

RESEARCH ARTICLE OPEN ACCESS

Improving Species Distribution Models for Stream Networks by Incorporating Spatial Autocorrelation in Multi-Sourced Datasets: A Range-Wide Assessment of Idaho Giant Salamander Status and Future Risk

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Received: 19 February 2025 | **Revised:** 15 August 2025 | **Accepted:** 1 September 2025

Editor: Chunlong Liu

Funding: The authors were supported by their respective agencies during the preparation of this manuscript.

Keywords: Idaho giant salamander | spatial autocorrelation | spatial stream network model | species distribution model

ABSTRACT

Aim: Fundamental to species conservation efforts is the development of accurate distribution models. Doing so is challenging for many stream organisms, where limited funding may necessitate the compilation of incidental observations from multiple sources which lack an overall sampling design and are often spatially clustered. We demonstrate the application of specialised spatial-stream-network models (SSNMs), which incorporate autocorrelation among observations and have the potential to improve species distribution models for many organisms.

Location: Rocky Mountains in west-central North America.

Methods: We compiled a comprehensive presence-absence dataset for Idaho giant salamander (IGS; *Dicamptodon aterrimus*) from previous studies, natural resource agencies, museum collections and new surveys, and linked these data to geospatial habitat covariates. The dataset was modelled using a suite of candidate SSNMs, and results were compared to those from non-spatial generalised linear models (GLMs). The top-ranked models were used to predict range-wide IGS occurrence probabilities for scenarios that represented historical baselines and futures associated with two model covariates (water temperature and riparian tree canopy density) that are changing with environmental trends in the study area.

Results: The classification accuracy of salamander observations was higher with SSNMs than GLMs (90.8% vs. 63.2%) and the spatial models identified fewer significant habitat relationships, which simplified model interpretation. Baseline range estimates from the models were similar (13,090–14,114 stream km) and both predicted small range expansions (2.0%–24.8%) with future warming because many streams were sub-optimally cold for IGS. However, these expansions were partially offset in scenarios which included decreases in riparian canopy density.

Main Conclusions: SSNMs significantly improved species distribution models on stream networks by incorporating spatial autocorrelation and provide an inexpensive means of developing new information from many existing datasets. This incentivises

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1 | Introduction

Freshwater ecosystems are disproportionately biodiverse and increasingly impaired due to declining water quality, species invasions, increasing disease incidence and habitat loss (Dudgeon et al. 2006; Arthington et al. 2016). Freshwaters host ~9.5% of the Earth's described animal species on only 2.3% of the Earth's surface (Reid et al. 2019), yet recent estimates suggest 25% of this fauna is at risk of extinction (Sayer et al. 2025). Despite decades of biodiversity inventories that underpin these estimates, our understanding of the distribution of many aquatic organisms remains incomplete (the Wallacean shortfall; Hortal et al. 2015). For taxa with poor distribution information, development of accurate species distribution models (SDMs) is often a key conservation step that provides insight into the importance of different habitat factors, enables mapping of habitat suitability, and facilitates vulnerability assessments to highlight where risks from disturbance agents are greatest (Elith and Leathwick 2009; Sillero et al. 2021). There is particular urgency for delineating and adding resolution to the distributions of many freshwater amphibians, which are believed to be the most threatened class of vertebrates (Luedtke et al. 2023). Of these, salamander species inhabiting montane regions are especially vulnerable, with numerous case histories documenting population losses (Stuart et al. 2004; Wake and Vredenburg 2008) and future warming projected to take an increasing toll (Carey and Alexander 2003; Araújo et al. 2006; Luedtke et al. 2023).

For non-game freshwater species like salamanders and others which lack societal cachet, range-wide targeted surveys are rare due to a lack of funding. Inventory and monitoring efforts must often rely on incidental observations made during surveys for other taxa or on convenience surveys in accessible locations (Kadmon et al. 2004; Hortal et al. 2008). These sources usually consist of survey information archived at natural history museums and local studies where clusters of observations were made, which combined with the lack of an a priori spatially balanced sampling design (Stevens and Olsen 2004; Dumelle et al. 2023), may lead to an inaccurate perspective on habitat preferences and distributions. Moreover, SDMs developed from aggregated datasets are more likely to have spatially autocorrelated error structures (i.e., closer locations exhibit more similar values than those further apart) that violate the statistical assumption of independent and identically distributed residuals. This typically results in underestimation of standard errors and increased Type I error rates (incorrectly rejecting the null hypothesis of no effect) that ultimately translate to overparameterized SDMs (Legendre 1993; Dormann 2007).

Addressing spatial autocorrelation has long been standard practice in SDMs for terrestrial organisms where latitude and longitude coordinates provide convenient means of developing autocovariance structures (Dormann et al. 2007; Cressie 2015). Patterns of autocorrelation on flow-directed networks such as streams differ substantially, however, so an obstacle to the adoption of spatial statistical models for fluvial systems was the lack of appropriate autocovariance structures (Peterson et al. 2007; Ver Hoef and Peterson 2010). Development of statistical theory for a valid class

of spatial-stream-network models (SSNMs; Ver Hoef et al. 2006; Cressie et al. 2006) and software to run these analyses have overcome these limitations only relatively recently (Peterson and Ver Hoef 2014; Ver Hoef et al. 2014; Dumelle et al. 2024), and efforts to fully generalise SSNMs to match the breadth of non-stream models (e.g., MacKenzie et al. 2002; Guillera-Arroita et al. 2015; Fletcher et al. 2019) remain ongoing. Over the last decade, SSNMs have been used extensively to improve inference from autocorrelated water quality datasets (Peterson et al. 2013; Isaak et al. 2014; Rushworth et al. 2015), but few studies have developed SDMs for aquatic species based on SSNMs (Mota-Ferreira and Beja 2020; Sharma et al. 2021; Winkowski et al. 2024). Of these, none have made detailed comparisons of parameter estimates and predicted distributions with non-spatial models to fully understand the disadvantages potentially incurred by ignoring spatial autocorrelation in stream SDMs.

Here, we developed a large presence-absence dataset from multiple sources for Idaho giant salamander (IGS; *Dicamptodon aterrimus*), a species of conservation concern that inhabits mountain streams in the Rocky Mountains of western North America. We contrasted SDMs developed from this dataset based on SSNMs with non-spatial generalised linear models (GLMs) that assumed spatial independence among observations, used both models to estimate habitat relationships, and predicted range-wide occurrence probabilities for baseline and future scenarios. Our results highlight the utility of using SSNMs with aggregated datasets and suggest similar approaches could benefit many stream species for which poor distribution information exists.

2 | Materials and Methods

2.1 | Target Species

The IGS is one of four members of a genus endemic to mesic coniferous forests in mountainous areas of west-central North America. Although initially thought to be present only in central Idaho of the U.S. (Carstens et al. 2005; Wagner 2014), recent observations of IGS revealed a small portion of its range extending into the upper St. Regis river basin of northwestern Montana (Maxell et al. 2003; Figure 1). Individuals in this genus attain large body sizes (150–300 mm), are long-lived (20 years; Dudaniec and Richardson 2012), and exhibit varying degrees of paedomorphosis, that is, the retention of larval morphology in reproductively mature and fully aquatic adults. Observations of terrestrial adults are few and anecdotal; hence, metamorphosis is regarded as rare (Sepulveda and Lowe 2009). Giant salamanders have limited dispersal abilities and a genetic population structure that is strongly related to stream network structure at distances of a few kilometres, with little evidence of genetic exchange beyond that distance (Steele et al. 2009; Mullen et al. 2010). Historical conditions within the IGS range are characterised by cold, wet winters with heavy snow accumulations at high elevations and warm, dry summers. Stream hydrographs exhibit pronounced peak flows in the spring and

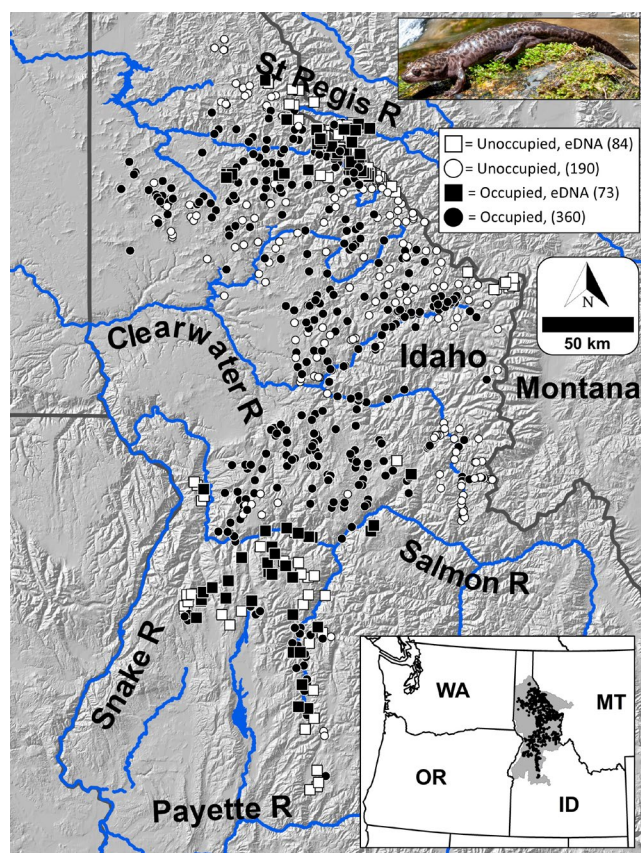


FIGURE 1 | Locations and occupancy status of 707 Idaho giant salamander survey sites in northern Idaho and western Montana that were used to develop species distribution models. Parenthetical numbers in the legend are sample sizes. The species range spans 44.5°–47.6° N latitude in the northwestern U.S. Photo by John Cossel.

low flows during late summer, fall, and winter. Vegetation in these landscapes is dominated by coniferous forests in which wildfire is a common disturbance (Morgan et al. 2008; Alizadeh et al. 2021). Most of the ~40,000 km² IGS range is sparsely populated by humans and publicly administered by the U.S. Forest Service. Land uses include domestic livestock grazing, timber harvest, and recreational activities, although the species' range also encompasses large wilderness areas where human impacts are limited.

2.2 | IGS Occurrence Dataset

We attempted to obtain all sampling data for this species ($n = 888$ locations). This included information from biologists with local datasets, museum records, state natural heritage program observations, and data in the peer-reviewed and grey literatures. We verified that all observations were within the plausible range of IGS and had geocoordinates. The stream network was represented using the 1:100,000-scale National Stream Internet layer (NSI; Nagel et al. 2024; <https://research.fs.usda.gov/rmrs/projects/national-stream-internet>), which is a derivative of the National Hydrography Dataset Plus Version 2 (NHDPlus; McKay et al. 2012; Moore and Dewald 2016) that has been customised to facilitate SSNM analysis by correcting topological errors. Next, we devised an eDNA sampling campaign ($n = 438$ samples) to

supplement the existing observations. These samples were taken following a standardised field protocol (Carim et al. 2016) and focused on the northern range margin near the recently reported range expansion and in sparsely sampled basins elsewhere within the IGS range (Figure 1). In addition, many streams within this region already had eDNA water samples collected to support inventories of other species (Young et al. 2018), and a subset of these falling within target basins were re-analysed to assess the presence of IGS (cf. Dysthe et al. 2018). All eDNA samples were processed at the National Genomics Center for Wildlife and Fish Conservation, and analysed using single-species qPCR with an assay (Pilliod et al. 2013) optimised for lab protocols as described by Franklin et al. (2019).

Of the 1326 total samples, we restricted SDM development to a subset of observations obtained in recent decades, that is, since 1990, that were collected using electrofishing or eDNA sampling, which both have high detection efficiencies for IGS and result in few false absences (Sepulveda and Lowe 2009; Cossel et al. 2012; Pilliod et al. 2014; Kieran et al. 2020; Plante et al. 2021). Although eDNA surveys did not involve the capture of organisms in the field, as was the case with electrofishing, we considered eDNA results to be equivalent to direct observation for two reasons. First, detection probabilities decline rapidly downstream from point sources of animals in small streams and rivers, especially at densities typical of IGS (Pilliod et al. 2014), and our sampling intervals (generally > 5 km) exceeded the downstream transport distance of eDNA in small streams (< 1 km; Jane et al. 2015; Robinson et al. 2019). Second, most of our eDNA-based IGS detections (75%) involved amplification in all three laboratory replicates, a pattern indicative of high eDNA copy numbers associated with organisms that occurred near the sampling location (Wilcox et al. 2016; Young et al. 2022).

Descriptive plots of the dataset in initial quality control checks revealed that IGS were never absent from survey sites in the upstream portions of networks where reach slopes exceeded 20%. Although this pattern may have arisen in part from a preference for habitat conditions in these areas (Isaak et al. 2025), examination of the data sources revealed that presence-only surveys were used exclusively in the steepest reaches. Because surveys in reaches > 20% slope composed a small portion of the dataset (~5%) and our goal was development of predictive models that drew information from the many informative absences for this species (Guillera-Aroita et al. 2015), we truncated the dataset to surveys conducted in reaches < 20% slope. Further examination of the dataset revealed it was common for multiple surveys to occur in close proximity (i.e., < 1 km) on the same reach of stream. The large majority of these surveys showed the same occupancy status, that is, IGS absent (present) at all survey sites within a reach, which prompted us to winnow the dataset by eliminating redundant surveys. When surveys from the same stream reach showed mixed results, that is, IGS both present and absent (which occurred in 21 reaches), the survey indicating species presence was retained. This winnowing resulted in minor information loss because the spatial resolution of habitat covariates was no finer than the reach lengths in the NSI network, which averaged ~2 km in extent. A last set of IGS samples were excluded because poor location information precluded accurate cross-referencing to stream reaches (40 sites) or because the NSI network layer did not show streams at the survey

locations (7 sites). This screening reduced the size of the final dataset used in SDM development to 707 sites where the status of IGS was known (433 presences and 274 absences; Figure 1).

As a preliminary check for spatial autocorrelation in the dataset, we calculated a Torgegram (Zimmerman and Ver Hoef 2017) using the SSN2 package in R (version 0.1.1; Dumelle et al. 2024; R Core Team 2024). Torgegrams are similar to the semivariograms commonly used in spatial statistics (Cressie 2015) but split semivariance values into categories based on flow-connected (linkages between sites are traced by passive, one directional downstream flow) and flow-unconnected (linkages between sites require both upstream and downstream movement) relationships that better represent the types of spatial patterns characteristic of stream networks. Semivariance values were calculated as the average variation between measurement values separated by an intervening distance and had the following empirical estimator:

$$\gamma(h) = 0.5 \frac{1}{N(h)} \sum_{\|x_i - x_j\| \in c(h)} [z(x_i) - z(x_j)]^2 \quad (1)$$

where $\gamma(h)$ is the semivariance for distance lag h , $N(h)$ is the number of data pairs (x_i, x_j) separated by the distance h , $\|x_i - x_j\|$ is the distance between locations x_i and x_j , $c(h)$ is the interval around h (chosen to be mutually exclusive and exhaustive so that all distances h fall into one interval), and $z(x_i)$ is the data value at location x_i (Matheron 1963; Cressie 2015). When spatial autocorrelation does not occur in a set of observations, a semivariance plot shows no trend but if autocorrelation is present, the semivariance values are small near the origin and increase at greater distances (Ver Hoef et al. 2001). The Torgegram for the IGS dataset exhibited the latter pattern for both flow categories although a stronger trend was apparent among flow-connected sites (Figure 2).

2.3 | Stream Habitat Attributes

The IGS sites were linked to ecologically relevant habitat descriptors associated with channel morphology, thermal and

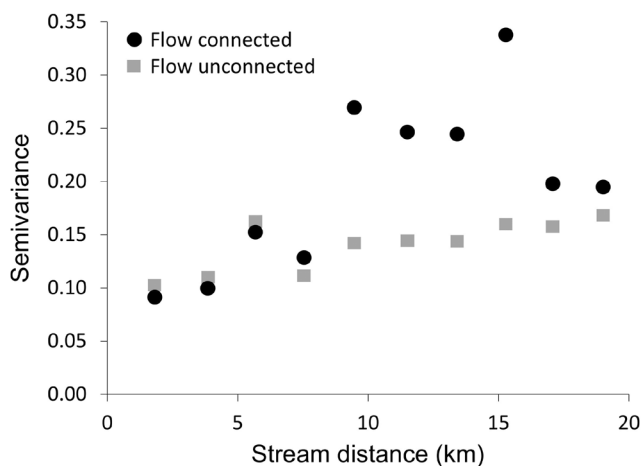


FIGURE 2 | Empirical Torgegram describing spatial patterns of correlation among 707 presence-absence surveys for Idaho giant salamander.

flow regime attributes, riparian vegetation conditions, and disturbance agents (Appendix S1). For a habitat attribute to be considered, we required a plausible hypothesis of its effect on IGS based on literature descriptions or our understanding of the organism's ecology and distribution (hypotheses summarised in Appendix S1). Because of the geographic scope of the project, the habitat descriptors were derived from geospatial datasets that were available throughout the IGS range. Most instream attributes were obtained from datasets designed for compatibility with NSI and NHDPlus networks that linked directly to reach segments. However, for watershed characteristics such as wildfire prevalence and road density, mean values were summarised by 12-digit hydrologic units (Seaber et al. 1987) and the same value was assigned to IGS sites that fell within a unit boundary. For more details on the road density and wildfire covariates, see Isaak et al. (2022).

2.4 | IGS Distribution Models

To prepare the dataset for SSNM analysis, the survey sites were complimented with a set of prediction sites spaced at 1-km intervals throughout the species' range, and the SSNbler software (Peterson et al. 2024) which replaces the earlier STARS software (Peterson and Ver Hoef 2014) was used with ArcPro to create a landscape network object that contained the required spatial distance matrices, topological elements, and attribute information (Peterson and Ver Hoef 2014). As a part of model fitting, covariates were initially screened for multicollinearity using variance inflation factors, but these were not problematic (all VIFs < 3) due to relatively low correlations among covariates ($r < 0.6$; Appendix S2; Dormann et al. 2013). The SSNMs were fit using the SSN2 package with the landscape network object and specifying a binomial distribution with a logit link, whose parameters were estimated using a version of the Laplace approximation (Ver Hoef et al. 2024). These models paired an autocovariance function with different combinations of fixed-effect covariates that included a global model, reduced models, and an intercept-only model, which was equivalent to ordinary geostatistical kriging (Ver Hoef 2008; Isaak, Ver Hoef, et al. 2017).

The SSNMs were of the general form:

$$g(p) = \mathbf{X}\boldsymbol{\beta} + \mathbf{z}_{TU} + \mathbf{z}_{TD} + \mathbf{z}_{EUC} + \epsilon \quad (2)$$

where $g(p)$ is the logit function that links the probability of IGS presence, p , to the other model components; $\mathbf{X}$ is a matrix of covariate values, $\boldsymbol{\beta}$ is a vector of regression coefficients, and ϵ is a vector of independent and normally distributed random errors. Spatial structure in the residuals was described using vectors of zero-mean random variables ($\mathbf{z}_{TU}$, $\mathbf{z}_{TD}$, $\mathbf{z}_{EUC}$) with a mixed-model autocorrelation structure composed of tail-up (TU), tail-down (TD) and/or Euclidean (EUC) covariance functions (Peterson and Ver Hoef 2010). The functions in the autocorrelation structure can be represented by different models in the SSN2 software (Dumelle et al. 2024; see Appendix S3 for more details). To select an autocovariance structure for the IGS dataset, a global model with the full set of fixed effects was fit with 10 different autocovariance specifications. The models were ranked from most plausible to least plausible based on the Akaike information

TABLE 1 | Descriptive statistics for covariates associated with 707 Idaho giant salamander survey sites that were used to develop species distribution models.

Variable	Occupancy status	<i>n</i>	Mean	Median	SD	Minimum	Maximum
Riparian canopy (RC, %)	Absent	274	58.4	63.5	23.9	0	95.0
	Present	433	63.8	69.0	22.8	0	94.0
Reach slope (S, %)	Absent	274	6.42	5.15	4.55	0.01	18.8
	Present	433	7.26	6.41	4.67	0.38	19.8
Precipitation (P, mm)	Absent	274	1166	1138	329	538	2388
	Present	433	1070	1044	257	462	1899
Baseflow index (BI, %)	Absent	274	67.6	68.5	4.88	47.0	74.0
	Present	433	66.6	68.0	5.30	45.0	73.0
Stream temperature (T, °C)	Absent	274	11.1	10.8	1.94	6.66	16.9
	Present	433	11.5	11.4	1.58	7.35	16.0
Summer flow (SF, m ³ /s)	Absent	274	0.48	0.21	0.65	0.01	3.78
	Present	433	0.35	0.13	0.58	0.01	4.68
Winter floods (WF, days)	Absent	274	2.57	0.95	3.33	0	13.0
	Present	433	3.02	1.70	3.26	0	14.6
Road density (R, km/km ²)	Absent	274	1.25	1.28	1.03	0	4.01
	Present	433	1.45	1.51	1.02	0	4.24
Fire extent (F, %)	Absent	274	9.62	0.97	14.5	0	66.4
	Present	433	7.11	1.08	12.5	0	66.4

Note: Abbreviations and measurement units are in parentheses.

criterion (AIC; Akaike 2003) and estimation was done using restricted maximum likelihood.

Once an autocovariance structure was selected, SSNMs with different fixed effects were fit and ranked based on AIC. The predictive performance of these models was also assessed by computing the mean square prediction error (MSPE; Cressie 2015), classification accuracy based on leave-one-out cross-validation (LOOCV; James et al. 2013), and the area under the curve (AUC) of the receiver operator characteristic (Pearce and Ferrier 2000; Robin et al. 2011) in the SSN2 package. When determining classification accuracy, the logit scores from the SSNMs were converted to IGS occurrence probabilities and used with a 0.61 threshold that matched the prevalence of occurrences in the dataset (Liu et al. 2005). For comparison with the SSNMs, we also fit non-spatial GLMs to the IGS dataset using identical sets of fixed effects covariates and assessed these models with the same performance metrics.

2.5 | IGS Distribution Scenarios

Top-ranked models were used to create prediction maps of IGS occurrence probabilities throughout the species' range under different scenarios. The length of reaches with predicted probabilities greater than 0.61 was also calculated and mapped to estimate the extent of habitat likely to be occupied

in each scenario. Seven scenarios were developed to represent: (1) baseline conditions which coincided with the IGS survey decades, (2) moderate future warming (+1°C water temperatures) relative to the baseline scenario in conjunction with reductions in riparian tree canopy densities of 0%, 25%, or 50%, and (3) extreme future warming (+2°C water temperatures) in conjunction with riparian canopy reductions of 0%, 25%, or 50%. The future scenarios represent the amount of stream warming expected in the next 50–100 years based on estimates of historical warming rates and projections specific to our study region (Isaak, Wenger, et al. 2017; Isaak et al. 2018). Future changes in riparian canopy tree density have greater uncertainty because they may result from transitions between vegetation types along streams (Clark et al. 2016), in many cases prompted by extended droughts, insect outbreaks, or wildfires which are patchy and difficult to forecast (Allen et al. 2010; Parisien et al. 2012). However, there is evidence that forest and riparian canopy densities are becoming more open within the IGS range (Morgan et al. 2008; Alizadeh et al. 2021; Ball et al. 2021), thus the wide range of values used in our scenarios should usefully bound future conditions. Because we excluded IGS samples from reaches with slopes >20% in the modelling dataset, these steeper reaches were also excluded from the prediction scenarios to avoid model extrapolation. Similarly, because no IGS presences occurred in large streams with summer flows >4.68 m³/s (Table 1), downstream portions of networks that exceeded this value were excluded from prediction scenarios.

Creating prediction maps from GLMs is straightforward as the probability predictions are based only on generalised linear model slope estimates (Allison 2012). However, SSNMs generate predictions by empirical best linear unbiased prediction (Zimmerman and Ver Hoef 2024), or synonymously, universal kriging (Schabenberger and Gotway 2005; Cressie 2015) adapted to the generalised linear model context (Ver Hoef et al. 2024), which combines predictions from the model with adjustments based on local spatial autocorrelation as:

$$\hat{w}(s_0) = \mathbf{x}(s_0)' \hat{\boldsymbol{\beta}} + \hat{\mathbf{c}}(s_0)' \hat{\boldsymbol{\Sigma}}^{-1} (\mathbf{w} - \mathbf{X} \hat{\boldsymbol{\beta}}) \quad (3)$$

where $\hat{w}(s_0)$ indicates the probability of occurrence at s_0 , $\mathbf{x}(s_0)$ is a vector containing the covariate values at prediction location s_0 , and the vector $\hat{\boldsymbol{\beta}}$ contains the estimated regression coefficients, so $\mathbf{x}(s_0)' \hat{\boldsymbol{\beta}}$ forms the linear regression prediction. The remaining portion of Equation (3) is an adjustment for spatial autocorrelation, where $\hat{\mathbf{c}}(s_0)$ is a vector of covariances among observed data and the prediction sites, $\hat{\boldsymbol{\Sigma}}$ is the covariance matrix among observed data, and $\mathbf{w}$ is an estimate of the underlying latent (i.e., unobserved) probability of occurrence for the occurrence response variable, $\mathbf{y}$ (see Ver Hoef et al. 2024 for details). Prediction variances (Ver Hoef et al. 2024) are given by:

$$\widehat{\text{var}}[\hat{w}(s_0)] = \Lambda (-\mathbf{H}_{\mathbf{w}})^{-1} \Lambda^T + \hat{\sigma}_0^2 - \hat{\mathbf{c}}(s_0)' \hat{\boldsymbol{\Sigma}}^{-1} \hat{\mathbf{c}}(s_0) + \mathbf{d}' (\mathbf{X}' \boldsymbol{\Sigma}^{-1} \mathbf{X})^{-1} \mathbf{d} \quad (4)$$

where $\Lambda = \mathbf{x}(s_0)' \mathbf{B} + \hat{\mathbf{c}}(s_0)' \hat{\boldsymbol{\Sigma}}^{-1} - \hat{\mathbf{c}}(s_0)' \hat{\boldsymbol{\Sigma}}^{-1} \mathbf{X} \mathbf{B}$ and $\mathbf{B} = (\mathbf{X}' \boldsymbol{\Sigma}^{-1} \mathbf{X})^{-1} \mathbf{X}' \boldsymbol{\Sigma}^{-1}$, $-\mathbf{H}_{\mathbf{w}}$ is the observed Fisher information matrix evaluated at $\mathbf{w}$, $\hat{\sigma}_0^2 = \text{var}[w(s_0)]$ (the sum of all the variance components) and $\mathbf{d} = \mathbf{x}(s_0)' - \mathbf{X}' \hat{\boldsymbol{\Sigma}}^{-1} \hat{\mathbf{c}}(s_0)$.

3 | Results

Samples in the modelling dataset were spread throughout the putative IGS range (Figure 1). These sites encompassed diverse conditions on small to moderately sized streams, across

ranges of thermal environments, riparian canopy densities, and reach slopes (Table 1). Disturbances associated with roads (0–4.24 km/km²) and wildfires (0%–66.4%) within the IGS watersheds ranged from negligible to extensive.

3.1 | SSNM Autocovariance Structure

The top-ranked autocovariance structure included a two-part mixture of TD and EUC components, which were both represented with spherical models (Table 2). However, this autocovariance was only slightly better than several others that employed different models and were ranked within 1–2 AIC points. A one-part TD autocovariance structure was also closely ranked ($\Delta\text{AIC} = 1$) but we chose the two-part mixture because of the additional flexibility that inclusion of the EUC component provided. This was useful because IGS can disperse short distances overland between stream reaches in addition to moving up- and downstream—patterns that the TD component represented. Three-part autocovariance mixtures were the lowest ranked and the variance associated with the TU component in these mixtures suggested it made a negligible contribution.

3.2 | Distribution Model Comparisons

Eight SSNMs and GLMs with different fixed effects were fit to the dataset (Table 3). The worst SSNM was the global version (model #1) but it was 143 AIC points better than the best GLM (#3a), had a smaller MSPE (0.111 versus 0.216), and a higher AUC (0.973 versus 0.678). Moreover, a minority of the fixed effects in the global SSNM (4 of 10) had probability levels < 0.1 whereas most effects were below this threshold in the GLM global model (7 of 10). The top-ranked SSNM (#3) included positive linear effects for riparian canopy and reach slope, as well as a quadratic effect for mean August stream temperature. The third-ranked SSNM (#4) was an intercept-only model without fixed effects, yet it outperformed the best GLM by 146 AIC points.

TABLE 2 | Rankings of autocovariance mixtures in SSNM species distribution models for Idaho giant salamander.

Covariance mixture	Model 1	Model 2	Model 3	Variance component	Δ AIC
TD/EUC	Spherical	Spherical		0.47/0.47 ^a	0
TD/EUC	Exponential	Spherical		0.57/0.38	1
TD/EUC	Spherical	Gaussian		0.58/0.36	1
TD	Spherical			0.94	1
TD/EUC	Exponential	Gaussian		0.59/0.36	2
TD/EUC	Exponential	Exponential		0.42/0.52	2
TD/EUC	Spherical	Exponential		0.32/0.63	2
TD	Exponential			0.94	3
TU/TD/EUC	Spherical	Spherical	Gaussian	0/0.62/0.32	5
TU/TD/EUC	Exponential	Exponential	Gaussian	0/0.53/0.41	6

Note: Mixtures are ordered from most plausible to least plausible based on differences in AIC values.

Abbreviations: EUC, Euclidean; TD, tail-down; TU, tail-up.

^aProportion of the covariance mixture associated with each model.

Parameter estimates for the top-ranked SSNM and GLM are provided in Table 4 and model diagnostic plots are summarised in Appendix S4. As expected, standard errors from the SSNM were larger than the GLM because of redundancy and spatial autocorrelation among the IGS sample sites. However, there were also slight differences in the fixed-effect parameter estimates between the two models which affected the IGS response curve relationships (Figure 3). For example, although the temperature curves indicated unimodal responses, the SSNM curves were shifted ~1°C towards warmer temperatures than the GLM curves. Despite general similarities in response curve shapes, the classification accuracy of the SSNM was considerably higher than the GLM (90.8%

vs. 63.2%) due to the inclusion of an autocovariance structure and the correlation between the probabilities predicted by the two models was relatively weak (Appendix S5).

3.3 | Range-Wide IGS Scenarios

Application of SSN Model 3 to create a range-wide prediction scenario of baseline conditions revealed high probabilities of IGS occurrence along the western portion of the species range at low to mid-elevations in several major river drainages (Figure 4a). Low occurrence probabilities were predicted in the coldest streams

TABLE 3 | Rankings of SSNM and GLM species distribution models that predict Idaho giant salamander occurrence probabilities.

Model # and type	Fixed effects	Δ AIC	AUC	MSPE	Comments
3, SSNM ^a	T, T ² , RC, S	0	0.973	0.111	T ² indicates a quadratic unimodal stream temperature effect
2, SSNM	T, T ² , RC, S, P ^b	11	0.973	0.111	
4, SSNM	None	21	0.981	0.114	Intercept-only model
1, SSNM	T, T ² , RC, S, BI , P , R , F , SF , WF	24	0.973	0.111	Global model
3a, GLM	T, T ² , RC, S	167	0.678	0.216	
2a, GLM	T, T ² , RC, S, P	179	0.683	0.215	
1a, GLM	T, T ² , RC, S, BI , P , R , F , SF , WF	182	0.708	0.210	Global model
4a, GLM	None	207	0.612	0.237	Intercept-only model

Note: Models are ordered from most plausible to least plausible based on differences in AIC values. Leave-one-out cross-validation mean square prediction error (MSPE) and the area under the curve (AUC) provide measures of predictive accuracy.

Abbreviations: BI, baseflow index; C, riparian canopy density; F, wildfire prevalence; P, precipitation; R, road density; S, reach slope; SF, summer flow; T, water temperature; WF, winter high-flow frequency.

^aSSNMs include a mixed model autocovariance structure composed of tail-down and Euclidean spherical functions.

^bFixed effects in bold had probability values > 0.1 and were considered statistically non-significant.

TABLE 4 | Parameter estimates ($\hat{\beta}$) and classification accuracy of the top ranked SSNM and GLM used to predict range-wide occurrence probabilities of Idaho giant salamander.

Model # and type	Fixed effect	$\hat{\beta}$	$\widehat{SE}$	<i>p</i>	Classification accuracy ^a
3, SSNM ^b	Intercept	-22.0	5.22	< 0.01	90.8% (84.5%)
	T	3.24	0.881	< 0.01	
	T ²	-0.121	0.0374	< 0.01	
	S	0.111	0.0321	< 0.01	
	RC	0.0152	0.00637	0.02	
3a, GLM	Intercept	-17.9	3.04	< 0.01	63.2% (63.2%)
	T	2.76	0.519	< 0.01	
	T ²	-0.108	0.0222	< 0.01	
	S	0.0731	0.0193	< 0.01	
	RC	0.0130	0.00368	< 0.01	

Note: Values in parentheses are based on leave-one-out cross-validation predictions.

^aModel predictions were transformed from logits to probabilities and a 0.61 threshold was used to determine classification accuracy.

^bSSNM includes a five-parameter mixed model autocovariance structure composed of a nugget effect (0.0250), partial sill and range estimates for a tail-down spherical function (5.99 and 76,700 m, respectively), and partial sill and range size estimates for a Euclidean spherical function (0.281 and 21,110 m, respectively). See Appendix S3 for more details.

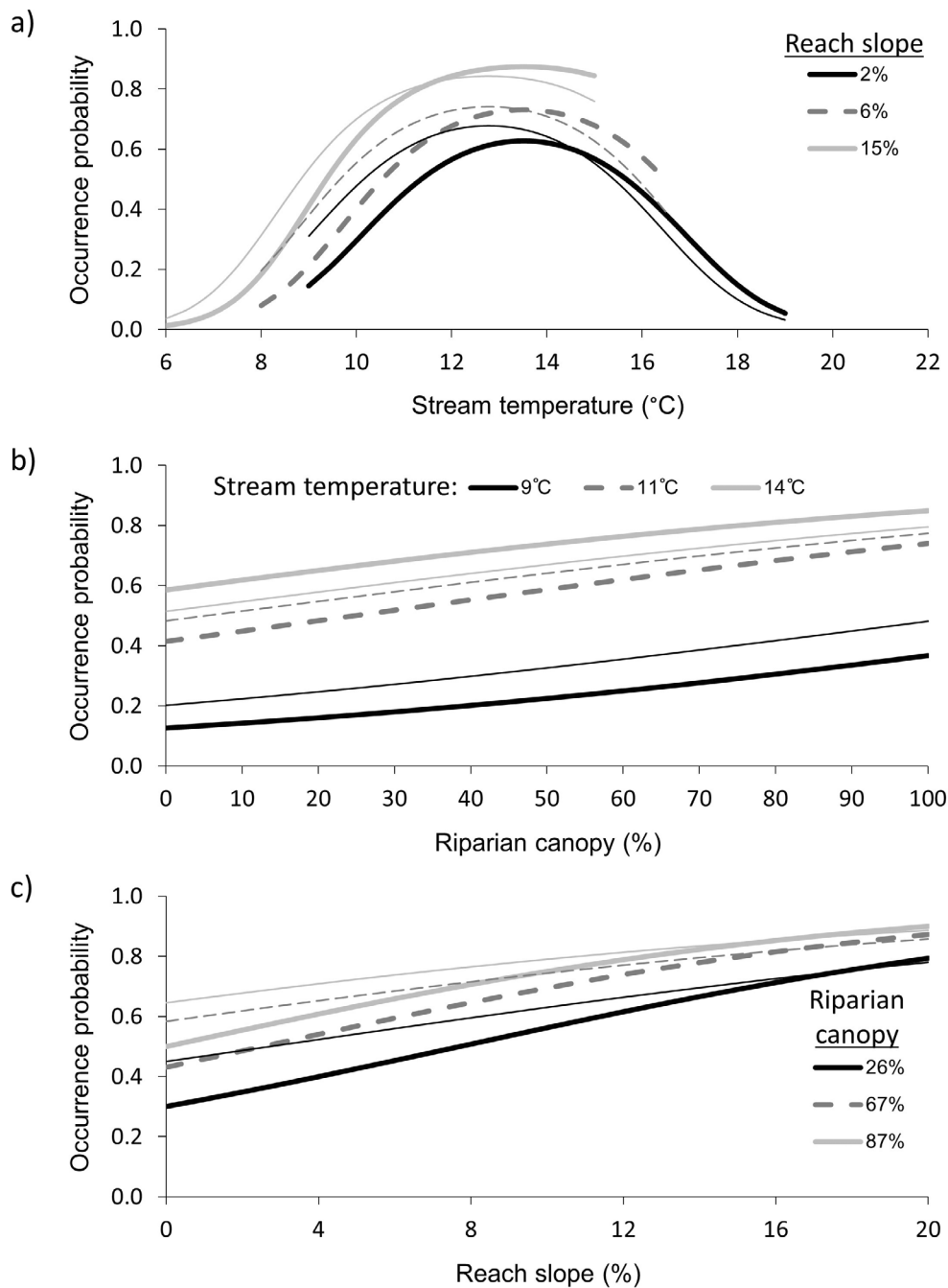


FIGURE 3 | Response curves from the top-ranked SSNM (thick lines) and GLM (thin lines). Curves are based on the 10th, 50th, and 90th percentile values in the survey dataset and are conditioned on the median value of the third covariate not represented within a panel. Portions of the response curves in the top panel are truncated to avoid extrapolation beyond the range of conditions that occurred within the Idaho giant salamander range.

at high elevations along the border between Idaho and Montana and at the northern and southern range extents. Interestingly, the intercept-only SSN Model 4 predicted similar patterns but did so more patchily because it lacked stream covariates to represent within-stream habitat variation (Figure 4b). Both SSNM probability scenarios contrasted with GLM scenarios in which the predicted probabilities from GLM Model 3a tended towards mid-range values that were spread more evenly throughout the IGS range (Figure 4c). The absence of an autocovariance structure in the GLM also meant that the probabilities derived from an intercept-only GLM were the equivalent of the 0.61 IGS

prevalence level within the dataset predicted uniformly across the range (Figure 4d).

In the baseline scenarios, the top-ranked SSNM (#3) and GLM (#3a) estimated IGS occupied 13,090–14,114 km of stream (Figure 5a,c; Table 5). The occupied extent was smaller but more contiguous based on the SSNM, which reflected patterns in the underlying occurrences and probability maps (Figures 1 and 4). Future scenarios associated with warmer temperatures (scenarios 2 and 5) suggested small to moderate increases in occupied habitat even as IGS distributions were predicted to shift

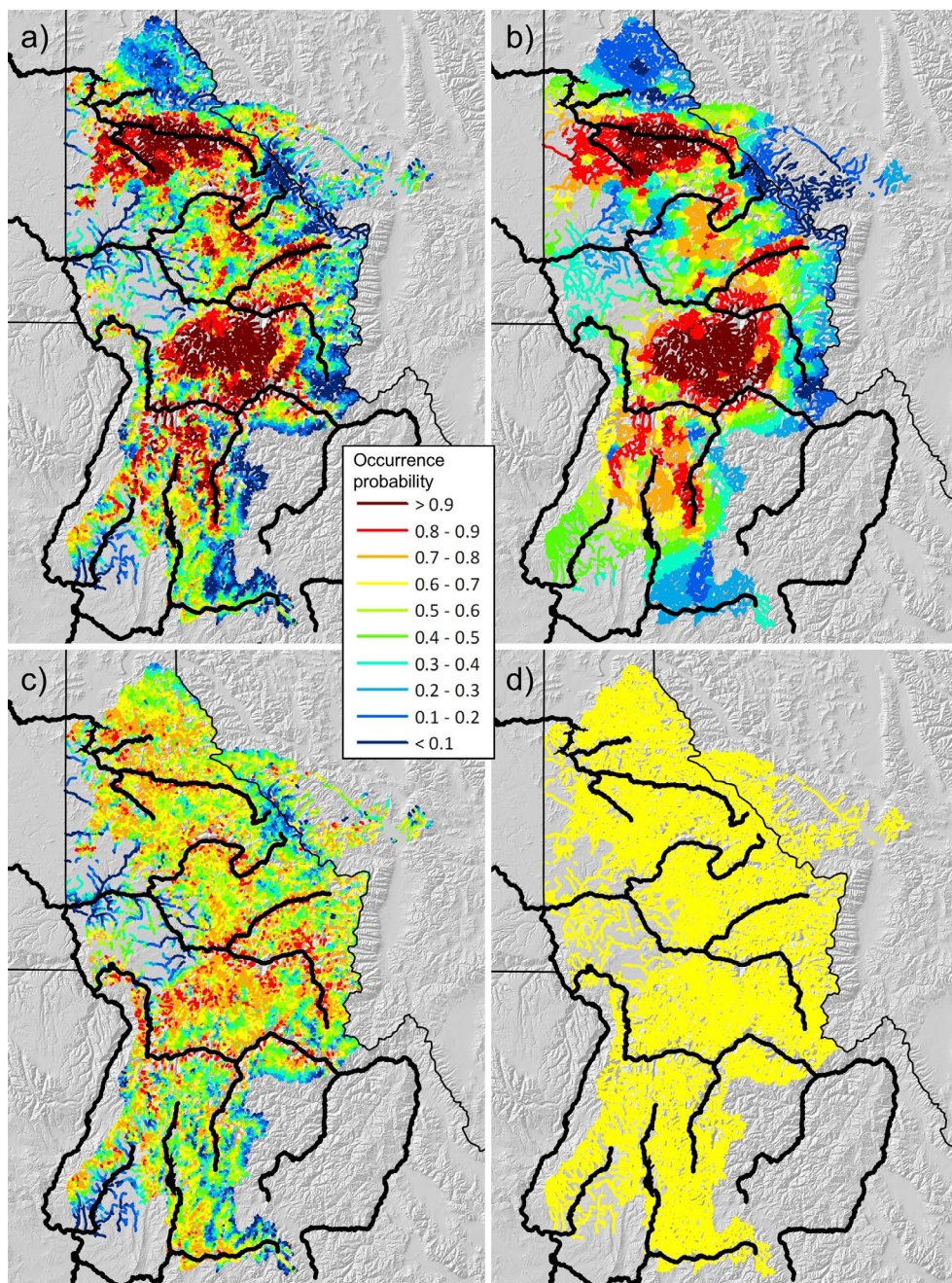


FIGURE 4 | Range-wide occurrence probability maps for Idaho giant salamander derived from SSNM with fixed effects (Model 3, panel a) and without fixed effects (Model 4, panel b). Bottom panels show probability maps from GLMs with the same sets of fixed effects (Model 3a, panel c; Model 4a, panel d).

eastward in the northern half of the range and show a mixed pattern elsewhere (Figure 5b,d). However, scenarios which included future riparian canopy reductions (Table 5) suggest these gains could be partially or entirely offset. Interestingly, the magnitude of declines associated with riparian canopy reductions in GLM-based scenarios was larger than SSNM-based scenarios, despite a smaller parameter estimate for this effect in the GLM (Table 4). This occurred because the range-wide probability map derived from the GLM (Figure 4c) contained many intermediate values near the classification threshold which moved into unoccupied status with reductions in riparian canopy.

A spatial uncertainty map based on the prediction variances from SSN Model 3 provides important auxiliary information about the interpolated distribution of IGS (Figure 6). Notably, standard errors were relatively small in proximity to survey sites but increased gradually as the distance from these sites increased out to several kilometres. An exception to this pattern occurred where straight-line distances were interrupted by mountain ridgelines—resulting in abrupt breaks in standard error sizes. An example of this was evident along a portion of the border between Idaho and Montana where the potential distribution of IGS was in both states.

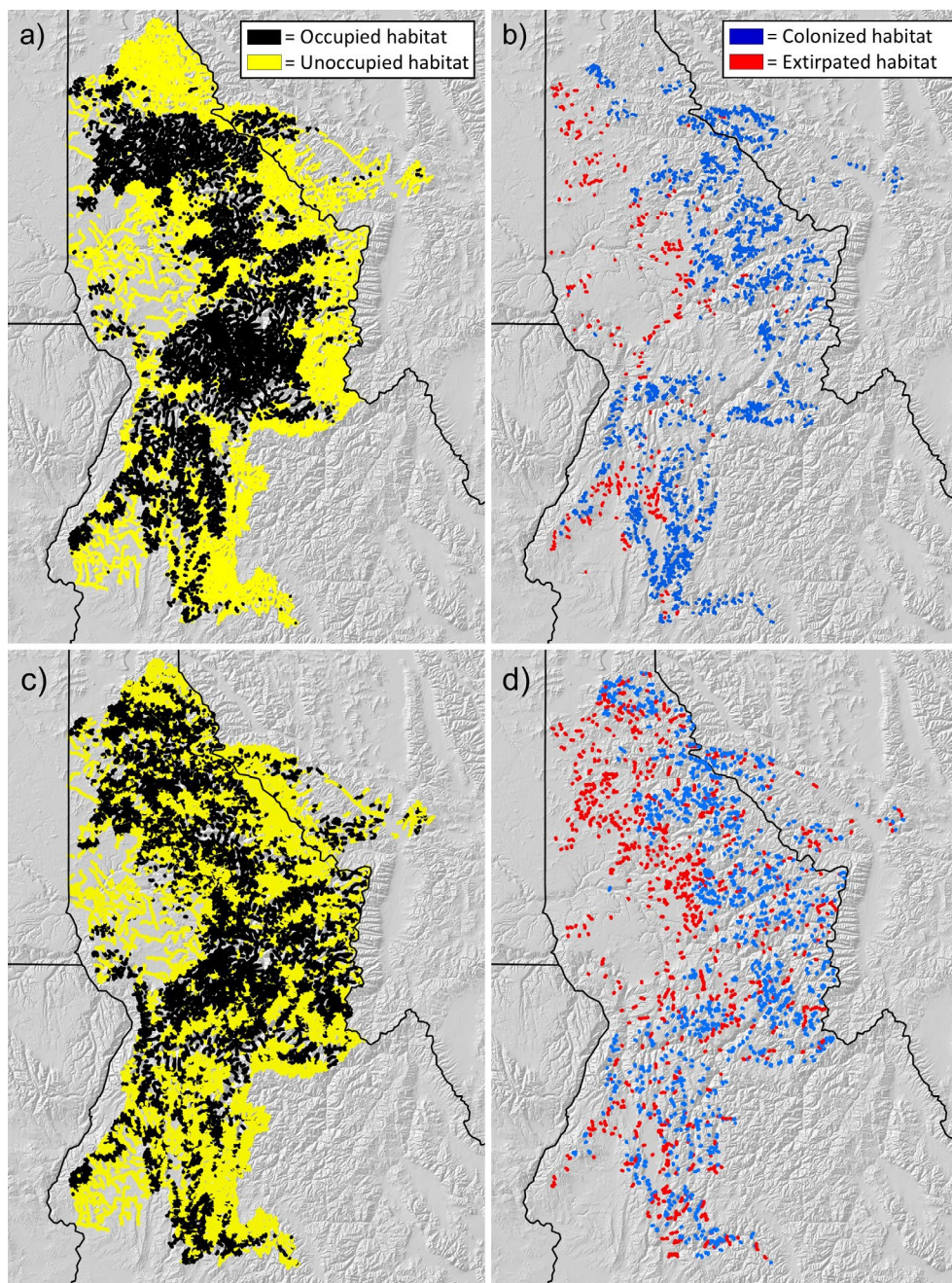


FIGURE 5 | Potential occupied range of Idaho giant salamander in baseline Scenario 1 predicted by classifying SSN Model 3 (a) and GLM Model 3a (c) probabilities using a 0.61 threshold. Right panels show changes in range extent predicted under Scenario 2, which represents a 1°C increase in mean August stream temperature for the SSN (b) and GLM (d).

4 | Discussion

By applying SSNMs to a dataset aggregated from multiple sources, we developed an SDM with good fit that added resolution to the distribution of IGS, provided a range-wide status assessment, and addressed potential future risks. In many regards, our results parallel those in the terrestrial SDM literature concerning the improved predictive performance of spatial statistical models and their identification of fewer significant fixed effect relationships (Dale and Fortin 2009; Dormann 2007). It was noteworthy that an intercept-only SSNM which lacked fixed effects outperformed non-spatial GLMs by a large margin

with our data. This suggests autocorrelation was particularly strong and the autocovariance structure enhanced the ability of the models to identify and leverage spatial patterns among observations. Similar performance of this “bare-bones” modeling approach is not guaranteed with other datasets but would depend on the density of observations relative to the range of autocorrelation. Whenever possible, building models based on ecologically motivated hypotheses and covariates that enhance understanding of the factors regulating species’ distributions should be preferred over a reliance on spatial interpolation (Austin 2002). However, intercept-only SSNMs could provide interesting null models for comparison and perhaps an initial

TABLE 5 | Occupied habitat extents for Idaho giant salamander under different scenarios.

Scenario	SSNM predicted occupied habitat (km)	GLM predicted occupied habitat (km)
1. Baseline	13,090	14,114
2. +1°C T	14,900 (13.8%)	14,393 (2.0%)
3. +1°C T, −25% RC	13,833 (5.7%)	11,398 (−19.2%)
4. +1°C T, −50% RC	12,744 (−2.6%)	8300 (−41.2%)
5. +2°C T	16,044 (22.6%)	17,615 (24.8%)
6. +2°C T, −25% RC	14,745 (12.6%)	14,688 (4.1%)
7. +2°C T, −50% RC	13,541 (3.4%)	11,387 (−19.3%)

Note: Values in parentheses are changes relative to the baseline scenario.

means of predicting distributions for aquatic species with limited ecological information.

4.1 | IGS Range Interpretation

The IGS SDMs predicted 13,090–14,114 stream kilometres were occupied in the baseline scenarios, a figure that should be viewed as conservative because model predictions were constrained to stream reaches <20% slope to avoid extrapolation. Moreover, some of the excluded network areas may have constituted good habitat because model response curves indicated IGS occurrence probabilities were highest in the steepest reaches. The amount of occupied IGS habitat was probably underestimated by 5%–10% given the frequency of occurrences observed in steep reaches, but this figure could be greater if higher-resolution stream networks were used in model development (Moore and Dewald 2016). Networks at resolutions higher than the 1:100,000-scale National Stream Internet we used include more first-order headwater channels and therefore depict longer network extents, but the prevalence of dispersal barriers associated with geologic features (i.e., vertical waterfalls) and intermittent flows in these channels make it uncertain how much additional area IGS could actually occupy (Latterell et al. 2003; Isaak et al. 2025).

Within the stream network prediction domains we used, however, the baseline scenarios also highlighted an abundance of suitable but unoccupied habitat near the northern range boundary of IGS, a pattern indicative of dispersal limitation for many amphibians in North America (Cunningham et al. 2016). Moreover, comparison to the modern ranges of other amphibians that likely occupied the Rocky Mountain Refugium during the last Ice Age but now extend much farther north, east, and west, for example, Rocky Mountain tailed frogs *Ascaphus montanus* and Coeur d'Alene salamander *Plethodon idahoensis* (Metzger et al. 2015; Pelletier et al. 2015), supports the conclusion of a limited capacity for movement by IGS. Notably, seasonal, up- or downstream ranging movements by *Dicamptodon* are common but relatively short (most direct observations <1 km; Sepulveda and Lowe 2011; Honeycutt et al. 2016), and recolonisation of defaunated reaches (on the scale of tens of meters) may require

several years (Ferguson 2000). There is also no obvious biotic factor—a predator, competitor, or congener—restricting IGS to its current range, because similar and sometimes identical suites of these guilds are found in many basins inside and surrounding this range. Even more striking, however, is the limited expansion of IGS up- and downstream along the Salmon River (in the south) and upstream, downstream, and across the valley of the St. Regis River basin (in the north). Multiple authors have suggested that large rivers constitute migration barriers for salamanders because of biotic resistance or habitat insuitability (Richardson 2012; Trumbo et al. 2013; Covarrubias et al. 2021; Figueiredo-Vázquez et al. 2021). The absence of IGS occurrences in large rivers substantiates that argument, but the abiotic components of our model do not identify how large rivers might be unsuitable.

4.2 | Factors Affecting Distributions

Although many environmental factors have been regarded as influencing the distribution of IGS (Appendix S1), our most plausible models included just three effects associated with water temperature, riparian tree canopy density, and reach slope. It was notable that neither of the major natural and anthropogenic disturbances thought to affect amphibian distributions, which we tested—recent wildfire and road density (Pilliod et al. 2003; Hossack and Pilliod 2011; Carstens et al. 2005; Sepulveda and Lowe 2009; Covarrubias et al. 2021; Ochs et al. 2024), had measurable effects on habitat occupancy at the range-wide scale of our analysis, although others have also failed to observe effects on salamanders (Dudaniec et al. 2012; Swartz and Warren 2023). The three significant effects in our models have been repeatedly associated with the presence of salamanders in stream ecosystems (Roni 2002; Stoddard and Hayes 2005; Dudeniac and Richardson 2012; Elliott et al. 2022; Olson and Ares 2022) and two of these—water temperature and riparian canopy density—formed the basis of our future scenarios. Greater riparian canopy density positively affected IGS, so more open forest canopies resulting from a suite of ongoing factors (Allen et al. 2010; Clark et al. 2016; Alizadeh et al. 2021; Ball et al. 2021) were projected to negatively affect their occupied habitat extent and overall status. Partially countering that negative trend could be small habitat gains predicted to result from water temperature increases. Idaho giant salamanders, like most other stream vertebrates in this region (Isaak, Ver Hoef, et al. 2017; Isaak, Wenger, et al. 2017), exhibit a unimodal temperature response curve in which habitat losses along warm-edge niche boundaries are offset by gains in sub-optimally cold streams at higher elevations where channel densities are also higher. These results contrast with the dire predictions for many montane amphibians in tropical areas where the range of thermal conditions is often more limited (Wake and Vredenburg 2008; Luedtke et al. 2023). However, another mitigating factor may be the increased resolution of our SDM, which relied on stream-specific covariates and a dense survey dataset that improved accuracy relative to coarser approaches, a finding that parallels previous studies (Isaak et al. 2015; Chauvier et al. 2022). Viewed in combination, IGS could retain future amounts of suitable habitat that are similar to the baseline scenarios but their distributions will have to shift, which may increasingly fragment populations or cause potential mismatches with habitat availability due to dispersal

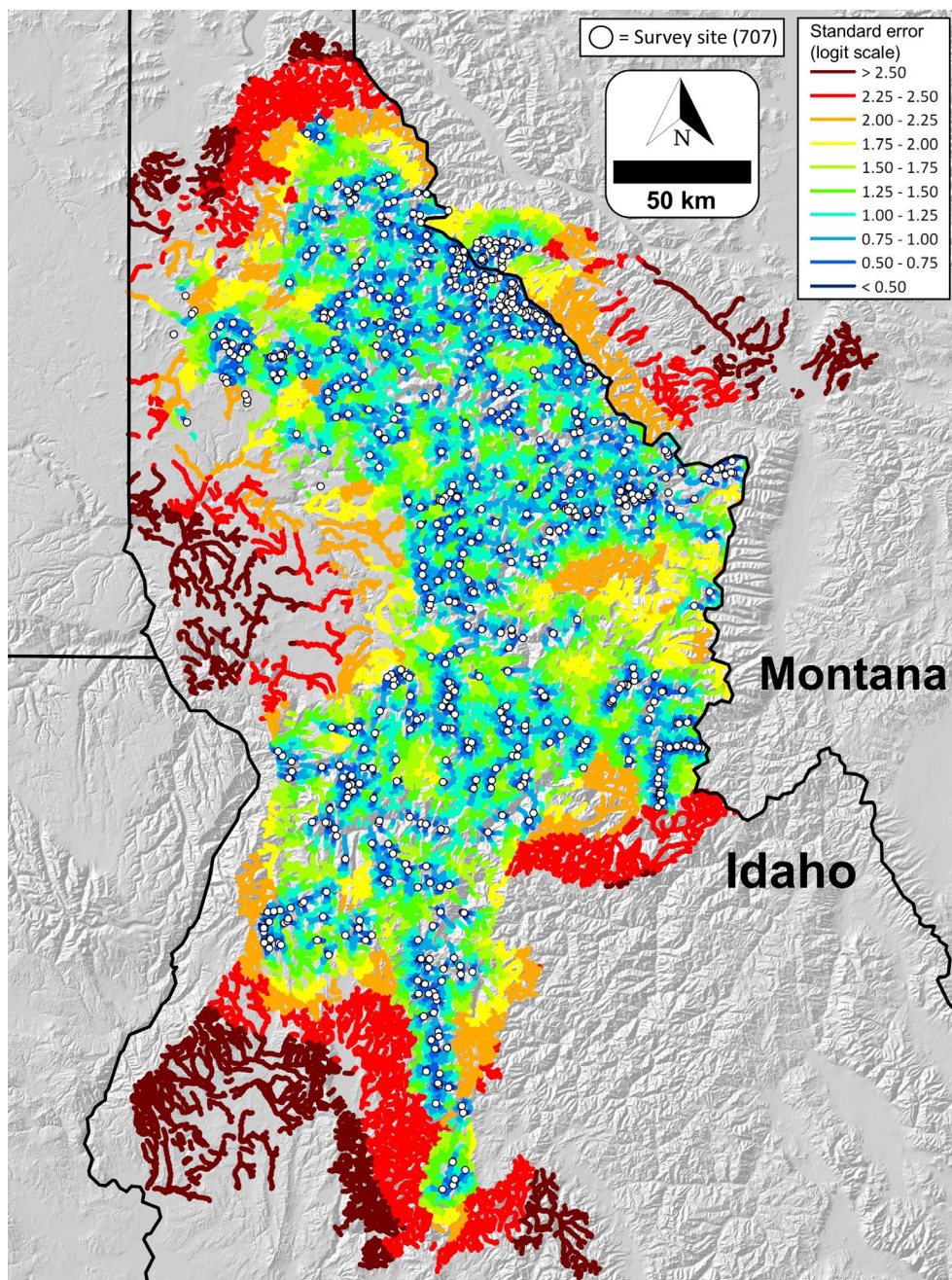


FIGURE 6 | Prediction uncertainty map for the Idaho giant salamander distribution based on standard errors of the logit values predicted by SSN Model 3.

limitations (Araújo et al. 2006; Mullen et al. 2010; Sepulveda and Lowe 2011).

4.3 | Monitoring Program Considerations

Given current and future ambiguities in IGS distributions, monitoring and inventory programs will be important for conservation efforts. The SDM predictions and survey dataset we compiled could be used to direct new sampling efforts to stream reaches which are most likely to support IGS and lack surveys, as has been done for other species (Fois et al. 2018; Neto et al. 2020; Isaak et al. 2022; Young et al. 2022; Winkowski et al. 2024). Uncertainty maps based on the prediction variances of the

SSNMs are another complimentary asset and could be used to further refine survey allocation to those areas where the distribution model is least precise. The pattern of spatial autocorrelation among IGS surveys indicates that sampling a few sites in many watersheds—rather than many sites within a few watersheds—should be more efficient for identifying occupied basins. A second phase of sampling at multiple sites within occupied basins could then refine upstream and downstream distributions (cf. Young et al. 2022). A portion of these surveys could extend upstream into reaches exceeding 20% slope to supplement our survey dataset and improve future revisions of the SDM. To monitor temporal trends in IGS distributions which may emerge from changes in habitat conditions, resurveys of historical sample sites and assessments of changes in occupancy status

could be employed (Tingley and Beissinger 2009; Comte and Grenouillet 2013). Targeting some resurveys at habitats where changes are anticipated, for example, unoccupied cold reaches upstream of extant IGS populations, could also be done to resolve key uncertainties about the ability of IGS to track shifting conditions or whether problematic lags were developing.

4.4 | Applying SSNMs

Spatial-stream-network models were valuable for developing information from the IGS datasets aggregated for this study but are more complex than non-spatial statistical techniques to implement. Moderately advanced skills in geographic information systems are required to preprocess datasets and develop the topological information among networked observation and prediction locations (Peterson and Ver Hoef 2014; Peterson et al. 2024). The SSNMs are also more computationally demanding than non-spatial models, although much less so with the updated estimation routines in the SSN2 package compared to the original SSN package (Ver Hoef et al. 2014; Dumelle et al. 2024). Moreover, the latest versions of SSN2 (versions $\geq 0.3.0$) have incorporated big data routines to further reduce model fit times (Ver Hoef et al. 2023). A separate issue is that SSNMs have larger recommended minimum data requirements because of the additional parameters that are estimated for the autocovariance structure. A simple structure requires two or three parameters, but a full mixed-model autocovariance with tail-up, tail-down, and Euclidean components has seven parameters (Peterson and Ver Hoef 2010; Ver Hoef and Peterson 2010). These are in addition to parameters for the fixed effects, so minimum sample sizes generally range from 50 to 100 based on model complexity and the recommendation of having ~ 10 observations for each parameter estimate (Van Belle 2011). As a result, the benefits that SSNMs provide will most often be realised for species with moderate to large numbers of observations obtained from multiple sources which in aggregate show some level of clustering and likelihood of spatial autocorrelation. Going forward, additional generalisation of the theory and software supporting SSNMs is also needed to expand the utility of the models for application to a wider breadth of ecological datasets. These could include datasets composed of presence-only surveys, mixed survey types with variable detection efficiencies that require integration, or datasets with information on multiple species suitable for Joint SDMs (Pollock et al. 2014; Guillera-Arroita et al. 2015; Fletcher et al. 2019; Gimenez 2024).

5 | Conclusions

Species distribution models and addressing the Wallacean shortfall (Hortal et al. 2015) are fundamental to improving species conservation efforts, but the large sample sizes required to ensure robust model parameterisation are often difficult to achieve for many stream organisms. Aggregating biological survey data from multiple sources is one potential solution, which is increasingly aided by the rapid growth and availability of massive species occurrence databases (Beck et al. 2014; Young et al. 2018) and the recent adoption of eDNA sampling techniques which provide reliable presence-absence information (Valentini et al. 2016; Bernos et al. 2023). However, because

composite samples derived from these sources will usually lack an overarching spatially balanced sampling design and often exhibit spatial clustering, specialised analytical techniques are required to provide unbiased inference. Spatial stream network models which incorporate autocorrelation among observations and account for the unique forms of spatial dependence on flow-directed networks appear particularly well suited to these datasets. As such, SSNMs may provide a means of developing significant amounts of new information from existing datasets to better resolve distributions, provide insight into habitat relationships, and help assess future risks for many stream-dwelling organisms of conservation concern.

Author Contributions

Daniel J. Isaak: conceptualization (co-lead); formal analysis (lead); visualization (lead); writing – original draft, revision, and editing (co-lead). **Michael Dumelle:** software (lead); writing – revision and editing (supporting). **Dona L. Horan:** visualization (supporting); data curation (supporting). **Daniel H. Mason:** methodology (supporting); data curation (supporting); writing – revision and editing (supporting). **Thomas W. Franklin:** methodology (supporting); data curation (supporting); writing – revision and editing (supporting). **David E. Nagel:** data curation (supporting). **Jay M. Ver Hoef:** software (supporting); writing – revision and editing (supporting). **Michael K. Young:** conceptualization (co-lead); methodology (lead); data curation (lead); writing – original draft, revision, and editing (co-lead); funding (lead).

Acknowledgements

We appreciate John Cossel's contribution of the Idaho giant salamander photograph used in Figure 1 and comments by Matt Fuller and Naomi Detenbeck during preparation of the manuscript. The views expressed in this article are those of the author(s) and do not necessarily represent the views or policies of the U.S. Environmental Protection Agency.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The IGS survey dataset, habitat covariates, and statistical files (annotated R code and .ssn landscape network object files) for replicating the analyses are available in Dryad at <https://doi.org/10.5061/dryad.h18931zxb>. These files are accompanied by a large format .pdf poster showing the IGS sample sites overlaid on a baseline occurrence probability scenario and an ArcGIS shapefile which contains the predictions and standard errors for use in conservation planning.

Peer Review

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.70085>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** ddi70085-sup-0001-Appendices S1-S5.docx. **Appendix S2:** ddi70085-sup-0001-AppendicesS1-S5.docx. **Appendix S3:** ddi70085-sup-0001-AppendicesS1-S5.docx. **Appendix S4:** ddi70085-sup-0001-AppendicesS1-S5.docx. **Appendix S5:** ddi70085-sup-0001-AppendicesS1-S5.docx.