

Ecography

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**Supplementary material**  
**Appendix 1**

1 Modelling habitat distributions for multiple species  
2 using phylogenetics  
3 (Appendix)

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## 15 **Field sampling**

16 During the summer months (late June – early September) of the years 2011 – 2013, the  
17 Hydronet research group (hereafter simply referred to as “Hydronet”) surveyed 28 rivers  
18 (15 unregulated and 13 regulated) located in four Canadian provinces (New-Brunswick,  
19 Quebec, Ontario, and Alberta). Each river was sampled at multiple locations hereafter  
20 referred to as the sampling sites. Sampling sites had 300 m<sup>2</sup> surface area (5 m across by  
21 60 m along the river) and were positioned in alternation (site width was often substantially  
22 narrower than river sections), near the left shore (facing downstream), in the middle, and  
23 near the right shore of the river, starting randomly, while ensuring that the habitat within  
24 them was fairly homogeneous. Locations of the beginning and end of each sampling site  
25 were recorded using a GPS unit (GPSMAP® 76sc: Garmin International Inc. 1200 E. 151<sup>st</sup>  
26 Street, Olathe, KS 66062, USA).

27 Fish sampling consisted in electrofishing (using an LR24® Backpack electrofisher:  
28 Smith-Root Inc., 14014 NE. Salmon Creek Ave., Vancouver, WA 98686, USA;  
29 electroshocking duration per site: 900 s; mean power: 200 W) and snorkelling surveys  
30 performed during daytime hours (between 0830 and 1800). These two sampling methods  
31 were used in tandem to minimise the bias associated with because each of these methods  
32 shows selectivity toward catching fish of particular species and size classes (Macnaughton  
33 et al., 2014). Sampling with both methods involved zigzagging in the upstream direction to  
34 cover the whole sampling area. Fish were identified to species or else to the nearest  
35 taxonomic level that electrofishers or snorkelers could discriminate visually. Electrofishing  
36 was performed by teams of three fishers: one operating the electrofisher and two catching

37 the electroshocked fish with dip nets 38 mm long  $\times$  33 mm wide  $\times$  20 mm deep, mesh size:  
38 6.35 mm (Smith-Root Inc.). Fish were identified, measured (Total length,  $TL \pm 0.1$  cm),  
39 allowed to recover in cool aerated water, and released at the location where they had been  
40 captured. Visual observations were performed by teams composed of two trained  
41 snorkelers. Fish with total lengths  $\geq 3$  cm (fish with total lengths  $< 3$  cm could not be  
42 identified reliably by snorkelers) were categorised into size classes, with the first class going  
43 from 3 to 5 cm (median size approximately 4 cm), and then in classes 5 cm apart (median  
44 sizes: 7.5 cm, 12.5 cm, 17.5 cm, etc.).

45 Descriptors of the local physical environment that are often regarded as key drivers  
46 shaping community structure were estimated in the sampling sites (Knouft et al., 2011;  
47 Michel and Knouft, 2014). We estimated water depth ( $z$ , in cm, measured using a  
48 graduated pole) and velocity ( $v$ , in  $\text{cm s}^{-1}$ ; Flo-Mate 2000: Marsh-McBirney Inc., 4539  
49 Metropolitan Court Frederick, MD 21704-9452, USA), substrate median grain size ( $D_{50}$ , in  
50 cm), and the proportion of macrophyte cover ( $MC$ , in %) in ten 50 cm  $\times$  50 cm plots  
51 randomly dispatched within each sampling site (Wolman, 1954; Latulippe et al., 2001).  
52 Water temperatures was measured in the field using HOBO UA-002-62 logging  
53 thermometers (precision:  $\pm 0.5^\circ\text{C}$ ; Onset Computer Corp., 470 MacArthur Blvd., Bourne,  
54 MA 02532, USA; 3-10 devices / river). Devices were deployed in riffle, run, or shallow pool  
55 habitats and set to record water temperature at 15 min intervals for at least 9 weeks. We  
56 used the number of heating degree-days ( $DD$ , in  $^\circ\text{C d}$ ) as an environmental descriptor,  
57 which we estimated as the sum of mean daily water temperatures above  $0^\circ\text{C}$  for a period of  
58 nine weeks encompassing the four weeks preceding the hottest week of the summer, and  
59 the four weeks following it (between late-May to late-September). During the low summer

60 flows and on days without rain, we took between one and nine water samples in the main  
61 stream of the rivers. These samples were collected in 250 mL acid-washed, high-density  
62 polyethylene bottles (Nalgene®, Nalge Nunc International Corporation), kept at 4 °C, and  
63 shipped to the University of Alberta’s Biogeochemical Laboratory for analysis. Total  
64 phosphorus ( $TP$ , in  $\mu\text{g L}^{-1}$ ) was determined using persulfate oxidation (Ng, 2010). For  
65 each river, individual  $TP$  values that differed by 15 standard deviations or less from the  
66 river mean were retained; we took the average of the latter as the total phosphorus for the  
67 whole river.

## 68 **Data processing**

69 In the present study, we used fish density (fish  $(100\text{ m}^2)^{-1}$ ) by species and size class as the  
70 response variable of the phylogenetic habitat model. To obtain a *species*  $\times$  *location*  
71 response matrix that was not overly sparse (i.e. did not contain too many zeros) as well as  
72 to facilitate computations, modelling was performed on the basis of whole rivers. For each  
73 river, values of  $z$ ,  $v$ ,  $D_{50}$ , and  $MC$  were averaged. Mean densities for whole rivers were  
74 estimated separately for each combination of species and size class using Generalised Linear  
75 Models (GLM: Hastie and Pregibon, 1991; Poisson distributed) fitted with the values of  
76 depth, velocity and substrate grain size for each sampling site as descriptors. We took the  
77 fitted values of each GLM (one per river for each combination of species and size-class),  
78 estimated for the average environmental conditions observed in the river, as the mean fish  
79 density. Species and size class combinations that were not observed in a given river were  
80 assumed to be absent from that river and assigned a density value of 0 fish  $(100\text{ m}^2)^{-1}$ .

81 For any given species, we discarded all size classes for which no fish was observed,  
82 and merged the size classes for which fish were present in two rivers or less. Size class  
83 merging was performed by coalescing size classes with insufficient numbers of observations  
84 with an adjacent size class. When two adjacent size classes were present on either side of  
85 the class with low number of observations, the one with the smallest number of  
86 observations was chosen. The mean size of the newly formed size class was taken as the  
87 mean of their median sizes weighted by their respective numbers of observations. Size class  
88 merging stopped when all those remaining had been observed in two rivers or more. The  
89 species represented by a single size class that were present in only one river were discarded.

90 We used the phylogeny published by Hubert et al. (2008), which was estimated using  
91 K2P distances (Kimura, 1980) calculated from a standard 652 base pairs «bar code» region  
92 of the Cytochrome Oxidase subunit I (COI) mitochondrial gene. That tree was used to  
93 calculate Phylogenetic eigenvector maps (PEM; Guénard et al., 2013). PEM required a  
94 tree tip for every combination of species and size class. Therefore, every single tree tip  
95 representing species with more than one size class was merged into a star tree having  
96 branch lengths of 0 and as many tips as the species had size classes. Since the merged star  
97 tree had branch lengths of 0, the number of phylogenetic eigenvectors with non-zero  
98 eigenvalues obtained from the approach remain one minus the number of species, with each  
99 eigenvector defined for all the species and size classes; they are, however, invariant across  
100 observations involving the same species.

101 We used spatial eigenvector maps (SEM; Borcard and Legendre, 2002; Dray et al.,  
102 2006; Diniz-Filho et al., 2013; Legendre and Legendre 2012, Chapter 14) to model patterns  
103 of spatial variation among the rivers and account for spatial auto-correlation (Legendre,

104 1993; Dormann et al., 2007). These eigenfunctions were calculated from the geodesic  
105 distances among rivers.

106 In the present study, the design matrix  $\mathbf{X}$  contained the species descriptors, which  
107 included the median standard length of the fish in each size class as a species trait in  
108 addition to the PEM descriptors that represented the among-species phylogenetic patterns  
109 of trait variation. It is noteworthy that, in the model, variation among species and size  
110 classes was explained in part by the median fish size and the PEM, because fish of different  
111 species had different median sizes, on average, but within-species variation was only  
112 associated to variation in the median fish size, because PEM were constant across size  
113 classes for a given species. The design matrix  $\mathbf{Z}$  of site descriptors included environmental  
114 variables and the spatial eigenfunctions. Since two types of row descriptors were used with  
115 two types of column descriptors, there were eight types of bilinear model terms. Among  
116 them, four were modelling main effects acting alone in the model: 1) the traits, 2) the  
117 phylogeny (PEM), 3) the environment, 4) space (spatial eigenvectors). There were also four  
118 second-order interaction terms: 1) trait-environment, 2) trait-space,  
119 3) phylogeny-environment, 4) phylogeny-space. Therefore the first two columns of matrix  
120  $\mathbf{R}$  represent the different types of row descriptors, namely *trait* (fish total length; column  
121 1) and *phylogeny* (PEM; column 2), the next two columns represent the column  
122 descriptors, namely *environment* ( $z$ ,  $v$ ,  $D_{50}$ ,  $MC$ ,  $DD$ , and  $TP$ ; column 3) and *space*  
123 (SEM; column 4), and the last four columns of  $\mathbf{R}$  represent their interactions (column 5:  
124  $trait \wedge environment$ , column 6:  $trait \wedge space$ , column 7:  $phylogeny \wedge environment$ , and  
125 column 8:  $phylogeny \wedge space$ ). We fitted the model using a Poisson-distributed  
126 Generalized Linear Model (GLM).

## 127 **Details on model estimation**

128 To ensure that the resulting model was general, rendered dependable predictions, and  
129 avoided over-fitting, we regularised the bilinear regression model using elastic net  
130 regularisation (Zou and Hastie, 2005), which is a combination of the Least Absolute  
131 Shrinkage and Selection Operator (LASSO; Tibshirani, 1996; the  $L_1$  regularisation norm)  
132 and Tikhonov regularisation (Tikhonov and Arsenin, 1977, the latter being also known as  
133 ridge regression; the  $L_2$  regularisation norm). That method involves estimating matrix  $\mathbf{B}$   
134 as the solution minimising an objective function  $f$  involving size of the (standardised)  
135 regression coefficients as follows:

$$f_{\alpha,\lambda,\xi}(y; x, z|\beta) = \sum_{i=1}^n \sum_{j=1}^m \varepsilon_{i,j}^2 + \lambda \sum_{k=1}^p \sum_{l=1}^q \xi_{k,l} \left( \alpha |\beta_{k,l}| + \frac{(1-\alpha)}{2} |\beta_{k,l}|^2 \right) \quad (1)$$

136 where  $\alpha$  is a parameter varying between 0 and 1, which controls the relative importance of  
137 the regularisation norms,  $\lambda$  is the average penalty of all the descriptors ( $0 \leq \lambda < \infty$ ), and  
138  $\xi_{k,l}$  are penalty factors specific to particular terms of the model,  $\beta_{k,l}$  are the standardised  
139 regression coefficients, and  $\varepsilon_{i,j}$  are the residuals of the regression model. Therefore, any  
140 variable with  $\lambda \xi_{k,l} > 0$  (the minimum value) experiences an effective shrinkage of its  
141 contribution to the model. In that framework, parameter  $\lambda$  controls the average amount of  
142 shrinkage for all the regression coefficients whereas parameters  $\xi_{k,l}$  allows one to attribute  
143 greater shrinkage to certain groups of regression coefficients with respect to others. That  
144 feature can be exploited for the purpose of maximising the predictive power. We estimated  
145  $\alpha$ ,  $\lambda$ , and  $\xi_{k,l}$  using embedded models estimated by cross-validation as those maximising  
146 the predictive power of the models. Parameters  $\alpha$  and  $\lambda$  were estimated as constants

147  $c_\alpha = \text{logit } \alpha$  and  $c_\lambda = \log \lambda$ , respectively, to ease optimisation (since the domain of  $c_\alpha$  and  
 148  $c_\lambda$  need not be bounded), whereas parameters  $\xi_{k,l}$  were estimated through a logistic model  
 149 with a factorial design that was defined as follows:

$$\mathbf{R}[c_\xi] = [\text{logit } \xi_{k,l}], \quad (2)$$

150 where  $\mathbf{R}$  is a binary design matrix with  $(p \cdot q - 1)$  rows, each of them representing the  
 151 columns of  $\mathbf{Z} \otimes \mathbf{X}$ , with the exception of the model intercept (the first column), which is  
 152 assigned a constant penalty factor of 0.5, and  $(r + 1)(s + 1) - 1$  columns, where  $r$  is the  
 153 number of types of row descriptors and  $s$  is the number of types of column descriptors,  
 154 while  $[c_\xi]$  is a column vector of the regularisation model coefficients. It is noteworthy that  
 155 following Eq.2, penalty values are equal for all the variables involved in the same model  
 156 term. We chose a logistic rather than a linear model to represent the penalty factors  
 157 because constraining the penalty factors between 0 and 1 avoids interference with the  
 158 estimation of  $c_\lambda$  during the optimisation process. The columns of matrix  $\mathbf{R}$  represent the  
 159 different types of row descriptors, column descriptors, as well as their interactions.  
 160 Elements in each column of  $\mathbf{R}$  take the value 1 whenever the descriptor is involved in the  
 161 type of descriptor it represents, or their interactions, and 0 otherwise.

162 For phylogenetic habitat modelling, there will be at least one type of each of the row  
 163 and column descriptors (i.e.  $r = 1$  and  $s = 1$ ), namely a set of variables representing the  
 164 phylogeny, and a set of variables representing the environment. In the simplest scenarios,  
 165 matrix  $\mathbf{R}$  will therefore have three columns: one that represents the marginal effect of the  
 166 phylogeny, one that represents the marginal effect of the environment, and a third  
 167 representing the interaction between phylogeny and the environment. In such a scenario,

168 rows of  $\mathbf{R}$  corresponding to the columns of  $\mathbf{Z} \otimes \mathbf{X}$  representing the marginal effect of the  
169 the phylogeny will take the value 1 in the first column of  $\mathbf{R}$  and 0 elsewhere. On the other  
170 hand, rows of  $\mathbf{R}$  corresponding to the columns of  $\mathbf{Z} \otimes \mathbf{X}$  representing the  
171 phylogeny-environment interaction will also take the value 1 in the first column of  $\mathbf{R}$ , but  
172 also in the second, which represents the environment, and in the third column, which  
173 represents the phylogeny-environment interaction, thereby allowing the penalties applied to  
174 the marginal effects of phylogeny and environment to be non-additive with that applied to  
175 their interactions. In practice, it may be useful to use traits alongside the variables  
176 describing the phylogeny as row descriptors and variables describing spatial variation  
177 alongside environmental variables as column descriptors.

## 178 **Assessing the effect of flow regulation**

179 We assessed the effect of flow regulation on fish density by subtracting the predicted fish  
180 density values by species and size classes, obtained using the unregulated river model, from  
181 the fish densities observed at the sampling sites. The density differences thus obtained were  
182 negative when the model predicted higher densities than that observed in the field; positive  
183 values were obtained for observed densities that were higher than those predicted. Prior to  
184 further analysis, we  $\log(x + 1)$ -transformed these density differences on the basis of their  
185 absolute values while conserving their signs as follows:

$$x_{transformed} = \text{sign}(x_{original}) \log(|x_{original}| + 1), \quad (3)$$

186 where  $x_{original}$  and  $x_{transformed}$  are the original and transformed differences in fish density,  
187 respectively, and function  $\text{sign}(x)$  returns  $-1$  when  $x < 0$ ,  $0$  when  $x = 0$ , and  $1$  when  $x > 0$ .  
188 The necessity for that transformation was consequential to the fact that a Poisson  
189 distribution was assumed for modelling. It was used to mitigate over-dispersion and avoid  
190 conclusions driven only by a few extreme values.

## 191 Data collected

192 A total of 989 sites were sampled in the 28 rivers but because of malfunctioning equipment  
193 during field sampling, information about water velocity was not available for 48 sites  
194 located on four rivers (St-Jean: 17 sites, Elbow: 12, Kananaskis: 10, and Petit-Saguenay:  
195 9); these sites were thus discarded, leaving us with 941 usable sites for modelling. Mean  
196 river environmental conditions and species densities were calculated using numbers of sites  
197 ranging from 16 (in Petit-Saguenay) to 50 (in Au saumon and Bécancour). Water depth  
198 was left-skewed and was log-transformed before further treatment as were water velocity  
199 and substrate grain size; both were  $\log(x + 1)$ -transformed because values of 0 were  
200 present. Water depth ( $z$ ) ranged 25.8–55.1 cm (mean= 36.82 cm),  $v$  ranged 0.07–0.59 m s<sup>-1</sup>  
201 (mean= 0.296 m s<sup>-1</sup>),  $D_{50}$  ranged from 0.29 to 38.68 cm (7.057 cm),  $MC$  ranged from 0 to  
202 21%,  $DD$  ranged from 367 to 1540 °C d, and  $TP$  ranged from 1.00 to 3.42  $\mu\text{g L}^{-1}$  among  
203 the rivers. A total of 244 combinations of species and size classes, involving 61 species,  
204 were observed in at least one of the 28 rivers. After merging the sparsely observed size  
205 classes, 143 combinations of species and size classes, involving 48 species, were retained (see  
206 Fig. 1 in the main text). On average, each species was represented by 2.6 size classes, with

207 numbers ranging from one (six species) to nine (one species: the white sucker, *Catostomus*  
208 *commersoni*). The characteristic (median) sizes of these classes ranged from 4.0 to 42.5 cm  
209 (mean: 9.50 cm). The sample size ( $np$ ) for the present application scenario was 2145  
210 observations (143 combinations of species and size class sampled in the 15 unregulated  
211 rivers).

## 212 **Details on the interactions between phylogeny and the** 213 **environment**

214 We found a total of 22 interactions terms between phylogenetic eigenfunctions and five of  
215 the six environmental descriptors ( $v$ ,  $D_{50}$ ,  $DD$ ,  $TP$ , and  $MC$ ). Mean current velocity  
216 interacted with one phylogenetic eigenfunction (PE36) and described the Common shiner  
217 (*Luxilus cornutus*), the Bluntnose (*Pimephales notatus*), and the Fathead (*P. promelas*)  
218 minnows as being more abundant in rivers with faster current than are the eastern shiners  
219 (i.e. species of genus *Notropis*). Substrate grain size interacted with five phylogenetic  
220 eigenfunctions (PE12, PE17, PE27, PE30, and PE36); their overall effect indicated that, in  
221 the family Cyprinidae, riffle daces (i.e. the Longnose dace, *Rhinichthys cataractae*, and the  
222 Blacknose dace, *R. atralutus*) tended to be more abundant in rivers with coarser substrate  
223 than the average, while the Fallfish (*Semotilus corporalis*), the Bluntnose and fathead  
224 (genus *Pimephales*) minnows, the eastern shiners, and the Golden shiner (*Notemigonus*  
225 *crysoleucas*) tended to be abundant in rivers with finer substrate. Temperature interacted  
226 with three phylogenetic eigenfunctions (PE17, PE19, and PE35), their overall contributions  
227 indicating that the White sucker (*Catostomus commersoni*), the redhorses (i.e. the Silver

228 redhorse, *Moxostoma anisurum*, and the Shorthead redhorse, *M. macrolepidotum*), the  
229 Lake chub (*Couesius plumbeus*), and the Creek chub (*Semotilus atromaculatus*) were  
230 observed in greater densities in cold environments whereas the Longnose dace, the Fallfish,  
231 the White sucker, the Brown bullhead (*Ameiurus nebulosus*), and the Stonecat (*Noturus*  
232 *flavus*) were denser in warmer environments. Total phosphorus interacted with a total of  
233 11 phylogenetic eigenfunctions and their combined effects were associated to a wide range  
234 of differential species responses to *TP*, which we enumerate as follows:

- 235 1. The complex formed of the Johnny darter and the Tessellated darter (*Etheostoma*  
236 *olmstedii nigrum* - *E. olmstedii*; these species could not be discriminated by  
237 phylogenetic analysis) is found in higher densities in high *TP* environments, while the  
238 Fantail darter (*E. flabellare*) is denser in lower *TP* environments. Two phylogenetic  
239 eigenfunctions were involved in that interaction: PE33 and PE42.
- 240 2. Among the Percidae, the Walleye (*Sander vitreus*) appears to be favoured in high *TP*  
241 conditions whereas the Yellow perch (*Perca flavescens*) and two roughbelly darters  
242 (Genus *Percina*: the Common logperch, *P. crapodes*, and the Channel darter, *P.*  
243 *copelandi*) were denser in lower *TP* environments. PE23 and PE45 were involved in  
244 that interaction.
- 245 3. Among the eastern shiners, the Sand shiner (*Notropis stramineus*) is more prevalent  
246 in high *TP* in comparison with the Mimic shiner (*N. volucellus*). PE44 was involved  
247 here.
- 248 4. In genus *Semotilus*, higher *TP* is concomitant with higher densities of the Fallfish  
249 compared to the Creek chub and the Lake chub. PE17 and PE22 were behind that

250 interaction.

- 251 5. The riffle daces and the Cutlips minnow (*Exoglossum maxillingua*; the effect was  
252 described by PE29) as well as the Fathead minnow (the effect was, this time,  
253 associated with PE30 and PE40) seem to find high *TP* environments more favourable  
254 than the other Cyprinids.
- 255 6. Among the Catostomidae, the White sucker are found to be denser in high *TP*  
256 environments while the Longnose (*Catostomus catostomus*) and Mountain (*C.*  
257 *platyrhynchus*) suckers as well as the redhorses appear to be denser in rivers with  
258 lower *TP*. Here, PE19 and PE45 were involved.

259 Macrophyte cover interacted with three phylogenetic eigenfunctions; their combined effects  
260 described the riffle daces, the Cutlips minnow, the Golden shiner, and the Fathead minnow  
261 as being found in higher densities in rivers with low *MC*, compared to the eastern shiners,  
262 the Common shiner (*Luxilus cornutus*), the Fallfish and the Bluntnose minnow, which had  
263 higher densities in rivers with higher *MC*. These examples illustrate the capacity of the  
264 method described in this paper to represent, in a single model, many details about the  
265 habitat requirements of many species, using knowledge of their common evolutionary  
266 history, and how these factors drive community structure.

## 267 **Analysis data and script**

268 The raw data and analysis script used for the exemplary scenario are available online at  
269 [urltobepostedhereuponpaperacceptance].

## Tables

Table 1: Bilinear model coefficients estimated by the elastic net procedure.

	<i>Int.</i>	<i>TL</i>	<i>PE</i> <sub>1</sub>	<i>PE</i> <sub>12</sub>	<i>PE</i> <sub>17</sub>	<i>PE</i> <sub>19</sub>	<i>PE</i> <sub>22</sub>	<i>PE</i> <sub>23</sub>	<i>PE</i> <sub>27</sub>
<i>Int.</i>	-3.58	—	-8.79	—	—	—	—	—	—
$\log z$	—	-0.0193	—	—	—	—	—	—	—
$\log(v + 1)$	—	-0.0837	—	—	—	—	—	—	—
$\log(D_{50} + 1)$	—	-0.0158	—	-1.11	0.107	—	—	—	0.72
<i>DD</i>	0.00131	-4.4e-05	—	—	0.000964	0.000785	—	—	—
$\log TP$	1.79	—	—	—	0.725	0.95	0.441	0.987	—
<i>MC</i>	—	-0.0242	—	0.395	—	—	—	—	—
<i>SE</i> <sub>1</sub>	0.313	-0.0316	—	—	—	—	—	—	—
<i>SE</i> <sub>2</sub>	—	0.103	—	—	—	—	—	—	—
<i>SE</i> <sub>3</sub>	—	-0.0777	—	—	—	—	—	—	—
<i>SE</i> <sub>4</sub>	—	0.0238	—	—	—	—	—	—	—
<i>SE</i> <sub>7</sub>	—	-0.00938	—	—	—	—	—	—	—
<i>SE</i> <sub>8</sub>	—	0.102	—	—	—	—	—	—	—
<i>SE</i> <sub>11</sub>	—	-0.00975	—	—	—	—	—	—	—
<i>SE</i> <sub>12</sub>	—	0.0272	—	—	—	—	—	—	—
<i>SE</i> <sub>13</sub>	—	0.0679	—	—	—	—	—	—	—
<i>SE</i> <sub>14</sub>	—	-0.0182	—	—	—	—	—	—	—

  

	<i>PE</i> <sub>29</sub>	<i>PE</i> <sub>30</sub>	<i>PE</i> <sub>33</sub>	<i>PE</i> <sub>35</sub>	<i>PE</i> <sub>36</sub>	<i>PE</i> <sub>40</sub>	<i>PE</i> <sub>42</sub>	<i>PE</i> <sub>44</sub>	<i>PE</i> <sub>45</sub>
<i>Int.</i>	—	—	—	—	—	—	—	—	—
$\log z$	—	—	—	—	—	—	—	—	—
$\log(v + 1)$	—	—	—	—	4.8	—	—	—	—
$\log(D_{50} + 1)$	—	0.127	—	—	0.318	—	—	—	—
<i>DD</i>	—	—	—	-0.000554	—	—	—	—	—
$\log TP$	-0.224	0.0298	-2.5	—	—	-0.295	0.256	0.624	-0.165
<i>MC</i>	—	—	—	—	—	-0.105	—	—	—
<i>SE</i> <sub>1</sub>	—	—	—	1.91	—	—	—	—	—
<i>SE</i> <sub>2</sub>	—	—	—	—	—	—	—	—	—
<i>SE</i> <sub>3</sub>	—	—	—	—	—	—	—	—	—
<i>SE</i> <sub>4</sub>	—	—	—	—	—	—	—	—	—
<i>SE</i> <sub>7</sub>	—	—	—	—	—	—	—	—	—
<i>SE</i> <sub>8</sub>	—	—	—	—	—	—	—	—	—
<i>SE</i> <sub>11</sub>	—	—	—	—	—	—	—	—	—
<i>SE</i> <sub>12</sub>	—	—	—	—	—	—	—	—	—
<i>SE</i> <sub>13</sub>	—	—	—	—	—	—	—	—	—
<i>SE</i> <sub>14</sub>	—	—	—	—	—	—	—	—	—

*Int.*: intercept, *TL*: total length (cm), *PE*<sub>*x*</sub>: *x*<sup>th</sup> phylogenetic eigenvector, *z*: depth (cm), *v*: velocity (cm s<sup>-1</sup>), *D*<sub>50</sub>: median grain size (cm), *DD*: cumulative number of degree-day (°C d), *TP*: total phosphorus (μg L<sup>-1</sup>), *MC*: percent macrophyte cover (%), *SE*<sub>*x*</sub>: *x*<sup>th</sup> spatial eigenvector, —: placeholder for coefficients estimated to numerically 0; all logarithms are base *e*

## References

- 271  
272 Borcard, D. and Legendre, P. (2002). All-scale spatial analysis of ecological data by means  
273 of principal coordinates of neighbour matrices. *Ecol. Model.*, 153:51–68.
- 274 Diniz-Filho, J. A. F., Diniz, J. V. B. P. L., Rangel, T. F., Soares, T. F., de Campos Telles,  
275 M. P., Garcia Collevatti, R., and Bini, L. M. (2013). A new eigenfunction spatial  
276 analysis describing population genetic structure. *Genetica*, 141:479–489.
- 277 Dormann, C. F., McPherson, J. M., Araújo, M. B., Bivand, R., Bolliger, J., Carl, G.,  
278 Davies, R. G., Hirzel, A., Jetz, W., Kissling, W. D., Kühn, I., Ohlemüller, R.,  
279 Peres-Neto, P. R., Reineking, B., Schröder, B., Schurr, F. M., and Wilson, R. (2007).  
280 Methods to account for spatial autocorrelation in the analysis of species distributional  
281 data: a review. *Ecography*, 30:609–628.
- 282 Dray, S., Legendre, P., and Peres-Neto, P. (2006). Spatial modelling: a comprehensive  
283 framework for principal coordinate analysis of neighbor matrices (pcnm). *Ecol.*  
284 *Modelling*, 196:483–493.
- 285 Guénard, G., Legendre, P., and Peres-Neto, P. (2013). Phylogenetic eigenvector maps  
286 (PEM): a framework to model and predict species traits. *Meth. Ecol. Evol.*, 4:1120–1131.
- 287 Hastie, T. J. and Pregibon, D. (1991). *Generalized linear models*, volume Statistical models  
288 in S, chapter 6, pages 195–247. Wadsworth, Pacific Grove, CA.
- 289 Hubert, N., Hanner, R., Holm, E., Mandrak, N. E., Taylor, E., Burrridge, M., Watkinson,  
290 D., Dumont, P., Curry, A., Bentzen, P., Zhang, J., April, J., and Bernatchez, L. (2008).  
291 Identifying canadian freshwater fishes through DNA barcodes. *PLOS ONE*, 3:e2490.

292 Kimura, M. (1980). A simple method for estimating evolutionary rate of base substitutions  
293 through comparative studies of nucleotide sequences. *J. Mol. Evol.*, 16:111–120.

294 Knouft, J. H., Caruso, N. M., Dupre, P. J., Anderson, K. R., Trumbo, D. R., and  
295 Puccinelli, J. (2011). Using fine-scale gis data to assess the relationship between  
296 intra-annual environmental niche variability and population density in a local stream fish  
297 assemblage. *Meth. Ecol. Evol.*, 2:303–311.

298 Latulippe, C., Lapointe, M. F., and Talbot, T. (2001). Visual characterization technique  
299 for gravel-cobble river bed surface sediments; validation and environmental applications  
300 contribution to the programme of CIRSA (Centre Interuniversitaire de Recherche sur le  
301 Saumon Atlantique). *Earth Surf. Process. Landforms*, 26:307–318.

302 Legendre, P. (1993). Spatial autocorrelation: trouble or new paradigm? *Ecology*,  
303 74:1659–1673.

304 Legendre, P. and Legendre, L. (2012). *Numerical Ecology, 3rd English edition*. Elsevier  
305 Science B.V., Amsterdam, The Netherlands.

306 Macnaughton, C. J., Harvey-Lavoie, S., Senay, C., Lanthier, G., Bourque, G., Legendre, P.,  
307 and Boisclair, D. (2014). A comparison of electrofishing and visual surveying methods for  
308 estimating fish community structure in temperate rivers. *River Res. Appl.*, 31:1040–1051.

309 Michel, M. J. and Knouft, J. H. (2014). The effects of environmental change on the spatial  
310 and environmental determinants of community-level traits. *Landscape Ecol.*, 29:467–477.

311 Ng, J. (2010). Subsampling water samples in the field. Technical report, Biogeochemical  
312 Analytical Laboratory, University of Alberta, Edmonton, AB, Canada.

- 313 Tibshirani, R. (1996). Regression shrinkage and selection via the lasso. *J. R. Stat. Soc. B*,  
314 58:267–288.
- 315 Tikhonov, A. N. and Arsenin, V. Y. (1977). *Solution of Ill-posed Problems*. Winston &  
316 Sons, Washington, DC, USA. ISBN 0-470-99124-0.
- 317 Wolman, M. G. (1954). A method of sampling coarse river-bed material. *Trans. Am.*  
318 *Geophy. Union.*, 35:951–956.
- 319 Zou, H. and Hastie, T. (2005). Regularization and variable selection via the elastic net. *J.*  
320 *R. Stat. Soc. B*, 67:301–320.