

# A spatial autocorrelative model for targeting stream restoration to benefit sensitive nongame fishes

Matthew W. Diebel, Jeffrey T. Maxted, Olaf P. Jensen, and M. Jake Vander Zanden

**Abstract:** Stream restoration projects often aim to benefit aquatic biota and frequently use the reappearance of sensitive nongame fish species as a measure of restoration success. However, mitigation of human influence will only benefit a given species where static habitat characteristics are suitable for that species and where potential source populations are within the range of their dispersal capability. We used spatial autoregressive habitat models to simulate the effect of watershed-scale stream restoration on the distributions of six sediment-sensitive fish species in Wisconsin, USA, streams. These models consider the probability of occurrence of a species in a given stream segment as a function of characteristics of that segment as well as the characteristics of neighboring segments. Populations of individual species are predicted to be restorable in 0.2%–2.8% of Wisconsin streams. Streams with high restoration potential for one or more species generally have high watershed human land use but are also closely connected through the stream network to relatively undisturbed streams. These results indicate that habitat restoration for nongame stream fishes will be most effective when it builds onto existing suitable habitat because of both dispersal limitation and spatial autocorrelation of habitat characteristics.

**Résumé :** Les projets de restauration des cours d'eau visent souvent à favoriser les organismes aquatiques et utilisent fréquemment la réapparition d'espèces de poissons non sportifs sensibles comme mesure du succès de la restauration. Cependant, la mitigation de l'influence anthropique ne va bénéficier à une espèce seulement là où les caractéristiques statiques de l'habitat sont adéquates pour cette espèce et lorsque des populations sources potentielles existent dans la portée de leur capacité de dispersion. Nous utilisons des modèles spatiaux autorégressifs de l'habitat pour simuler l'effet d'une restauration à l'échelle du bassin versant sur la répartition de six espèces de poissons sensibles aux sédiments dans des cours d'eau du Wisconsin, É.-U. Ces modèles tiennent compte de la probabilité de la présence d'une espèce dans un segment donné d'un cours d'eau comme une fonction des caractéristiques de ce segment et aussi des caractéristiques des segments voisins. Nous prédisons que des populations des différentes espèces particulières peuvent être restaurées dans 0,2 % – 2,8 % des cours d'eau du Wisconsin. Les cours d'eau qui présentent un fort potentiel de restauration pour une ou plusieurs espèces ont généralement une importante utilisation humaine de leur bassin versant, mais ils ont aussi par leur réseau hydrographique des connexions proches à des cours d'eau relativement peu perturbés. Nos résultats indiquent que la restauration des habitats pour les poissons lotiques non sportifs sera la plus efficace si elle se base sur un habitat existant adéquat, étant donné les limites de la dispersion et l'autocorrélation spatiale des caractéristiques de l'habitat.

[Traduit par la Rédaction]

## Introduction

A common goal of stream restoration is to benefit aquatic biota, particularly fish. The “field-of-dreams” hypothesis (Palmer et al. 1997) suggests that if habitat is restored, species of interest will return. The reappearance of these sensitive target species is thus often used as a measure of restoration success and may determine whether a particular approach to restoration is deemed effective (Wang et al. 2002; Pretty et al. 2003). However, there are several reasons why the return of target species may not automatically follow habitat restoration.

First, when restoration is carried out at any scale smaller than an entire watershed, upstream sources of disturbance or pollution may continue to degrade habitat in the “restored” section (Smokorowski et al. 1998; Moerke and Lamberti 2003; Wang et al. 2006). Watershed-scale stream restoration requires substantial effort and is thus most commonly attempted with less-intensive restoration approaches, such as implementation of agricultural conservation practices and riparian buffers. In contrast with approaches such as channel reshaping or remeandering, which directly recreate an image of a natural stream, these indirect approaches restore watershed functions such as runoff and sediment retention and

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rely on vegetation and geomorphic processes to translate these changes into changes in stream habitat (Kauffman et al. 1997). These changes are likely to be more subtle and occur after longer lags than with direct restorations (Kondolf 1995). Thus, a given species will only find such changes meaningful if they happen where fixed characteristics, such as stream size and gradient, are already suitable.

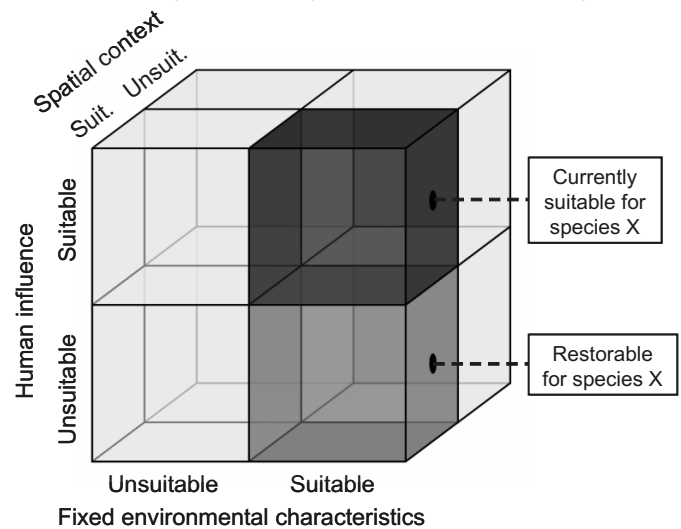
Even when stream restoration creates suitable habitat, it may fail to induce recolonization by desired species if there are no source populations nearby (Wang et al. 2006). This factor is particularly relevant for many small-bodied nongame stream fishes that have small home ranges and are not stocked by fisheries managers. Furthermore, even when a stream is recolonized, it will not necessarily support a persistent population unless it is part of a habitat patch of sufficient size for the species (Lowe 2002). Both of these factors are exacerbated by the presence of dams and other anthropogenic impedances, such as road crossings (Morita and Yamamoto 2002; Bond and Lake 2003). Thus, the spatial context and connectedness of a particular stream within the larger stream network have the potential to determine its suitability for biologically oriented stream restoration.

In this study, we introduce a conceptual and operational model for partitioning the relative influence of three types of factors that control stream fish habitat suitability: fixed environmental characteristics, human influence, and spatial context (Fig. 1). In this model, restoration is capable of reducing human influence but cannot affect fixed environmental characteristics or spatial context. The model thus modulates the potential effectiveness of restoration based on these unchangeable attributes. The limiting effects of fixed environmental characteristics (Reeves et al. 1989) and spatial context (Bond and Lake 2003; Hughes 2007) on the potential outcomes of habitat restoration have been recognized before; this study provides a method for integrating them into a quantitative, predictive framework (Urban 2006). In its general form, this framework could also be applied to other taxa and habitat types.

Our specific objective was to create predictive models of stream fish distributions for the state of Wisconsin that could be used to target stream restoration where it would most likely result in recolonization and population persistence by six pollution-sensitive nongame fish species. Alternatively stated, we aimed to set realistic expectations, or benchmarks, for the biological outcomes of stream restoration. Predictions from these models were used as one component in a broader scheme for geographically targeting agricultural conservation practices in Wisconsin (University of Wisconsin-Madison, College of Agricultural and Life Sciences 2005).

Species distribution models are commonly used in the broad arena of conservation planning (reviewed by Rodríguez et al. 2007) but have been infrequently used to target ecological restoration (e.g., Pearce and Lindenmayer 1998; Carroll et al. 2003). There are two main reasons for this. First, most distribution models describe the occurrence or abundance of a species as a function of one or more environmental predictor variables. If the value of one or more of those predictor variables can be modified through restoration, the impact of restoration on the probability of species occurrence can be simulated. However, confidence in these simulations requires sufficient statistical isolation of the “re-

**Fig. 1.** Conceptual diagram of the modeling approach. Streams vary along three axes: (1) fixed environmental characteristics (e.g., stream size, gradient), (2) human influence (represented as the percent agricultural plus urban land in the watershed), and (3) spatial context (suitability of connected neighboring habitat). Streams must be suitable on all three axes to support a population of species X. Streams that are suitable on axes 1 and 3 but not suitable on axis 2 are considered restorable. All other streams are considered unsuitable and unrestorable. The boundaries among cells in this space are shown as distinct for clarity, but in reality, these boundaries are fuzzy.



storation variable(s)” from other variables (Dormann 2007). It also requires evidence that an observed correlation between the restoration variable and the species’ occurrence is actually causation and that this relationship will hold up across the range of values aimed for by restoration (Thuiller 2004; Dormann 2007). These conditions may not be met in complex multivariate models and when simulated conditions lie outside of the range of existing conditions.

Second, most species distribution models (e.g., generalized linear models, bioclimatic envelope models) are actually nonspatial in that occurrence at a location is independent of the predictors and (or) responses at neighboring locations (Lichstein et al. 2002). Predictions from these models can be mapped and therefore create spatial model output, but there are typically no explicit spatial processes (i.e., dispersal, aggregation) represented in the model structure. While this model form may actually be a realistic representation of the static distributions of some species, it is not suitable for simulating recolonization, which is an inherently spatial process.

In developing the modeling approach for this study, our priorities were to address these two issues. We began by building relatively simple logistic regression models for the six species so that the influence of the restoration variable would not be obscured or biased by collinearity. We then tested whether adding a spatial autocorrelative term to these models was warranted and, if so, whether these autologistic models (Augustin et al. 1996) more accurately predicted observed species distributions. To better represent how fish move in streams, the autocorrelative term in these models is based on distances measured through the stream network rather than on Euclidean distance. Using predictions from the autologistic models, we mapped current distributions of

each species and then predicted where watershed restoration would induce recolonization and population persistence.

## Materials and methods

The spatial extent of our study was the state of Wisconsin. Model inputs and outputs were associated with confluence-bounded stream segments ( $n = 35\,855$ , mean length = 2.5 km) in the 1:100 000-scale National Hydrography Dataset (NHD) (US Geological Survey 2003). Model inputs included species occurrence (presence–absence) data and Geographic Information System (GIS) derived environmental variables and were obtained from the US Geological Survey's Aquatic GAP database (Jana Stewart, US Geological Survey, 8505 Research Way, Middleton, WI 53562, USA, unpublished data) for Wisconsin.

### Species occurrence data

Fish surveys were conducted on 7581 (21% of total) NHD segments between 1970 and 2003, primarily by the Wisconsin Department of Natural Resources, using standard stream survey methods, including electrofishing, netting, and trapping (Fago 1992). Survey reach length was typically 20 times mean wetted width. Some stream segments contained more than one survey reach and (or) date; a species was considered present in a segment if at least one individual was captured during at least one survey.

Species were selected for this study based on their likelihood of responding to watershed restoration efforts. These species have documented sensitivity to sediment or turbidity (Becker 1983; Berkman and Rabeni 1987; Lyons 1992). They are also all primarily lotic and tend to occur in smaller streams (Becker 1983) whose watersheds could feasibly be restored. Among species that met these criteria, we selected six (Table 1) that had a sufficient proportion of occurrences (>3%) in survey data to model their distributions. Four of these species are absent, or only have a few isolated occurrences, in one or two of the three major drainage basins in Wisconsin (Lake Michigan, Lake Superior, and Mississippi River) (Table 1). We only modeled distributions of each species in basins with >20 occurrences in the survey data.

### Environmental variables

The variables we considered as potential predictors of fish species occurrence were selected to facilitate addressing the “restoration variable” and “spatial process” priorities described above. We selected seven variables (Table 2), which are all relatively uncorrelated with one another (maximum Pearson's  $r = 0.50$ ). Six of these variables are considered “fixed” (i.e., unchanging) characteristics. The sum of watershed agricultural and urban land (a measure of human influence) is the restoration variable. Agriculture and urban land uses have different effects on streams (reviewed in Allan 2004), but because urban land makes up a small proportion of Wisconsin (1.5%; Wisconsin Department of Natural Resources 1998) and is absent from the watersheds of most streams, we did not expect to be able to detect its independent effect at the statewide scale. All of these variables have been shown to influence fish habitat at local scales (Wang et al. 2003; Sowa et al. 2007) but are also able to be estimated over broad spatial extents and unsampled locations using

widely available GIS data, thus allowing the use of the autologistic model described below.

Predictor variables were calculated by the Wisconsin Aquatic GAP Project using unpublished methods similar to those described by Sowa et al. (2005). In brief, watersheds were delineated for each NHD stream segment with the ArcHydro (Maidment 2002) extension to ArcGIS (ESRI, Redlands, California) using a 30 m resolution digital elevation model (DEM) (US Geological Survey 1999). The percentages of four land cover classes (agriculture, urban, wetland, and open water) were then calculated for each watershed from a 1990 land cover classification of Wisconsin (Wisconsin Department of Natural Resources 1998). Other land cover classes (e.g., forest) were not considered because they are highly correlated with at least one of these four classes. The average land slope of each watershed was calculated from the DEM. Average soil permeability of each watershed was calculated from the US Department of Agriculture STATSGO soil layer for Wisconsin (US Department of Agriculture 2005). The average gradient of each stream segment was calculated by dividing the DEM-derived elevation difference between the ends of the segment by the length of the segment. The expected influences of these variables on local habitat conditions are reported along with summary statistics (Table 2). To satisfy assumptions of normality and constant variance, we transformed all of the predictor variables by log or square root (Table 2) and then created  $z$ -scores by subtracting the mean and dividing by the standard deviation. We also tested quadratic terms ( $z$ -score<sup>2</sup>) of all of the variables. Because we intended to build simple models, variable interactions were not considered, except for (soil permeability  $\times$  slope), which is a good predictor of groundwater inputs to streams (Baker et al. 2003).

### Modeling approach

We began by fitting nonspatial (i.e., with no spatial autocorrelation) logistic regression models in SPSS (SPSS Inc., Chicago, Illinois) for each of the six species. Variables were selected for inclusion in each model using the stepwise forward-selection method with  $\alpha = 0.05$ . Because the candidate variables were relatively uncorrelated, we expected estimated coefficients to remain relatively stable through the addition of other variables to the models. To check this expectation, we monitored all variable coefficients through the stepwise procedure. In no case did a coefficient switch signs, and coefficient estimates generally varied by <20% through the selection procedure.

To test whether these nonspatial models captured spatial autocorrelation in the observed distributions, we calculated Pearson residuals from the nonspatial models as the standard residual (observation (0 or 1) minus the model prediction ( $0 < \text{prob} < 1$ )) divided by the standard deviation of the standard residuals (Bio et al. 2002). We then measured the distance through the stream network between all pairs of sampled segments. Next, we plotted the mean Pearson residual for pairs of segments separated by 1 km increments of stream network distance. The resulting semivariograms describe residual spatial autocorrelation after accounting for environmental variation. The statistical significance of residual spatial autocorrelation was assessed using Moran's  $I$ .

**Table 1.** Species names, occurrence, and prevalence in survey data.

Common name	Scientific name	Family	Basin(s)	Prevalence (%)
American brook lamprey	<i>Lampetra appendix</i>	Petromyzontidae	M	6.9
Logperch	<i>Percina caprodes</i>	Percidae	M, N, S	8.8
Mottled sculpin	<i>Cottus bairdii</i>	Cottidae	M, N, S	6.3
Northern hog sucker	<i>Hypentelium nigricans</i>	Catostomidae	M, N	19.1
Rainbow darter	<i>Etheostoma caeruleum</i>	Percidae	M	11.0
Redside dace	<i>Clinostomus elongatus</i>	Cyprinidae	M, N	3.1

**Note:** Basins: M, Mississippi River; N, Lake Michigan; S, Lake Superior.

When residual autocorrelation was detected in a nonspatial model, we fit an autologistic model for that species. The autologistic model (Augustin et al. 1996) adds a term (the autocovariate) to the nonspatial logistic model to account for the effect of conditions in neighboring segments. The model is

$$(1) \quad \log\left(\frac{p_i}{1-p_i}\right) = \alpha + \beta_{\text{cov}} \times X_i + \beta_{\text{auto}} \text{autocov}_i$$

where  $p_i$  is the probability of presence in segment  $i$ ,  $\alpha$  and  $\beta_{\text{auto}}$  are regression coefficients,  $\beta_{\text{cov}}$  is a vector of regression coefficients,  $X_i$  is a vector of covariates for segment  $i$ , and  $\text{autocov}_i$  is the average predicted probability of presence ( $\hat{p}$ ) in neighboring segments. Neighboring segments were defined as within 10 stream km of segment  $i$  and not obstructed by a dam. Dam locations ( $n = 4103$ ) were obtained from a comprehensive statewide database (Wisconsin Department of Natural Resources 2000). Specifically, we considered segment  $j$  excluded from the neighborhood of segment  $i$  if, while moving from  $j$  to  $i$ , a dam was encountered on an upstream leg of the route. All segments, including unsampled ones, were included in the autocovariate calculation. The 10 km neighborhood distance was a compromise between two priorities: (1) capturing most of the structural variance in the semivariograms and (2) limiting the number of segments in the average neighborhood. There were 20 segments in the average 10 km neighborhood; accounting for a larger radius would have had diminishing effects on the value of the autocovariate. We did not include a distance-weighting function in the calculation of the autocovariate because exploratory analyses indicated that it had no appreciable influence on the fitted values of  $\beta_{\text{auto}}$  or on the predictive ability of the models.

Autologistic models were fit using an iterative approach, the modified Gibbs sampler method (Augustin et al. 1996). First, the nonspatial model was used to generate  $\hat{p}$  for every stream segment, including unsurveyed ones. The autocovariate was then calculated from these nonspatial  $\hat{p}$ , allowing fitting of the first iteration of the autologistic model. This procedure was repeated until values of  $\alpha$ ,  $\beta_{\text{cov}}$ , and  $\beta_{\text{auto}}$  stabilized. All significant covariates from the nonspatial models were retained in the autologistic models, even if their coefficients became nonsignificant through the autologistic fitting process.

### Model validation

We validated models with 10-fold cross-validation. Model structure (i.e., which variables were included) was deter-

mined with all of the observation data. We then fitted regression coefficients using 90% of the data and generated  $\hat{p}$  for the remaining 10%. Using this approach, predictions for each observation were made with models constructed from independent data.

We used receiver operating characteristic (ROC) curves as a measure of model accuracy. The ROC curve describes the relationship between the number of observed presences correctly predicted as present and the number of false presences (Hanley and McNeil 1982). The area under the ROC curve (AUC) is a single index that integrates model discriminatory ability across all possible probability thresholds for distinguishing presence from absence (Manel et al. 2001). With null models,  $\text{AUC} = 0.5$ , and models with AUC values  $>0.7$  are considered to have high discriminatory ability (Hosmer and Lemeshow 2000). To test statistical significance of model AUCs, we divided the difference between the model AUC and 0.5 by a nonparametric estimate of the standard error of the AUC (Hanley and McNeil 1982). To test whether autologistic models outperformed their nonspatial counterparts, we used the method of Hanley and McNeil (1983). This test reduces the expected null difference between AUCs based on the correlation between predictions produced by the two models.

### Simulating stream restoration

We used the autologistic models to simulate the effect of watershed-scale stream restoration on the probability of occurrence of each species. We simulated restoration by changing the percentage of watershed agricultural plus urban land use (HUM) from its actual value to 30% for each stream segment where  $\text{HUM} > 30\%$ . We did not explicitly assign a land cover type to which the human land was converted but rather assumed some combination of natural land cover types (i.e., forest, grassland). We then calculated the predicted probability of occurrence following restoration ( $\hat{p}_i^r$ ) for each segment  $i$  without updating  $\text{autocov}_i$ . This procedure simulated restoration of each segment independently, in the context of existing conditions in neighboring segments. Restoration potential ( $\text{RP}_i$ ) was calculated for each segment as the joint probability that the species is currently absent but would be present following restoration:

$$(2) \quad \text{RP}_i = (1 - \hat{p}_i) \hat{p}_i^r$$

Total restoration potential (RP) across the study area was calculated as the length-weighted probability of occurrence following restoration minus the current length-weighted probability of occurrence:

**Table 2.** Variables used to model stream fish distributions.

Variable	Description	Represents	Units	Transform	Sampled streams			All streams in Wisconsin		
					10%	Median	90%	10%	Median	90%
WAREA	Watershed area	Stream size	km <sup>2</sup>	log	6.1	33	613	1.5	8.0	216
GRAD	Stream segment gradient	Channel substrate, water velocity	m·m <sup>-1</sup>	Square root	0	0.002	0.010	0	0.004	0.022
PERM	Watershed mean soil permeability	Flow variability	cm·h <sup>-1</sup>	Square root	3.0	7.9	19	2.7	6.1	19
SLOPE	Watershed mean land slope	Flow variability, channel substrate	%	Square root	0.8	1.9	8.1	0.5	1.8	8.0
WET	Watershed wetland	Riparian vegetation, organic carbon	%	Square root	0.1	8	26	0	5.9	29
WAT	Watershed open water	Access to lentic habitats	%	log	0	0.2	5.2	0	0	3.2
HUM	Watershed agricultural plus urban land	Pollution, hydrologic alteration	%	Square root	0.3	33	74	0.3	38	80

**Note:** Percentiles are reported for all 35 855 confluence-bounded stream segments in Wisconsin and for 7581 streams where fish were sampled. HUM (human land cover) is the restoration variable; all others are considered fixed (unchanging).

$$(3) \quad RP = \frac{\sum \hat{p}_i^r L_i}{\sum L_i} - \frac{\sum \hat{p}_i L_i}{\sum L_i}$$

where  $L_i$  is the length of segment  $i$ . To quantify the influence of spatial context on the extent of restorable streams for each species, we also followed this same procedure with the nonspatial models.

We chose a value of 30% for HUM because five of the species models included a negative squared term for HUM, suggesting threshold relationships where reductions in HUM below approximately 10%–25% would not result in any further increase in probability of occurrence. A study in Wisconsin found that a threshold of 30% watershed agriculture best distinguished streams with intact fish communities from those with degraded ones (Fitzpatrick et al. 2001). Thus, 30% was a compromise between what might be feasible and what would cause the largest restoration effect. It is a benchmark for assessing the relative scope for change among streams, not a prescription for exactly how much or what kind of land conversion should be done.

## Results

### Nonspatial models

Multiple logistic regression models for the six species contained between six and 12 significant variables, including squared terms (Table 3). All seven variables were significant for at least three species. Sixty-three percent of the significant variables included squared terms, indicating that estimated relationships between the value of these variables and species' occurrence were often nonlinear. The variables with the most consistent effects, indicated by the sign of the coefficient, were WAREA, which for five species was positive (with negative WAREA<sup>2</sup>), and HUM, which for five species was negative (five species with negative HUM<sup>2</sup>). Based on the cross-validation, all six models predicted species' occurrences better than null models (all  $p < 0.0001$ ) and all had AUC > 0.75, indicating very good discriminatory ability. Correct classification rates that are based on the probability threshold that maximizes the average percent correct absences and presences ranged from 70% to 79% (Table 3). Correct classification rates for probability-based models are highly dependent on the choice of a discriminatory probability threshold and generally reflect a trade-off between correctly predicting presence and correctly predicting absence. The maps of probability of presence and restoration potential (Supplementary Figs. S1–S12<sup>3</sup>) portray these variables in three classes (low, middle, and high) to acknowledge the ambiguity of marginal probabilities. Specifically, the middle category for probability of presence spans the range between the two probability values that, if used as binary discriminants, would result in 90% correct presences and 90% correct absences, respectively.

### Autologistic models

Strong spatial autocorrelation was detected in the residuals from all six of the nonspatial models (Moran's  $I$ ,  $p < 0.0001$  for all species). For most species, semivariance (an inverse measure of autocorrelation) was lowest for pairs of observations separated by distances of <10 km (Fig. 2). As expected given this finding, the autocovariate was a statisti-

**Table 3.** Model performance and structure for the six stream fish species.

	American brook lamprey	Logperch	Rainbow darter	Mottled sculpin	Northern hog sucker	Redside dace	
NS % correct	74.8	76.7	78.5	69.9	77.5	74.4	
AL % correct	76.2	77.7	78.9	70.9	78.5	76.5	
Nonspatial AUC	0.836	0.838	0.866	0.766	0.844	0.808	
Autologistic AUC	0.852	0.843	0.869	0.773	0.851	0.832	
<i>p</i> value of $\Delta$ AUC	0.034	0.053	0.352	0.016	0.019	0.008	
Variable	Model						
WAREA	NS	<b>0.66 (-0.39)</b>	<b>1.46 (-0.26)</b>	<b>1.65 (-0.51)</b>	<b>0.21 (-0.54)</b>	<b>2.17 (-0.54)</b>	(-0.37)
	AL	<b>0.65 (-0.40)</b>	<b>1.24 (-0.23)</b>	<b>1.36 (-0.41)</b>	<b>0.22 (-0.47)</b>	<b>1.87 (-0.47)</b>	(-0.24)
GRAD	NS	(-0.14)	—	0.23	—	<b>(-0.36)</b>	—
	AL	(-0.15)	—	0.18	—	<b>(-0.34)</b>	—
PERM	NS	0.25 (0.15)	<b>(-0.17)</b>	-0.20	<b>-0.23</b>	<b>-0.51</b>	<b>-1.52</b> (-0.36)
	AL	0.00* (0.11*)	(-0.12)	-0.14*	<b>-0.17</b>	<b>-0.40</b>	-0.45 (-0.11*)
SLOPE	NS	<b>0.65 (-0.35)</b>	<b>-0.40</b>	<b>-1.64 (-0.62)</b>	<b>(-0.87)</b>	<b>-0.40 (-0.23)</b>	<b>-1.24</b> (-0.16)
	AL	0.26* (-0.14*)	<b>-0.22</b>	<b>-0.99</b> (-0.38)	<b>(-0.55)</b>	-0.24 (-0.17)	-0.37 (-0.05*)
PERM $\times$ SLOPE	NS	—	—	—	<b>-0.88</b>	<b>-0.56</b>	<b>-0.90</b>
	AL	—	—	—	<b>-0.58</b>	<b>-0.41</b>	-0.27*
WET	NS	<b>-0.48 (-0.56)</b>	—	-0.33	<b>(-0.15)</b>	-0.24	(-0.27)
	AL	-0.29* (-0.30)	—	-0.22	<b>(-0.12)</b>	-0.16	(-0.11*)
WAT	NS	<b>-0.91</b>	<b>0.23</b>	<b>-0.30</b>	<b>-0.55</b>	(-0.09)	<b>-1.30</b> (0.33)
	AL	-0.47	0.14	-0.23	<b>-0.40</b>	(-0.07)	-0.64 (0.18*)
HUM	NS	<b>-0.58 (-0.99)</b>	<b>-0.25</b>	<b>(-0.94)</b>	<b>-0.77 (-0.43)</b>	<b>-0.50 (-0.40)</b>	<b>-0.47 (-0.43)</b>
	AL	-0.26* (-0.58)	-0.14	<b>(-0.60)</b>	<b>-0.46 (-0.27)</b>	<b>-0.31 (-0.30)</b>	-0.20 (-0.14*)
AUTOCOV	AL	<b>0.58</b>	<b>0.52</b>	<b>0.97</b>	<b>0.44</b>	<b>0.37</b>	<b>1.38</b>

**Note:** Cross-validated correct classification rates are based on the probability threshold that maximizes the average percent correct absences and presences. AUC (area under the curve) values were determined with receiver operating characteristic analysis for both autologistic and nonspatial models. The *p* values are for the difference between AUC values of the two models. Reported values for predictor variables are coefficients on significant variables (bolded numbers,  $p < 0.001$ ; all others,  $p < 0.05$ ) in the autologistic (AL) and nonspatial logistic (NS) models. Variables with an asterisk became nonsignificant during the autologistic fitting process. Numbers in parentheses are coefficients on squared variables. See Table 1 for variable definitions. AUTOCOV is defined in eq. 1.

cally significant addition to the models for all six species (Table 3). After fitting the autologistic models, the values of coefficients on most other variables were reduced and the associated *p* values increased (Table 3). The *p* values for several variables increased above 0.05, notably in models for species with the lowest prevalence. Correct classification rates were generally higher, and all of the autologistic models had higher AUCs than their nonspatial counterparts, but these differences were only significant for four species (Table 3). Despite accounting for some of the residual spatial autocorrelation with the autocovariate, significant spatial autocorrelation remained in the autologistic residuals (Moran's *I*,  $p < 0.0001$  for all species), and the autologistic semivariograms are nearly identical to those of the nonspatial models (Fig. 2).

### Stream restoration scenarios

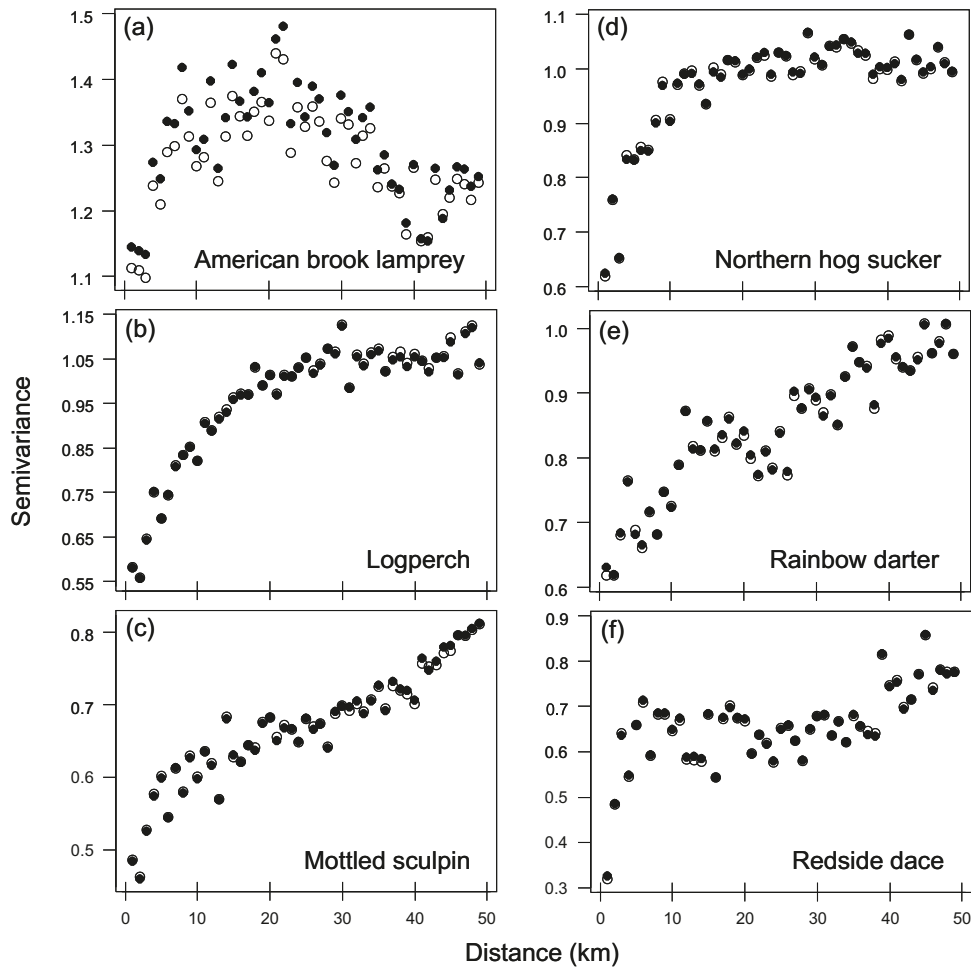
According to our models, the probability that watershed restoration will result in the presence of a previously absent species is generally low. The maximum value of  $RP_i$  from the autologistic models is 0.39 (rainbow darter), and generally, the best opportunities for restoration of each species represent a one in three chance of success (Fig. 3). Nevertheless,

these odds are much higher than for the majority of streams; the length-weighted average value of  $RP_i$ ,  $RP$ , ranges from 0.002 (logperch) to 0.028 (mottled sculpin). The  $RP$  values from the nonspatial models were on average twice as high as their autologistic counterparts (Fig. 4). Differences among species in  $RP$  can primarily be explained by differences in the strength of influence of human land use ( $\beta_{HUM}$ ), the total length of streams in the preferred size (WAREA) range, and the extent to which potentially suitable habitat is near existing suitable habitat (spatial context, sensu Fig. 1). The three species that tend to occur in the smallest streams, as indicated by their  $\beta_{WAREA}$  (American brook lamprey, mottled sculpin, and redside dace), had the largest discrepancies between  $RP$  values from the two model types. This trend may stem from the geometric structure of drainage networks where headwater basins are relatively isolated from one another.

Patterns in predicted distributions are highly variable among species (Supplemental Figs. S1–S12<sup>3</sup>). In maps from both types of model, streams with higher restoration potential for a species are generally adjacent to its predicted current distribution, which reflects autocorrelation in the environmental variables that shape those distributions. This pattern is more pronounced with the autologistic models

<sup>3</sup>Supplementary data for this article are available on the journal Web site (<http://cjfas.nrc.ca>) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 5303. For more information on obtaining material, refer to <http://cisti-icist.nrc-cnrc.gc.ca/eng/ibp/cisti/collection/unpublished-data.html>.

**Fig. 2.** Semivariograms of model residuals from the nonspatial logistic models (open circles) and the autologistic models (solid circles). Points are the mean semivariance (variance/2) of Pearson residuals for pairs of sample points separated through the stream network by each 1 km distance class.



due to the influence of the autocovariate. Streams with high restoration potential ( $RP_i > 0.25$ ) for one or more species tended to be near streams with less human influence. Specifically, these restorable streams had an average of 3.6% more human land use in their watersheds than the watersheds of their respective neighboring streams. On the maps (Supplemental Figs. S1–S12<sup>3</sup>), the middle class for displaying restoration potential is bounded on the lower end by  $RP_i = 0.25$  to avoid including marginal streams ( $\hat{p}_i = 0.5$ ) that have no room for improvement ( $\hat{p}_i = \hat{p}_i^r$ ). The upper class was arbitrarily set as  $RP_i > 0.3$ .

## Discussion

The good predictive performance (average correct classification rate = 77%) of all the models developed in this study indicates that stream fish species distributions are to a large extent driven by broad-scale environmental factors. These factors can be considered ultimate influences, which determine the smaller-scale habitat features to which fish proximately respond (Frissell et al. 1986; Poff 1997). Error in these models can be attributed to several sources: nuances of the scale relationships that link watersheds to streams (e.g., the influence of land cover pattern rather than simply

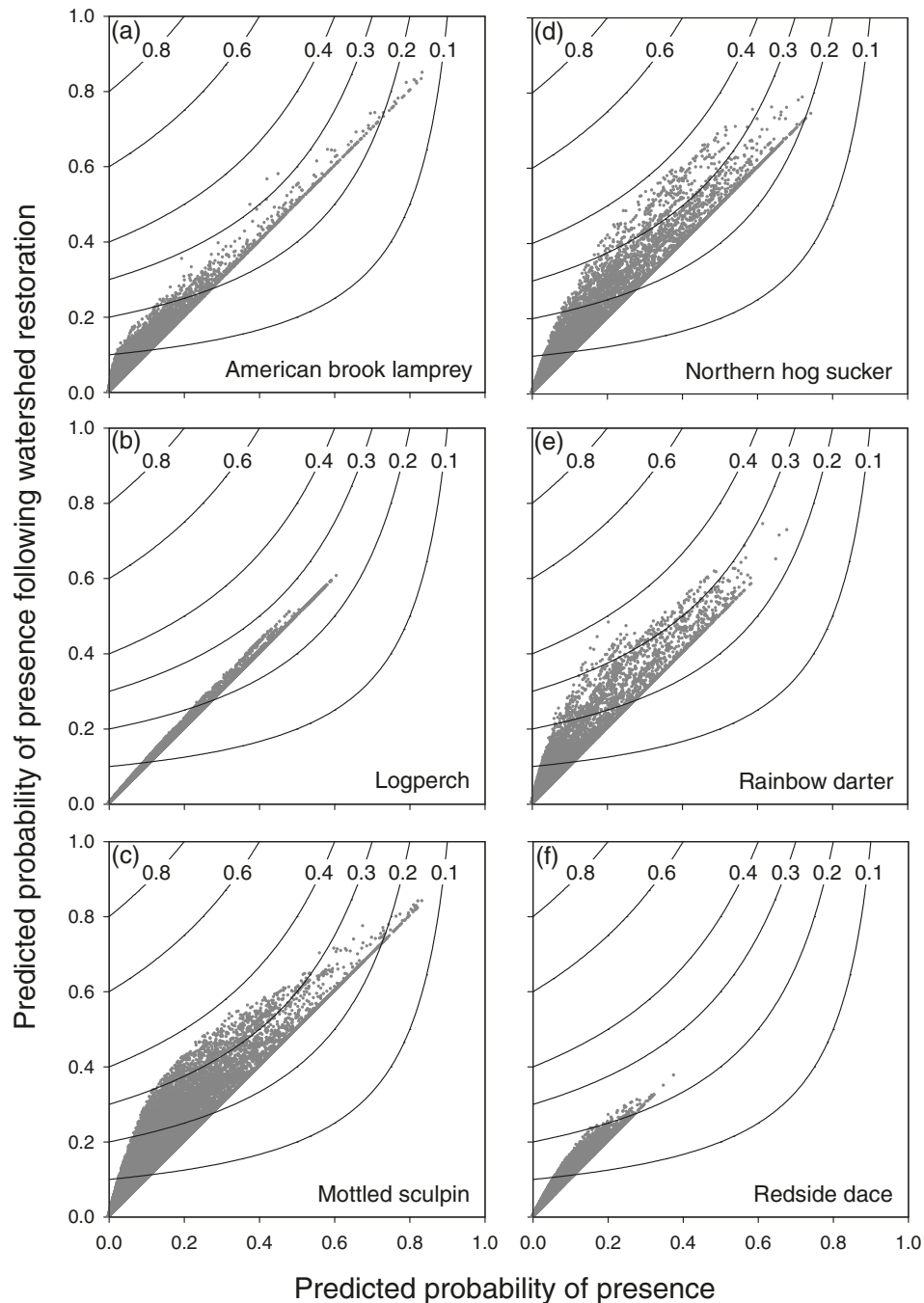
composition) (Gergel 2005; King et al. 2005), biotic interactions (e.g., predation, competition), and population processes (e.g., stochastic local extinctions).

We are reasonably confident that the statistical relationships between environmental variables and species' occurrence represent causation. Several other studies have identified these, or similar, factors as primary determinants of stream fish species' distributions (Wall et al. 2004; Oakes et al. 2005; McCleary and Hassan 2008) and community assemblages (Poff and Allan 1995; Lyons 1996; Wang et al. 2003). All of the model variables span broad gradients in Wisconsin and the sampled streams are representative of all streams, one exception being that the smallest streams were underrepresented in surveys. As a consequence, the predicted ranges of species generally found in smaller streams (mottled sculpin and redbside dace) may be overestimated.

## Simulating restoration

Agricultural and urban land uses have been unequivocally linked to changes in stream habitat and subsequent changes in fish community composition (Richards et al. 1996; Wang et al. 1997; Fitzpatrick et al. 2001). Our results support these general findings by demonstrating a consistent negative influence of human land use on the probability of occurrence

**Fig. 3.** Restoration potential (represented by contour lines) for each stream segment is the joint probability that the species is currently absent ( $1 - \hat{p}_i$ ) but would be present following restoration ( $\hat{p}_i^r$ ). For most species, the highest restoration potential occurs where  $\hat{p}_i$  is near 0.5 and where  $\hat{p}_i^r \gg \hat{p}_i$ .

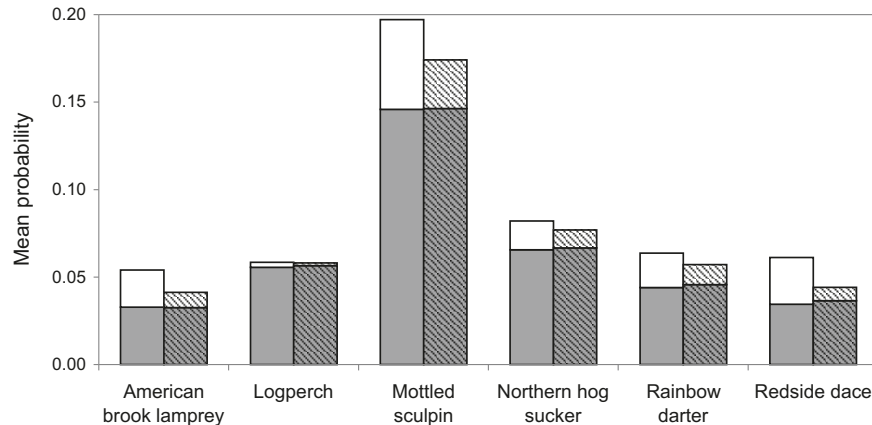


of six sediment-sensitive fish species. To simulate stream restoration, we reduced this negative influence everywhere and then asked where the reduction made a difference for each species. Because wholesale conversion of land to natural cover is rarely practical, this reduction in human influence is more likely to be achieved through the implementation of watershed best management practices (Allan 2004). Watershed and riparian best management practices can effect positive changes on fish habitat (Wang et al. 2002), although in some cases these changes are not

sufficient to cause fish community changes (Nerbonne and Vondracek 2001; Shields et al. 2007).

Five of the study species exhibited nonlinear relationships with human land use, where the probability of occurrence was maximized at 10%–25% human land use. These simple empirical functions probably represent either threshold or subsidy-stress relationships. In two separate studies of Wisconsin streams, fish index of biotic integrity scores only declined when watershed agriculture exceeded 30%–50% (Wang et al. 1997; Fitzpatrick et al. 2001). In some settings,

**Fig. 4.** Length-weighted mean probability of presence (shaded bars) and restoration (open bars) for the six fish species according to the autologistic (hatched) and nonspatial (not hatched) models.



limited amounts of human land use may actually improve conditions for some species by increasing primary production through nutrient inputs or clearance of shading riparian vegetation (Quinn and Hickey 1990). However, these same factors become detrimental at higher levels. Regardless of their nuances, the relationships that we observed suggest that the total elimination of human influence is not necessary for the existence of sensitive species.

### Spatial models

Despite the good predictive performance of the nonspatial logistic regression models in this study, their residuals remained spatially autocorrelated. It is unclear whether this pattern is due to the influence of unmeasured environmental characteristics that are themselves spatially autocorrelated or whether it represents aggregative behavior (Lichstein et al. 2002). Regardless of the mechanism, the independent errors assumption of logistic regression was violated. The autologistic model addressed this violation by simultaneously assessing the effects of environmental characteristics at multiple spatial scales. However, despite accounting for relationships in the dominant zone of spatial autocorrelation (10 km), residuals from the autologistic models were still autocorrelated. This outcome may be due to misspecification of the autocovariate (e.g., the lack of a distance-weighting term) or, more likely, to biased estimates of  $\beta_{\text{auto}}$  caused by inclusion of unsampled stream segments in the autocovariate. Most applications of spatial autoregressive models have not included predicted probabilities for unsampled locations in the autocovariate (or more generally, the neighborhood term: Klute et al. 2002; Lichstein et al. 2002; Betts et al. 2006). This approach allows the fitting routine to eliminate spatial autocorrelation in residuals by incorporating it into the neighborhood term. It is appropriate when environmental variables are only available for sampled locations and when the primary goal of the modeling exercise is to describe the scale(s) at which those variables are relevant. In contrast, our goal was to predict species' distributions with variables that have been measured at all locations. Unless the mechanisms that underlie spatial autocorrelation have a precise and consistent manifestation, our approach is unlikely to eliminate it. However, the inclusion of unsampled locations provides a more complete picture of the habitat

neighborhood and therefore may be more likely to produce accurate predictions at unsampled locations.

The predictive abilities of the autologistic models were only slightly better than those of their nonspatial counterparts. From this view, there is little reason to introduce their theoretical and computational complexity if the goal is simply to predict static distributions. However, from a priori reasoning, the dynamic process of dispersal and recolonization is likely to be better represented with spatial models. The dispersal ability of most stream fishes is poorly understood; although most small-bodied species are considered relatively sedentary (Hill and Grossman 1987; Warren and Pardew 1998), a small fraction of individuals in a population may be highly mobile (Freeman 1995; Smithson and Johnston 1999) and thus drive dispersal and colonization (Neely and George 2006). In our models, the likelihood of recolonization was implicitly modeled as a function of proximity to existing populations, interpreted from the primary range of spatial autocorrelation in the observed distribution data. Because the neighborhood of each segment is defined by stream network distance and excludes segments blocked by dams, it probably represents a conservative estimate of potential colonist sources. The routes of some of these potential colonists may be effectively blocked by unsuitable habitat, which can act as a de facto barrier for some species. For example, most of the study species are river or stream specialists and may not be able to traverse lakes, even if suitable lotic habitat is available on the other side. If unsuitable habitat could be defined for a species, it could be represented as a barrier in our modeling approach.

To our knowledge, this study is the first to use a spatial autoregressive model on a landscape composed of networked linear habitats rather than grid cells or other polygons. This is surprising because potential movement pathways are more constrained in stream networks than across terrestrial landscapes (Fagan 2002). Thus, the manifestation of spatial processes should be more apparent in streams (Cumming 2004). Other methods have been used to describe the influence of spatial context on stream fish distributions, notably connectivity metrics (Mattingly and Galat 2002; Isaak et al. 2007). However, these methods require a priori specification of the connectivity metric at each site rather than allowing its construction to adapt as the overall model fit converges. Different objectives may require differ-

ent approaches, but in general, models of dynamic processes in aquatic ecosystems (e.g., recolonization, climate change, species invasions) should account for constraints on movement of organisms imposed by the connectivity of habitats.

### Restoration potential

Based on comparison with the autologistic models, non-spatial logistic regression models grossly overpredicted the extent of streams that are restorable for the study species. This was especially true for species that prefer small streams, which supports the notion that spatial constraints on dispersal and colonization are particularly relevant for headwater species (Meyer et al. 2007). Simulating changes in the distribution of a species with a nonspatial model does not account for dispersal. It also assumes that if site-scale habitat is sufficient, a population will be able to persist, even at a site located in a matrix of unsuitable habitat. Because the movement of stream fishes is constrained by distance and network connectivity and because the autologistic models support the importance habitat suitability at two scales (segment and neighborhood), nonspatial models are inappropriate for this application.

The autologistic models indicate that most streams are unsuitable and (or) unreachable for most species, even if human influence is moderated. The distributions of stream fishes are limited by a suite of environmental factors, most of which cannot be modified by stream restoration. Despite having a common trait, sensitivity to sediment, the species that we modeled are influenced differently by these fixed variables and thus have very different predicted distributions. As a consequence, there is little overlap in the streams that are predicted to be restorable for these six species (Supplemental Figs. S1–S12<sup>3</sup>). This finding supports our decision to model the effects of land use scenarios on individual species rather than on summary statistics of overall biological condition (Van Sickle et al. 2004). Conservation approaches based on biological condition have the advantage of providing a consistent metric that can be applied across broad heterogeneous regions. However, it is unclear whether the nuanced responses of individual species can be successfully integrated in these approaches.

The maps and associated GIS layers from this study can be used in both the planning and evaluation stages of stream restoration projects. Managers could use the maps to target watershed restoration where it would most likely result in recolonization and population persistence by one or more of these sensitive species. This would be an appropriate approach when the goal of restoration is to induce a biological response. To hedge against errors in predicted distributions, streams with high restoration potential that are also near verified occurrences might be chosen first. Alternatively, because predictions for individual streams indicate which species could be expected following watershed restoration, they provide a standard for evaluating project outcomes.

The model for reddsides dace suggests that the best opportunities for restoration are also the locations most likely to currently support this species. This unintuitive outcome is the result of a combination of three factors: first, because of the structure of the logistic model, the range of predicted probability of presence for rare species will rarely extend above 0.5, second, the first factor is exacerbated when the overall

model fit is less than excellent, and third, when the influence of the restoration variable is relatively weak, the simulated restoration will not raise the probability of presence of any stream very much, making  $RP_i$  mostly a function of  $\hat{p}_i$ . Thus, for species such as reddsides dace, the best restoration opportunities may be on streams with the highest probability of presence but where surveys reveal that the species is absent.

Even though game fish dominate most stocking programs, nongame fish have recently begun to be stocked in some locations. For example, slimy and mottled sculpin are being reintroduced to streams in southeastern Minnesota where they historically occurred but where habitat degradation in the early part of the twentieth century resulted in local extirpations (Minnesota Department of Natural Resources 2003). Although habitat conditions have improved, many streams have not been recolonized because of the presence of both hard (e.g., dams) and soft (e.g., intervening unsuitable habitat) barriers. Our approach could aid in the identification of suitable locations for assisted recolonization. These efforts will likely be most successful where barriers to dispersal are also removed.

Watershed-scale stream restoration has the potential to benefit sensitive aquatic species, but this outcome has rarely been observed (Allan 2004). In some cases, the failure of restoration to induce a biological response may indicate that human influences on the stream have not been sufficiently mitigated. However, our models suggest that several other static environmental factors, as well as the spatial context of the restored stream, place comparable or greater limits on where stream restoration is likely to induce recolonization and population persistence of a given species.

Species distribution models have contributed greatly to understanding of the environmental niche, but most paint a static picture. Our modeling approach provides an example of how species distribution models can be tailored to simulate dynamic processes. Human modification of Earth's ecosystems, for better, worse, or just different, will only accelerate in the future. Forecasting the effects of these modifications on species distributions promises to be one of the next major challenges in ecology.

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