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# Dendritic prioritization through spatial stream network modeling informs targeted management of Himalayan riverscapes under brown trout invasion

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## Abstract

1. With the concept of 'riverscapes' long pending to be acknowledged in the 'landscape-centric' legislative framework of Himalayan nations, conservation of native riverine species stays practically unheeded. This necessitates urgent prioritization of stream networks to conserve the lotic taxa under invasion pressures. Himalayan riverscapes are pervaded with the invasive-exotic brown trout *Salmo trutta*, posing serious threats to the co-occurring native, the snow trout *Schizothorax richardsonii*.
2. Using intensive surveys (218.7 km) and geostatistical stream network models ($n = 537$), we contrasted snow trout in two stream networks with and without invasives, for assessing differences in their spatial distribution.
3. Our models indicate invasion-induced relegations of natives from the river mainstem into headwaters, with large sections of mainstem occupied by invasives. Furthermore, a concerningly small percentage of potential habitat left for natives to occupy in the mainstem is threatened, where a 100% overlap of native and invasive trout distributions is predicted.
4. With a higher presence probability for the natives in headwaters of invaded watershed as compared to the non-invaded watershed, we highlight the headwater streams as potential refugia for the natives under invasion.
5. *Synthesis and Applications*. Our approach of basin-scale dendritic prioritization provides immediate management solutions to tackle brown trout invasion threats in Himalaya. We inform decisions on delineation of headwaters as invasion refugia for native fish, with assisted recovery of their fragmented populations in the river mainstems through targeted management of invasives.

KEYWORDS

freshwater ecosystems, headwaters, Himalaya, invasion refugia, invasive species management, native-invasive overlaps, riverscape topology, stream network models

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## 1 | INTRODUCTION

Reaching habitats of retreat is critical for native species under invasion, more so, when the invasive species are aggressively territorial (Kirk et al., 2018). This facilitates a potential recolonization of natives, when favourable environments return (Mota-Ferreira & Beja, 2020). However, access to such invasion refugia is strongly contingent upon the native species' dispersal ability and direction (Berger-Tal et al., 2016; Hoare, 2007). The rivers, nonetheless, are network-constrained environments (Lois & Cowley, 2017), where in-stream dispersal is constrained by network topology and flow directionality (Rubenson & Olden, 2017). This is quite unlike seascapes or landscapes, which proffer multidirectional range shift opportunities (Lenoir et al., 2020; Pinsky et al., 2020). Understandably, there is surmounting evidence on invasions in riverscapes being much more detrimental than terrestrial or marine realms (Moorhouse & Macdonald, 2015; Ricciardi & Kipp, 2008; Sala et al., 2000) as restricted movement pathways lead to higher native-invasive conflict zones resulting in native species' relegations, range contractions and at times, local extinctions (Fausch & White, 1981; Kirk et al., 2018; McKenna et al., 2013). Identifying directionalities of species' movements in invaded riverscapes is thus crucial for prioritizing stream networks for effective management of native species (Filipe et al., 2017; Mota-Ferreira & Beja, 2020).

Native species movement to seek invasion refugia is evident when riverscapes are invaded by an interference competitor like the brown trout *Salmo trutta* (Lobón-Cerviá & Sanz, 2018), which is ranked among the top 30 worst invasive species on the globe (McIntosh et al., 2012). Brown trout has expanded beyond its native Eurasian range to pervade high-elevation stream networks worldwide (Lobón-Cerviá & Sanz, 2018; McIntosh et al., 2012). Its agonistic behaviour to occupy energy-efficient foraging and resting sites (Piccolo & Watz, 2018) spares enhanced energy reserves for paced-up growth, eventually escalating its establishment rates and in the process, relegating native fish out from suitable sites of rest, a critical and scarce resource (Fausch & White, 1981; Hoxmeier & Dieterman, 2016). With surmounting evidences of native ecosystem collapses resulting from its invasions in most mountain systems (Boddy, 2018; Fausch & White, 1981; Kirk et al., 2018; Ohlund et al., 2008), the condition in Himalayan stream networks is assumingly detrimental owing to limited research available on its interactions with natives.

One of the most primitive natives that co-evolved with Himalayan orogeny is the snow trout *Schizothorax richardsonii*, a fish species representative of high-altitude stream networks (He & Chen, 2006). Categorized as Vulnerable on the IUCN Red List (Vishwanath, 2010), snow trout currently faces serious threats owing to ongoing hydropower developments (Rajvanshi et al., 2012), flow alterations (Grumbine & Pandit, 2013), and as per recent evidences, by competitive interactions with invasive brown trout (Sharma et al., 2021a). Although research ranging from its phylogenomics to ecology and life history has upsurged in the recent years (Kamalam et al., 2019; Regmi, 2019; Sharma et al., 2021a, 2021b), the effect of invasion on snow trout distribution stays inexplicit. This is concerning, as delineating invasion refugia for a species is rather challenging unless its distribution is well studied.

Distribution in dendritic riverscapes is governed by a combination of stream geology (Strahler, 1950; Townsend, 1996), in-stream autocovariances (Peterson & Ver Hoef, 2014; Peterson et al., 2007) and species ecology (Bruckerhoff et al., 2019) apart from interactions with invaders (Filipe et al., 2017). Modeling of such distributions thus requires a riverscape-based conjoined approach. Globally however, native freshwater fauna has been largely managed with techniques developed for terrestrial environments which are not optimized for streams (Chee & Elith, 2012; Van Looy et al., 2014), consequentially undermining the existing invasion threats in riverscapes. We thus stand at an inadequate protocol for freshwater species management, more so for the Himalayan nations, where conservation policies are not framed to address inherent riverscape processes structuring the native-invasive interactions.

How efficient can native species conservation be in invaded riverscapes, thus strongly depends on addressal of in-stream processes. We thereby utilize our intensive sampling with spatial stream network (SSN) modeling approach to account for hydrologic spatial dependencies in geophysical and native-invasive interaction dynamics. By comparing the spatial distribution of native snow trout in Himalayan stream networks invaded and non-invaded with brown trout, we set out to answer the questions (a) whether invasion brings any evident differences in distributional patterns of the natives, if so, (b) does the dendritic structure of river network govern their spatial segregation? By answering these questions, we aim to highlight potential invasion refugia for natives in high-altitude Himalayan streams. Furthermore, by identifying streams of highest native-invasive overlaps, we delineate well-defined spatial stream networks for informed invasive species management and control.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

The watersheds namely Asiganga (N30°45′–30°55′, E78°25′–78°34′) and Tirthan (N31°31′–31°43′, E77°13′–77°38′) are located in western Himalaya characterized by high elevations (>1,000 m), whence the region witnesses snowfall (Figure S1). They represent the last few free-flowing Himalayan rivers and major part of their networks fall under protected area boundaries, thus proffering unaltered habitats for freshwater biota. These watersheds share similar elevational ranges (Asiganga: 1,158–4,400 m, Tirthan: 990–4,880 m) and temperature profiles (Figure S2). While Tirthan harbours a snow trout population which co-occurs with invasive brown trout, snow trout in Asiganga occurs in complete absence of brown trout.

### 2.2 | Field sampling

Fishes were sampled monthly from 2016 to 2019, where we took a downstream to upstream approach progressing from the river mouth up to its origin. Sampling in both watersheds was conducted by trekking along the stream beds covering a total river stretch of 218.7 km. We followed an intensive design with sampling points placed every 500 m for higher-order streams (4th and higher) and 200 m for lower orders (3rd and lower), as the latter often covered a stream length of <500 m. In total, 25 and 108 sampling points were sampled in Asiganga and Tirthan respectively (Figure S1). At each sampling location, a 100 m stream reach was surveyed where we estimated the presence/absence of snow trout and brown trout using cast nets (10 and 30 mm mesh sizes), ensuring an equal sampling effort.

## 2.3 | Stream geoprocessing and environmental covariates selection

We generated topologically accurate stream rasters, using AW3D30 (Advance Land Observation System World 3D –30 m Digital Elevation Model; JAXA, 2015) at a horizontal resolution of 30 m mesh. Hydrological distances were calculated and geometrical details of stream reaches, nodes and reach contributing areas—landscapes surrounding individual reaches—were delineated to create landscape networks (LSNs) for each watershed. As per our study requirements, we made subjective alterations (Supplementary Information) in the workflow proposed by Peterson (2019) to build the LSNs using Spatial Tools for the Analysis of River Systems (STARS) toolset version 2.0.7 (Peterson, 2019; Peterson & Ver Hoef, 2014) in ArcGIS version 10.8 (ESRI). In addition to the sampling locations, we generated 812 and 2,781 prediction points across stream networks of Asiganga and Tirthan, respectively, evenly spaced at a stream distance of 200 m. The same pre-processing was performed for sampling and prediction locations in each watershed. To build the SSN models, we used a total of 13 environmental covariates, representing an envelope of climatic, topographic and soil attributes potentially influencing the distribution of our target species (Table S1). Relatively, uncorrelated predictor variables (Spearman correlation coefficient, $r < 0.85$) were selected for incorporation in the final LSN object for each species. Additionally, spatial Torgegrams were used to check for the presence of spatial autocorrelation (Zimmerman & Ver Hoef, 2017) separately for sites connected and unconnected by flow as a function of increasing hydrologic distance (Figure S3).

## 2.4 | Building spatial stream network models

As the number of variables still remained large post-multicollinearity check, we performed a two-step procedure to filter a final subset of predictors affecting species presence. First, we used all-possible regression choosing the best set based on a high adjusted $R^2$ and a Mallow's Cp close to the number of predictors plus constant (Olejnik et al., 2000) using the package OLSRR (Hebbali, 2020). Second, best five sets of covariates were used to build non-spatial models (nugget-only model) maintaining the assumption of spatially independent residual errors and using no autocovariance structure in the SSN package (Ver Hoef et al., 2014). The best non-spatial model was then chosen based on lowest root mean squared prediction error (RMSPE; Ver Hoef et al., 2014). We further dropped the non-significant variables ($p > 0.05$) from the best non-spatial model using a stepwise-backward elimination procedure and used the final set of predictors as fixed-effects component of the SSN mixed model (spatial model). We used the fixed-effects component with a random component—attributing to the spatial dependencies and covariance structure in the stream network—to build the SSN mixed models. For details on data pre-processing and model building, see Supplementary Information.

We fit a total of 537 SSN mixed models including every possible combination of spatial components namely Tail-up (TU), Tail-down (TD) and Euclidian (EUC), in random errors and different moving average functions (Peterson & Ver Hoef, 2010). We used linear-with-sill, spherical, exponential, mariah and epanechnikov moving average constructions for TU and TD models, while spherical, exponential, Gaussian and Cauchy for EUC models, assuming stream networks as dendritic and not braided (for details on moving average constructions, see Ver Hoef et al., 2014). We used binomial link function within the SSN package for model fitting (Ver Hoef et al., 2014). The range parameters were used to capture spatial patterns of intermediate scale undetected by explanatory variables. The relative strength of each component was assessed with its partial sill while any possible measurement errors or variability at finer resolution than the closest measurements on stream (<200 m) was accounted for by the nugget effect (Cressie, 1993). The model minimizing the RMSPE was chosen as best model. We estimated the bias using RMSPE and assessed model performance from predictions through leave-one-out cross validation (Ver Hoef et al., 2014). We retained all autocovariance models selected in the best spatial model, regardless of their partial sill values (Table S5). This was done to elucidate the role of individual autocovariance functions and make the model predictions ecologically meaningful (Frieden et al., 2014; Garreta et al., 2010). We performed variance decomposition on covariance matrices of SSN models to quantify the variance not explained by the fixed effects, by apportioning it into the relative fractions of residual variance explained by TU, TD and EUC functions (having a spatial structure), and the nugget (representing the independent error). Additionally, spatial models per species were compared with their non-spatial models to examine differences in their predictive performance.

The predictions for both species were mapped across the stream network using universal kriging (Cressie, 1993). We used predicted distribution of brown trout as an additional regressor along with other environmental variables to build SSN models for snow trout in the invaded basin. This was done to investigate the distributional association of native and invasive trout. All the analyses were performed in R (R Core Team, 2020).

## 3 | RESULTS

Of the 25 and 108 sampling points covered in Asiganga and Tirthan, our field efforts indicate a widespread distribution of snow trout when free from invasion, with its presence recorded in 52% (*n* = 13) sites in Asiganga. Whereas, in the invaded Tirthan, snow trout was recorded in 34.25% (*n* = 30) of the sites. The invasive brown trout was found to be much more prevalent (52.78%; *n* = 57) in Tirthan.

### 3.1 | Environmental regressors governing native-invasive spatial structuring

Based on the significance levels, sets of environmental covariates used in non-spatial models were retained for the mixed models of both snow trout populations unlike those of brown trout. The estimates and significance scores, however, differed among both model types for each population (Table 1). The parameter estimates for fixed-effects component in SSN mixed models indicated a positive influence of annual mean temperature and clay on presence probability of natives in non-invaded watershed (Table 1). The natives co-occurring with brown trout contrarily were majorly governed by the presence of the invasive and area-weighted mean elevation, indicative of a greater presence probability in higher elevations with an evident overlap with invasive brown trout. While Strahler stream order and annual mean temperature positively affected the presence probability of brown trout, area-weighted mean elevation affected it negatively, indicating its preference for higher-order streams at lower elevation in Tirthan (Table 1).

### 3.2 | Variance decomposition and performance of geostatistical SSN models

The spatial models fit separately for each population distinctly outperformed their non-spatial models in terms of RMSPE (Tables S3 and S4). This was further evident from a relatively small variance in presence probability explained by non-spatial models (natives-Asiganga: 57.83%, natives-Tirthan: 30.02%, invasive brown trout: 36.38%) as compared to spatial models (natives-Asiganga: ≈100%, natives-Tirthan: 94.38%, invasive brown trout: ≈100%). Furthermore, the variance decomposition for all spatial models revealed a higher variance explained by the autocovariance moving-average functions (random effects) vis-à-vis the environmental covariates (fixed effects; Table 2), underpinning the explicit role of spatial autocorrelations in structuring the distribution of all populations in our study. While fixed and random effects contributed 42.34% and 57.66%, respectively, in determining the presence probability of snow trout in Asiganga, the Tirthan snow trout was majorly governed by random effects contributing to 74.75% of the total explained variance. The invasive brown trout presence probability likewise was found to be majorly (80.47%) explained by random effects (Table 2). Cross-validation statistics of all spatial models indicated relatively small bias, with the model performance of snow trout in Asiganga

**TABLE 1** Parameter estimates for non-spatial and mixed SSN models for snow trout in Asiganga, brown trout and its co-occurring snow trout in Tirthan. Estimates (*B*), standard errors (*SE*) and *p*-values (*p*) of the regression coefficients are provided for each model. The predictions of the geostatistical mixed models of brown trout were used as one of the regressors to model the snow trout in Tirthan with the regressor indicated as 'Invasive'

| | | Intercept | | | AMT | | | AWElev | | | Sord | | | Clay | | | Invasive | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Population** | **Models** | ***B*** | ***SE*** | ***p*** | ***B*** | ***SE*** | ***p*** | ***B*** | ***SE*** | ***p*** | ***B*** | ***SE*** | ***p*** | ***B*** | ***SE*** | ***p*** | ***B*** | ***SE*** | ***p*** |
| Snow trout (Asiganga) | Non-spatial | −2.441 | 0.756 | <0.05 | 0.070 | 0.017 | <0.05 | | | | | | | 0.009 | 0.004 | <0.05 | | | |
| | Mixed | −2.768 | 1.036 | <0.05 | 0.081 | 0.025 | <0.05 | | | | | | | 0.010 | 0.005 | <0.05 | | | |
| Brown trout (Tirthan) | Non-spatial | −0.554 | 0.163 | <0.05 | 0.047 | 0.091 | <0.05 | ≈−0.000 | ≈0.000 | <0.05 | 0.184 | 0.058 | <0.05 | | | | | | |
| | Mixed | −0.310 | 0.211 | 0.15 | 0.041 | 0.015 | <0.05 | | | | 0.088 | 0.041 | <0.05 | | | | | | |
| Snow trout (Tirthan) | Non-spatial | 0.003 | 0.068 | 0.97 | | | | ≈0.000 | ≈0.000 | <0.05 | | | | | | | 0.733 | 0.109 | <0.05 |
| | Mixed | 0.059 | 0.120 | 0.02 | | | | ≈0.000 | ≈0.000 | <0.05 | | | | | | | 0.649 | 0.154 | <0.05 |

comparatively better than that of Tirthan. The models for brown trout and its co-occurring snow trout performed almost in equivalence (Table 3).

## 3.3 | Autocovariance structures and Torgegrams

We found the TD linear-with-sill autocovariance structure as the major determinant of snow trout distribution in Tirthan (partial sill = 0.176, range = 1,106.081 m), indicating their explicit movement both along and against the flow (Table 2), unlike that in Asiganga where sites in close proximity seemingly shared similar presence probabilities, evident with major variance explained by the EUC Gaussian autocovariance (partial sill = 0.141, range = 1,218.140 m), with negligible effects of TU and TD models (Table S5). Conversely, the variance in brown trout presence probability was majorly structured by the TU epanechnikov function (partial sill = 0.126, range = 1,163.846 m) as well as TD mariah (partial sill = 0.051, range = 219,514.619 m) autocovariance models, indicative of their distribution being majorly flow governed. Furthermore, our interpretations of Torgegrams corroborated the covariance parameter estimates suggesting occurrence of spatial dependencies in model residuals (Figure S3).

## 3.4 | Predictions on the spatial stream networks

We mapped the SSN model predictions and associated uncertainties for the populations of snow trout (Figure 1) and brown trout (Figure 2). While the distribution of brown trout was spatially contiguous across Tirthan, that of its co-occurring snow trout was evidently disjunct. In similitude to the brown trout, the snow trout in non-invaded Asiganga was contiguously distributed.

For snow trout in non-invaded Asiganga, 76.77% of the total prediction points in fourth-order streams formed the highest 30% quantile predictions (>0.70 presence probability; Figure 3). Contrarily, for snow trout in the invaded Tirthan, only 17.65% of fourth-order points showed highest quantile predictions, which were further lower for fifth order (16.56%). The absence of fifth-order streams in Asiganga network, however, restricted us from making comparisons among presence probabilities of natives with and without invasion therein (Figure 3). Noteworthily, while the presence probability of snow trout was relatively low in mainstems of Tirthan (fourth- and fifth-order streams), brown trout in mainstem was predicted with distinctly high percentages (fourth order: 80.15%; fifth order: 81.60%; Figure 4).

Unlike mainstem, the headwaters (second and third orders) in our best-fit SSN models showed greater presence probability for snow trout in invaded (second order = 0.489; third order = 0.481), as compared to the non-invaded watershed (second order = 0.451; third order = 0.446) which were predicted with lower medians of probability distributions (Figure 3). Brown trout presence probabilities (second order = 0.493; third order = 0.523), however, dominated that of its co-occurring snow trout (Figure 4), indicating a higher prevalence of brown trout in headwaters as well. Brown trout dominance was further underpinned through highest 30% quantile predicting a 100% overlap of brown trout and its co-occurring snow trout in fourth- and fifth-order streams of Tirthan, with a considerable, albeit lower overlap in second and third orders (61.54% and 85.71%, respectively). Although we present the results for first-order streams in Figures 3 and 4, we refrain from making statistical comparisons for the same, as majority of them are dry or glaciated, thus uninhabitable for fishes.

The LOESS smoothened GAM fitted on our model predictions revealed a distinctly low presence probability for snow trout at lower elevations (<2,200 m) in Tirthan, where brown trout was predicted with higher presence. In Asiganga contrarily, snow trout was predicted with highest presence probabilities in the same elevational range (Figure 5). Furthermore, we found a higher presence

**TABLE 2** Variance decomposition indicating the selected covariance structure in the final SSN mixed-models for snow trout in Asiganga, brown trout and its co-occurring snow trout in Tirthan. The percentage of variance contributed by fixed effects and each random effect in the mixed-models and the function selected for every random effect component is indicated for all the models

| | | Random effects (Autocovariance models) | | | |
|---|---|---|---|---|---|
| Population | Fixed effects | Tail up | Tail down | Euclidean | Nugget |
| Snow trout (Asiganga) | 42.338 | ≈0.00 (Linear-with-sill) | ≈0.00 (Epanechnikov) | 57.662 (Gaussian) | ≈0.00 |
| Brown trout (Tirthan) | 15.531 | 56.625 (Epanechnikov) | 22.362 (Mariah) | 5.483 (Spherical) | ≈0.00 |
| Snow trout (Tirthan) | 15.629 | | 74.691 (Linear-with-sill) | 4.060 (Gaussian) | 5.620 |

**TABLE 3** Cross-validation statistics of the geostatistical mixed SSN models for snow trout in Asiganga, brown trout and its co-occurring snow trout in Tirthan. The RMSPE denotes root mean-squared prediction error, MSPE denotes the mean-squared prediction error

| Population | RMSPE | Standardized MSPE | Bias | Standardized bias |
|---|---|---|---|---|
| Snow trout (Asiganga) | 0.2634 | 1.0012 | 0.0044 | 0.0085 |
| Brown trout (Tirthan) | 0.3606 | 0.9389 | 0.0058 | 0.0088 |
| Snow trout (Tirthan) | 0.3676 | 1.0581 | 0.0082 | 0.0110 |

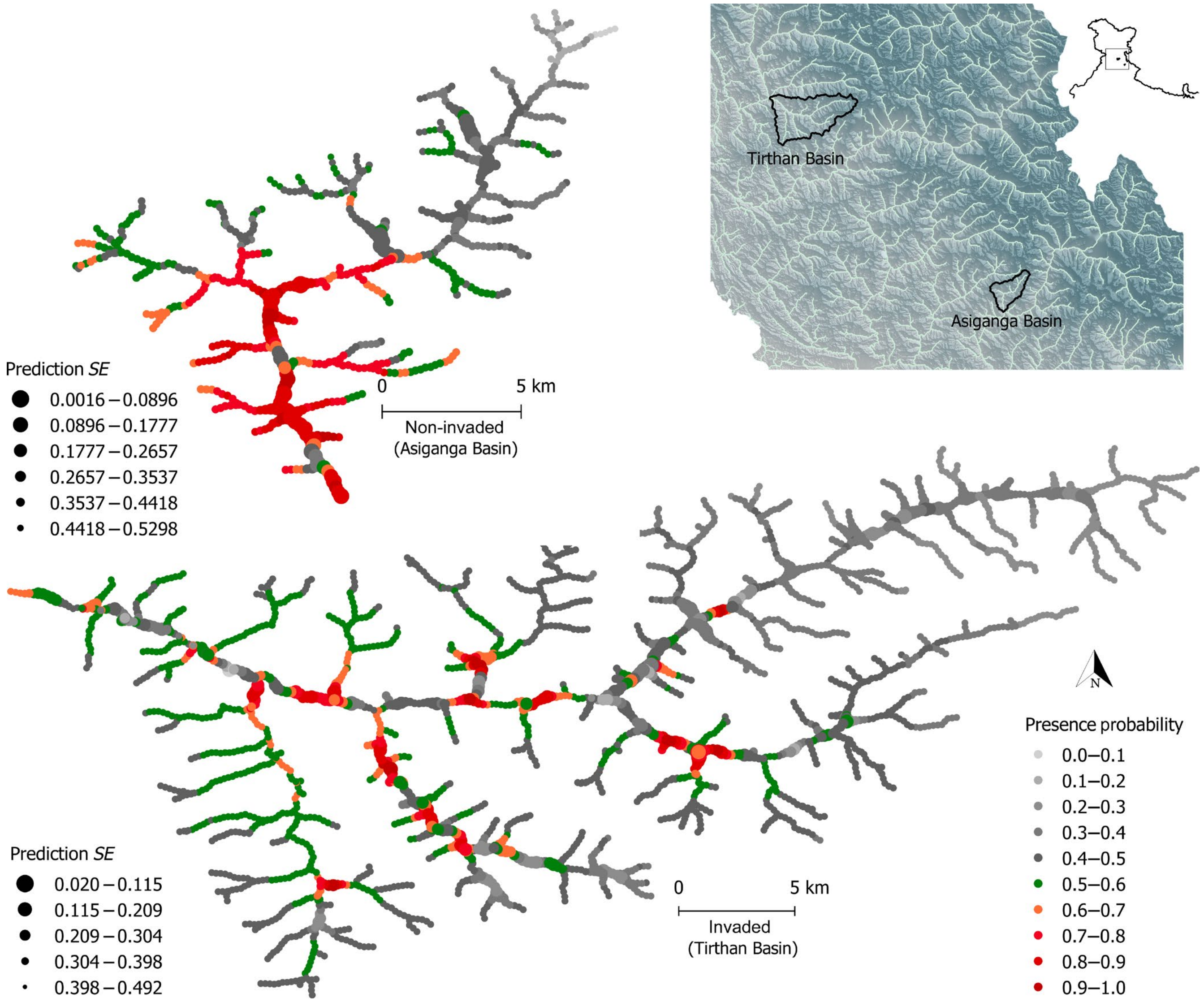


**FIGURE 1** Spatial stream network model predictions for native snow trout in non-invaded (upper panel) and invaded (lower panel) watersheds, respectively. The universally kriged potential distribution and associated uncertainties (Prediction SE) indicate a spatially contiguous distribution of snow trout without invasion

probability of snow trout in Tirthan than in Asiganga at an elevation >3,100 m.

## 4 | DISCUSSION

Our results indicate a strong role of stream network topology in structuring the distribution of native snow trout and invasive brown trout populations; nonetheless, biotic interaction likely plays a role in governing their spatial segregation. Our models predict that a river free from exotic-invasives proffers an undisrupted spread of natives throughout the stream network, with predominant distribution in the river mainstem, that is, fourth and fifth orders, as compared to its headwaters, that is, second and third. Conversely, in invaded networks, our predictions indicate invasion-induced relegations of native snow trout from the mainstem towards headwaters, with a concerningly small percentage of potential habitat left for them in the mainstem. What raises further concern is that natives in remnant mainstem habitats are predicted to exhaustively overlap with invasives, warranting urgent prioritization of these river channels. Furthermore, our approach combining the biotic interactions and geostatistical models aids in stringent identification of invasion refugia.

Unaltered stream networks provide a high degree of habitat heterogeneity, thus promoting the coexistence of strongly interacting natives and invasives (Cantrell et al., 2007). Our selection of unaltered watersheds thus allows clear interpretability of native-invasive spatial interactions. Although classical models for biological invasions suggest that homogeneous landscapes favour invasion success (Kareiva et al., 1990; Okubo, 1980; Skellam, 1973), most invasions in fact, occur in heterogeneous environments (Lutscher & Musgrave, 2017; Melbourne et al., 2007), more so, for lotic

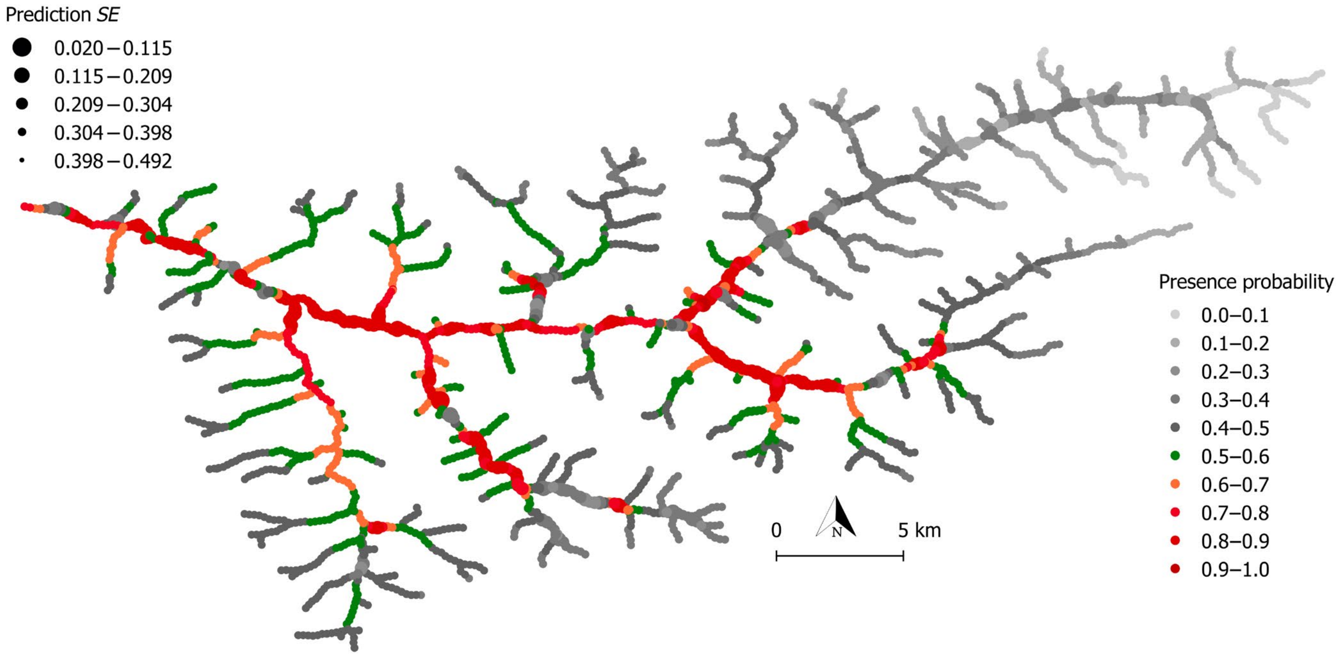
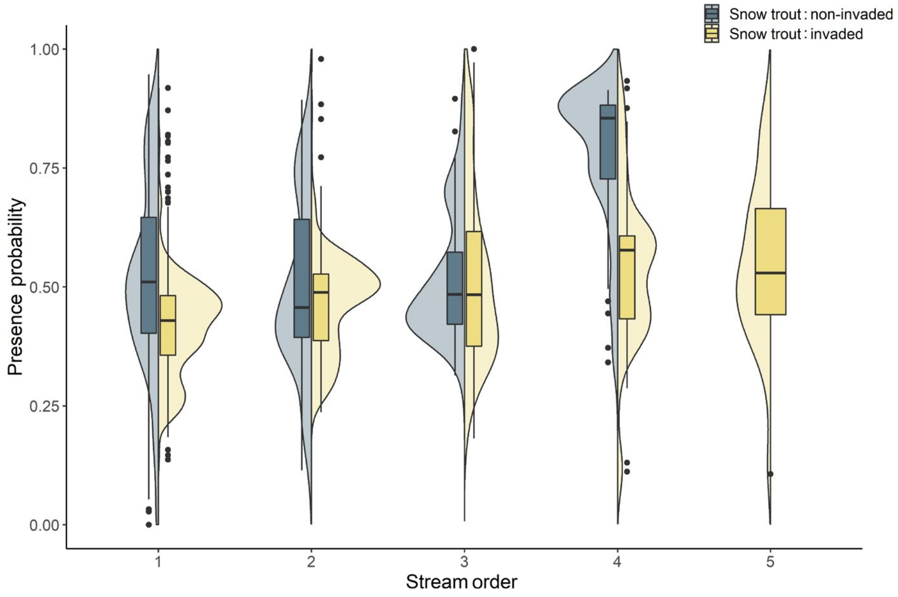


**FIGURE 2** Spatial stream network model predictions for invasive brown trout in Tirthan watershed. The universally kriged potential distribution and associated uncertainties (Prediction SE) indicate its spatially contiguous distribution across the mainstem, unlike its co-occurring snow trout (Figure 1 lower panel), where a disjunct distribution is evident

**FIGURE 3** Vertical violin plots for predicted presence probabilities of snow trout in non-invaded and invaded watersheds. The predictions of the spatial stream network models are separately plotted per stream order (1–5) and juxtaposed for both populations. The boxes and whiskers represent interquartile range and 95% confidence intervals, respectively, while the shape of violins indicates the frequency of kernel distribution



ecosystems. Environmental heterogeneity and invasive species presence, thus collectively influence the native species distribution (Vander Zanden et al., 2017). In congruence, our SSN models indicate the distribution of natives to be contingent upon the combined effects of environmental variations and invasive species presence. We predict a positive association of the invasive brown trout and their co-occurring native snow trout in Tirthan, indicative of their common habitat preferences. With brown trout in other invaded networks circumstantially evidenced to be detrimental for natives when their habitat preferences overlap (Ellender & Weyl, 2014; Hasegawa & Maekawa, 2008; McIntosh et al., 1992), our results raise concerns on the conservation of native species in Himalaya. Furthermore, best fit model parameters for invasives in Tirthan and natives in uninvaded Asiganga indicate their positive association with mean annual temperature, and thus, their analogous preferences for streams with relatively warmer temperatures than the cold headwater reaches.

Although brown trout is coldwater species, what makes them opt for rather cool-to-warm stretches in their invaded habitats? These salmonids in their non-native montane rivers are documented

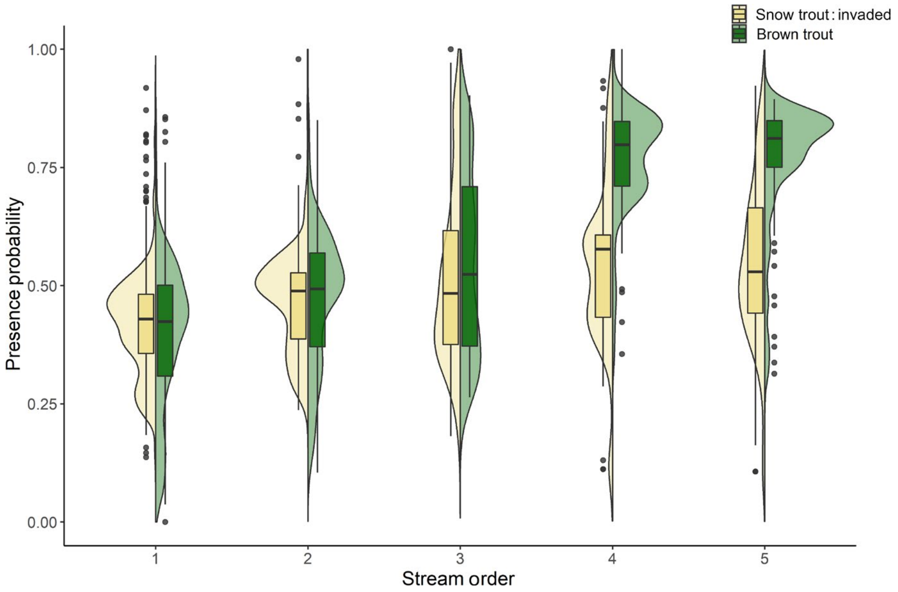


**FIGURE 4** Vertical violin plots for the predicted presence probabilities of snow trout and the invasive brown trout in Tirthan watershed. The predictions of the spatial stream network models are separately plotted per stream order (1–5) and juxtaposed for both the species. The boxes and whiskers represent the interquartile range and 95% confidence intervals, respectively, while the shape of violins indicates the frequency of kernel distribution

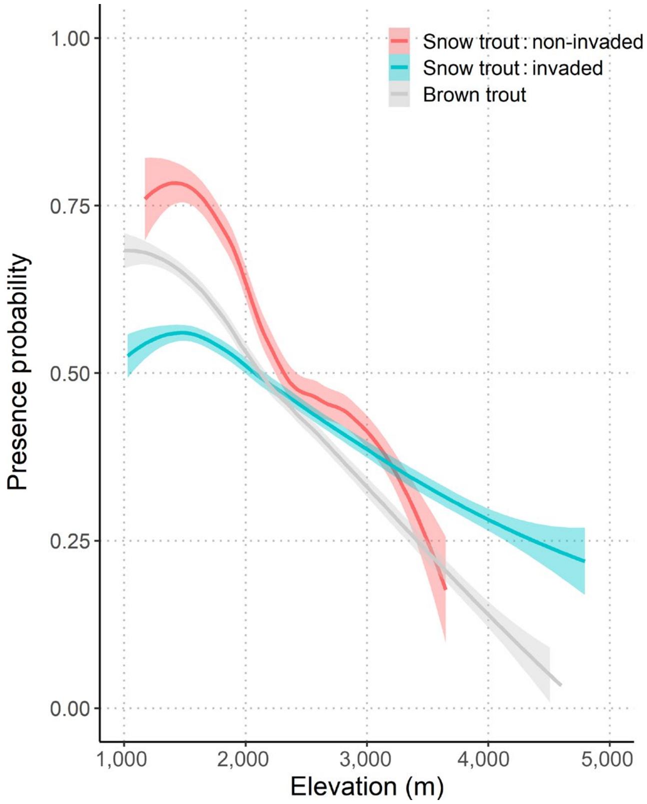


**FIGURE 5** The LOESS smoothened GAM curve fit on the SSN model predictions for snow trout with and without invasion, and the brown trout relating their presence probabilities with stream elevational gradients

with a competitive superiority and long-term survival in relatively lower elevation streams with warmer thermal regimes (McKenna et al., 2013; Ohlund et al., 2008). The aggressive competitive behaviour of brown trout is energy-consuming, which turns out to be beneficial if the surroundings are warmer, and thus more productive (Finstad et al., 2011). Contrariwise, snow trout is inherently cool-water species (Kamalam et al., 2019; Sehgal, 1999), evident with their distribution across low- to mid-elevation tributaries across Himalaya (Sharma et al., 2021b). Understandably, lower elevation mainstems being optimal for both brown trout and native snow trout, we expected higher competitive interactions therein. Much inline, our predictions indicate highest native-invasive overlaps across mainstems, with evidently fragmented distribution of natives under invasion, hinting on the competitive dominance of invasive brown trout for space. Being strong interference competitors, brown trout agonistically interacts with native species (Lobón-Cerviá & Sanz, 2018), displacing the latter from sites of favourable rest and forage (McKenna et al., 2013). Additionally, studies in other montane stream networks, irrefutably indicate that population fragmentations are consequential in long-term disjunctions of natives (Kirk et al., 2018; Letcher et al., 2007), ensuing in sub-populations prone to inbreeding, reduced viability and local extinctions (Robinson et al., 2017). With our previous investigations in Tirthan highlighting an invasion-induced disrupted size structure of snow trout (Sharma et al., 2021a), the situation is already grave. As it stands, the brown trout standing stock is continually enhanced by propagule pressure under the auspices of various angling associations across Himalaya. The disjunct distribution of natives is thus a major conservation concern, as replacement of cent-per-cent native populations to predominantly brown trout are commonplace (Lobón-Cerviá & Sanz, 2018), which can be the case with snow trout in other Himalayan watersheds where stocking is still continued, like that in Tirthan.

Brown trout invasions forcing natives from favourable mainstems to harsher headwater habitats is strongly evidenced in other major mountain systems, ranging from the Appalachians of North America to Scandinavian mountains in Europe and Southern Alps in New Zealand (Boddy, 2018; Fausch & White, 1981; Kirk et al., 2018; McKenna et al., 2013; Ohlund et al., 2008). With snow trout in Himalaya facing similar relegations, our predictions indicate a striking global parallelism in the invasion strategies used by brown trout across high-elevation riverscapes. However, what interests is the uniformity in refuge-seeking strategies of natives across these brown trout invaded mountain ranges. As majority of native populations are directionally oriented towards headwaters to evade brown trout invasion, the question arises, why do they do so? The natives seemingly benefit from the inefficiency of brown trout in fully exploiting headwaters (Boddy, 2018). Brown trout has, in their native ranges, occupied niches of stable flow regimes and reduced flow perturbations, much unlike their invaded territories where unstable headwater tributaries deter their establishment (Lobón-Cerviá & Sanz, 2018). Contrarily, faster flow and deeper pools in mainstems enhance their territorial competitiveness by proffering more space to swim, more drift-feeding opportunities and an enhanced net energy intake, overall leading to a faster growth (Piccolo & Watz, 2018). This clearly reflects in the tail-up autocovariance in brown trout distribution models apart from their strong correlation with stream orders, indicating their predominance in larger stream segments. This gives native species an upper stance, as they being co-evolved with the regional hydrogeography and orogeny are flood-resilient. Thereby, albeit less favourable for sustenance, the natives prefer to relegate and establish in headwaters to seek refuge under competition (Kirk et al., 2018; McKenna et al., 2013), as evidenced by the snow trout distribution under invasion in our results. With other native species documented to be constrained in headwaters under invasion, our results further underpin the potential of headwaters to act as invasion refugia.

The headwaters have continued to garner attention as conservation priorities for native freshwater fauna in the past decade (Ellender et al., 2015; Quaglietta et al., 2018; Weyl et al., 2014). The hierarchical organization of dendritic stream networks interacts with a species' movement behaviour and structures its population distribution (CampbellGrant et al., 2007), noticeably enhancing its demographic resilience as intersecting or confluent branches increase (Lowe & Bolger, 2002). In fact, dendritic networks promote asynchrony in the headwater populations, thereby favouring their persistence via portfolio effect (Larsen et al., 2021). This complex stream topology in headwaters, seemingly, proffers refuge to natives in the invaded watersheds of our study, whose movement against flow is evident with the tail-down model.

## 4.1 | Management implications

While there exists a strong legislative framework for conservation of terrestrial biodiversity in the Himalayan nations, freshwaters are concerningly unheeded. The current policies in the Indian part of Himalaya, for example, the Indian Fisheries Act 1897, the Wildlife (Protection) Act 1972, the Environment Protection Act 1986, and the Wetlands (Conservation and Management) Rules 2017, although safeguard certain threatened species and their habitats, are still inadequate to address the management of 'riverscapes'. With our models strongly indicating an intricate connection of native freshwater species to riverscape topology, the current landscape-based management policies in Himalaya need an urgent review to accommodate riverscape-based species conservation. Such dendritic prioritization will also aid in developing mitigation measures against exotic-invasives such as *Cyprinus carpio* and *Oncorhynchus mykiss* in other Himalayan riverscapes.

We thus strongly suggest that conservation of snow trout and their associated species such as *Tor*, *Neolissochilus*, *Euchiloglanis*, *Glyptothorax*, *Barilius* and *Nemacheilus* can be benefited if headwater streams are prioritized, with concurrent restoration in mainstems, thus going by the 'protect the best, restore the rest' conservation approach (Young et al., 2018). While protecting headwaters proffers constant availability of nursery grounds to snow trout during breeding seasons (Sehgal, 1999), the restoration of mainstems would enhance possibilities of native species recolonization.

With predictions of maximum conflict in mainstems, halting brown trout stocking is immediately warranted while existing distribution of natives in the remnant patches can be expanded by 'catch-and-harvest' angling specifically targeting the invasive. We further suggest a landscape-to-riverscape-to-socialscape approach, as brown trout provides angling-based revenues to the local angling associations, which can be promoted to shift from brown trout towards native species angling primacies. The policymakers in the Himalayan nations are thus requested to frame overarching national conservation policies taking a cue from this study.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## AUTHORS' CONTRIBUTIONS

A.S., V.K.D., J.A.J., K.S.: Study concept and design; A.S., V.K.D.: Data collection and analysis; A.S., V.K.D., J.A.J., K.S., Y.K.R.: Data interpretation. Manuscript writing: led by A.S. and V.K.D. All authors contributed to the drafts and gave final approval for publication.

## DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.f1vhhmgxh (Sharma et al., 2021).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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