivore, omnivore, or carnivore (Pigot et al., 2020). Species habitat was classified as either dense or semi-open, and territoriality was classified as strong, weak, or none. Both habitat and territoriality were based on scores from Tobias et al. (2016).

### *Statistical analyses*

We modeled the relationships between GST and combinations of barrier permeability, average population size, and ecological variables using Bayesian phylogenetic mixed models as implemented in the R package MCMCglmm (Hadfield, 2010). To characterize phylogenetic relationships, a variance-covariance matrix was created using a comprehensive phylogeny of all birds (Jetz et al., 2012). 1,000 of the most likely trees from the posterior distribution were summarized into a 50% maximum clade credibility tree using DendroPy (Sukumaran & Holder, 2010) following Rubolini et al. (2015). To account for the difference in resolution and methods used in calculating barrier costs, species pairs that were separated by mountains were modeled separately from those separated by rivers. Prior to model fitting, both categories of barrier costs were scaled to have a mean of 0 and SD of 1. An uninformative prior was specified for all fixed effects where  $V = 1$  and  $\nu = 0.002$  for R and G. Models were run for 100,000 iterations, with the first 10,000 iterations discarded as burn-in. Six models were fit for each barrier type, and from each barrier type's set of models, the first included barrier cost, HWI, and an interaction between the two while the second included only barrier cost and HWI as predictors. Each barrier type's other four models included HWI, barrier cost, average population size, diet type, habitat type, or territoriality classification without interactions. We then compared each barrier type's set of models using the deviance information criterion (DIC). The best river and mountain models were run an additional two times each and tested for convergence using the Gelman-Rubin (Gelman & Rubin, 1992) and Geweke's convergence diagnostics (Geweke, 1991) using the R package coda (Plummer et al., 2006). We also examined trace and density plots to confirm model convergence visually. For each best performing model, we calculated marginal and conditional

R<sup>2</sup> (Nakagawa & Schielzeth, 2013) as metrics of the variance explained by the fixed effects only and by the entire model, respectively.

## **Results**

After removing specimens that did not meet our criteria, our final dataset included 141 populations for 30 bird species across 17 families of passerines (90%) and non-passerines (10%). Our final dataset showed a strong bias towards species in the Amazon basin. Of these 141 populations, 106 were sampled across rivers; 35 were sampled across mountains. From our pool of 30 total species, 25 species were sampled across rivers for an average population size of 17.4. 18 species were sampled across mountains for an average population size was 6.4. GST was calculated using the cytochrome b gene, except for our three mountain populations that were sampled in Australia and used the ND2 gene. Most specimens sampled were not classified by sub-species.

Based on the DIC score (Table 1), the best river model only included barrier cost and HWI without an interaction (marginal R<sup>2</sup> = 0.02, conditional R<sup>2</sup> = 0.48). The Gelman-Rubin diagnostic was performed on the three independent runs of this model and produced potential scale reduction factors approaching 1, suggesting the model had converged. The Geweke's convergence diagnostic was also performed on this river model, with output values being within the 95% confidence interval of the standard normal (i.e.,  $|x| < 1.96$ ). We also confirmed convergence by visually inspecting parameter density and trace plots. The scaled width of the river barriers had a significant positive association with genetic differentiation (estimate = 0.0218; 95% CI: 0.0013, 0.043; PMCMC < 0.05), supporting our hypothesis that river permeability had a significant effect on population differentiation. HWI did not predict genetic

differentiation (PMCMC = 0.95). River width was a positive and significant predictor of genetic differentiation throughout all six models, while morphology, habitat, diet, territoriality, and average population size were consistently insignificant.

Barrier Type	Models	df	logLik	DIC	delta	weight
Rivers	Barrier cost + HWI	6	92.9593	-167.5154	0.0000	0.2660
	Barrier cost + HWI + Habitat	7	92.8688	-166.8637	0.6517	0.1920
	Barrier cost + HWI + Territoriality	8	92.6229	-166.7838	0.7316	0.1845
	Barrier cost + HWI + Diet	8	92.8176	-166.1434	1.3720	0.1340
	Barrier cost + HWI + Avg Population Size	7	92.6252	-166.1117	1.4037	0.1319
	Barrier cost * HWI	7	92.3272	-165.3837	2.1317	0.0916
Mountains	Barrier cost + HWI + Avg Population Size	7	13.0050	-14.7712	0.0000	0.6079
	Barrier cost + HWI	6	10.3680	-11.3427	3.4285	0.1095
	Barrier cost + HWI + Territoriality	8	10.6855	-11.1580	3.6132	0.0998
	Barrier cost + HWI + Habitat	7	10.3053	-10.5064	4.2648	0.0721
	Barrier cost + HWI + Diet	8	10.2523	-10.0892	4.6819	0.0585
	Barrier cost * HWI	7	10.0149	-9.8600	4.9111	0.0522

**Table 1.** Model fit comparison using Deviance Information Criterion (DIC). Model selection was categorized by river or barrier type, and lowest DIC scores indicate best fit.

The mountain model with the lowest DIC score (Table 1) included barrier cost, HWI, and average population size without an interaction between HWI and barrier cost (marginal  $R^2 = 0.1$ , conditional  $R^2 = 0.48$ ). The Gelman-Rubin diagnostic was performed on three independent runs of this model, and scale reduction factors approached 1. Geweke's convergence diagnostic was also performed and output values within the 95% confidence interval of the standard normal. These outputs confirmed convergence, as did our visual analyses of parameter density and trace plots. However, unlike the rivers model, our metric of mountain permeability was not predictive

of genetic differentiation of cross-barrier populations (estimate = 0.0118; 95% CI: -0.0571, 0.0809; PMCMC = 0.726), and the effects of diet, habitat, and territoriality were also insignificant across all mountain barrier models (Table S3).

## **Discussion**

Rates of intraspecific population divergence are correlated with speciation rates, suggesting the processes that impact population differentiation may be important determinants of macroevolutionary processes (Harvey et al., 2017). Identifying the factors that facilitate or hinder population differentiation is therefore not only important to understanding population dynamics, but in furthering our understanding of speciation. While geographic barriers have long been recognized as having an important role in structuring populations, developing a nuanced understanding of the impacts of barrier variation on divergence is challenging.

We find river barrier cost to have a significant positive association with genetic differentiation (PMCMC < 0.05), suggesting that rivers that are narrower are more permeable, allowing for higher rates of dispersal and gene flow. However, rivers as barriers to gene flow are complex given that their location and permeability are dynamic over time and biogeographic space. The inability to account for this complexity imposes limitations on the interpretations of our results. For example, headwaters present less of an obstacle to gene exchange among populations (Sandoval-H et al., 2017; Weir et al., 2015), while the drainage network of lowland rivers is more dynamic than those from the upland (Bicudo et al., 2019; Cremon et al., 2016). In these instances, our metric of river width may not reflect rates of dispersal at the point at which river width is measured but may instead be correlated with distance to headwaters or elevation and slope.

Our data are also strongly biased towards tropical regions (Figure 1), where rivers have long been known to be important to diversification (Aleixo, 2004; Ribas et al., 2012). Because tropical birds tend to have lower flight capacity (Sheard et al., 2020), and population differentiation in tropical regions may be more strongly associated with speciation rates (Cutter & Gray, 2016; Harvey et al., 2017; Smith et al., 2017), our findings on the significance of rivers as barriers may be less reflective of their effects on gene flow in temperate regions. More empirical work is therefore needed to understand the generality and implications of our findings on speciation. Conversely, we do not find that the cost to travel between populations separated by mountains to be predictive of population structure. Mountains are known to be significant barriers to gene exchange in the tropics (Janzen, 1967), and there is also some evidence that largescale variation in cost-distance can drive differences in genetic divergence (White, 2016). Our results suggest that for some taxa, mountains may all be similarly insurmountable, with either unpredictable long-distance dispersal events, or dynamic histories of changing connectivity driving inter-population dynamics (Weeks et al., 2016).



**Figure 1.** The geographic distributions of 30 species sampled across river or mountain barriers with a strong bias towards South America.

While geographic features may be the basal drivers of differentiation in birds, the impacts of these features are expected to be mediated by species ecologies. There is considerable evidence that flight efficiency (i.e., HWI) is associated with dispersal at small scales (e.g., natal dispersal distances; Weeks et al. 2022) and is associated with population differentiation (Chua et al., 2017) and diversification rates (Claramunt et al., 2012; Weeks & Claramunt, 2014). Given this, we expected that HWI would predict population differentiation and that species with higher HWI would show lower rates of population divergence across barriers given their elevated abilities to maintain gene flow. However, we find no evidence of this relationship, with HWI consistently not significantly associated with GST in our models. We are cautious in interpreting this result, as our models have limited statistical power, but the failure to find a relationship between HWI and GST does suggest that more work is necessary to understand the link between flight efficiency and dispersal at scales that are intermediate between ecological dispersal events (e.g., natal dispersal) and macroevolutionary processes playing out in deep time.

An outstanding question related to the importance of dispersal ability to evolutionary processes is how the relationship between dispersal ability and dispersal changes across scales. For example, while subtle differences in HWI may predict dispersal rates across small barriers (e.g., roads), they become less important in predicting dispersal rates across larger barriers (e.g., oceans). Given this, we expected that the impacts of HWI on GST would be determined in part by HWI. However, we find no evidence of this, as the interaction between HWI and barrier permeability was not significant and not included in the best model. However, we do not know if our measurements of genetic differentiation reflected rates of exchange in genetic material rather than reproductive isolation, as most specimens comprising our cross-barrier populations did not have sub-species classifications assigned. The scale of our analyses and the relatively limited

differences in barrier permeability may also have been insufficient in revealing an interaction between these variables. Future work including a broader range of barriers with greater variation in permeability is needed.

Furthermore, although morphological, ecological, and life history variables affect species interactions with the landscape, we find no evidence for a relationship between any of the tested variables and GST. Previous models exploring the determinants of dispersal distance in birds have found that differences in diet and habitat explain little variation in dispersal beyond what is captured by morphological metrics of dispersal ability (Claramunt, 2021; Dawideit et al., 2009; Weeks et al. 2022). However, it is possible that our metrics of ecological differences are too coarse to recover inter-specific differences at this scale, and our model is only able to explain a small proportion of the variance in GST, suggesting a potential role for ecology that we are unable to capture.

## **Conclusion**

River width was the only predictor found to have a significant effect on population structure, with lower levels of population genetic differentiation across less permeable rivers. Although our metric of permeability did not account for the complexity of rivers as barriers to gene flow, our results suggest that the width of rivers may be an informative indicator of barrier cost. And while we find no evidence that dispersal ability predicts population structure in our study, we interpret this finding cautiously given the breadth of empirical work linking HWI to a range of ecological and evolutionary processes. The results of this study suggest that more work on the relationship between dispersal ability, landscape connectivity, and population divergence is warranted.



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## Supplemental Materials

Order	Family	Genus	Species
Passeriformes	Furnariidae	Dendrocincla	fuliginosa
Passeriformes	Thamnophilidae	Cymbilaimus	lineatus
Passeriformes	Furnariidae	Glyphorhynchus	spirurus
Passeriformes	Thamnophilidae	Myrmotherula	axillaris
Passeriformes	Tityridae	Schiffornis	turdina
Passeriformes	Furnariidae	Sclerurus	mexicanus
Passeriformes	Furnariidae	Xenops	minutus
Passeriformes	Tyrannidae	Attila	spadiceus
Passeriformes	Furnariidae	Automolus	ochrolaemus
Cuculiformes	Cuculidae	Piaya	cayana
Passeriformes	Thraupidae	Tersina	viridis
Passeriformes	Thraupidae	Chlorophanes	spiza
Passeriformes	Thraupidae	Cyanerpes	caeruleus
Passeriformes	Pipridae	Lepidothrix	coronata
Passeriformes	Cotingidae	Querula	purpurata
Passeriformes	Thraupidae	Tangara	gyrola
Passeriformes	Tityridae	Tityra	semifasciata
Trogoniformes	Trogonidae	Trogon	rufus
Passeriformes	Troglodytidae	Microcerculus	marginatus
Passeriformes	Furnariidae	Xiphorhynchus	elegans
Passeriformes	Vireonidae	Hylophilus	ochraceiceps
Coraciiformes	Momotidae	Baryphthengus	martii
Passeriformes	Thraupidae	Saltator	grossus
Passeriformes	Pycnonotidae	Bleda	syndactylus
Passeriformes	Pycnonotidae	Bleda	notatus
Passeriformes	Troglodytidae	Henicorhina	leucosticta
Passeriformes	Icteridae	Psarocolius	angustifrons
Passeriformes	Meliphagidae	Lichenostomus	leucotis
Passeriformes	Petroicidae	Petroica	multicolor
Passeriformes	Artamidae	Artamus	superciliosus

**Table S1.** The final dataset included 30 bird species across 17 families of passerines (90%) and non-passerines (10%).

<b>Model: Cost distance *</b>						
<b>HWI</b>	<b>Posterior mean</b>	<b>Lower 95% CI</b>	<b>Upper 95% CI</b>	<b>Effective sample</b>	<b>pMCMC</b>	<b>Effect</b>
(Intercept)	0.0846	0.0080	0.1613	47375.7330	0.0433	fixed
Cost distance	0.0218	0.0003	0.0430	84233.4475	0.0449	fixed
HWI	0.0014	-0.0389	0.0408	52168.7298	0.9489	fixed
Cost distance:HWI	-0.0003	-0.0219	0.0211	86247.0178	0.9746	fixed
Phylogenetic	0.0044	0.0002	0.0131	4893.8811	NA	random
Species	0.0045	0.0003	0.0103	10958.4107	NA	random
Units	0.0104	0.0074	0.0138	47051.8171	NA	residual
<b>Model: Cost distance +</b>						
<b>HWI</b>	<b>Posterior mean</b>	<b>Lower 95% CI</b>	<b>Upper 95% CI</b>	<b>Effective sample</b>	<b>pMCMC</b>	<b>Effect</b>
(Intercept)	0.0844	0.0047	0.1577	52522.5182	0.0420	fixed
Cost distance	0.0218	0.0013	0.0435	79161.1152	0.0441	fixed
HWI	0.0014	-0.0380	0.0412	49622.3230	0.9510	fixed
Phylogenetic	0.0044	0.0002	0.0129	4544.2068	NA	random
Species	0.0045	0.0004	0.0104	11095.9877	NA	random
Units	0.0103	0.0073	0.0135	48207.0711	NA	residual
<b>Model: Cost distance +</b>						
<b>HWI + Avg. Pop. Size</b>	<b>Posterior mean</b>	<b>Lower 95% CI</b>	<b>Upper 95% CI</b>	<b>Effective sample</b>	<b>pMCMC</b>	<b>Effect</b>
(Intercept)	0.0779	-0.0019	0.1528	56898.2709	0.0560	fixed
Cost distance	0.0187	-0.0045	0.0409	74876.3277	0.1084	fixed
HWI	0.0011	-0.0391	0.0400	53191.9147	0.9606	fixed
Avg. pop. size	0.0006	-0.0011	0.0023	67850.6232	0.4687	fixed
Phylogenetic	0.0042	0.0002	0.0126	4581.2138	NA	random
Species	0.0046	0.0004	0.0104	10724.8515	NA	random
Units	0.0104	0.0073	0.0137	49894.9324	NA	residual
<b>Model: Cost distance +</b>						
<b>HWI + Diet</b>	<b>Posterior mean</b>	<b>Lower 95% CI</b>	<b>Upper 95% CI</b>	<b>Effective sample</b>	<b>pMCMC</b>	<b>Effect</b>
(Intercept)	0.0633	-0.0543	0.1756	76902.7085	0.2526	fixed
Cost distance	0.0226	0.0017	0.0439	78587.5154	0.0386	fixed
HWI	0.0058	-0.0368	0.0492	72328.0901	0.7837	fixed
Diet (invertebrates)	0.0352	-0.0862	0.1524	82667.9474	0.5394	fixed
Diet (omnivore)	-0.0142	-0.1614	0.1292	90000.0000	0.8437	fixed
Phylogenetic	0.0047	0.0002	0.0145	4395.1859	NA	random
Species	0.0051	0.0003	0.0117	10504.9685	NA	random
Units	0.0103	0.0073	0.0136	45842.8532	NA	residual
<b>Model: Cost distance +</b>						
<b>HWI + Habitat</b>	<b>Posterior mean</b>	<b>Lower 95% CI</b>	<b>Upper 95% CI</b>	<b>Effective sample</b>	<b>pMCMC</b>	<b>Effect</b>
(Intercept)	0.1506	-0.0704	0.3750	60062.4962	0.1748	fixed
Cost distance	0.0215	0.0004	0.0428	73291.9830	0.0474	fixed
HWI	0.0061	-0.0364	0.0480	63196.7452	0.7736	fixed
Habitat	-0.0634	-0.2634	0.1381	74253.2596	0.5188	fixed
Phylogenetic	0.0043	0.0002	0.0129	4542.8330	NA	random
Species	0.0048	0.0003	0.0110	10702.7476	NA	random
Units	0.0103	0.0073	0.0137	49225.6912	NA	residual
<b>Model: Cost distance +</b>						
<b>HWI + Territoriality</b>	<b>Posterior mean</b>	<b>Lower 95% CI</b>	<b>Upper 95% CI</b>	<b>Effective sample</b>	<b>pMCMC</b>	<b>Effect</b>
(Intercept)	0.0356	-0.0849	0.1495	69437.3327	0.5088	fixed
Cost distance	0.0220	0.0006	0.0429	72632.3921	0.0429	fixed
HWI	0.0069	-0.0331	0.0479	79345.1523	0.7305	fixed
Territoriality (Strong)	0.0378	-0.0776	0.1543	51319.5154	0.5027	fixed
Territoriality (Weak)	0.1082	-0.0210	0.2356	77799.2832	0.0968	fixed
Phylogenetic	0.0051	0.0002	0.0143	4760.0036	NA	random
Species	0.0036	0.0002	0.0092	7491.5272	NA	random
Units	0.0103	0.0073	0.0136	44531.4001	NA	residual

**Table S2.** Results of MCMCglmm multivariate river models.

<b>Model: Cost distance *</b>						
<b>HWI</b>	<b>Posterior mean</b>	<b>Lower 95% CI</b>	<b>Upper 95% CI</b>	<b>Effective sample</b>	<b>pMCMC</b>	<b>Effect</b>
(Intercept)	0.1476	0.0108	0.2743	63585.4110	0.0388	fixed
Cost distance	0.0269	-0.0433	0.0975	79894.2007	0.4441	fixed
HWI	0.0062	-0.0755	0.0911	90000.0000	0.8762	fixed
Cost distance:HWI	0.0166	-0.0414	0.0760	85299.5490	0.5696	fixed
Phylogenetic	0.0087	0.0002	0.0303	3555.0780	NA	random
Species	0.0085	0.0002	0.0251	7837.3438	NA	random
Units	0.0347	0.0168	0.0561	40130.2741	NA	residual
<b>Model: Cost distance +</b>						
<b>HWI</b>	<b>Posterior mean</b>	<b>Lower 95% CI</b>	<b>Upper 95% CI</b>	<b>Effective sample</b>	<b>pMCMC</b>	<b>Effect</b>
(Intercept)	0.1450	0.0125	0.2780	75086.8875	0.0427	fixed
Cost distance	0.0279	-0.0406	0.0989	81442.7899	0.4220	fixed
HWI	0.0001	-0.0786	0.0801	90000.0000	0.9977	fixed
Phylogenetic	0.0090	0.0001	0.0310	3395.1804	NA	random
Species	0.0081	0.0002	0.0237	7759.0303	NA	random
Units	0.0338	0.0168	0.0544	36745.6663	NA	residual
<b>Model: Cost distance +</b>						
<b>HWI + Avg. Pop. Size</b>	<b>Posterior mean</b>	<b>Lower 95% CI</b>	<b>Upper 95% CI</b>	<b>Effective sample</b>	<b>pMCMC</b>	<b>Effect</b>
(Intercept)	0.2484	0.0676	0.4288	86170.0389	0.0110	fixed
Cost distance	0.0118	-0.0571	0.0809	82129.9624	0.7261	fixed
HWI	-0.0064	-0.0867	0.0725	90000.0000	0.8678	fixed
Avg. pop. size	-0.0187	-0.0382	0.0017	41848.7935	0.0662	fixed
Phylogenetic	0.0122	0.0002	0.0410	3693.8390	NA	random
Species	0.0092	0.0002	0.0279	7211.1352	NA	random
Units	0.0295	0.0136	0.0488	29453.1710	NA	residual
<b>Model: Cost distance +</b>						
<b>HWI + Diet</b>	<b>Posterior mean</b>	<b>Lower 95% CI</b>	<b>Upper 95% CI</b>	<b>Effective sample</b>	<b>pMCMC</b>	<b>Effect</b>
(Intercept)	0.1083	-0.1282	0.3579	90000.0000	0.3593	fixed
Cost distance	0.0377	-0.0337	0.1103	86543.9193	0.2888	fixed
HWI	-0.0046	-0.0858	0.0737	90000.0000	0.9011	fixed
Diet (invertebrates)	0.0795	-0.1789	0.3406	87894.2912	0.5306	fixed
Diet (omnivore)	-0.0979	-0.4105	0.2123	90000.0000	0.5232	fixed
Phylogenetic	0.0090	0.0002	0.0321	3557.7085	NA	random
Species	0.0079	0.0002	0.0238	7799.9653	NA	random
Units	0.0342	0.0167	0.0551	43625.1886	NA	residual
<b>Model: Cost distance +</b>						
<b>HWI + Habitat</b>	<b>Posterior mean</b>	<b>Lower 95% CI</b>	<b>Upper 95% CI</b>	<b>Effective sample</b>	<b>pMCMC</b>	<b>Effect</b>
(Intercept)	0.3298	-0.0846	0.7532	81100.4662	0.1166	fixed
Cost distance	0.0196	-0.0522	0.0924	75242.0548	0.5826	fixed
HWI	0.0144	-0.0707	0.0998	90000.0000	0.7296	fixed
Habitat	-0.1701	-0.5367	0.1937	90000.0000	0.3429	fixed
Phylogenetic	0.0086	0.0001	0.0308	3259.1033	NA	random
Species	0.0084	0.0002	0.0246	8044.9629	NA	random
Units	0.0340	0.0169	0.0552	38499.8128	NA	residual
<b>Model: Cost distance +</b>						
<b>HWI + Territoriality</b>	<b>Posterior mean</b>	<b>Lower 95% CI</b>	<b>Upper 95% CI</b>	<b>Effective sample</b>	<b>pMCMC</b>	<b>Effect</b>
(Intercept)	0.0810	-0.1265	0.2849	87461.4132	0.4076	fixed
Cost distance	0.0269	-0.0413	0.0961	84411.1400	0.4331	fixed
HWI	0.0230	-0.0622	0.1038	90000.0000	0.5718	fixed
Territoriality (Strong)	0.1170	-0.1033	0.3329	82431.6387	0.2760	fixed
Territoriality (Weak)	-0.0720	-0.3506	0.2027	81157.2313	0.5996	fixed
Phylogenetic	0.0086	0.0001	0.0296	3872.1883	NA	random
Species	0.0069	0.0002	0.0213	7996.8299	NA	random
Units	0.0333	0.0164	0.0532	47577.5541	NA	residual

**Table S3.** Results of MCMCglmm multivariate mountain models.