



# The effectiveness of surrogate taxa to conserve freshwater biodiversity

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**Abstract:** *Establishing protected areas has long been an effective conservation strategy and is often based on readily surveyed species. The potential of any freshwater taxa to be a surrogate for other aquatic groups has not been explored fully. We compiled occurrence data on 72 species of freshwater fishes, amphibians, mussels, and aquatic reptiles for the Great Plains, Wyoming (U.S.A.). We used hierarchical Bayesian multispecies mixture models and MaxEnt models to describe species' distributions and the program Zonation to identify areas of conservation priority for each aquatic group. The landscape-scale factors that best characterized aquatic species' distributions differed among groups. There was low agreement and congruence among taxa-specific conservation priorities (<20%), meaning no surrogate priority areas would include or protect the best habitats of other aquatic taxa. Common, wideranging aquatic species were included in taxa-specific priority areas, but rare freshwater species were not included. Thus, the development of conservation priorities based on a single freshwater aquatic group would not protect all species in the other aquatic groups.*

**Keywords:** biogeography, conservation planning, reserve design, surrogates

La Efectividad de los Taxones Sustitutos en la Conservación de la Biodiversidad de Agua Dulce

**Resumen:** *La creación de áreas protegidas ha sido durante mucho tiempo una estrategia efectiva de conservación y frecuentemente está basada en especies censadas sin inconvenientes. El potencial que cualquier taxón de agua dulce tiene para ser el sustituto de otros grupos acuáticos no se ha explorado en su totalidad. Recopilamos los datos de incidencia de 72 especies de peces, dulceacuícolas, anfibios, mejillones y reptiles acuáticos en las Grandes Planicies, Wyoming (EUA). Utilizamos modelos jerárquicos bayesianos de mezclas multi-especies y modelos MaxEnt para describir la distribución de las especies y el programa Zonation para identificar las áreas de prioridad de conservación para cada grupo acuático. Los factores a escala de paisaje que mejor caracterizaron la distribución de las especies acuáticas difirieron entre los grupos. Hubo bajo acuerdo y congruencia entre las prioridades de conservación específicas para cada taxón (<20%), lo que significa que ningún área de prioridad sustituta incluiría o protegería los mejores hábitats de otros taxones acuáticos. Las especies acuáticas comunes y de amplia distribución fueron incluidas en las áreas de prioridad específicas para cada taxón, pero las especies dulceacuícolas raras no fueron incluidas. Por eso, el desarrollo de las prioridades de conservación con base en un solo grupo dulceacuícola no protegería a todas las especies de otros grupos acuáticos.*

**Palabras Clave:** biogeografía, diseño de reservas, planeación de la conservación, sustitutos

## Introduction

North American freshwaters are among the world's most threatened ecosystems. Based on current trends,

projected mean future extinction rates of freshwater fauna are 5 times greater than predicted extinction rates for terrestrial fauna (Ricciardi & Rasmussen 1999). During the twentieth century, 123 freshwater species went

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extinct, and 200 have been listed as threatened or endangered in North America (Ricciardi & Rasmussen 1999), primarily due to synergistic effects of human threats (i.e., habitat alterations and non-native species) that appear to be accelerating and will continue to undermine conservation efforts (Williams et al. 2011). Reactive single-species approaches have been used with limited effectiveness (Williams et al. 2011). By contrast, proactive approaches that prioritize areas for conservation are widely recognized as a viable alternative for ensuring maintenance of aquatic ecosystems and protecting biodiversity (Williams et al. 2011).

Protected areas have long been used as a terrestrial conservation strategy (Suski & Cooke 2007). In general, protected areas are established to sustain native communities by maintaining habitat diversity and connectivity and protecting against human disturbance and management mistakes (Edgar et al. 2014). There have been calls to manage native freshwater communities through protected areas, but few areas have been created (Saunders et al. 2002), likely because distribution data are limited for many aquatic species (Mellin et al. 2011).

Ideally, aquatic protected areas should be planned with the intention of conserving all aquatic groups. However, because of limited distribution data, practitioners rely on data characterizing distributions of more readily surveyed species. Any mismatch in distribution patterns means that some species in other freshwater aquatic groups may not be fully protected, and this approach could result in misguided development of aquatic protected areas (Wiens et al. 2008). However, given that monitoring surveys are expensive and time consuming, if some freshwater aquatic taxa are identified as reliable surrogates, then surveys could be avoided as a requirement for making management decisions for taxa whose distributions are less well known. This situation is especially marked for freshwater aquatic species, for which most aquatic surveys are engineered to acquire information on readily surveyed species such as fish.

In the absence of distribution data for species, conservation planners have often relied on shortcuts such as surrogate species (Grantham et al. 2010). Studies show mixed success of biological surrogates (Vessby et al. 2002; Kati et al. 2004). Moreover, conservationists have not identified 1 method that is more effective than the others (Grantham et al. 2010), given that factors such as spatial scale, surrogate type (i.e., taxonomic and environmental), and methods used to construct surrogates differ in performance (Grantham et al. 2010). Higher-taxon surrogates tend to perform better than cross-taxon surrogates (Ruhi & Batzer 2014). For example, there is little evidence to suggest that birds, mammals, or amphibians are effective surrogates for aquatic taxa (Kirkman et al. 2012). However, the potential of freshwater fishes, mussels, or aquatic reptiles to serve as surrogates for the distribution patterns of other freshwater aquatic taxa has

not been explored. Research assessing the effectiveness of surrogates in freshwater aquatic ecosystems is needed to avoid the risk of poor conservation planning and ineffective implementation (Grantham et al. 2010).

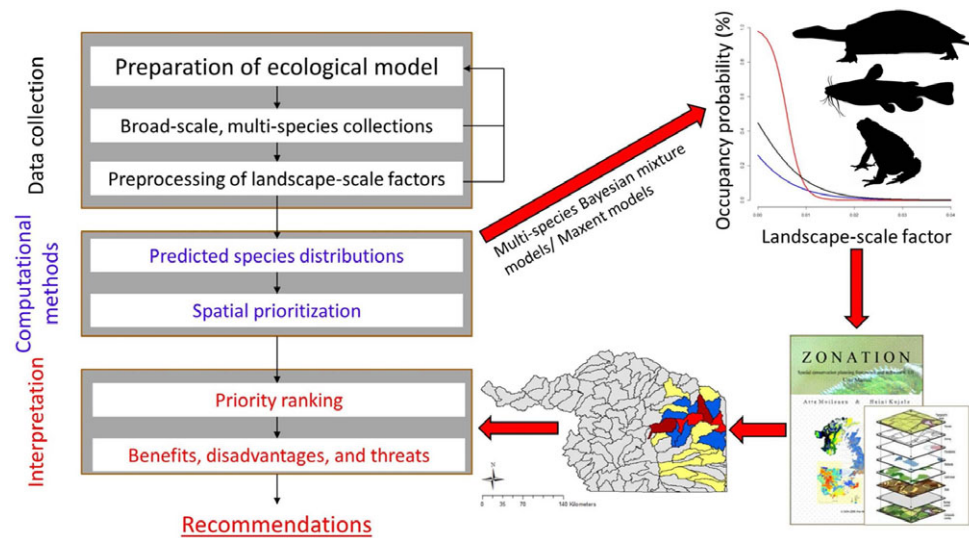
We used a comprehensive modeling approach to describe distributions of aquatic species within the Missouri River drainage, Wyoming (Fig. 1), and then delineated taxa-specific conservation areas to test effectiveness of biological surrogates of freshwater taxa. First, we determined species representation in taxa-specific and cross-taxon conservation areas. Second, we examined relatedness of cross-taxon conservation areas to determine how effectively surrogate areas represented key habitats of other aquatic species.

## Methods

### Species' Distribution Models

We developed a comprehensive database of aquatic species based on survey data of the Wyoming Game and Fish Department and collection histories from the Wyoming Natural Diversity Database (Table 1). From 1993 to 2014, species were collected using random and stratified random sampling designs throughout the Missouri River drainage in Wyoming (Fig. 2). Fish communities were sampled using seining and pulsed DC electrofishing. A backpack electrofisher was used to sample small streams and bank units, whereas for larger streams electrofishing was conducted from a raft or boat (Quist et al. 2004). Sampled reaches were at least 200 m long. Mussel communities were sampled using timed search surveys, where searches of all possible habitats where mussels could occur were conducted using snorkeling and glass bottomed viewing buckets (Howard & Cuffey 2003). Amphibian and reptile communities were surveyed via visual-encounter methods (Heyer et al. 1994). Surveys involved canvassing all available habitats such as pools, ponds, and wetlands in designated riparian reaches on foot during morning and afternoon periods. Sites were sampled by two observers and visited at least two times during the field season (Heyer et al. 1994). Samples were considered independent if they were sampled more than a week apart.

We used landscape-scale data from online sources to determine relative importance of landscape-scale factors thought to influence the ecology of aquatic species throughout the Missouri River drainage (Table 2 & Supporting Information). Because amphibian and reptile data were presence-only data and fish and mussel data were presence-absence data and were collected using different survey designs, we used three different modeling approaches (Table 3). For amphibian and reptile species, we created distribution models with MaxEnt, which uses maximum-entropy algorithms to make predictions from presence-only data by estimating the geographic



**Figure 1.** A modified flow diagram from Lehtomäki and Moilanen (2013) illustrating the stages of the conservation-planning assessment used in this study. The first stage requires collection of species and habitat (see landscape-scale factors Table 1) data. The second stage requires the development of species distribution models to illustrate species-habitat relationships (i.e., multispecies Bayesian mixture models and Maxent models) to incorporate biological realism into the spatial prioritization analysis that identifies priority conservation areas with Zonation program. The third stage requires input from stakeholders to evaluate the benefits, disadvantages, and threats associated with the priority watershed rankings (identified by the boundaries). Those areas in color represent the highest ranking priority rankings (red, top 2%; brown, top 5%; blue, top 10%; yellow, top 25%). Images courtesy of PhyloPic (<http://www.phylopic.org/>) and Scott Hartman (<https://creativecommons.org/licenses/by-nc-sa/3.0/>).

probability distribution from point data (Phillips et al. 2006). We used the target-group background method so that background data represented the range of conditions available to each species (Phillips et al. 2009), where all other localities in our data set that were within 0.50 km of a species known occurrences comprised the background data. By using a 0.50-km buffer around each locality, the background data were subject to the same spatial bias as the sighting data, given the low dispersal ability of most amphibians and aquatic reptiles (Phillips et al. 2009).

We used a model-selection procedure to tune the MaxEnt multiplier that balanced model fit and complexity by reducing the number of landscape-scale variables for each species (Wright et al. 2015). MaxEnt runs were based on hinge-only features. This feature exhibits high predictive ability while not significantly increasing model complexity (Phillips & Dudik 2008). These methods allowed us to identify a model balanced for fit and complexity for each species (Supporting Information). We evaluated model accuracy and the contribution of each landscape-scale variable to model performance. Model accuracy was determined using a cross-validation technique in which we divided the occurrence data into a training data set (75% of occurrence data) and a held-out test data set (25% of occurrence data). This procedure was repeated 10 times for each model, and the mean output was used to determine overall model performance.

We evaluated performance based on the area under the receiver operating characteristic curve (AUC) (Ling et al. 2003). We evaluated 2 statistics produced by MaxEnt—percent contribution and permutation importance—to determine relative importance of each variable. We used percent contribution to determine percent increase in model fit associated with each landscape-scale variable and permutation importance to determine potential loss in predictive power with removal of the variable (Phillips et al. 2006).

We used a mixture modeling technique to determine fish and mussel distributions. We developed model-based hypotheses organized by stream size and context, human disturbance, geology, and land-use predictors based on previous investigations (Wenger et al. 2008; Kirsch & Peterson 2014; Supporting Information). We developed competing candidate models with hierarchical Bayesian multispecies mixture models to evaluate occupancy as it relates to landscape-scale factors for multiple species. The model was constructed to estimate species-specific probability of detection and occupancy values from the spatially replicated observations compiled in a species-by-reach-by-survey occurrence matrix from the multiple occupancy surveys. The model was structured to estimate species-specific parameter estimates by assuming that terms among species and site-level random effects are independent and exchangeable.

**Table 1.** Information on species considered in distribution and Zonation models of fishes, mussels, and reptiles, number of sites having amphibians and mussels (presence only) and number of sites with occurrences and percent occurrence of fish and mussels (presence or absence).

Common name	Scientific name	Species code	Origin <sup>b</sup>	Sites (%) <sup>a</sup>
<b>Amphibians</b>				
American Bullfrog	<i>Rana catesbeiana</i>	ABF	N	4
Columbia Spotted Frog	<i>Rana luteiventris</i>	CSF	N	104
Bighorn Mountain Wood Frog	<i>Lithobates sylvaticus</i>	BMWF	N	146
Boreal Chorus Frog	<i>Pseudacris maculata</i>	BCF	N	609
Eastern Clade Western Toad	<i>Anaxyrus boreas</i>	ECWT	N	88
Great Basin Spadefoot	<i>Spea intermontana</i>	GBS	N	4
Great Plains Toad	<i>Anaxyrus cognatus</i>	GPT	N	34
Northern Leopard Frog	<i>Lithobates pipiens</i>	NLF	N	1 640
Plains Spadefoot	<i>Spea bombifrons</i>	PSF	N	176
Rocky Mountain Toad	<i>Anaxyrus woodhousii woodhousii</i>	RMT	N	1 393
Southern Rockies Wood Frog	<i>Lithobates sylvaticus</i>	SRWF	N	74
Tiger Salamander	<i>Ambystoma mavortium</i>	TS	N	134
Wyoming Toad	<i>Anaxyrus baxteri</i>	WT	N	195
<b>Fishes</b>				
Bigmouth Shiner	<i>Notropis dorsalis</i>	BMN	N	68 (13)
Black Bullhead	<i>Ameiurus melas</i>	BLB	N	111 (22)
Black Crappie	<i>Pomoxis nigromaculatus</i>	BLC	E	7 (1)
Brass Minnow	<i>Hybognathus bankinsoni</i>	BMN	N	61 (12)
Brook Stickleback	<i>Culaea inconstans</i>	STK	E	8 (2)
Brook Trout	<i>Salvelinus fontinalis</i>	BKT	E	5 (1)
Brown Trout	<i>Salmo trutta</i>	BNT	E	23 (5)
Central Stoneroller	<i>Camptostoma anomalum</i>	STR	N	71 (12)
Channel Catfish	<i>Ictalurus punctatus</i>	CCF	N	115 (23)
Common Carp	<i>Cyprinus carpio</i>	CRP	E	185 (36)
Common Shiner	<i>Luxilus cornutus</i>	CSH	N	53 (10)
Creek Chub	<i>Semotilus atromaculatus</i>	CKC	N	202 (40)
Emerald Shiner	<i>Notropis atherinoides</i>	EMS	E	5 (1)
Fathead Minnow	<i>Pimephales promelas</i>	FHM	N	343 (68)
Finescale Dace	<i>Pboxinus neogaeus</i>	FSD	N	18 (4)
Flathead Chub	<i>Platygobio gracilis</i>	FHC	N	155 (31)
Gizzard Shad	<i>Dorosoma cepedianum</i>	GZS	E	87 (17)
Goldeye	<i>Hiodon alosoides</i>	GDE	N	54 (11)
Green Sunfish	<i>Lepomis cyanellus</i>	GSF	E	166 (33)
Hornyhead Chub	<i>Nocomis biguttatus</i>	HHC	N	13 (3)
Iowa Darter	<i>Etheostoma exile</i>	IDT	N	26 (5)
Johnny Darter	<i>Etheostoma nigrum</i>	JDT	N	71 (14)
Lake Chub	<i>Couesius plumbeus</i>	LKC	N	8 (2)
Largemouth Bass	<i>Micropterus salmoides</i>	LMB	E	8 (2)
Longnose Dace	<i>Rhinichthys cataractae</i>	LND	N	297 (58)
Longnose Sucker	<i>Catostomus catostomus</i>	LNS	N	63 (12)
Mountain Sucker	<i>Catostomus platyrhynchus</i>	MTS	N	44 (9)
Northern Pearl Dace	<i>Margariscus margarita</i>	NPD	N	8 (2)
Northern Plains Killifish	<i>Fundulus zebrinus</i>	PKF	N	155 (31)
Orangethroat Darter	<i>Etheostoma spectabile</i>	OTD	N	7 (1)
Plains Minnow	<i>Hybognathus placitus</i>	PMN	N	45 (9)
Plains Topminnow	<i>Fundulus sciadicus</i>	PTM	N	45 (9)
Quillback	<i>Carpionodes cyprinus</i>	QBC	N	7 (1)
Rainbow Trout	<i>Oncorhynchus mykiss</i>	RBT	E	9 (2)
Red Shiner	<i>Cyprinella lutrensis</i>	RDS	N	45 (9)
River Carpsucker	<i>Carpionodes carpio</i>	RCS	N	111 (22)
Rock Bass	<i>Ambloplites rupestris</i>	RKB	E	13 (3)
Sand Shiner	<i>Notropis stramineus</i>	SDS	N	310 (61)
Sauger	<i>Sander canadensis</i>	SAR	N	12 (3)
Shorthead Redhorse	<i>Moxostoma macrolepidotum</i>	NRH	N	75 (5)
Shovelnose Sturgeon	<i>Scaphirhynchus platyrhynchus</i>	SNS	N	21 (4)
Smallmouth Bass	<i>Micropterus dolomieu</i>	SMB	E	76 (15)
Spottail Shiner	<i>Notropis budsonius</i>	STS	E	1 (< 0)
Stonecat	<i>Noturus flavus</i>	STC	N	127 (25)
Sturgeon Chub	<i>Macrhybopsis gelida</i>	SGC	N	9 (2)

continued



**Table 1. Continued.**

Common name	Scientific name	Species code	Origin <sup>b</sup>	Sites (%)
Suckermouth Minnow	<i>Phenacobius mirabilis</i>	SMM	N	8 (2)
Walleye	<i>Sander vitreus</i>	WAE	E	3 (1)
Western Silvery Minnow	<i>Hybognathus argyritis</i>	SMN	N	11 (2)
White Crappie	<i>Pomoxis annularis</i>	WHC	E	1 (< 0)
White Sucker	<i>Catostomus commersonii</i>	WHS	N	330 (65)
Yellow Perch	<i>Perca flavescens</i>	YEP	E	11 (2)
<b>Mussels</b>				
Cylindrical Papershell	<i>Anodontoides ferussacianus</i>	CPM	N	32 (24)
Fatmucket	<i>Lampsilis siliquoidea</i>	FMM	N	48 (40)
Giant Floater	<i>Pyganodon grandis</i>	GFM	N	13 (8)
Plain Pocketbook	<i>Lampsilis cardium</i>	PPM	N	31 (23)
Western Pearlshell	<i>Margaritifera falcate</i>	WHM	N	16 (11)
<b>Reptiles</b>				
Common Snapping Turtle	<i>Chelydra serpentina</i>	CST	N	96
Eastern Spiny Softshell Turtle	<i>Apalone spinifera spinifera</i>	ESST	N	94
Western Painted Turtle	<i>Chrysemys picta bellii</i>	WPT	N	207

<sup>a</sup>Fish and mussel species that occurred at <2% of sampling locations were not included in the species distribution models. All species were included in the Zonation models.

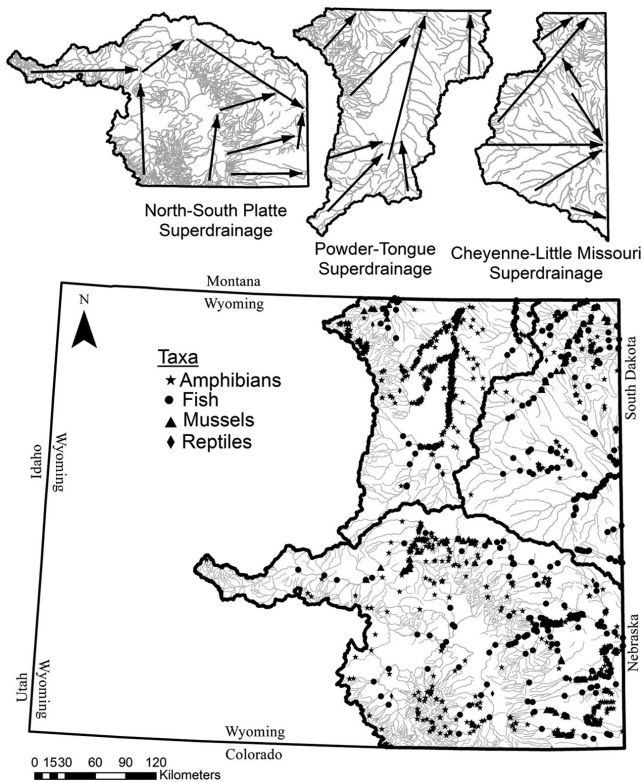
<sup>b</sup>Abbreviations: N, native; E, non-native.

**Table 2. Mean and range of watershed and reach variables for rivers and watersheds in the Missouri River drainage, Wyoming.**

Scale	Variable group	Variable	Mean (SD)	Range
Reach	Stream size and context	downstream link magnitude (d link)	47 (87)	1–764
		link magnitude	1,967 (1,373)	15–4,581
		aspect (degrees)	175.86 (0.21)	0.45–359.82
		gradient (%)	4.09 (5.30)	0.00–38.93
		elevation (m; elev)	1,363 (263)	953–2,288
	land use	residential development (% study reach area)	2.56 (2.32)	0.00–100.00
		barren (% study reach area)	0.33 (1.26)	0.00–10.32
		forest (% study reach area)	1.74 (1.27)	0.00–9.45
		shrub land (% study reach area)	24.15 (8.48)	0.00–93.18
		grass land (% study reach area)	41.79 (22.37)	0.00–100.00
		agriculture (% study reach area)	6.25 (14.17)	0.00–94.84
		wetland (% study reach area)	22.73 (14.20)	0.00–89.84
Watershed	landscape geology	alluvium (% watershed)	57.94 (36.79)	0.00–100.00
		limestone-dolomite (% watershed)	1.16 (6.93)	0.00–100.00
		sandstone (% watershed)	36.16 (38.30)	0.00–100.00
		gravel (% watershed)	3.68 (10.44)	0.00–100.00
	watershed context	dams (dams/km <sup>2</sup> ) (%)	0.01 (0.01)	0.00–0.04
		road density (km/km <sup>2</sup> ; road)	10.34 (3.69)	3.16–32.88
		oil and gas (no./km <sup>2</sup> ; oil)	0.01 (0.01)	0.00–0.03
		coal-bed mines (no./km <sup>2</sup> ; mines)	0.02 (0.04)	0.00–0.31
		diversions (no./km <sup>2</sup> )	1.97 (2.01)	0.21–11.53
		area (km <sup>2</sup> ; area)	786.33 (198.97)	284.77–1267.97
		impervious surface (%; imp)	0.28 (0.35)	0.06–3.32

The integrated likelihood representing the survey design is denoted as

$$\begin{aligned}
 [y_{ik} | \psi_{ik}, p_{ijk}] = & I_{\{\sum_{j=1}^J y_{ijk} > 0\}} \left( \psi_{ik} \prod_{j=1}^J p_{ijk}^{y_{ijk}} (1-p_{ijk})^{1-y_{ijk}} \right) \\
 & + \left( 1 - I_{\{\sum_{j=1}^J y_{ijk} > 0\}} \right) \\
 & \times \left( (1-\psi_{ik}) + \psi_{ik} \prod_{j=1}^J (1-p_{ijk}) \right), \quad (1)
 \end{aligned}$$



**Figure 2.** Collection locations of amphibians, fishes, mussels, and reptiles in the study area (bottom map) and watershed boundary lines of 3 large-scale drainages (hydrologic unit code 2) (arrows indicate direction of flow) in the Missouri River drainage, Wyoming.

where  $y_{ik}$  is the observations of the  $J$ th number of surveys at reach  $i$  for species  $k$ . The true occurrence probability of species  $k$  at reach  $i$  is represented as  $\psi_{ik}$  and arises as Bernoulli random variables—represented as a logit-linear function of landscape-scale factors:

$$\text{logit}(\psi_{ik}) = \beta_{0,k} + \sum_{v=1}^n \beta_{v,k} x_{v,i} + \delta_{i(j)}, \quad (2)$$

where  $x_{v,i}$  are landscape-scale predictors,  $v = 1, 2, \dots, n$  measured at reach  $i$ ,  $\beta_{0,k}$  and  $\beta_{v,k}$  are species-specific parameter estimates, and  $p_{ijk}$  is the probability that the species is detected given that it is present (i.e., detectability). Detection probability was calculated using encounter histories from a subsample of reaches ( $n = 40$ ) sampled 2–3 times to reduce the uncertainty in the estimated occupancy of the target species at the sampled sites (Kirsch & Peterson 2014; Stewart & Long 2016). With this modeling approach, we assumed species-specific detection probabilities are constant for all individuals, population is demographically closed, and occurrence at each site does not change over the sam-

pling period. We believe we met the latter assumption of a closed population given that reaches were resampled within the same season and year. It is possible to include covariates of detectability to account for differences in sample effort and methods, but we did not do so because we lacked relevant collection-level data across all samples. Therefore, we modeled  $p_{ijk}$  as a logit linear model,  $\text{logit}(p_{ijk}) = \gamma_k$ , where  $\gamma_k$  allowed for extra among-species variation and  $\delta_{i(j)}$  allowed for extra site  $i$  within watershed  $j$  variation with an exchangeable term  $N \sim (0, \sigma)$ . The  $\beta$ s are the fixed-effect coefficients. We were not able to account for imperfect detection for mussels; thus, observations were compiled in a species-by-reach occurrence matrix, and the model was reduced by removing the detection function  $p_{ijk}$  from the integrated likelihood.

We developed and then ranked models based on a priori hypotheses relative to the effects of reach- and watershed-specific factors on occupancy (Table 1 & Supporting Information). Candidate hierarchical models were fit with covariates standardized with a mean = 0 and SD = 1. Only predictor variables that had a correlation coefficient ( $r$ ) < 0.60 were used in the same model to reduce intercorrelation due to potential multicollinearity (Dormann et al. 2013). Correlated predictor variables ( $r \geq 0.60$ ) were not used in the same model but were considered when developing models based on a priori hypotheses (Supporting Information). We used cross-validation techniques, Bayesian  $p$  values (quantifies the probability that simulated data are more extreme than the original data [ $p(y) = \Pr(T(y_{\text{sim}}) > T(y))$ ] [Gelman & Hill 2007]), and an information theoretic approach (Burnham & Anderson 2002) to rank competing model-based hypotheses. We used mean deviance from Markov chain Monte Carlo (MCMC) iterations to calculate Akaike information criteria with small-sample bias adjustment ( $\text{AIC}_c$ ). A Bayesian  $p$  value close to 0 or close to 1 indicates poor model fit, and a value around 0.50 indicates adequate model fit (Gelman & Hill 2007). We assumed models with  $\Delta\text{AIC}_c \leq 6$  were plausible, and relative fit of candidate models were determined by calculating Akaike weights ( $w$ ). Strength of evidence ( $\epsilon$ ) was calculated using the ratios of the Akaike weights (Burnham & Anderson 2002).

Species' distribution models for fishes and mussels were implemented in WinBUGS software version 1.4 (Lunn et al. 2000), and MCMC algorithms were used to generate posterior distributions of parameters. Noninformative priors (i.e., diffuse priors) were used and models were fit using three parallel chains simulated for 850,000 iterations with a burn-in of the first 200,000 iterations. The number of required iterations was estimated using the global model and testing for convergence with the Gelman–Rubin diagnostic convergence statistics, examination of chain histories, and the posterior density plots (Gelman & Rubin 1992).

**Table 3.** Species group, data type, and models used to determine which variables affected distributions of fishes, mussels, amphibians, and reptiles.

<i>Species group</i>	<i>Data type</i>	<i>Model</i>	<i>Mean area-under-curve<sup>a</sup></i>	<i>Mean Bayesian p<sup>b</sup></i>	<i>Landscape-scale factors<sup>c</sup></i>
Fish	presence-absence	hierarchical, multispecies Bayesian mixture model <sup>d</sup>	0.83	0.63	stream context (elevation, stream position and size, gradient); human use (density of diversions, dams, roads, and oil and gas well development)
Mussel	presence-absence	hierarchical, multispecies Bayesian mixture model <sup>d</sup>	0.87	0.69	stream context (stream position and gradient); human use (density of diversions and impervious surface)
Amphibians	presence only	Maxent	0.85	–	elevation, gradient, alluvium (geology), land cover (water, wetlands, forest)
Reptiles	presence only	Maxent	0.79	–	land cover (wetlands, water)

<sup>a</sup>Model performance based on the overall average area-under-curve statistic computed for the species group.

<sup>b</sup>Model performance based on mean Bayesian *p* value estimated for the hierarchical multispecies Bayesian mixture models (Bayesian *p* values close to 0.5 indicate good model fit).

<sup>c</sup>The listed landscape-scale factors are the most important variables identified.

<sup>d</sup>Accounts for probability of detection.

### Spatial Conservation Planning

All predicted localities were checked for accuracy against range maps from field guides (Baxter & Stone 1995), and field maps were developed by the Wyoming Natural Diversity Database (<http://www.uwyo.edu/wyndd/>) and by contacting original data sources such as biologists and staff working with Wyoming Game and Fish Department. Species' distribution maps were developed using both known and predicted probability occurrences. Only amphibian and aquatic reptile species caught at more than one watershed (fifth order, 10 level HUC) and fish and mussel species caught at >2% of the sampling locations were considered in species' distribution models to avoid making predictions of occurrence based on model parameters that could be biased due to insufficient information (Kirsch & Peterson 2014). For rare species (Supporting Information), we developed species' distribution maps based on known occurrences. We assigned a value of 1 to sampled areas where the species were collected (indicating 100% occurrence) and a 0 to all other areas.

Species' distribution maps for each species were used to evaluate and prioritize watersheds (HUC10) of high conservation value with the Zonation software package (version 4.0; Moilanen et al. 2009). We used HUC10 watersheds as planning units ( $n = 199$ ) so that watershed-scale conservation actions would conserve species assemblages and the larger ecosystem (Williams et al. 2011). We used the additive benefit function cell removal rule, specified an exponent of the power function of 0.25 for all species, and used directed connectivity relationships between upstream and downstream planning units in Zonation. This configuration allowed us to prioritize

areas that benefit multiple species while considering connectivity among watersheds following methods by Moilanen et al. (2008). Thus, tributaries of watersheds that had high importance would also receive some prioritization (Moilanen et al. 2009; Supporting Information). We also compared these Zonation results with models that did not include connectivity or rare species to evaluate the sensitivity of our results to connectivity and presence of rare species.

In addition to prioritizing watersheds on the basis of species presence, we also developed cost layers that represented human threats and non-native fish species presence. The rationale for including cost layers is that areas with few human threats and few non-native species may be relatively easier to manage and conserve. For human threats, we included landscape-level land use (density of dams, oil and gas wells, coal-bed methane mines, diversions, roads, and impervious surface) and land use (percent agriculture and residential development). The use of cost layers down weights species occurrences because areas with high conservation value but low human threats or non-native species presence are selected (Strecker et al. 2011). Human and non-native species threat layers were developed by scaling human threats and non-native species to range between 0 and 100 so that watersheds with low and high relative threats could be identified.

The other modification we made to the prioritization was to use species weights of 10, 5, and 1 to maximize inclusion of rare, less common, and common species (Supporting Information; Early & Thomas 2007). To evaluate how species weights affected landscape prioritization, we doubled and halved weights and used chi-square tests based on log-linear models to provide standardized

Pearson residuals to determine if significant differences in responses existed among species weightings.

Zonation produces a full, continuous nested ranking of the landscape. Specifically, this means that the top 1% of the most important conservation areas is nested within the top 2%, which is in turn nested in the top 10%, 25%, and 100% of watershed rankings, and top-ranking watersheds rank among the best 1% of the landscape. We assessed agreement among prioritization rankings of watersheds with or without cost layers (native species only rankings, native species + human threat cost layer rankings, and native species + non-native fish species cost layer rankings), connectivity, and rare species by calculating agreement of watershed ranks and congruence coefficients to determine level of association (uncentered correlation) (Smilde et al. 2009) for all pairwise comparisons in R (R Development Core Team 2010).

We determined the validity of surrogate schemes based on the top-ranking watersheds identified for each aquatic group. We developed a hybrid approach in which we incorporated information from occurrence points and modeled ranges that were then reviewed by biologists and staff working with the conservation agencies (e.g., Wyoming Game and Fish Department) that were the source of the original data as a means to determine whether or not a species occurred in the conservation-priority watersheds identified in the Zonation analysis (Supporting Information). This produced species-accumulation estimates and the number of nontarget species included in the best conservation priorities (top 25% of landscape) identified for the surrogate. Because these conservation priorities represented the best areas to conserve for each taxon, we calculated percent agreement and used congruence coefficients to determine relatedness of cross-taxon conservation areas across taxa. These relationships represented the relatedness of the unique characteristics of taxa and landscape-scale factors affecting their distribution (Wiens et al. 2008).

## Results

### Species' Distribution Analysis

Mean AUC calculated from the cross-validation procedures indicated that MaxEnt models described the distributions of amphibians (0.85) and reptiles (0.79) well (Table 3 & Supporting Information). For fish and mussel species mean AUC values of the best-approximating multispecies Bayesian models were 0.83 and 0.87, and the mean Bayesian  $p$  value, which indicates the discrepancies between simulated and observed data, also indicated adequate model fit for both fishes (0.63) and mussels (0.69) (Table 3).

The distributions of aquatic species were affected by different sets of landscape-scale variables (Table 3). For

example, variable contribution analyses indicated that land-use variables were the best predictors of amphibian and reptile occurrences; whereas, fish and mussel distributions were better described by stream context and watershed context variables (Supporting Information). Landscape geology was not an important predictor of occurrence for any aquatic species group. Most spatially restricted amphibians species were predicted to occur in and around high-elevation, low-gradient wetlands; whereas occurrences of broadly distributed amphibian species were better described by land-cover variables such as percent forest, percent residential development, and percent grassland (Supporting Information). Species-specific differences in fish and mussel distributions were strongly related to longitudinal changes in elevation and stream size and position. The occurrence of most fish and mussel species was greatest in low-elevation, large, low-gradient streams located downstream of small to medium-size streams, but there were also species that occurred at higher elevation sites (Supporting Information). There were few species-specific differences among aquatic reptiles, which were typically found near lotic and lentic systems at lower elevations (Supporting Information).

### Landscape Conservation Planning with Zonation

We identified 91 high-priority (top 25% watersheds for all groups) candidate watersheds, all of which contained large, low-elevation, low-gradient rivers (Fig. 3). Log-linear analysis indicated that species weights did not affect priority rankings, and watershed rankings did not vary significantly based on a species' weight by aquatic group by cost layer interaction effect ( $\chi^2 = 16.63$ ,  $p = 0.28$ ) (Supporting Information). Congruence statistics indicated that the top 25% of watersheds identified for fish (congruence estimate = 93%), mussels (congruence estimate = 87%), amphibian (82%), and aquatic reptiles (congruence estimate = 77%) were not highly affected by inclusion of human threat and non-native species cost layers; thus, final analysis was based on the average watershed rankings from the cost-layer and no-cost-layer scenarios to account for watershed-ranking variability.

There was limited agreement among priority watersheds for amphibians, fishes, mussels, and aquatic reptiles (Supporting Information). On average, greatest agreement was between fishes and aquatic-reptile priority rankings. Agreement (<20%) and concordance were low regardless of whether connectivity or rare species were included in the Zonation model (Supporting Information). Overall, agreement among the top 10% of watersheds for aquatic-group combinations was, on average, <10%, indicating that most optimal habitats were not shared among aquatic species. For example, when we no longer considered regional ranking of each watershed, <10% of amphibian priority watersheds were shared with fishes and mussels priorities, 23% of aquatic-reptile



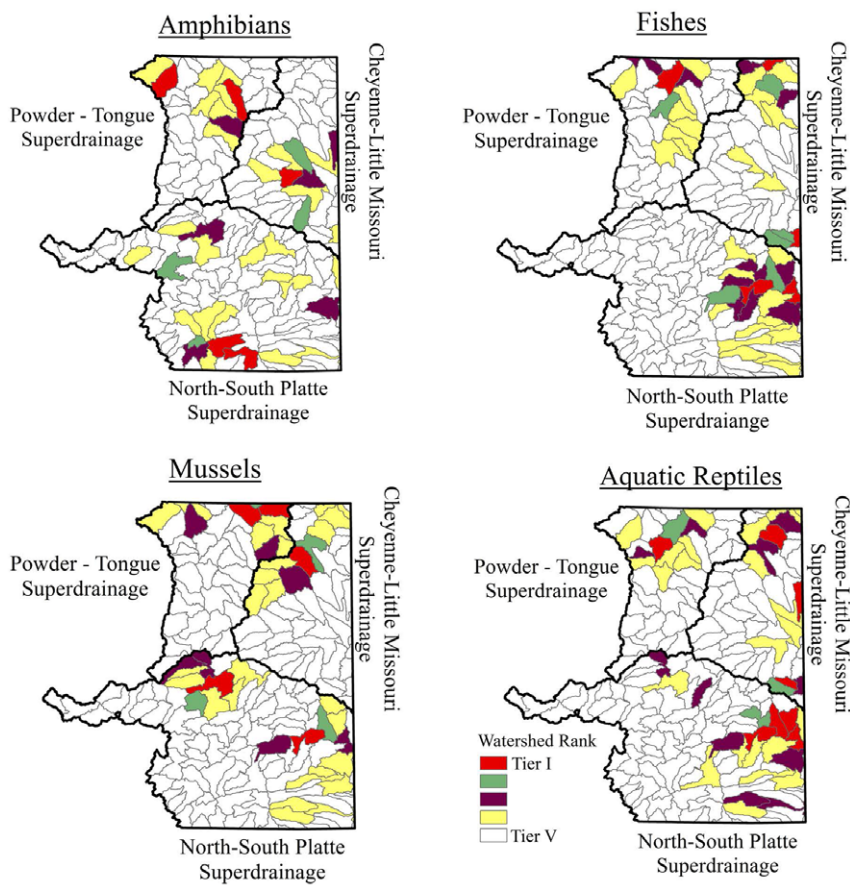


Figure 3. Prioritization rankings of the Missouri River drainage, Wyoming, watersheds for landscape-scale conservation of amphibians, fishes, mussels, and aquatic reptiles (red, top 2% of sites; green, top 5%; purple, top 10%; yellow, top 25%).

priority watersheds were shared with amphibian priorities, 27% of mussel priority watersheds were shared with fishes and aquatic-reptile priorities, and 45% of conservation priority watersheds were shared between fishes and aquatic reptiles. These results were corroborated by the low congruence among the top ranking priorities and aquatic groups: fishes versus mussels (18% [SD 5]), fishes versus amphibians (19% [10]), fishes versus aquatic reptiles (26% [11]), amphibians versus mussels (12% [10]), mussels versus aquatic reptiles (15% [6]), and amphibians versus aquatic reptiles (15% [8]).

There was high inclusion (nearly 100%) for aquatic species within the top 10% of watersheds identified for their target species group, but inclusion was variable when priorities were based on other aquatic groups. The top 10% of watersheds identified for amphibians included 75% of fish species, 45% of mussel species, and 100% of reptile species. The top 10% of watersheds for fish included 50% of amphibian species, 77% of mussel species, and 100% of aquatic reptile species. The top 10% of both mussel and aquatic reptile priority areas included <55% of amphibians species and >80% of fish species. Yet aquatic-reptile priority areas included 75% of mussel species, whereas 100% of aquatic reptile species were included in mussel priority areas. All common, wide-ranging aquatic species were included in most priority areas, regardless of taxa. But spatially restricted species

like the eastern clade western toad, Great Plains toad, Southern Rockies wood frog, and the Wyoming toad were not included in the top priority rankings identified for fishes, mussels, or aquatic reptiles.

## Discussion

We used a set of novel modeling approaches and systematic conservation prioritization techniques to evaluate factors controlling occurrence of aquatic species and to identify conservation priorities for management. This permitted a comprehensive evaluation of the extent to which conservation priorities based on one freshwater aquatic taxon would also include other aquatic species (Hitt & Frissell 2004). Our results indicated that percent inclusion of the species within a particular taxon was relatively high when considering the top 25% of the priority areas for each surrogate type, but it did not insure persistence of these species in the long term given that the top-ranking priority areas (or the best habitats) were significantly different. Moreover, many rare and spatially restricted aquatic species that currently require conservation were not included in any of the priority watersheds selected for the other taxa. Based on these results, a surrogate approach would not be effective, and

relying only on representation of the most common species would not translate to responsible conservation of other aquatic taxa, given that the surrogate landscape did not include the best habitats for the background taxa.

We identified optimal areas for each aquatic group and their associated habitats with a systematic prioritization tool that considered both common and rare species, yet we found the agreement and concordance of these conservation priorities across taxa to be low. Agreement was <10% in most cases, and congruence was <15%. Removing rare species and connectivity did not improve agreement across taxa (Supporting Information). Part of the reason for the lack of agreement among priority areas was that different landscape-scale factors affected the distribution of aquatic species differently. Our analysis of species-specific distributions shed light on the processes that control the occupancy and assemblage structure of aquatic species. The 3 main factors were habitat quality, habitat complexity, and environmental stability (Supporting Information). We found that habitat quality differed among aquatic groups; the low overlap between the distributions of amphibians and the other three taxa reflected the fact that the cool, fishless wetland and riparian habitats favored by these species occur in higher-elevation watersheds in the Missouri River drainage in Wyoming. Habitat complexity was likely a primary driver of fish distributions; occurrences of many fish species were positively related to stream size and position and negatively related to elevation, similar to results of previous studies that show longitudinal changes in fish assemblage structure as a result of zonal and additive patterns (Rahel & Hubert 1991). Further, anthropogenic disturbances such as oil and gas development, density of dams, diversions, and roads are known to have a negative effect on environmental stability (Davis et al. 2010). Previous work indicates these factors are positively related to non-native fish species and negatively related to many native aquatic species in the Missouri River drainage within Wyoming (Stewart et al. 2016). When this information is related to the locations of the conservation priorities, it is easy to understand why the large, low-elevation streams better suited for conservation of fish and reptiles did not spatially co-occur with top-ranking priorities identified for amphibians (Semlitsch & Bodie 2003). Thus, development of conservation priorities based on a single aquatic group would not protect many species in the other aquatic groups.

Other attempts to identify and test surrogate approaches have also reported disappointing results or inconsistencies (Larsen et al. 2009), and the methods used may affect these conclusions (Grantham et al. 2010). For example, Mellin et al. (2011) concluded that surrogacy methods based on representation (i.e., inclusion) may achieve goals related to conservation planning, whereas congruence methods are better suited for predicting biodiversity. Similarly, others suggest that the success of

surrogate approaches depends on congruence in species co-occurrence patterns among regions (Hess et al. 2006). If one were to base success on species representation, then one would conclude that using cross-taxon biodiversity surrogates has value in protecting the most common aquatic species, although spatially restricted and rare aquatic taxa were not represented in any watersheds identified as being important for any cross-taxon surrogate. We identified incongruences and low agreement among conservation priority watersheds among aquatic groups, indicating that representation may not insure long-term persistence of these species because one runs the risk of working to conserve these species in suboptimal habitats, given that more suitable areas were identified for each aquatic group (Rodrigues et al. 2000). Therefore, investing effort into collecting information on all species from a broad representation of environments and then using an integrated modeling approach that prioritizes the landscape for all species may be the most effective approach (Strecker et al. 2011). For example, using the Zonation conservation planning tool, we identified taxa-specific priority rankings that protected 100% of the species for each aquatic group. The ideal scenario would be to include all species in a single analysis, thus avoiding the surrogacy problem and increasing the representation of rare species across all taxa (Kremen et al. 2008).

We used a comprehensive modeling approach to identify the different landscape-scale factors that controlled the distribution of aquatic species as a framework for developing and integrating models for multiple species across a broad geographic area into the conservation planning analysis. In our study area, the inclusion of rare species did not significantly affect watershed rankings because they were typically in areas with many common species—similar to results reported by Bond et al. (2014). However, others, such as Carroll et al. (2010) found the opposite to be true: rare species occupied restricted or narrow habitats that did not contain other species. Because the influence of rare species on Zonation solutions is likely to be context dependent, it is worth computing and comparing the solutions both with and without the inclusion of rare species. However, our primary question was how well do taxa-specific freshwater conservation priorities protect other nontarget freshwater aquatic species? We found little congruence and agreement among the top-ranking taxa-specific priorities and priorities identified for the other freshwater taxa, with the primary exception being between fish and aquatic-reptile priorities. Top-ranking watershed priorities identified for fishes often failed to include rare and spatially restricted species of other aquatic groups, precisely the species that would most likely need conservation attention. This pattern remained true when considering any of the other taxa. Thus, we urge caution against surrogate approaches that rely on representation because priority

conservation areas identified for the focal taxon may not include many of the species in other taxonomic groups that are also in need of relying on these watersheds to protect.

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## Supporting Information

Model-based hypotheses (Appendix S1) and model results (Appendix S2) are available online. The authors are solely responsible for the content and functionality of these materials. Queries should be directed to the corresponding author.

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