**SUPPLEMENTARY INFORMATION**

**Title:** Dendritic prioritization through spatial stream network modelling informs targeted management of Himalayan riverscapes under brown trout invasion

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**Figure S1** The sampling locations for the River Tirthan (snow trout under invasion) and Asiganga (snow trout without invasion) shown in the upper and lower insets respectively.

**Comparisons of climatic similarities in Asiganga and Tirthan Basins**

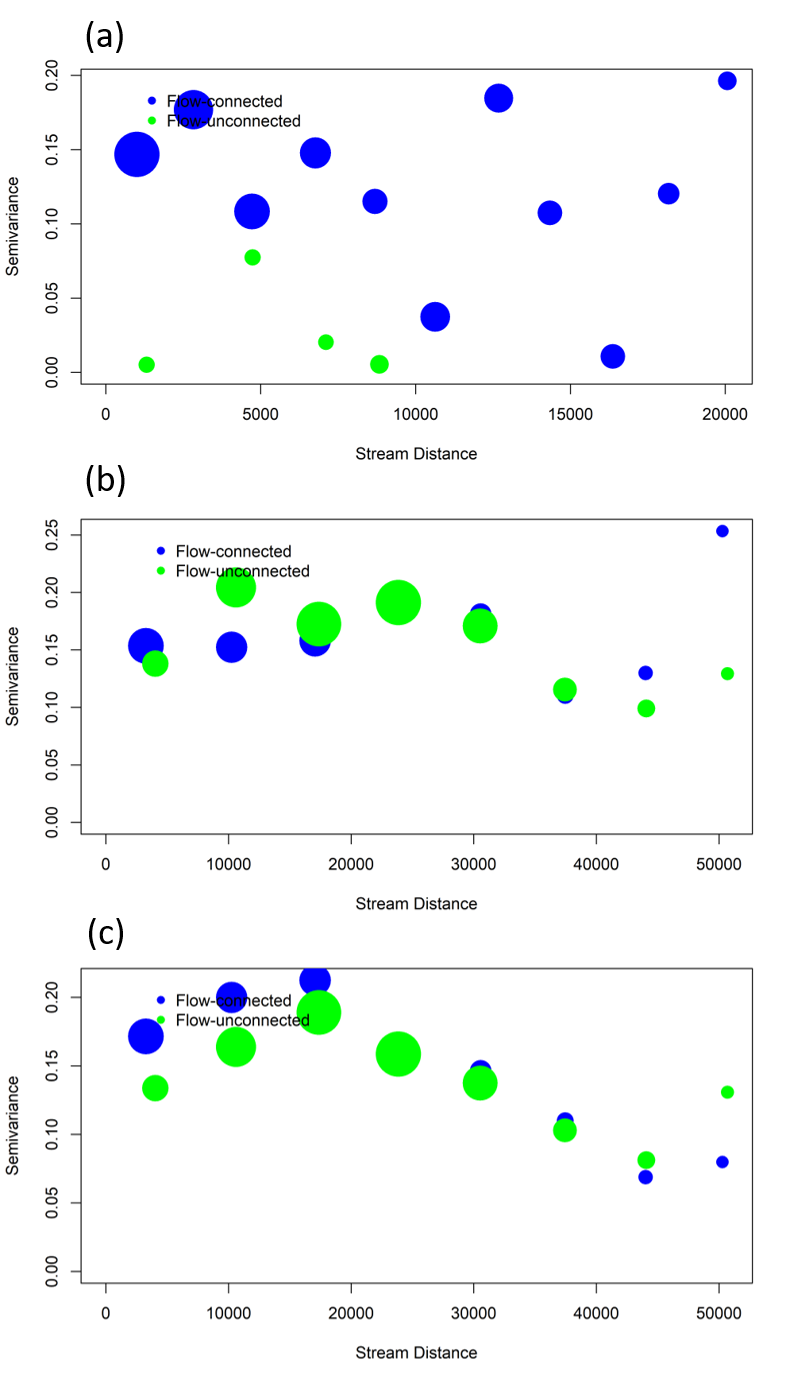
We also checked whether Asiganga and Tirthan share similar climatic profiles for which we compared mean annual temperatures (30 seconds resolution) extracted from the Worldclim Climate Database (version 2.1) (Fick and Hijmans, 2017) for both the basins. The mean annual temperature was chosen for comparison as it has been widely reported to be a prime factor governing the metabolism and hence the distribution of organisms on earth (Pearson and Dawson 2003; Brown, et al. 2004). We found both the basins, Asiganga and Tirthan to be climatically similar. The comparisons of mean annual temperatures across Asiganga and Tirthan basins revealed similar thermal gradients (Figure S2), with the values at the occurrence locations of snow trout ranging between 13.2-18.7 °C in Asiganga and 11.9-18.9 °C in Tirthan, respectively. Furthermore, the Welch’s t-test performed on mean annual temperatures at the occurrences failed to find evidence for any difference in the two basins at an alpha of 0.05 (Welch's t-test statistic=-2.5584, p=0.02).



**Figure S2.** Annual mean temperature gradients for Tirthan and Asiganga watersheds indicating similar thermal profiles available for the snow trout populations. Sampling locations are represented in the Figure S1.

**Torgegrams describing fluvial variography of presence probabilities**

We used torgegram-based fluvial variography to analyse spatial structuring in presence probabilities. The interpretations of the torgegram corroborated the covariance parameter estimates (as described in the main text). The lower semivariance (higher autocorrelation) at short lags among flow-unconnected sites as visualised in the torgegram for the snow trout in the non-invaded Asiganga (Fig. S3a), underpinned their distribution to be insignificantly governed by the topological positioning of sites. Noteworthily for the snow trout under invasion in Tirthan, we observed a distinct structure of autocovariance along the stream distance indicated with a relatively strong correlation at shorter lags for sites both connected and unconnected by flow, indicating their distribution being bi-directionally associated with the stream flow. The higher influence of TU models in the brown trout distribution was evident with the torgegrams showing a distinct pattern for the flow-connected sites (Fig. S3 b & c).



**Figure S3.** Torgegrams depicting spatial dependencies in the distribution of (a) native snow trout in Asiganga, (b) invasive brown trout in Tirthan and (c) native snow trout in Tirthan, after fitting the fixed effects. The torgegrams show the semivariance separately for the flow-connected and flow-unconnected sites. The sizes of the circles are proportional to the number of pairs in each bin of distance class.

**Table S1.** Environmental covariates used for spatial stream network modelling of invasive brown trout and native snow trout in Asiganga and Tirthan watersheds. The set of covariates selected post Spearman multicollinearity check (<0.85) is indicated by the symbol √.

|  |  |  |  |
| --- | --- | --- | --- |
| Predictor Covariates | Description | Covariates Chosen | |
| Asiganga | Tirthan |
| Bioclimatic |  |  |  |
| AMT | Annual Mean Temperature (°C) | √ | √ |
| TWM | Max Temperature of Warmest Month (°C) |  |  |
| TCM | Min Temperature of Coldest Month (°C) |  |  |
| APT | Annual Precipitation (mm) |  |  |
| Topological |  |  |  |
| AWElev | Area-weighted mean elevation (m) | √ | √ |
| AFVarea | Additive function |  |  |
| UPDist | Distance from river mouth (m) | √ |  |
| Sord | Strahler stream order (1-6) |  | √ |
| Soil Physical |  |  |  |
| Clay | Proportion of clay (< 0.002 mm) in fine earth fraction (g/kg) | √ |  |
| Sand | Proportion of sand (> 0.05 mm) in fine earth fraction (g/kg) |  | √ |
| Bulk density | Bulk density of fine earth fraction (particle size <2 mm) (cg/cm³) | √ |  |
| Soil Chemical |  |  |  |
| Soil pH | Soil pH (in water) (pHx10) | √ | √ |
| Total Nitrogen | Total Soil Nitrogen (cg/kg) | √ | √ |

**Variable selection, extraction and pre-processing of spatial layers**

As we also aimed at making predictions on points where no samplings were conducted, the covariates had to be available across all the sampling and prediction locations (Isaak et al. 2020), thus we chose explanatory variables available as geospatial data layers from accessible geostatistical products. We extracted bioclimatic variables (30 seconds resolution) reflecting annual trends in rainfall (annual precipitation-APT) and temperature (annual mean temperature-AMT) from Worldclim Climate Database, Version 2 (http://www.worldclim.org/) (Fick and Hijmans 2017). While annual precipitation dictates the energy flow of montane stream networks apart from cueing the fish spawning phenology (Poff et al. 2006; Goode *et al*. 2013), the annual mean temperature is a widely reported prime factor in governing metabolism and hence, the distribution of organisms on earth (Pearson and Dawson 2003; Brown *et al.* 2004). To account for thermal extremities across the species range, we used the maximum temperature of warmest month (TWM) and minimum temperature of coldest month (TCM), which are reported to govern snow trout distribution across Himalaya apart from triggering changes in lotic fish assemblage structure (Chea *et al.* 2017; Sharma *et al*. 2021b).

We extracted the spatial data on soil properties of river beds from the global gridded soil information platform – ‘SoilGrids’, which maps pedometric attributes based on soil profile data, climate, terrain morphology and land cover (Hengl et al. 2017). We obtained soil properties at a spatial resolution of 250 m and a depth interval of 0-5 cm to incorporate the effects of hyporheic transport on fluvial characteristics of the river. Soil properties of hyporheic zones control autochthonous nutrient enrichment and fuel zooplankton production, thus enhancing food subsidies for the fishes (Cardenas et al. 2016, Humphries et al. 2020). Further, the spawning site preferences for nest construction in brown trout and egg laying in snow trout are strongly dictated by the soil composition of hyporheic zones, which maintain continuous flow of oxygenated water over the eggs (Sharma 1991, Sear et al. 2016), thereby necessitating the inclusion soil data to refine our models. We thus extracted the layers of bulk density of fine earth fraction (particle size <2 mm) and the proportion of clay (< 0.002 mm) and sand (> 0.05 mm) in the fine earth fraction to account for the soil physical properties. Additionally, layers for soil pH in water and total nitrogen were also extracted for the chemical attributes of the river bed soil.

We then generated the predictor variables describing the stream topography, of which, the Strahler order for each stream segment was generated using a club of tools under the hydrology and map algebra toolsets of ArcGIS. Additionally, three geostatistical variables were generated from the LSN: (i) distance from river mouth (UPDist) to account for variability in species presence with topological positioning of sites on the stream network, (ii) accumulated value of area-weighted mean elevation (AWElev) to assess the effect of upstream reach contributing areas and segment mean elevations, and (iii) the additive function (AFVarea) value representing the product of proportional influences of the area-weighted mean elevation of downstream segments, thus accounting for the stream dendritic structure and the influence of confluences on species distribution, using STARS. Procedures entailing the subjective selection of environmental covariates for building SSN models per population (snow trout in Asiganga, snow trout in Tirthan, and brown trout in Tirthan), are presented in Tables S1-S3.

**Details on SSN models**

The SSN models are based on a recent geostatistical approach accommodating a mixture of spatial covariances specifically designed to account for multitude of spatial relationships across dendritic stream networks, including clustered observations (Peterson *et al.* 2007, 2013; Ver Hoef and Peterson 2010; Isaak *et al*. 2014; Ver Hoef *et al.* 2014). Unlike the conventional linear mixed-models which ignore stream topology, the geostatistical SSN models explain autocovariance between sites on a dendritic stream network, arising through three components (Ver Hoef and Peterson 2010). These components explain the spatial autocorrelations between sites as a function of either (i) the hydrologic distances between sites connected by flow (tail-up (TU) model)- indicating ‘passive’ movement of chemical particles or biota along the river flow, (ii) the hydrologic distances between sites irrespective of flow connectivity (tail-down (TD) model)- as is the case of biota swimming ‘actively’ against or with the flow, or (iii) straight-line distances between sites (Euclidean (EUC) model)- indicative of geological and topographic processes spanning across the basin which generate covariance irrespective of the river topological attributes (Ver Hoef *et al.* 2006). The SSN models are extensions of the standard linear models described by Ver Hoef and Peterson (2010) as:

Y= Xβ + zTD + zTU + zEUC + ε

Where, Y is the response variable vector, X is a design matrix of fixed effects (predictor variables), β are the parameters. The vectors zTD, zTU and zEUC are the autocovariance models for tail-down, tail-up and euclidean components, while ε is a vector of independent and normally distributed random errors. To deal with the dichotomous nature of streams we addressed the effects of confluences (in TU models) using the catchment area weighted mean elevations to apportion the autocovariance in the upstream branching segments (Peterson & Ver Hoef, 2010).

**Table S2.** Best 5 models selected through the ‘all possible regression’ for the native snow trout in Asiganga, the invasive brown trout in Tirthan with its co-occurring snow trout. Best models were selected using a parsimony between a low adjusted R2 and a Mallow’s Cp close to the number of predictors plus constant. The predictions of the SSN models of brown trout were used as one of the regressors to model its co-occurring snow trout, indicated as ‘Invasive’ in the table.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Population | Model Rank | Predictors | R2 | Adjusted R2 | Mallow’s Cp | AIC |
| Snow trout (Asiganga) | 1 | Total Nitrogen + Soil pH + Bulk density + Clay + AMT | 0.6301 | 0.5327 | 4.7045 | 25.3881 |
| 2 | Total Nitrogen + Soil pH + Clay + Sord + AMT | 0.6301 | 0.5327 | 4.7050 | 25.3889 |
| 3 | Soil pH + Bulk density + Clay + Sord + AWElev + AMT | 0.6423 | 0.5231 | 6.1194 | 26.5481 |
| 4 | Total Nitrogen + Soil pH + Bulk density + Clay + AWElev + AMT | 0.6409 | 0.5211 | 6.1882 | 26.6484 |
| 5 | Bulk density + Clay + AWElev + AMT | 0.5870 | 0.5044 | 4.7647 | 26.1402 |
| Brown trout (Tirthan) | 1 | Total Nitrogen + Soil pH + Sord + AWElev + AMT | 0.3680 | 0.3370 | 5.3481 | 120.8836 |
| 2 | Soil pH + sand + Sord + AWElev + AMT | 0.3681 | 0.3372 | 5.3222 | 120.8561 |
| 3 | Total Nitrogen + sand + Sord + AWElev + AMT | 0.3690 | 0.3381 | 5.1764 | 120.7005 |
| 4 | Soil pH + Sord + AWElev + AMT | 0.3651 | 0.3405 | 3.8034 | 119.3677 |
| 5 | Total Nitrogen + Sord + AWElev + AMT | 0.3653 | 0.3406 | 3.7807 | 119.3437 |
| Snow trout (Tirthan) | 1 | Total Nitrogen + Soil pH + AWElev + AMT + Invasive | 0.3020 | 0.2678 | 5.9465 | 120.6656 |
| 2 | Total Nitrogen + Soil pH + Sord + AWElev + AMT + Invasive | 0.3109 | 0.2699 | 6.6546 | 121.2883 |
| 3 | Total Nitrogen + Soil pH + Sand + Sord + AMT + Invasive | 0.3119 | 0.2710 | 6.5034 | 121.1259 |
| 4 | Soil pH + Sand + AWElev + AMT + Invasive | 0.3062 | 0.2722 | 5.3405 | 120.0218 |
| 5 | Soil pH + Sand + Sord + AWElev + AMT + Invasive | 0.3132 | 0.2724 | 6.3069 | 120.9146 |

**Table S3.** Cross validation statistics for the best non-spatial (nugget only) spatial stream network models for the native snow trout in Asiganga, invasive brown trout in Tirthan and its co-occuring snow trout in Tirthan. For each model, the best fixed effects retained are shown with stepwise backward elimination for the non-significant predictors indicated with every model. A low root mean squared prediction error (RMSPE) was used as a model selection criterion. The predictions of the SSN models of brown trout were used as one of the regressors to model its co-occurring snow trout, indicated as ‘Invasive’ in the table. The final models selected for each population are indicated in bold.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Population | Best model | RMSPE | Standardised MSPE | AIC | Bias | Standardised Bias |
| Snow trout (Asiganga) | **Clay\*\* + AMT\*\*\*\*** | **0.3483** | **0.9444** | **36.0473** | **0.0007** | **0.0009** |
| Brown trout (Tirthan) | Soil pH + Sord\*\*\* + AWElev\*\* + AMT\*\*\*\* | 0.4171 | 0.9990 | 160.6126 | 0.0000 | -0.0000 |
| **Sord \*\*\* + AWElev\*\* + AMT\*\*\*\*** | **0.4126** | **0.9974** | **155.6077** | **-0.0012** | **-0.0014** |
| Snow trout (Tirthan) | Soil pH + Sand + AWElev\* + AMT + Invasive\*\*\*\* | 0.4132 | 0.9867 | 167.4187 | -0.0006 | -0.0007 |
| Sand + AWElev\*\* + AMT + Invasive\*\*\*\* | 0.4085 | 0.9945 | 155.3543 | -0.0000 | -0.0000 |
| Sand + AWElev\*\* + Invasive\*\*\*\* | 0.4085 | 0.9945 | 155.3543 | -0.0000 | -0.0000 |
| **AWElev\*\* + Invasive\*\*\*\*** | **0.4075** | **0.9976** | **145.3002** | **-0.0008** | **-0.0010** |

The significance levels of predictors are indicated as 0 ‘\*\*\*\*’ 0.001 ‘\*\*\*’ 0.01 ‘\*\*’ 0.05 ‘\*’

**Table S4.** Cross validation statistics for the best mixed spatial stream network models for the native snow trout in Asiganga, invasive brown trout in Tirthan and its co-occurring snow trout in Tirthan. For each model, the best fixed effects represent the set of regressors selected from the previous step which were further filtered based on the high p values (>0.05) in the mixed model (Table S3). Model selection is based on a low root mean squared prediction error (RMSPE) and Akaike Information Criterion (AIC). The predictions of the SSN models of brown trout were used as one of the regressors to model its co-occurring snow trout indicated, indicated as ‘Invasive’ in the table.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Population | Model Rank | Fixed Effects | Autocovariance models | RMSPE | Standardised MSPE | AIC | Bias | Standardised Bias |
| Snow trout (Asiganga) | 1 | AMT + Clay | LinearSill.tailup + Epanech.taildown + Gaussian.Euclid + Nugget | 0.2634 | 1.0012 | 32.2922 | 0.0044 | 0.0085 |
| 2 | AMT + Clay | Epanech.tailup + Epanech.taildown + Gaussian.Euclid + Nugget | 0.2634 | 1.0013 | 32.2922 | 0.0044 | 0.0085 |
| 3 | AMT + Clay | Epanech.tailup + LinearSill.taildown + Gaussian.Euclid + Nugget | 0.2634 | 1.0012 | 32.2939 | 0.0044 | 0.0085 |
| 4 | AMT + Clay | Mariah.tailup + LinearSill.taildown + Gaussian.Euclid + Nugget | 0.2640 | 0.9654 | 32.5715 | 0.0042 | 0.0083 |
| 5 | AMT + Clay | Mariah.tailup + Epanech.taildown + Nugget | 0.2681 | 0.8131 | 33.3008 | 0.0011 | 0.0028 |
| Brown Trout (Tirthan) | 1 | AMT + Sord | Epanech.tailup + Mariah.taildown + Spherical.Euclid + Nugget | 0.3606 | 0.9389 | 93.0743 | 0.0058 | 0.0088 |
| 2 | AMT + Sord | Spherical.tailup + LinearSill.taildown + Gaussian.Euclid + Nugget | 0.3685 | 0.9207 | 97.4698 | 0.0097 | 0.0146 |
| 3 | AMT + Sord | LinearSill.tailup + Exponential.taildown + Spherical.Euclid + Nugget | 0.3583 | 0.8641 | 97.8428 | 0.0047 | 0.0071 |
| 4 | AMT + Sord | LinearSill.tailup + LinearSill.taildown + Cauchy.Euclid + Nugget | 0.3696 | 0.9637 | 101.9160 | 0.0064 | 0.0092 |
| 5 | AMT + Sord | Epanech.tailup + LinearSill.taildown + Cauchy.Euclid + Nugget | 0.3581 | 1.0125 | 102.4311 | 0.0051 | 0.0079 |
| Snow trout  (Tirthan) | 1 | AWElev + Invasive | LinearSill.taildown + Gaussian.Euclid + Nugget | 0.3676 | 1.0581 | 135.0417 | 0.0082 | 0.0110 |
| 2 | AWElev + Invasive | LinearSill.tailup + LinearSill.taildown + Gaussian.Euclid + Nugget | 0.3811 | 1.0120 | 147.2788 | -0.0004 | -0.0004 |
| 3 | AWElev + Invasive | LinearSill.tailup + LinearSill.taildown + Nugget | 0.3812 | 1.0105 | 143.5266 | -0.0004 | -0.0005 |
| 4 | AWElev + Invasive | Spherical.tailup + LinearSill.taildown + Nugget | 0.3812 | 1.0111 | 143.5271 | -0.0004 | -0.0005 |
| 5 | AWElev + Invasive | LinearSill.tailup + LinearSill.taildown + Spherical.Euclid + Nugget | 0.3812 | 1.0103 | 147.3570 | -0.0004 | -0.0004 |

**Table S5.** Covariance parameter estimates for the best mixed-models based on the root mean squared prediction error (RMSPE) and Akaike Information Criterion (AIC) for the native snow trout in Asiganga, invasive brown trout in Tirthan and its co-occurring snow trout in Tirthan. For each model, the moving-average functions (TU:tail-up, TD:tail-down and EUC: Epanechnikov) are provided with their partial sill and range estimates. The variance decomposition is provided in the Table 2 of the main manuscript.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Population | Covariance Model | Function | Estimate | |
| Partial sill | Range (m) |
| Snow trout (Asiganga) | TU | Linear-with-sill | ≈0.000 | 48478.658 |
| TD | Epanechnikov | ≈0.000 | ≈0.000 |
| EUC | Gaussian | 0.141 | 1218.140 |
| Nugget | - | ≈0.000 | - |
| Brown trout (Tirthan) | TU | Epanechnikov | 0.126 | 1163.846 |
| TD | Mariah | 0.051 | 219514.619 |
| EUC | Spherical | 0.012 | 929.788 |
| Nugget | - | ≈0.000 | - |
| Snow trout (Tirthan) | TU | - | - | - |
| TD | Linear-with-sill | 0.176 | 1106.082 |
| EUC | Gaussian | 0.010 | 40811.500 |
|  | Nugget | - | 0.013 | - |

**Detailed workflow of the methodology**

The complete workflow is presented under 3 major steps for clarity. All the procedures were implemented in the ArcGIS ver. 10.8. and R ver 4.0.2.

**A. Generation of stream rasters**

1. To ensure a topologically accurate stream raster generation, we used the Digital elevation model (DEM) raster at a resolution of 30 m for the study basins.
2. We used the *Hydrology* tools provided under the Spatial Analyst Toolbox in ArcGIS.
3. To create a depression less DEM, we filled the sinks in the DEM using the *Fill* tool.
4. The flow accumulation raster generated from the flow direction was classified with a lower break value of 1000 to ensure significant representation of the smaller order tributaries. The classified break point was then used to create a new flow accumulation raster using the *Raster Calculator*.
5. Stream orders were generated using the *Stream Order* tool using the flow accumulation raster created in step 4.
6. A vector of stream orders was created using the *Stream to Feature* tool.

**B. Spatial data generation using Spatial Tools for the Analysis of River Systems (STARS)**

For implementation of the Spatial Stream Network-SSN (Ver Hoef et al. 2014) in R, the pre-requisite files for the spatial stream data were generated using the STARS ver. 2.0.7 in ArcGIS. We followed the procedures detailed in the STARS tutorial available at: <https://www.fs.fed.us/rm/boise/AWAE/projects/SSN_STARS/downloads/STARS/STARS_tutorial_2.0.7.pdf> and procedures implemented by Mota-Ferreira and Beja (2021). We made subjective alterations in the workflow provided in the STARS tutorial based on the requirements of our study as detailed:

1. We visually examined the direction of flow in the stream raster generated in the step A. The *arrow at end* symbology was used to check for the topological details and digitization of the segments in the downward direction.
2. A landscape network (LSN) was used to build the geometrical details of stream reaches, nodes and the reach contribution area.
3. Node-to-node connectivity was delineated through edges representative of the flow paths.
4. Topological errors were checked with the:
5. Network topology: Source, confluence and outlet nodes were generated to visually examine the topology of the stream network using the *Check Network Topology tool* of the STARS toolkit.
6. Complex confluences identification: We checked for the confluences where three or more streams converge with their downstream node draining into a common edge using the *Identify Complex Confluences* tool.

No topological errors were identified in our stream networks, as such we proceeded to the generation of reach contributing areas (RCAs)

1. We used the *Create Cost RCAs* tool to generate the mesh of RCAs, which was checked for errors, multiple reach contributing areas for one edge which were corrected by dissolving the RCA grid to remove the duplicate polygons.
2. We calculated the RCA area (Km2) and mean elevation representing each stream segment using the RCA grid raster.
3. To weigh the relative influence of the upstream segments, we used a product of RCA area and mean elevation for each edge, which was then accumulated using the *Accumulate Values Downstream* tool.
4. We created prediction locations for the SSN modelling using the *Generate Points Along line* tool under *Sampling* in the *Data Management toolbox* by setting an interval of 200m.
5. Owing to common discrepancies in the sampling locations falling slightly away from the digitized stream networks, we snapped the sites to the nearest stream segments. We used the *Snap Points to Landscape Network Edges* tool with a search radius of 100m. As the method is performed statistically, we verified each site with manual inspections of the generated output.
6. Similar LSN feature was created for the prediction points with a search radius of 1m. the prediction points did not need ‘snapping’ as the points were generated from the river network file.
7. The accumulated product in step 10 was then assigned to the observation and prediction with the *Watershed Attributes* tool.
8. The *Upstream Distance– Sites* and *– Edges* tools were used to compute the distance of the sites and segments to the outlet.
9. The spatial weights needed to fit the SSN were performed as a three-tier procedure. The first two steps were undertaken using STARS in ArcGIS, while the third step was performed in R using the SSN package. In STARS:

i) We used the *Segment PI* tool, which calculates the relative influence of each segment on the segment directly downstream with respect to the accumulated product value.

ii) The additive function values (AFV) were then calculated for each site and edge. The additive function value basically is a product of the segment PIs of all the segments downstream, including that of the segment for which AFV is being calculated. The AFV of any prediction or observation site is the AFV value of the segment on which it is placed. We used the *Additive Function – Edges* and *– Sites* tools for the calculations of AFV.

1. The above series of steps were repeated for both the basins separately. Once the LSN was prepared, we incorporated the environmental covariates for each species separately before exporting the SSN object.
2. Rest of the procedures were implemented with codes written in R proposed by Hoef *et al.* 2014.

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