

A spatially-explicit assessment of the fish population response to flow management in a heterogeneous landscape

GUILLAUME GUÉNARD,^{1,†} GABRIEL LANTHIER,¹ SIMONNE HARVEY-LAVOIE,¹ CAMILLE J. MACNAUGHTON,¹ CAROLINE SENAY,¹ MICHEL LAPOINTE,² PIERRE LEGENDRE,¹ AND DANIEL BOISCLAIR¹

¹NSERC Hydronet – Département de Sciences Biologiques, Université de Montréal,
CP 6128, succ. Centre-Ville, Montréal, Québec H3C 3J7 Canada

²Department of Geography, McGill University, Room 619, Burnside Hall 805 Sherbrooke St. W.,
Montreal, Québec H3A 2K6 Canada

Citation: Guénard, G., G. Lanthier, S. Harvey-Lavoie, C. J. Macnaughton, C. Senay, M. Lapointe, P. Legendre, and D. Boisclair. 2016. A spatially-explicit assessment of the fish population response to flow management in a heterogeneous landscape. *Ecosphere* 7(5):e01252. 10.1002/ecs2.1252

Abstract. Ecological processes are structured in space and there are important benefits in incorporating spatial information for the analysis of data sets obtained from field studies. Assessing the effect of different flow management practices on river ecosystems is an example where such an exercise is highly relevant. Human activities such as hydroelectric power production are known to modify the temporal variability in river flow. Flow management strategies may have a direct influence on fishes and may trigger complex cascades of interactions involving different features of the river ecosystem. In this study, we performed an assessment of the effect of different flow management practices on fish count density (no. fish/m²), biomass density (g/m²), and species richness. Data were collected in 941 sites located along 28 Canadian rivers. These rivers were either naturally flowing or had altered flows from one of three flow management strategies: run of the river dams, storage with gradual release, or storage with peak release. Each site (300 m²) was surveyed using paired snorkeling and electrofishing techniques; environmental variables (water depth and velocity, and substrate composition) were also measured. The study spanned a broad geographic range (3497 km, geodesic distance) and involved repeated local observations (16–50 sites/river), and was therefore inherently spatially organized. We used spatial modeling to obtain a baseline to estimate the effect of flow management strategies on fishes. Our results indicate that rivers downstream of flow peaking storage dams have, by far, the lowest fish densities (count and biomass) and species richness, whereas those downstream of gradual release storage dams had higher fish biomass density than the unregulated rivers.

Key words: communities and ecosystems; fish ecology; habitat and water quality; management and policy; recreational fisheries; spatial filtering; statistics and modeling.

Received 23 June 2015; revised 5 October 2015; accepted 13 October 2015. Corresponding Editor: D. P. C. Peters.

Copyright: © 2016 Guénard et al. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** guillaume.guenard@gmail.com

INTRODUCTION

Incorporating spatial information about ecological processes is now widely recognized as a cornerstone paradigm for understanding ecological processes and obtaining dependable

statistical inferences from field study (Forman and Godron 1986, Legendre 1993, Wiens et al. 1993, Cottenie 2005, Wagner and Fortin 2005, Guénard et al. 2010). Ecologists commonly need to assess the influence of variables within a landscape. Whether these assessments

involve controlled field experiments or field observational surveys, the observations performed will inevitably be distributed into space and will therefore likely feature spatial variation patterns (e.g., gradients, patches) that are contextual to a particular study area (Dormann et al. 2007, Diniz-Filho et al. 2009, Peres-Neto and Legendre 2010). These spatial variation patterns incur pseudoreplication and may induce apparent but spurious relationships in field data. Modeling spatial variation is therefore important to ascertain that the observed relationships are indeed the outcome of underlying ecological processes. Quantifying the effect of hydroelectric power dams, which is a human activity impacting large areas, is one such scenario where spatial modeling comes in handy because of the need to estimate the local baseline conditions that would have prevailed had the river been unregulated.

Hydroelectric power production, as with most human activities, has its share of associated environmental costs (Bonner and Wilde 2000, de Ménora et al. 2005, Nilsson et al. 2005). Hydroelectric power facilities can be operated in different ways; certain flow management practices may exert more downstream flow impacts than others. Spatial variation in flow regimes are subject to other factors, such as climate, that shift the baseline for environmental assessment and further complicate the generalization of the effects of flow management practices on the ecosystems downstream of a dam. As the need for renewable energy increases, knowledge of the ecological consequences of hydroelectric power production across broad geographical ranges will undoubtedly be the cornerstone to develop more sustainable facilities, in terms of new constructions as well as upgrades of existing ones.

Flow management practices affect river flow in different manners, both in terms of intensity

and periodicity. Here, we categorize rivers into four different types with respect to the presence and operation mode of hydroelectric facilities (Table 1). Unregulated river (UR) are those without dam. The presence of a dam involves some sort of regulation, yet not all dams store large amounts of water. Dams with small water storage (i.e., a few hours or days worth of flow) are categorized as “run-of-the-river” (RR). Dams that store large amounts of water may also differ in the way water is released with time. Storage dams may generate power all day long, releasing water gradually (ST, for “storage”) or alternate between two (or more) very contrasting flow values, releasing short bursts of high flow (PE, for “peaking”; McLaughlin et al. 2014, Young et al. 2011). In northern latitudes, unregulated rivers experience flow patterns modulated by climatological processes, showing seasonal periodicity (i.e., spring floods) and occasional random flow peaks after large storms (Young et al. 2011). In contrast, dams may use all the water available for power production or allow the surplus of water flow to spill over a weir. The storage capacity of reservoirs and release of water from dams may also vary greatly from one hydroelectric facility to another, resulting in differences in the magnitude and periodicity of downstream flows. In rivers with RR dams, a small upstream reservoir volume relative to mean flow may occur but does not store more water than required for power production for a single day, resulting in downstream flows similar to a natural regime (Bratrich et al. 2004). In rivers with ST dams, larger storage volumes allow the natural seasonal runoff volumes to shift temporally, resulting in significant seasonal high flow attenuation and enhancement of low flows, especially during the winter months. Rivers with PE dams exhibit frequent periods of significant hourly or daily hydrological fluctuations over a year caused by

Table 1. Characteristics of the different rivers with respect to their flow management strategies.

Type	Abbreviation	Dam retention time	95th percentile hourly rate of flow increase or decrease
Unregulated	UR	No dam	0.2–3.1 m ³ /s
Run-of-the-river	RR	A few hours to a few days	0.5–3.3 m ³ /s
Storage	ST	Several months to a year	0.001–5 m ³ /s
Flow spiking (Hyropeaking)	PE	Several months to a year	6–135 m ³ /s

rapid opening and closing of the dam's sluice gates (ST dams do not produce such frequent burst of flow).

River regulation tends to increase minimum and decrease maximum flows, and that tends to make overall flow homogeneous among rivers (Poff et al. 1997, Magilligan and Nislow 2001, Pyron and Neumann 2008). Furthermore, Magilligan and Nislow (2005) have shown that regulated rivers have a greater number of high flow pulses of shorter duration than unregulated rivers. Each flow management practice may exert a range of influences on temporal flow patterns (McLaughlin et al. 2014). Because of the potentially complex effects of the flow management practices on temporal flow patterns downstream of the dam, generalizing their potential impacts on ecosystems is a challenging task (Richter et al. 1996, Magilligan and Nislow 2005).

The hydroelectric industry and stakeholders place substantial effort to accurately identify reference fish and flow conditions that serve as baseline data to quantify the changes to fish communities due to flow alteration in regulated rivers. Assessing the ecosystemic effect of different flow management strategies further requires that fish communities be sampled across a variety of flow management practices and rivers, in order for the data to be representative of the largest number of possible natural backgrounds. Since no two rivers are entirely comparable, the number of rivers that are needed to detect any effect is often fairly large, resulting in prohibitive survey costs.

In this study, we propose to use an observational approach involving survey data for the different flow management practices. Observational studies do not provide much control over variables other than those tested. That lack of control entails low statistical power: the many points in which the rivers differ can be regarded as many potentially confounding variables that may distort our perspective of the actual outcome of the effect of flow management on ecosystem functioning. Spatial variation stems from the spatially organized nature of the processes shaping the landscape (e.g., the climatological processes influencing rainfalls, the ecological processes whereby species dispersed, the geological processes that distributed minerals in the earth crust). In addition, statistical tests assume that observations are

independent of one another (Legendre and Legendre 2012) or, at least, that their dependence of one another is homogeneous. However, because the features and processes in the environment are spatially organized, observations taken at nearby locations (e.g., two consecutive locations) are more dependent of one another than observations taken at a greater distance (e.g., locations 10 km apart): observations are spatially autocorrelated (Legendre and Fortin 1989, Legendre 1993, Dormann et al. 2007). Similarly, observations on pairs of rivers located in the same region (e.g., 50 km apart) are expected to be more similar than observations on pairs of rivers located in different regions (e.g., 1000 km apart). Following that paradigm, the dependence of observations is expected to be some negative function of the distance separating them. Fortunately, methods exist that allow us to use the spatial dependence among observations in a predictive manner.

The goal of this study is to quantify the effect of different flow management strategies (i.e., RR, ST, and PE) on fish count density, biomass density and species richness. These ecosystem responses are of great societal value and good indicators of ecosystem status (Vörösmarty et al. 2010). We achieved that goal by using unregulated rivers as a baseline for comparison. For that purpose, we estimated local values of the response variables for unregulated conditions using spatial model. Observed fish responses were compared with spatially-explicit predictions obtained for unregulated sites to assess the effect of flow regulation. Spatial modeling allows us to assess the effects of flow management strategies and environmental variables by making spatially-explicit predictions for unsampled locations based on their distances from the sampled rivers. We use the ability of the models to make spatially-explicit predictions to generate prediction maps of expected fish count density, biomass density, and species richness for the different flow management strategies, thus highlighting the transferability of our approach to other impacted systems of the same types.

METHODS

Sampling

Our data set encompasses information from 28 rivers, of which 15 are unregulated and 13 are regulated. All these rivers are located in

Canada and are spread among four Canadian provinces: Alberta, Ontario, New-Brunswick, and Quebec. Sampling was performed during the summer months (late June, July and August) of years 2011–2013, and consisted in both electrofishing (using an LR24; Backpack electrofisher: Smith-Root Inc., Vancouver, Washington, USA) and snorkeling surveys performed during daytime (0830–1800). Because each of these sampling method shows selectivity toward catching fish of particular species and size classes, we used both methods in tandem to minimize the bias associated with sampling methods (Macnaughton et al. 2014). For example, electrofishing seemed to be more effective at sampling cryptic species than snorkeling, whereas the latter was more effective at sampling large noncryptic fish, possibly because the latter species can feel the electric field of the electrofisher earlier and hence avoid being caught. Also, snorkelers would often observe large schools of small fish (e.g., 1–10 cm Cyprinids) while electrofishing could only catch a few individuals.

Electrofishing was performed by teams consisting of an electro-fisher operator flanked by two fishers, each wielding a dip net (Smith-Root, dimension (cm): 38 long $\times$ 33 wide $\times$ 20 deep, mesh size (mm): 6.35) and moving in the upstream direction. The fish captured were identified to species, measured (total length; ± 0.1 cm) and weighed (± 0.1 g; Ohaus mod. CL201: Ohaus Corp., Parsippany, New Jersey, USA). They were allowed to recover in cool aerated water before being released at their point of capture. To standardize fishing effort, the electrofishing teams aimed for total electro-shocking periods of approximately 900 s per sampling site; the voltage was set at each sampling site to obtain a mean power of 200 W.

Observations were performed by teams consisting of three trained snorkelers moving upstream in a zigzagging manner to cover the whole sampling area. Fish were identified to species or else to the nearest taxonomic level that snorkelers could discriminate visually. It was not possible for the snorkelers to identify fish below 3 cm to species and, as a consequence, all fish observations with size < 3 cm were categorized as “fry”. The size of fish with total length ≥ 3 cm was visually estimated in a first class going from

3 to 5 cm (mean size taken as being 4 cm), and then in classes 5 cm apart (mean sizes taken as being 7.5 cm, 12.5 cm, 17.5 cm, etc.). Total lengths were converted to wet body mass using empirical length-mass relationships. The relationships used were computed using the fish captured by electrofishing. In order of preference, we used the relationship obtained using the fish from (1) the same river, (2) other rivers from the same Canadian province, or (3) all the sampled rivers, depending on available sample sizes.

Sampling sites having a surface area of 300 m² (5 m across by 60 m along the river) were positioned to ensure that the fish habitat within them was as homogeneous as possible. Because site width was often substantially narrower than river sections, they were transversally positioned in alternation, near the left shore (facing downstream), in the middle, and near the right shore of the river, starting randomly. The location of the beginning and end of each sampling site were measured using a GPS unit (GPSMAP; 76sc: Garmin International Inc. Olathe, Kansas, USA). Local environmental variables were estimated. Water depth and velocity, as well as substrate composition, are often regarded as key drivers shaping community structure (Knouft et al. 2011, Michel and Knouft 2014). Water depth (z in cm, measured using a graduated pole), velocity (v in cm/s; Flo-Mate 2000: Marsh-McBirney Inc., Frederick, Maryland, USA), and substrate median grain size (g in cm) were estimated in ten 50 cm $\times$ 50 cm plots randomly dispatched within each sampling site (Wolman 1954, Latulippe et al. 2001). These three variables were used as covariables to obtain a better assessment of the effect of flow management on fish count and biomass densities, and species richness.

Calculations

Total fish density was calculated as the maximum value obtained using electrofishing or visual sampling for each site within each river. That maximum was calculated on the basis of individual species and size classes, and was calculated separately for fish count density (no. fish/m²) and fish biomass density (g/m²; Macnaughton et al. 2014). Following that selection procedure, we summed all these taxon- and size-specific densities to obtain the total fish count density and the total fish biomass

density for each sampling site. We calculated species richness per sampling site. Fish of total lengths ≤ 3 cm were excluded because they could not be dependably identified at the species level in the field. We computed spatial eigenvector maps on the basis of the distance among sites. The distance between pairs of sites located in different rivers was taken as the geodesic distance between the rivers; this is the length of the spherical arc between two locations following Earth's curvature. We calculated the geodesic distances from the geographical coordinates of the sites (in degrees) using the haversine formula (Goodwin 1910). The distance between pairs of sites located in the same river was taken as the distance following the course of the river. That approach was used to calculate distances because the geodesic distance underestimates the distance that fish need to travel among sites of the same river.

Statistical analysis

Spatial eigenvectors.—We quantified spatial structures using spatial eigenvector maps (Legendre and Legendre 2012: Chapter 14). Since we use the sampling sites of all the rivers for the calculation of the spatial eigenvectors, sites within a river were very close to one another in comparison to distances among rivers. We therefore calculated a spatial eigenvector map using the approach proposed by Diniz-Filho et al. (2013), which consists in multiplying the among sites distances by -0.5 before centering the rows and columns of the resulting matrix to a value of 0 and calculating an eigenvalue decomposition as follows (Griffith 2003):

$$\mathbf{Q}(-0.5[d_{i,j}])\mathbf{Q} \quad (1)$$

where $\mathbf{Q} = \mathbf{I}_n - n^{-1}\mathbf{1}_n\mathbf{1}_n^T$ is an idempotent centering matrix (n : the number of sites, $\mathbf{I}_n$: an $n \times n$ identity matrix, $\mathbf{1}_n$: an $n \times 1$ all-ones matrix), $[d_{i,j}]$ is the among sampling sites distance matrix for all the rivers, $\mathbf{U}$ is a matrix of spatial eigenvector, and $\mathbf{D}_\lambda$ is a diagonal matrix whose diagonal elements are the nonzero eigenvalues λ . That calculation is equivalent to performing a Principal Coordinate Analysis of the square root of the distances among the sampling sites while skipping the last step

where the eigenvectors are multiplied by the square root of their eigenvalues. The square root of the distances was used in this study to decrease the importance of the among-river distances relatively to the within-river distances. Since no two sites occupy the same location and because of the centering of the distance matrix (Eq. 1), the number of nonzero eigenvalues is $n - 1$. Only the eigenvectors associated to nonzero eigenvalues were used for spatial modeling. Interestingly, a regularly sampled transect, these spatial eigenvectors are identical to the type-II discrete cosine transforms (DCT-II), which are commonly used to represent image details by image compression algorithms (e.g., jpeg), yet they remain applicable in irregular sampling scenarios, which is the case in this study. The higher order eigenfunctions represent large-scale spatial variation on the whole study area, whereas lower order eigenfunctions represent smaller features, first among rivers, and then within the rivers. By combining them, a multiple-spatial-scale picture of the spatial variation is obtained. Making predictions using eigenfunctions is straightforward, as was illustrated by Guénard et al. (2011) where predicting trait values was done using phylogenetic eigenvectors. Similarly, prediction scores (s_k) for a set of q arbitrary sampling sites can be obtained in the spatial context by re-arranging Eq. 1 and posing a matrix of new locations k located at known distances $[d_{i,k}]$ from the sampling points i as follows:

$$\mathbf{s}_k = -0.5 \left\{ [d_{i,k}] - n^{-1}(\mathbf{1}_q\mathbf{1}_n^T[d_{i,j}] + [d_{i,k}]\mathbf{1}_n\mathbf{1}_n^T) + n^{-2}\mathbf{1}_q\mathbf{1}_n^T[d_{i,j}]\mathbf{1}_n\mathbf{1}_n^T \right\} \mathbf{U}\mathbf{D}_\lambda^{-1}. \quad (2)$$

Models built using the eigenvectors in $\mathbf{U}$ can be used to predict values for new sites by using s_k as predictors. In this study, we used predictions obtained from spatial predictors s_k to cross-validate linear models as well as to draw prediction maps for all response variables.

Spatial model estimation.—We modeled fish count and biomass density, and species richness for UR rivers using water depth (z) and velocity (v) as well as median substrate grain size (g) and

spatial eigenvectors in an additive manner using a linear model defined as follows:

$$y_i = b_0 + b_z z_i + b_v v_i + b_s g_i + \sum_{l=1}^{n-1} b_l u_{i,l} + \varepsilon_i \quad (3)$$

where y_i is the response variable observed on site i , b_0 is the intercept of the model, which corresponds to unregulated rivers, b_z is the effect of depth, b_v is the effect of current velocity, b_s is the effect of substrate grain size, b_l is the effect of a spatial eigenvector l of which $u_{i,l}$ is an element and ε^i is a normally-distributed random error. Since the spatial modeling method presented above produces many $(n - 1)$ spatial eigenvectors in addition to the environmental variables, we built the spatially-explicit models using elastic net regression (Zou and Hastie 2005). Elastic net regression linearly combines norm (L_1) used for the Least Absolute Shrinkage Selection Operator (LASSO; Tibshirani 1996) with that (L_2) used for the ridge regression (Tikhonov and Arsenin 1977) in a single quadratic regularization norm. The parameter estimates thus minimize the following objective function:

$$F_{\alpha,\psi} = \sum_{i=1}^n (y_i - \hat{y}_i)^2 + \psi \left(\alpha \sum_{l=1}^{n-1} |b_l| + (1 - \alpha) \sum_{l=1}^{n-1} b_l^2 \right) \quad (4)$$

where y_i and $\hat{y}_i$ are the observed and fitted values of the response (fish count density, biomass density or species richness), b are the regression coefficients, α is a parameter varying between 0 and 1 that sets a trade-off between ridge ($\alpha = 0$) and LASSO ($\alpha = 1$) regression, and ψ is the penalty applied to the regression coefficients. As with LASSO regression (but unlike ridge regression), elastic net regression can produce a parsimonious model as it allows one to entirely deselect variables (i.e., make their coefficients numerically equal 0), while being more reliable than the LASSO at selecting variables within groups of correlated variables (Zou and Hastie 2005). The value of ψ imposes a constraint to the size of the regression coefficients to which it is applied, shrinking their contribution in the model. The smallest possible constraint is $\psi = 0$

and corresponds to a regular multiple regression model while increasing ψ would progressively pull an increasing number of coefficients toward 0, discarding them from the model. We used cross-validation to estimate the most appropriate value for α and ψ on the basis of the predictive power of the resulting spatial model as estimated using the cross-validation R -square (R_{cv}^2).

Because the number of observations was too great for leave-one-out cross-validation we performed it on groups of sites from the same river. We first determined the number of cross-validation groups in each river as the integer part of the division of its number of sampling sites by a value of minimum group size. Then, we proceeded in an interleaving manner by assigning the sampling sites to successive cross-validation groups. The number of observations varied among the different cross-validation groups because the numbers of sampling sites differed among the rivers and were often not multiples of the minimum group size (see Results).

The effect of flow regulation on the three fish responses was quantified by subtracting values predicted by the spatial model from the values observed on the regulated rivers. Inference tests of the effect of flow regulation were calculated separately for each type of flow regulation while controlling among-river differences. For that purpose, we used an ANOVA model calculated on the basis of type II sums of squares because sample size differed among rivers.

All calculations were performed using the R language for statistical computing (The R Development Core Team 2014). Spatial eigenfunctions were calculated using R package *codep* (Guénard et al. 2010) and elastic net regressions using R package *glmnet* (Friedman et al. 2010).

RESULTS

The number of sites sampled in each of the 28 rivers varied from 16 (one river: Petit-Saguenay) to 50 (two rivers: Au Saumon and Becaucour), for a total of 941 sites (513 in unregulated rivers and 428 in regulated rivers) spread over a vast area (Table 2). Sampling sites within river were located 368 m apart, on average, with separation distances ranging from 26 m to 11 km. In regulated rivers, sampling began from 200 m (Dee, Serpentine) to

Table 2. Summaries of parameter values for the models describing transformed ($\log(x + 1)$) fish count density, biomass density and species richness estimates for unregulated rivers with the number of spatial eigenfunctions and cross-validation R -squared (R_{cv}^2) for the model with and without spatial eigenfunctions.

Parameter	Model		
	Count density	Biomass density	Species richness
α	0.9984	0.9917	0.9996
ψ	0.010	0.029	0.032
Intercept	0.3829	0.7409	2.3302
Depth	-0.0015	–	-0.0062
Velocity	-0.2194	-0.3605	-0.8092
$\log(D_{50} + 1)$	–	–	–
Nb. of eigenfunctions	86	77	52
R_{cv}^2 w eigenfunctions	0.47	0.26	0.33
R_{cv}^2 w/o eigenfunctions	0.09	0.005	0.23

8 km (Magpie, Mississagi) downstream of the dam. Fish were observed in 910 sites (97%), where the range of fish count density was 0.003–4.57 fish/m² (median: 0.16 fish/m²), the range of biomass densities was 0.002–66.78 g/m² (median: 0.67 g/m²), and the maximum number of species observed per site was 18 (median: 5). Species richness as well as count and biomass densities were left-skewed (Richness: $\gamma_1 = 0.83$, count density: $\gamma_1 = 2.79$, biomass density: $\gamma_1 = 12.19$) and were therefore $\log(x + 1)$ -transformed to prevent models from being overly influenced by the few largest values.

We set a minimum group size of 15 for cross-validation, for a total of 31 cross-validation groups ranging in size from 15 (31 groups) to 22 (one group encompassing all sites of the Batchawana river). Petit-Saguenay River, was represented by a single group, two rivers (Au Saumon and Beaucour) by three groups and the remaining 12 rivers by two groups. The cross-validation estimates of α were slightly below 1, while that of ψ were ranged from 0.010 to 0.032 (Table 2). The predictive powers of the spatial models obtained from the elastic net regression models (R_{cv}^2) with spatial eigenfunctions ranged from 0.26 to 0.47 and were always higher than their counterpart without spatial eigenvectors (range: 0.09–0.23).

In the model predicting count density, the effect of two predictors, water depth and velocity, were retained by the elastic net model together with 17% of the 506 spatial eigenfunctions, whereas that of the median substrate size and the remaining

spatial eigenfunctions were discarded (Table 2). We found the flow management practices to affect count density, with PE dams having a 39% smaller density, on average than values predicted for unregulated rivers (a -0.059 fish per m² deviation from the predicted baseline of 0.150 fish per m²; $t_{(96)} = -5.922$, $P < 0.0001$). No statistically significant differences were found for RR and ST dams ($P > 0.05$; Fig. 1a).

In the model predicting biomass density, water velocity was the only retained significant predictors and was accompanied by 15% of the spatial eigenfunctions (Table 2). We found flow management to affect biomass density, with ST and PE dams having 33% higher and 47% lower biomass density, respectively, than predicted for UR (ST: a 0.350 g/m² deviation from the predicted average baseline of 0.795 g/m²; $t_{(162)} = 6.879$, $P < 0.0001$; PE: a -0.267 g/m² deviation from the 0.566 g/m² baseline; $t_{(96)} = -10.017$, $P < 0.0001$). RR dams were similar to UR conditions in terms of biomass density ($P > 0.05$; Fig. 1b).

In the model predicting species richness, water depth and velocity were selected as predictors together with 10% of the spatial eigenfunctions (Table 2). As in the two previous analyses, the flow management had an influence on species richness: PE and ST dams had 13% and 1.7% fewer fish species, respectively, than predicted for UR (PE: a -0.660 species deviation from the baseline of 5.088 species; $t_{(96)} = -12.744$, $P < 0.0001$; ST: a -0.091 species deviation from the baseline of 5.200 species; $t_{(162)} = -2.716$, $P < 0.01$), whereas RR

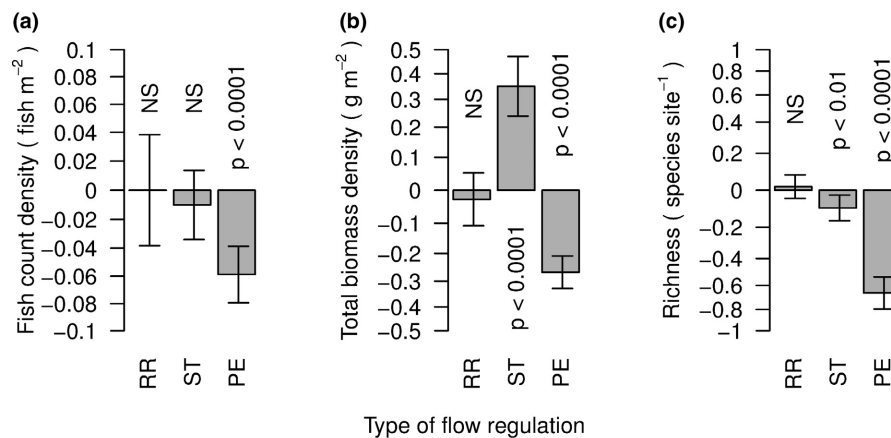


Fig. 1. Effect of flow management strategies on fish: (a) count density, (b) biomass density, and (c) species richness (RR: river with run-of-the-river dam, ST: river with a gradual release storage dam, PE: river with a peak release storage dam) Error bars are 95% confidence intervals.

dams had similar species richness than for UR ($P > 0.05$; Fig. 1c).

Because the selected rivers were spatially clustered in three groups, we predicted the three response variables in space in three regions: the western (from +49, -116° to +51, -113°; encompassing the four Albertan rivers), central (from +46, -85° to +49, -83°; encompassing the five rivers east of Lake Superior and north of Lake Uron), and eastern region (from +45, -77° to +49, -66°; encompassing the 19 rivers of Eastern Ontario, Québec, and New-Brunswick). Predictions were calculated using the average environmental conditions observed: depth 40 cm, flow velocity 32 cm/s, median substrate grain size 2.9 cm.

Predicted fish count density varied between -0.09–0.56 fish/m² (Fig. 2a), biomass density varied between 0.31 and 1.05 g/m² (Fig. 2b) whereas species richness varied between 1.58 and 2.18 species (Fig. 2c). The three response variables studied here show roughly similar spatial variation patterns across the three regions. For instances the highest values of all three responses were predicted in the eastern region, along the Saint-Lawrence River. The lowest count and biomass density values were predicted in the lower portion of the central region (north of Sault Ste.-Mary, Ontario), and the lowest species richness were predicted north of the western region.

DISCUSSION

In this study, we used spatial modeling to take the spatial context in which the observations were obtained into account to dependably assess the specific effect of flow management practices on fish density and species richness. It is important to state that the purpose of the spatial modeling method we described is not only to control for spatial variation as being a source of confounding variation; it is also to use the latter to make predictions for given segments of similar rivers located within the spatial scope of the models. Here, we illustrated that capacity by mapping fish count and biomass densities as well as fish species richness from spatially-explicit predictions across whole maps. The same computational approach remains applicable to other variables of interest and for other similar studies whose goal is to reliably assess the effect of variables using observation data obtained in survey studies.

The spatially-explicit models enabled us to highlight the effects of different flow management practices against the natural background of spatial variation. Our analysis strongly suggests that PE dams have deleterious effects on fish densities (count and biomass) and species richness (Fig. 1). Three out of the 28 rivers sampled had dams with PE management practices and given

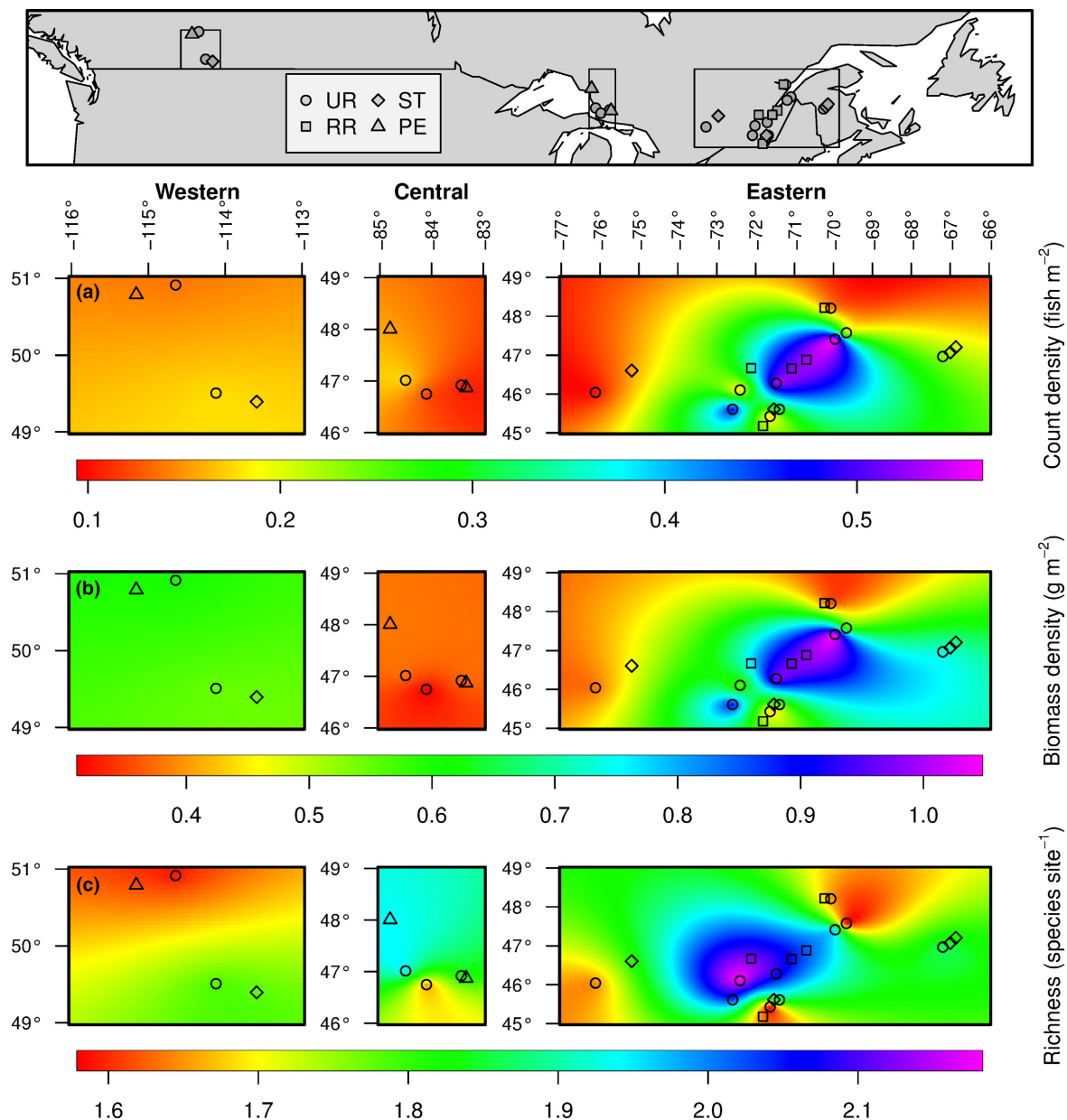


Fig. 2. Spatially-explicit estimates of fish: (a) count density, (b) biomass density, and (c) species richness, all three represented using a color scale, for the different flow management strategies in the three regions (Western, Central, and Eastern). The symbols on the maps represent the flow management strategies prevailing on a given location; management strategy symbols are shown in an inset in the upper map.

their geographic locations, the models would expect count density to be 83%, 0.36%, and 32% higher, biomass density to be 52%, 13%, and 7% higher, and species richness to be 15%, 1%, and 4% higher in the Kananaskis, Magpie, and Mississagi Rivers, respectively, had these rivers been

unregulated (Table 3). Possible mechanisms underlying the negative effects of PE dams may encompass, for example, fish stranding, downstream fish displacement, egg de-watering, increased predation on small fish, impeded fish migrations, lack of timing for fish reproduction

Table 3. Geographic locations (in degrees) of rivers in three regions of Canada (Western, Central, Eastern), their flow management strategies, and their mean observed and predicted count density (no. fish/m²), biomass density (g/m²), and species richness (species).

Region	River	Type	Latitude	Longitude	Count density		Biomass density		Species richness	
					Obs	Pred	Obs	Pred	Obs	Pred
Western	Kananaskis	PE	50.79013	-115.15707	0.01	0.15	0.06	0.76	0.73	3.99
	Elbow	UR	50.91403	-114.64483	0.04	NA	0.50	NA	2.76	NA
	Castle	UR	49.50713	-114.11905	0.15	NA	0.81	NA	4.25	NA
	Waterton	ST	49.39392	-113.59020	0.23	0.17	1.16	0.69	5.03	4.60
Central	Magpie	PE	48.00691	-84.80294	0.18	0.16	0.28	0.46	5.12	5.89
	Batchawana	UR	47.01422	-84.50238	0.18	NA	0.46	NA	5.81	NA
	Goulais	UR	46.74834	-84.09958	0.15	NA	0.31	NA	4.62	NA
	Aubinadong	UR	46.91840	-83.42486	0.05	NA	0.28	NA	4.20	NA
Eastern	Mississagi	PE	46.87216	-83.33139	0.08	0.14	0.40	0.50	3.67	5.57
	Picanoc	UR	46.04178	-76.11821	0.07	NA	0.40	NA	3.05	NA
	Kiamika	ST	46.60518	-75.18681	0.38	0.19	1.51	0.67	6.41	5.50
	Noire	UR	45.61028	-72.59266	0.48	NA	1.74	NA	8.84	NA
	Nicolet	UR	46.10445	-72.39958	0.27	NA	0.93	NA	7.95	NA
	Sainte-Anne	RR	46.66634	-72.11558	0.19	0.44	0.62	1.18	5.07	7.81
	Coaticook	RR	45.17841	-71.81062	0.45	0.28	0.88	0.71	5.49	4.38
	Eaton	UR	45.42903	-71.62786	0.40	NA	0.79	NA	4.52	NA
	St-Francois	ST	45.61350	-71.52945	0.06	0.35	1.18	0.77	3.93	5.73
	Bécancour	UR	46.27578	-71.47241	0.91	NA	3.00	NA	8.20	NA
	Au Saumon	UR	45.60874	-71.38894	0.38	NA	0.91	NA	6.77	NA
	Etchemin	RR	46.66083	-71.07681	1.17	0.70	2.44	1.66	7.38	7.23
	du Sud	RR	46.88161	-70.69758	0.43	0.68	1.10	1.63	8.61	6.21
	St-Jean	RR	48.21989	-70.22747	0.09	0.11	0.41	0.36	3.15	3.28
	Petit-Saguenay	UR	48.20977	-70.06994	0.06	NA	0.21	NA	2.82	NA
	Ouelle	UR	47.41224	-69.95785	0.79	NA	2.19	NA	7.43	NA
	du Loup	UR	47.57704	-69.66737	0.24	NA	0.68	NA	3.61	NA
	Gulquac	UR	46.96566	-67.19058	0.22	NA	0.88	NA	4.84	NA
	Dee	ST	47.07160	-66.99624	0.22	0.22	1.44	0.92	4.61	4.84
	Serpentine	ST	47.20665	-66.85522	0.22	0.24	1.89	0.95	3.80	5.40

and migration, and reduced fish shelter (see Young et al. 2011, for a review). Although we may consider the uneven spread of regulation practices across the study area as a limitation of this study, it is the goal of spatial modeling to make predictions assessing the effects of river management practices on fish through space.

Our analysis also revealed a positive effect of ST dams on biomass density. We found positive difference between observed and predicted biomass density ranging from 163% (Serpentine) to 35% (Dee) for all five rivers with ST dams. These results suggest that the ST dams may enable fish to grow to larger sizes than under unregulated flow. These results are similar to those reported by Kushlan (1976), who observed decreased fish density concomitantly with increased biomass, average fish size, species richness, and species

diversity following a period of stability of the water level in the Everglades marshes (Florida, USA). These changes were accompanied by a shift from the dominance of small-sized omnivorous species to a dominance of large-sized carnivorous species resulting from their immigration, because they were poorly adapted for surviving water level fluctuations in their native marshes. By contrast, we detected a small negative effect of ST dams on fish species richness compared to UR rivers. In this study, ST dams are associated with a similar number of individuals of fewer species growing to larger sizes. Although the effect of ST dams on species richness is small, similar species richness may imply radically different species composition. Further study on species composition may help detect what change in species assemblages underlying

the positive effect of ST dams on biomass density.

Nevertheless, our results suggest that the buffering of peak flow events associated with ST type dams may be favorable to larger individual fish, possibly because it is energetically more rewarding to have a larger size under that flow regime (Enders et al. 2005). Peak flow events, whether they are natural or anthropogenic in origin, may be difficult for larger fish to withstand, possibly because of their reduced ability to find refuge along the river bed and, therefore, they have a higher propensity to be flushed away from their preferred habitats. Similar peaking events might also be involved in the overall depression of ecosystem responses observed in rivers with PE dams. That result might seem counter-intuitive and contrast with that of other studies that found larger fish to be more powerful and better able to withstand peak flows than smaller fish (Bain et al. 1988, Kinsolving and Bain 1993). Because swimming against running water is energetically costly, simply swimming against strong current may not be sustainable in the long run, and this irrespective of fish size (i.e., swimming costs grow with fish size; Boisclair and Tang 1993, Guénard et al. 2015). In such a circumstance, fish would need to change their distribution toward more profitable habitat. It is possible that these alternate high flow habitat be rare for fish of any size given the magnitude of the flow peak downstream of PE dams.

King et al. (2010) have shown that too much flow stability can be detrimental to river ecosystems. ST dam operation also involves a few high flow events that could be instrumental to key processes for the maintenance of the habitat, such as preventing river bed silting. We hypothesize that ST dams may provide, on average, a good trade-off between the flow stability required for fish to thrive while ensuring sufficient high flow events to maintain suitable fish habitat.

The small negative impact of ST dams observed on species richness (0.2% on average) was not consistent among rivers. It was observed for three rivers out of five (Serpentine: -4%, St-François: -3%, and Dee: -0.1%), with the two remaining rivers, Waterton (4.4%) and Kiamika (3.9%), having higher species richness than predicted by the spatial model. That result suggests that under sets of circumstances not assessed in this study,

flow stability may become either detrimental or beneficial to local fish diversity.

Run-of-the-river management practices are thought to have minimal, if any, artificial influence on downstream river flows, suggesting that fish community metrics should not be significantly affected by these flows. This study supports that view as our results could evidence no effect of RR dams for any of the three fish community responses under study.

It is widely expected that the construction of hydroelectric dams on rivers and their subsequent operation may have profound impacts on ecosystems. Our results suggest that, besides for PE dams, the impacts on fish may be small and not systematically negative. Future studies should investigate whether and how flow management influence in community structure. For instance, the density of some species may increase, masking decrease in that of other species and resulting in similar total density. An analysis of species interaction may help strengthen our understanding the reason underlying the global fish responses that were observed in this study.

Using spatially-explicit modeling in this study has allowed us to take advantage of spatial variation to make predictions. These spatially-explicit predictions allowed us to extrapolate the effect of further hydroelectric development and flow management practices to other systems. Our study highlights the merits of including spatial modeling as a predictive tool in establishing environmental flows for regulated systems across large geographic extents. Spatial modeling is limited to representing spatial variation. To reliably estimate baseline conditions, it is important that models employ environmental variables representing any local particularity contrasting from the broad landscape picture. Let us consider, for instance, two nearby sites with very different depths have very contrasted fish density because of their different depth. A purely spatial model will not be able to grasp that difference without being helped by environmental variable depth. In revenge, it is often not practical to assess all the different driving broad- and medium-scale spatial variation and use them directly for prediction. Spatial modeling appears a pragmatic solution in such widespread situations. Spatial eigenfunctions represent variation that may arise from a multitude of environmental factors. The relevance

of these multiple factors driving spatial variation can be investigated in future studies using methods such as multiscale codependence analysis (MCA; Guénard et al. 2010). MCA allows to quantify the joint spatial dependence between variables, allowing one to identify the variables whose spatial distribution influences that of others.

From a more philosophical standpoint, we hope this study will help bridge the gap between theory and practice and encourage ecologists to use spatial ecological methods to tackle practical issues. Spatial structure and ensuing autocorrelation is expected in large-scale study such as the present. We recommend that spatial modeling be attempted in these scenarios. Spatial variation can only be assumed not to be relevant when no eigenfunctions can be evidenced to be a relevant predictor of the response under study.

ACKNOWLEDGMENTS

We are thankful to the many people who helped in collecting the field data used in this study. This study is a contribution of the strategic research network Hydronet, which aims at developing a better understanding of the effects of hydroelectric operations on aquatic ecosystems. HydroNet is funded by the National Research Council of Canada (NSERC) and through the coordinated efforts of Brookfield Power, Fisheries and Oceans Canada, the Ontario Ministry of Natural Resources, and the Ministère des Ressources Naturelles et de la Faune du Québec. All work reported herein was conducted in accordance with the guidelines of the Comité de Déontologie en Expérimentation Animale (CDEA) de l'Université de Montréal and was approved by Alberta Tourism, Parks and Recreation, Ministère des Ressources Naturelles et de la Faune, Fisheries and Oceans Canada, Ontario Ministry of Natural Resources and Ontario Parks.

LITERATURE CITED

- Bain, M. B., J. T. Finn, and H. E. Brooke. 1988. Stream-flow regulation and fish community structure. *Ecology* 69:382–392.
- Boisclair, D., and M. Tang. 1993. Empirical analysis of the influence of swimming pattern on the net energetic cost of swimming in fishes. *Journal of Fish Biology* 42:169–183.
- Bonner, T. H., and G. R. Wilde. 2000. Changes in the Canadian river fish assemblage associated with reservoir construction. *Journal of Freshwater Ecology* 15:189–198.
- Bratrich, C., B. Truffer, K. Jorde, J. Markard, W. Meier, A. Peter, M. Scheneider, and B. Wehrli. 2004. Green hydropower: a new assessment procedure for river management. *River Research and Applications* 20:865–882.
- Cottenie, K. 2005. Integrating environmental and spatial processes in ecological community dynamics. *Ecology Letters* 8:1175–1182.
- de Ménora, B., R. Vigouroux, and F. L. Tejerina-Garro. 2005. Alteration of fish diversity downstream from petit-saut dam in French Guiana. Implication of ecological strategies of fish species. *Hydrobiologia* 551:33–47.
- Diniz-Filho, J. A. F., J. C. Nabout, M. P. de Campos Telles, T. N. Soares, and T. F. Rangel. 2009. A review of techniques for spatial modeling in geographical, conservation and landscape genetics. *Genetics and Molecular Biology* 32:209–211.
- Diniz-Filho, J. A. F., J. V. B. P. L. Diniz, T. F. Rangel, T. F. Soares, M. P. de Campos Telles, R. Garcia Collevatti, and L. M. Bini. 2013. A new eigenfunction spatial analysis describing population genetic structure. *Genetica* 141:479–489.
- Dormann, C. F., et al. 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* 30: 609–628.
- Enders, E. C., D. Boisclair, and A. G. Roy. 2005. A model of total swimming costs in turbulent flow for juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Science* 62:1079–1089.
- Forman, R. T. T., and M. Godron. 1986. *Landscape ecology*. John Wiley and Sons Inc, New York, New York, USA.
- Friedman, J. H., T. J. Hastie, and R. J. Tibshirani. 2010. Regularization paths for generalized linear models via coordinate descent. *Journal of Statistical Software* 33:1–22.
- Goodwin, H. B. 1910. The haversine in nautical astronomy. *US Naval Institute Proceedings* 36:735–746.
- Griffith, D. A. 2003. *Spatial autocorrelation and spatial filtering: gaining understanding through theory and scientific visualization*. Springer-Verlag, New-York, New-York, USA.
- Guénard, G., P. Legendre, D. Boisclair, and M. Bilo-deau. 2010. Multiscale codependence analysis: an integrated approach to analyze relationships across scales. *Ecology* 91:2952–2964.
- Guénard, G., P. C. von der Ohe, D. de Zwart, P. Legendre, and S. Lek. 2011. Using phylogenetic information to predict species tolerances to toxic chemicals. *Ecological Applications* 21:3178–3190.
- Guénard, G., D. Boisclair, and P. Legendre. 2015. Phylogenetics to help predict active metabolism. *Ecosphere* 6:Article 62.

- King, A. J., K. A. Ward, P. O'Connor, D. Green, Z. Tonkin, and J. Mahoney. 2010. Adaptive management of an environmental watering event to enhance native fish spawning and recruitment. *Freshwater Biology* 55:17–31.
- Kinsolving, A. D., and M. B. Bain. 1993. Fish assemblage recovery along a riverine distance gradient. *Ecological Applications* 3:531–544.
- Knouft, J. H., N. M. Caruso, P. J. Dupre, K. R. Anderson, D. R. Trumbo, and J. Puccinelli. 2011. Using fine-scale gis data to assess the relationship between intra-annual environmental niche variability and population density in a local stream fish assemblage. *Methods in Ecology and Evolution* 2:303–311.
- Kushlan, J. A. 1976. Environmental stability and fish community diversity. *Ecology* 57:821–825.
- Latulippe, C., M. F. Lapointe, and T. Talbot. 2001. Visual characterization technique for gravel-cobble river bed surface sediments; validation and environmental applications contribution to the programme of CIRSA (Centre Interuniversitaire de Recherche sur le Saumon Atlantique). *Earth Surface Processes and Landforms* 26:307–318.
- Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? *Ecology* 74:1659–1673.
- Legendre, P., and M. J. Fortin. 1989. Spatial pattern and ecological analysis. *Vegetatio* 80:107–138.
- Legendre, P., and L. Legendre. 2012. *Numerical ecology*, Third English Edition. Elsevier Science B.V, Amsterdam, The Netherlands.
- Macnaughton, C. J., S. Harvey-Lavoie, C. Senay, G. Lanthier, G. Bourque, P. Legendre, and D. Boisclair. 2014. A comparison of electrofishing and visual surveying methods for estimating fish community structure in temperate rivers. *River Research and Applications* 31:1040–1051.
- Magilligan, F. J., and K. H. Nislow. 2001. Long-term changes in regional hydrologic regime following impoundment in a humid-climate watershed. *AWRA Journal of the American Water Resources Association* 37:1551–1569.
- Magilligan, F. J., and K. H. Nislow. 2005. Changes in hydrologic regime by dams. *Geomorphology* 71:61–78.
- McLaughlin, F., M. Lapointe, G. Bourque, and D. Boisclair. 2014. Using regional flow classes as references to analyse flow regime anomalies across a set of regulated canadian rivers. *Journal of Hydrology* 519A:307–328.
- Michel, M. J., and J. H. Knouft. 2014. The effects of environmental change on the spatial and environmental determinants of community-level traits. *Landscape Ecology* 29:467–477.
- Nilsson, C., C. A. Reidy, M. Dynesius, and C. Revanga. 2005. Fragmentation and flow regulation of the world's large river systems. *Science* 308:405–408.
- Peres-Neto, P. R., and P. Legendre. 2010. Estimating and controlling for spatial structure in the study of ecological communities. *Global Ecology and Biogeography* 19:174–184.
- Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime. *BioScience* 47:769–784.
- Pyron, M., and K. Neumann. 2008. Hydrologic alterations in the Wabash River watershed, USA. *River Research and Applications* 24:1175–1184.
- Richter, B. D., J. V. Baumgartner, J. Powell, and D. P. Braun. 1996. A method for assessing hydrologic alteration within ecosystems. *Conservation Biology* 10:1163–1174.
- The R Development Core Team. 2014. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Tibshirani, R. 1996. Regression shrinkage and selection via the lasso. *Journal of the Royal Statistical Society. Series B (Methodological)* 58:267–288.
- Tikhonov, A. N., and V. Y. Arsenin. 1977. *Solution of Ill-posed problems*. Winston & Sons, Washington, District Columbia, USA.
- Vörösmarty, C. J., et al. 2010. Global threats to human water security and river biodiversity. *Nature* 467:555–561.
- Wagner, E. H., and M. J. Fortin. 2005. Spatial analysis of landscapes: concepts and statistics. *Ecology* 86:1975–1987.
- Wiens, J. A., N. C. Stenseth, B. van Horne, and R. A. Ims. 1993. Ecological mechanisms and landscape ecology. *Oikos* 66:369–380.
- Wolman, M. G. 1954. A method of sampling coarse river-bed material. *Transactions American Geophysical Union* 35:951–956.
- Young, P. S., J. J. Cech, and L. C. Thompson. 2011. Hydropower-related pulsed-flow impacts on stream fishes: a brief review, conceptual model, knowledge gaps, and research needs. *Reviews in Fish Biology and Fisheries* 21:713–731.
- Zou, H., and T. Hastie. 2005. Regularization and variable selection via the elastic net. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)* 67:301–320.