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Conservation of interacting species in network-constrained environments

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ABSTRACT

Aim: We apply a novel approach in a spatial network context to identify factors influencing a parasite–host system and to distinguish focal areas for conservation of interacting species.

Location: Twenty river networks in southern Europe (Spain)

Methods: Spatial stream network (SSN) models were applied to analyse and predict density and biomass of interacting species in river networks. Density of an endangered freshwater mussel (parasite) and biomass data of its host fish were response variables for models with fixed-effect biotic and abiotic predictors and three random effect models for spatial covariance. Universal kriging with the SSN models was used to obtain predictions for parasite density and host biomass for the entire study region.

Results: Spatial stream network (SSN) models fitted separately for parasite density and host biomass explained 75% and 77% of the variance, respectively. Predictors explained 5% of the variance for the parasite and 14% for the host. Host biomass was the most important predictor of parasite density. The tail-up and tail-down spatial covariances fitted to the residual variance explained more than a half of the total variance in both models. Significant biotic and abiotic predictors differed between the parasite and host models. Combining model predictions for parasite density and host biomass identified areas where different strategies might be employed to conserve biotic interactions.

Main conclusions: Conservation of biotic interactions requires consideration of respective ecologies of the interacting species. In a network environment, connectivity of habitats can be an important determinant for occurrence of biotic interactions. Spatially explicit analyses, such as the SSN, can identify focal areas for conservation of biotic interactions. Conservation focused on biotic interactions, as opposed to a single species, could yield benefits to the focal species, the biotic community with which they occur and the ecosystem that supports them.

KEYWORDS

freshwater mussels, geostatistics, parasite–host biotic interactions, Salmonidae, spatial stream network models, universal kriging

1 | INTRODUCTION

Interactions between species are fundamental ecological processes that contribute to the evolution of life on earth (Levin, 1998) and they can affect other ecosystem processes from local (Wardle et al., 2004) to watershed (Lois et al., 2015) and/or continental scales of extent and resolution (Araújo & Luoto, 2007; Leathwick, 2002). Predation, herbivory, competition, parasitism and symbiosis are examples of biotic interactions that can influence species distribution and abundance (Wiens, 2011). Species interactions may affect species' responses to abiotic factors across space and time, and they may have cascading effects on habitats, resource availability and accessibility, thereby jointly affecting distribution and abundance of two or more species (Boulangeat, Gravel, & Thuiller, 2012).

Conservation focused on maintaining population densities and distributions of strongly interactive species is an important way to facilitate biodiversity conservation (Soulé, Estes, Miller, & Honnold, 2005). However, identifying factors that limit strongly interacting species can be challenging where there is spatial heterogeneity in environmental conditions. For instance, abundances of interacting species may depend on similar (or different) biotic and abiotic features at spatial extents larger than a single habitat where the species might coexist (Boulangeat et al., 2012). Thus, the potential for biotic interactions to occur can depend on factors acting over much broader spatial extents than local habitat conditions.

Many biotic interactions are constrained to natural environments with network topology such as caves, spider webs, rivers and road networks (Campbell Grant, Lowe, & Fagan, 2007). Within network-constrained environments, processes such as wind, animal movements, marine and freshwater currents or soil transport can cause spatial autocorrelation (Dormann et al., 2007). Rivers are a global example of network-constrained environments where movements of organisms and materials occur within the network structure with strong influences from the contributing watershed, regional topography and climate. River networks have directional topology caused by water flow that moves organisms and materials in the downstream direction. In contrast, active movements of freshwater organisms can occur within the network with or against the flow direction. These passive and active processes on the network are of special interest when considering the conservation of biotic interactions in network-constrained environments.

The study of biodiversity patterns and processes in river ecosystems was defined under the concept of riverscape (Fausch, Torgersen, Baxter, & Li, 2002; Wiens, 2002) that included the study of patterns and processes in several independent drainage basins. However, compared with terrestrial ecosystems, riverine systems have received less attention in development of appropriate statistical models and analytical techniques (Isaak et al., 2014; Lois, 2016) and river ecosystems have especially received less attention from a biogeographical perspective (Olden et al., 2010). Presently, most studies of biogeographical patterns in rivers have used techniques for terrestrial environments and conservation on rivers has been rarely addressed from a spatially explicit network perspective. Most prior work has focused on a catchment perspective by adapting techniques developed for terrestrial ecosystems, sometimes with inclusion of river connectivity (Chee & Elith, 2012; Linke, Norris, & Pressey, 2008; Moilanen, Leathwick, & Elith, 2008; Van Looy et al., 2014). However, an analysis that ignores network topology will likely fail to represent the spatial relationships and ecological processes occurring on rivers or other network environments (Peterson et al., 2013).

We analyse a freshwater parasite–host system of biotic interactions between an endangered freshwater pearl mussel (Unionoida, *Margaritifera margaritifera* L.) and its salmon and trout hosts. Freshwater mussel species are widespread in all freshwater ecosystems of the world except Antarctica and many species are critically endangered (Bogan, 2008). As a result, there is widespread interest in comprehensive studies that elucidate factors at various spatial scales that control mussel populations (Atkinson, Julian, & Vaughn, 2012; Hopkins, 2009; Strayer, 2008).

In our study region, *M. margaritifera* is an obligate parasite on host fish (Atlantic salmon, *Salmo salar* L. and brown trout, *Salmo trutta* L.) during the larval (glochidial) stage. The mussel can live to 200 years of age (Mutvei & Westermark, 2001), whereas its mobile host species' life spans are <20 years (http://www.demogr.mpg.de/longevityrecords/0503.htm). Freshwater mussels are benthic filter feeding organisms that are patchily distributed in the riverbed environment. Unionoid mussels have a characteristic life cycle where the parasitic larva depends on attachment to a mobile freshwater host for survival, metamorphosis and dispersal in the river network (Strayer, 2008).

Here, we analyse the parasite–host system in 20 river networks (independent drainage basins) in southern Europe. We use spatial stream network (SSN) models to identify significant biotic and abiotic factors influencing parasite density and host biomass. In addition, we use the estimated SSN models to predict parasite density and host biomass for the entire study region. Finally, we use model predictions to identify focal areas relevant for conservation of biotic interactions.

2 | METHODS

2.1 | Study area, spatial data and environmental predictors

We used spatial stream network models (Peterson et al., 2013; Ver Hoef & Peterson, 2010) to analyse data on density and biomass for strongly interacting aquatic species in 20 river networks in Galicia, Spain. We fitted separate SSN models for parasite density and host fish biomass.

For modelling parasite density, a total of 435 records for mussel density (density, ind./m^2) were selected following the criteria described in Lois et al. (2015). The estimates of mussel density (Lois, Ondina, Outeiro, Amaro, & San Miguel, 2014) came from a two-phase doubly stratified sampling method for efficient estimation of freshwater mussel densities in large areas (Villella & Smith, 2005); field sampling was conducted between 2008 and 2011. Additional details of sampling methods and estimation of mussel density were described in Lois et al. (2014). The frequency distribution of mussel density was

TABLE 1 Predictor variables (fixed effects) used for spatial stream network modelling of freshwater pearl mussel density and host fish biomass in 20 river networks in north-western Spain

Environmental predictor variables	Scale	Units
Climate[a]		
Average annual precipitation excluding summer	Site	mm
Average summer precipitation (July–September)	Site	mm
Average annual temperature	Site	°C
Maximum summer temperature	Site	°C
Minimum summer temperature	Site	°C
Host fish[b]		
Atlantic salmon density	Site	individuals/m^2
Migratory trout density	Site	individuals/m^2
Resident trout density	Site	individuals/m^2
Salmonid biomass	Site	g m^{-2} yr^{-1}
Landform[c]		
Slope	Site	%
Elevation	Site	m a.s.l.
Land use[c]		
Natural forest	Watershed	%
Forestry plantations	Watershed	%
Natural forest mixed with forestry plantations	Watershed	%
Agriculture	Watershed	%
Urban areas	Watershed	%
Geology[d]		
Granitic rocks	Watershed	%
Detrital deposits	Watershed	%
Metamorphic rocks	Watershed	%

Salmonid biomass was the response variable for host fish biomass, whereas it was a predictor variable for mussel density.

[a] Digital Climatic Atlas of the Iberian Peninsula (Ninyerola, Pons, & Roure, 2005)

[b] Fish Database of European Streams (Beier et al., 2007) and Xunta de Galicia.

[c] Sistema Información Teritorial de Galicia (SITGA, Spatial Data Infrastructure of Galicia) and CORINE Land Cover by the European Environmental Agency (EEA).

[d] SITGA.

skewed with a long right tail; therefore, the response variable was log-transformed prior to analyses.

For modelling host biomass, data from Galician streams on biomass (g m^{-2} yr^{-1}) of host fish for *M. margaritifera* [*Salmo salar* (Atlantic salmon), *Salmo trutta* (resident and anadromous (migratory) ecotypes)] were obtained from the European Fisheries Database (Beier, Degerman, Melcher, Rogers, & Wirlöf, 2007). A total of 391 records of host fish biomass located in the same 20 networks as used for mussel density were selected for modelling. With skewness similar to mussel density, host fish biomass values were log-transformed prior to analyses.

Model development for parasite density and host biomass began with a common set of 19 potential predictors for the parasite and 18 for the host. Biomass of host fish was used as a predictor variable in the model of parasite density and as the response variable in the host biomass model. Predictor variables were chosen to represent five general categories of factors that can affect biological productivity of a freshwater parasite–host system: climate, geology, landform, host fish and human land uses (Table 1). To represent climatic conditions, we used several measures of temperature and precipitation. We divided annual precipitation into two periods representing lower flow (summer, July–September) and higher flow conditions (not summer) in Galician rivers. Potential landform effects on parasite and host were represented with elevation and slope. Influences from geological rock types that contribute to streambed habitats needed for parasite and host were included as watershed scale predictors. Five categories of the predominant human land uses in the region were also evaluated as watershed scale predictors to assess possible effects from anthropogenic disturbances. Densities of three host fish types were evaluated as predictors in models for parasite density and separately for host biomass.

The spatial stream datasets necessary to analyse SSN models were generated using the STARS toolset in ARCMAP 10.2; watershed area was used to calculate spatial weights (Peterson & Ver Hoef, 2014). Eight predictors (geology and land use) were generated for use as watershed explanatory variables for each stream segment using a 40 m digital elevation model. The 11 remaining predictors were calculated as site-scale explanatory variables at each sampling location. The details of spatial data processing for SSN models are given in Peterson and Ver Hoef (2014).

2.2 | Modelling on-networks

A generalized approach for spatial statistical network models has been developed in the framework of geostatistics (Cressie, Frey, Harch, & Smith, 2006; Peterson et al., 2013; Ver Hoef, Peterson, & Theobald, 2006). The general idea is that SSN models, or models for other network-constrained environments, can include sources of spatial autocovariance arising from the topology of the network.

The SSN mixed models allow fitting of fixed-effect predictors and random effects (non-spatial and spatial autocovariance functions). A variance components approach is used to quantify the fraction of variance in the response variable explained by the predictors and the fraction of the residual variance that can be explained by spatial covariances. When spatial dependence is well explained by autocovariance functions, the SSN model (Ver Hoef & Peterson, 2010) produces predictions with generally smaller standard errors, at any point in the network, than do non-spatial methods or spatial methods that ignore the topology of river networks (Isaak et al., 2014). The SSN models can accommodate three possible sources of spatial covariance (Ver Hoef, Peterson, Clifford, & Shah, 2014). First, spatial covariance between flow-connected sites can occur in the same direction of the river flow (tail-up spatial covariance). Secondly, spatial covariance between flow-connected and flow-unconnected sites can occur in association with active movements of organisms against or with the flow (tail-down spatial covariance). Finally, features that span watershed boundaries of river networks, such as precipitation or exposed rock layers, may generate spatial covariance independently of the network topology, which can be included in the SSN models as Euclidean distance that is commonly used in terrestrial applications (Diniz-Filho, Bini, & Hawkins, 2003).

Analyses of SSN models of parasite density and host biomass were conducted with routines implemented in the SSN package (Ver Hoef et al., 2014) in R (R Development Core Team, 2010). Moving average functions for spatial covariance in river networks (Peterson & Ver Hoef, 2010), along with Euclidean distance, were evaluated. Further details on application of SSN models are given elsewhere (Frieden, Peterson, Webb, & Negus, 2014; Isaak et al., 2014).

Our SSN models for parasite density and host biomass used the Gaussian distribution. We used a multi-step process for model development by (1) evaluating initially the efficacy of a spatial stream network model relative to a non-spatial multiple regression model, (2) examining residuals of the selected model to identify and remove outliers, (3) implementing stepwise backward elimination to remove all non-significant predictors from the model and (4) comparing five moving average functions for tail-up and tail-down autocovariances (25 model combinations) to select a final model for parasite density and host biomass. Restricted maximum likelihood was used for parameter estimation for each final model. We used Akaike's Information Criterion (AIC; Akaike, 1973) for model selection. The model with the lowest AIC was identified as the final model for parasite density and for host biomass. For these final models, we inspected bias, root mean square prediction error and standardized mean square prediction error to ensure adequacy of final models. In addition, we conducted leave-one-out cross-validation (LOOCV) to further inspect model performance and obtained cross-validation statistics for model bias, standardized bias, root mean square prediction error and standardized prediction error.

In the framework of geostatistics (Matheron, 1963), the SSN models estimate the maximal variance (the sill) between pairs of uncorrelated sites, partition it into variance (partial sill) attributable to each source of spatial covariance and the distance at which spatial autocorrelation occurs (geostatistical range) for each spatial component. The nugget effect is composed of microscale variance in the spatial process and measurement error (Cressie & Wikle, 2011). These spatial parameters were estimated for parasite density and host biomass models using the SSN package in R.

2.3 | Model predictions

The model predictions of mussel density and host fish biomass were made using universal kriging implemented in the SSN package in R. Model predictions and their standard errors for parasite and host were obtained at 1-km point spacing in all river networks, which was convenient for viewing model predictions across the entire study region of 20 networks.

3 | RESULTS

Data were screened for outlying observations to reduce model bias; 31 outliers were eliminated in the data for parasite density ($N = 404$ in final model) and eight were removed from the host biomass data ($N = 383$). After data screening, frequency distributions for each response variable and the model residuals closely approximated a Gaussian distribution. Mean parasite density (logarithmic scale) and its standard error was 4.882 ± 0.071, the median was 4.695 and standard deviation was 1.422. Mean host biomass (logarithmic scale) was 9.093 ± 0.038, the standard deviation was 0.747 and median was 9.196. Observed parasite density and host biomass are shown in Figures 1a and 2a, respectively; model predictions for parasite density and for host biomass are shown in Figures 1b, and 2b,c, respectively.

The SSN models fitted separately for the mussel (parasite) and fish (host organisms) explained a majority of the variance (75% for mussel density, 77% for host fish biomass). For parasite and host, fixed-effect predictors explained less variance than did the random effects for tail-up and tail-down autocovariances (Table 2). For parasite density and host biomass, the Euclidean random effect explained less than 1% of the variance and it was excluded from each final model, based on AIC.

Significant predictors associated with increased parasite density included host biomass and percentages of granitic and metamorphic rocks in the watershed. Larger percentages of agricultural and urban land use within the watershed along with higher slope were associated with decreased mussel density. For parasite density, the tail-up autocovariance component explained 34.2% of total variance, whereas the tail-down component explained 35.6%. The geostatistical range for the tail-up random effect was approximately 14 km, whereas the tail-down range was approximately 0.2 km.

For the host fish, biomass was greater with increased resident trout density, migratory trout density, precipitation excluding summer months, average annual temperature and watershed percentage of detrital rocks. The coefficient for migratory trout density was larger than the coefficient for resident trout density. The percentage of urban area in the watershed was a significant negative influence on host biomass. For the host biomass model, the tail-up and tail-down autocovariances accounted for 35.1% and 27.6% of the variance, respectively. The geostatistical ranges for tail-up and tail-down autocovariances were approximately 13 km and 27 km, respectively.

Cross-validation analyses of the final models for parasite density and host biomass indicated relatively small bias and root mean square prediction error (Table 3) although the model for host fish was somewhat better than for the parasite. Cross-validation plots (Figure 3) indicated that in both models there was a tendency to over-estimate density or biomass at low observed values of the response variable and under-estimate at high-observed values. Model predictions for 1-km spaced points on each river network are shown for parasite density and host biomass in Figures 1b and 2b. To jointly visualize model predictions for parasite and host, we overlaid the highest 20% model predictions using a 50% transparency so that overlaid primary colours yielded a third colour to facilitate seeing important watersheds for conserving biotic interactions (Figure 4).

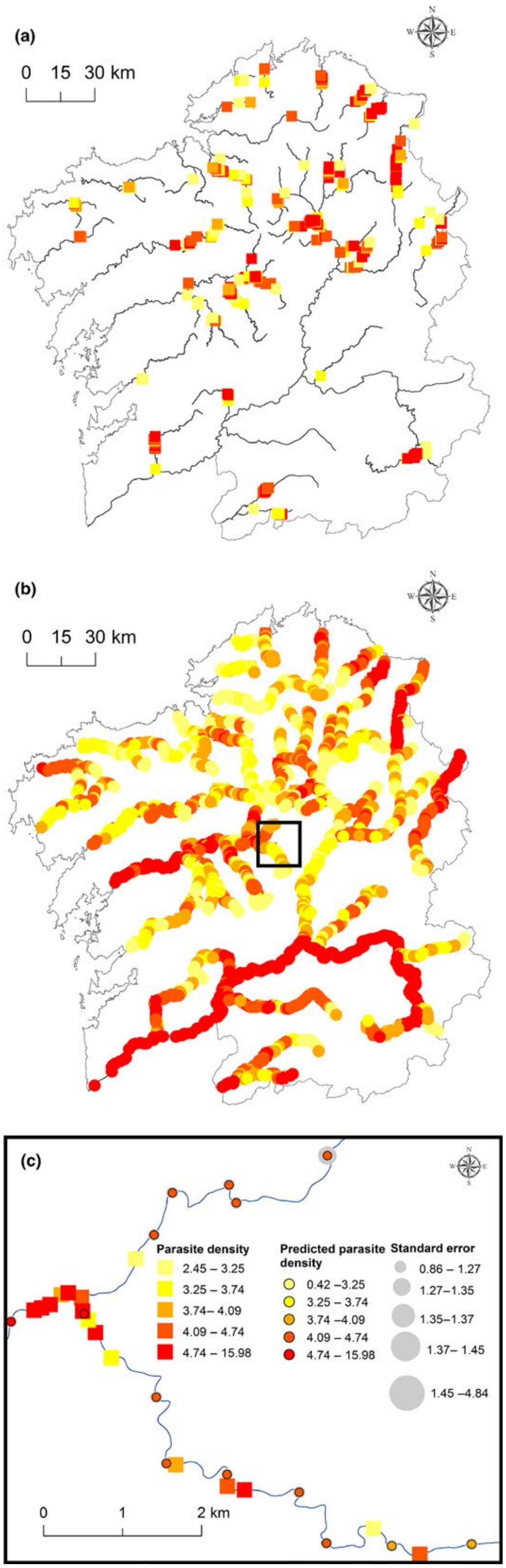

FIGURE 1 (a) Observed parasite (mussel) density used for spatial stream network (SSN) modelling after data screening (n=404) for the 20 networks of the study region, (b) universal kriging predictions for parasite density, (c) a map inset showing the area bounded by the black rectangle in (b) where observed parasite density, model predictions and their standard errors (in proportional grey dots) are shown together

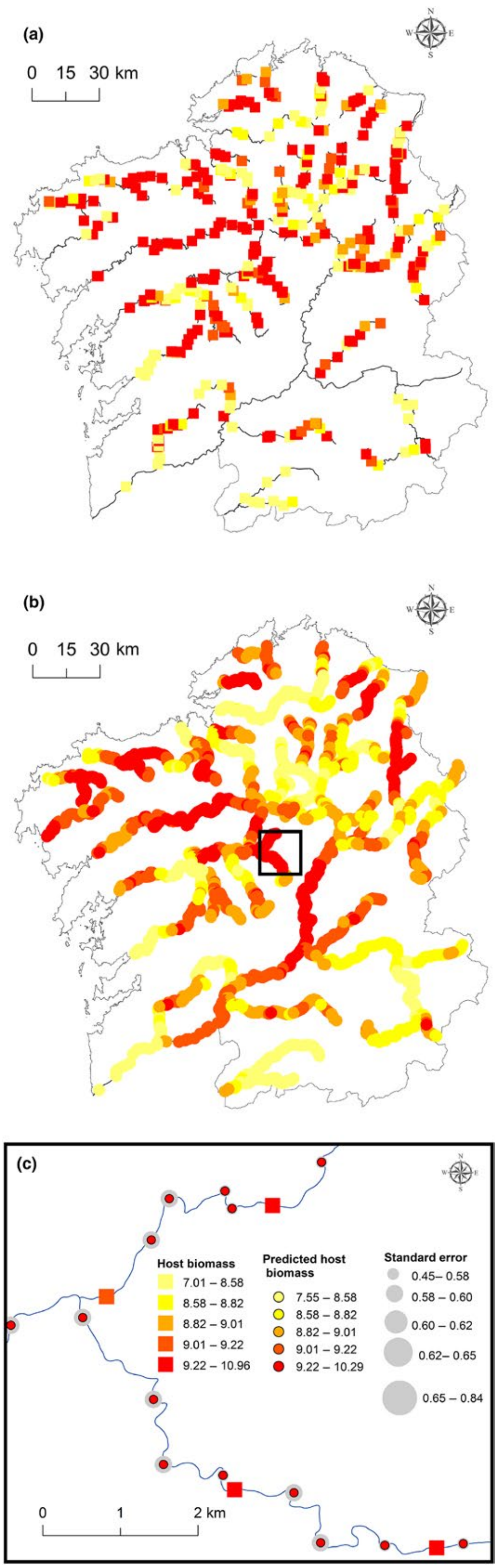

FIGURE 2 (a) Observed host fish biomass used for modelling after data screening (n=383) for the 20 networks of the study region, (b) universal kriging predictions for host biomass, (c) a map inset showing the area bounded by the black rectangle in (b) where observed host biomass, model predictions and their standard errors (in proportional grey dots) are shown together

TABLE 2 Parameter estimates for geostatistical mixed-model analyses of parasite density and host biomass for 20 river networks in north-western Spain. For each model, the fixed effects retained in the best (AIC-selected) models are shown. The proportion of variance is shown for fixed-effect predictors and autocovariances in the mixed model. Estimates, standard errors and *p*-values of the regression coefficients are given for fixed effects; estimates of the partial sill, geostatistical range (m) of spatial autocorrelation and the nugget are given for the autocovariances. The nugget effect is composed of microscale variance in the spatial process and measurement error

	Autocovariance parameter	Proportion of variance	Estimate	*SE*	*p*
Parasite model [response variable logarithm of mussel density]					
Fixed effects		0.052			
Intercept			3.107	0.404	<.01
Salmonid biomass			0.138	0.049	<.01
Slope			−0.018	0.009	.06
Granitic rocks			0.004	0.001	<.01
Metamorphic rocks			0.003	0.001	<.01
Agriculture			−0.004	0.001	<.01
Urban areas			−0.050	0.020	.01
Autocovariance models					
Tail-up: Linear with sill	Partial sill	0.342	0.651		
	Range		13747		
Tail-down: Exponential	Partial sill	0.356	0.678		
	Range		222		
	Nugget	0.250	0.465		
Host model [response variable logarithm of salmonid biomass]					
Fixed effects		0.143			
Intercept			6.364	0.909	<.01
Resident trout density			0.006	0.001	<.01
Migratory trout density			0.011	0.004	<.01
Ave. precipitation excluding summer			0.003	0.001	.02
Average annual temperature			0.113	0.054	.04
Detrital deposits			0.001	0.0005	.02
Urban areas			−0.019	0.006	<.01
Autocovariance models					
Tail-up: Mariah	Partial sill	0.351	0.193		
	Range		12847		
Tail-down: Linear with sill	Partial sill	0.276	0.151		
	Range		26720		
	Nugget	0.229	0.126		

4 | DISCUSSION

We applied a novel approach to explore interactions between two species in a spatial network context. Using geostatistical mixed models, we identified significant biotic and abiotic predictors of parasite density and host biomass. The mixed model approach quantified tail-up and tail-down spatial covariances for parasite and host models. The models for our datasets provided predictions of parasite density and host biomass for the entire study region at a resolution of 1 km. The semi-continuous model predictions enabled creation of a map showing where upper quantile model predictions for parasite and host co-occur, identifying focal watersheds relevant for conservation of biotic interactions in the study area.

4.1 | Predictor effects on parasite and host

Parasite density and host biomass had significant biotic predictors. For parasite density, the coefficient for host biomass was substantially larger than any of the abiotic predictors. Lois et al. (2015) previously noted the importance of larger size migratory hosts that produce more offspring as potential hosts for parasitism. The migratory hosts also make more extensive movements in river networks (Milner et al.,

TABLE 3 Cross-validation statistics for the spatial stream network (SSN) models of parasite density and host biomass; variables and autocovariances in each model are shown in Table 2; RMSPE denotes root mean-squared prediction error, MSPE is mean-squared prediction error

Model	Bias	Standardized bias	RMSPE	Standardized MSPE
Parasite	0.0309	0.0216	1.1220	0.9625
Host	0.0045	0.0042	0.6112	0.9932

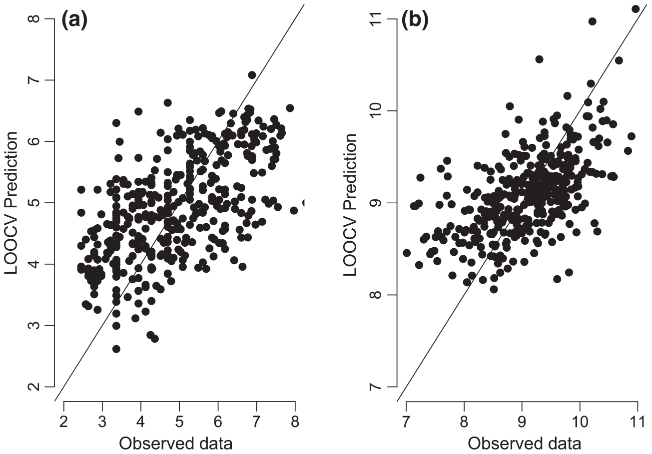

FIGURE 3 Kriging predictions plotted against observed values of the response variable using leave-one-out cross-validation (LOOCV) for (a) parasite density and (b) host biomass

2003) and they enhance dispersal of mussels into unoccupied habitats (Schwalb, Cottenie, Poos, & Ackerman, 2011). In the SSN model for host biomass, resident trout and migratory trout were significant positive effects but larger size migratory trout had a stronger influence on host biomass than did resident trout.

The SSN models indicated that different abiotic factors influence parasite density and host biomass. Mussel density was predicted to be higher in watersheds with more granitic and metamorphic rock, whereas host fish biomass was predicted to be higher in watersheds with detrital rock deposits. These results are consistent with other work showing that spatial patterns of geology are important watershed scale features controlling different mussel (McRae, Allan, & Burch, 2004) and fish habitats (Miller, Burnett, & Benda, 2008).

The significant negative influence of slope on mussel density but not host fish biomass highlights a notable habitat difference between parasite and host. Habitat suitable for mussels occurs in slower current velocity where deposition of finer sediments occurs, producing stable riverbed conditions (Hastie, Boon, & Young, 2000; Strayer, 1999). In contrast, host fish require higher velocity habitats with gravels free of fine sediment for successful spawning (Louhi, Mäki-Petäys, & Erkinaro, 2008). Dispersal of small host fish from their site of hatching into slower water habitats occupied by mussels provides the opportunity for parasitism to occur and parasitism enables subsequent dispersal of mussels into new habitats. The occurrence of the parasite in flow-unconnected sites in our study area evinces the importance of parasitized hosts dispersing mussels in a river network.

Significant land use predictors show somewhat different influences of habitat degradation on parasite density and host biomass. The area of urban development is a significant negative influence on parasite and host, whereas agricultural area is a second negative influence on the parasite. The impacts of urban areas on freshwaters include a wide range of anthropogenic stressors including pollution and habitat destruction that affect populations of the parasite (Bogan, 1993) and its host (Fenkes, Shiels, Fitzpatrick, & Nudds, 2016). Mussels, as benthic filter feeders with limited ability to move, may be more directly influenced by negative impacts in their habitats caused by sediment load associated with agricultural activities (Wood & Armitage, 1997). The differences in significant watershed influences in our models of parasite and host highlight a fundamental ecological difference between the long-lived, sedentary parasite and its comparatively short-lived, highly mobile host.

The predictors in our SSN model of parasite density affirm the results of Arbuckle and Downing (2002) and Atkinson et al. (2012), which indicated watershed scale predictors were important influences in the distribution and assemblage composition of freshwater mussels. However, we found that parasite density and host biomass are influenced by different predictors, suggesting that the spatial extent in network habitats needed to sustain occurrence of biotic interactions depends on environmental features that jointly control the interacting species. Thus, conservation of a parasitic mussel must consider both parasite and host habitat requirements in formulating an effective strategy to conserve biotic interactions.

4.2 | Spatial covariances for parasite and host

Validity of ecological interpretations of spatial covariance depends upon the tail-up and tail-down covariance functions accurately representing processes occurring in rivers. Because spatial covariances in our models are fit to the residuals after fitting the fixed-effect predictors, some of the spatial covariance captured by the tail-up and tail-down random effects could actually represent an important predictor not included in the model. Although we evaluated five categories of predictors likely to influence parasite and host in our study region, the models were limited by availability of geospatial predictor values. Another limitation, which we addressed, is that spatial covariances can be strongly affected by outliers in the data. The spatial covariance parameters (partial sill and range) can differ dramatically depending on the dataset and shape of the autocovariance functions included in the model. The range estimates for the same parasite–host system may be different in other regions where watersheds are larger or there is a greater spatial extent of lower slope river channels having more local sites of stable, fine sediment riverbed habitats needed by the mussel.

The estimates of geostatistical ranges of spatial autocorrelation and the amounts of variance accounted for by spatial covariances are consistent with the respective biology of parasite and host. Mussels have limited ability to move upstream and adults and larvae are biased in dispersal in a downstream direction (Terui et al., 2014), but a parasitized host could disperse juvenile mussels into upstream or downstream habitats. Hence, biology of mussels suggests that tail-up

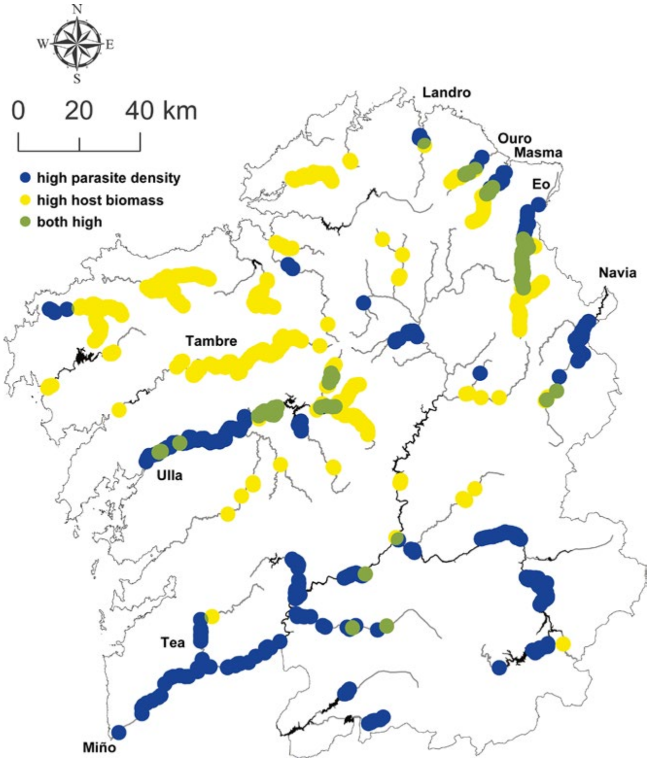

FIGURE 4 Overlay of the highest 20% quantile of spatial stream network (SSN) model predictions for parasite density (blue dots) and host fish biomass (yellow dots) for the 20 river networks in the study region. Higher predicted values of parasite density that overlap with higher values of predicted host biomass are shown in green dots, reservoirs are shown in black

spatial covariance would have a greater geostatistical range and appreciable variance would be accounted for by tail-up and tail-down spatial covariances. This is what we observed. Fish can move upstream and downstream, hence suggesting that tail-down spatial covariance should have a greater geostatistical range, as we also observed.

Lois et al. (2015) suggested that the geostatistical range for mussel density could be considered a spatial extent at which biotic interactions have occurred in the river networks of the study region. For species with low potential population growth rates, such as the long-lived parasite in our example, dispersal by host fish can be an important cause of spatial autocorrelation in abundance (Bahn, Krohn, & O'Connor, 2008).

It is notable that the geostatistical range of spatial autocorrelation is larger for host fish than for the parasite, which suggests that conservation of biotic interactions for an endangered mussel will require more habitat than might be targeted by simply focusing on the abundance and spatial distribution of the parasite. The geostatistical range is a useful metric for conservation biogeography by indicating a minimum amount of habitat in a river network necessary to sustain biotic interactions. In the case of strongly interacting species in our example, the larger range of the host is necessary to conserve the biotic interaction between parasite and host.

There may also be ecological information in the geostatistical range, which for the parasitic mussel can be considered the spatial extent at which river power and landform, a tail-up flow-connected context, combine to yield areas of fine sediment deposition that are required by the sedentary adult mussel and control their patchy distribution (Lois et al., 2014) at local spatial scales (Figure 1c). In contrast, the highly mobile host fish require multiple habitat types to support their various life history stages and this is consistent with the larger geostatistical range for host fish biomass (Table 2). The estimated geostatistical range for host biomass is consistent with the spatial extent of habitat required for conservation of salmonid fish in streams (Cowley, 2008; Hilderbrand, 2003).

4.3 | Conservation of biotic interactions

A map displaying the overlaid upper 20% quantile predictions of parasite density and host biomass (Figure 4) easily identifies watersheds with potential high host biomass (yellow), high parasite density (blue) and overlap of high parasite density and high host biomass (green). This depiction facilitates seeing in-network connectivity between parasite and host. The best watersheds supporting the parasite–host system have high host biomass in upstream headwaters, overlap of high parasite density and host biomass downstream from headwaters where watersheds are larger, and high parasite density farther downstream where watersheds are largest, a yellow-green-blue pattern on the map from upstream to downstream. Rivers Landro, Ouro, Masma, Eo and Tea (Figure 4) have connectivity between headwaters and the sea and they support migratory host fish. Some stream networks have no model predictions in the upper 20% quantile and hence have no colour in Figure 4, suggesting they may be impaired for parasite and host. The results suggest there are additional areas in the study region that may need habitat restoration for mussel and/or fish. Stream segments of blue without green or yellow indicate high values are predicted for parasite density, but there may be limitation in availability of hosts for parasitism (e.g. downstream portion of river Miño, Figure 4). Given the long life span of the mussel, conservation strategies here should aim at increasing fish biomass in connected network segments to facilitate biotic interactions. Watersheds with extensive yellow (e.g. river Tambre, Figure 4) are predicted to have higher host biomass, but abiotic conditions may be impaired for the parasite. Watersheds such as these indicate potential areas for further study to identify limitations on parasite density and to implement appropriate restoration strategies focused on the parasite. To recover mussel populations, connectivity of habitats within a watershed is necessary to maintain the biotic interaction between parasite and host.

4.4 | Broader implications for conservation

Our results show the utility of spatially explicit models that account for sources of spatial dependence in network-constrained environments, where movements of organisms (Frieden et al., 2014) and biotic interactions are constrained to occur within the network (Lois et al., 2015). Recent work has suggested that species persistence (Mari, Casagrandi, Bertuzzo, Rinaldo, & Gatto, 2014) and biodiversity (Seymour & Altermatt, 2014) are influenced by network geometry and connectivity. Our analyses emphasize the importance of a formal statistical modelling framework, such as the SSN models, for analysing data on interacting species in river networks. Presently, a limitation to broad application of SSN models is rapidly being reduced for North American stream networks with efforts of the National Stream Internet Project for the conterminous USA (http://www.fs.fed.us/rm/boise/AWAE/projects/NationalStreamInternet/NSI_network.html).

In our study region and in many rivers across Europe, conservation of the endangered freshwater pearl mussel depends critically on conservation of its host fish populations. Stocks of Atlantic salmon continue to decline in Spain and in much of the species' former European range (Chaput, 2012; Garcia de Leaniz & Martinez, 1988; Parrish, Behnke, Gephard, McCormick, & Reeves, 1998) and migratory trout have suffered a similar range-wide decline (Hastie & Cosgrove, 2001). The Atlantic salmon formerly occurred in nearly all rivers of northwest Spain, but the species' contemporary distribution is highly reduced by development of hydropower dams on most large rivers in the study area during the period 1955–1975 (Hervella & Caballero, 2002). The few remaining undammed rivers in our study region occur in small coastal watersheds and some of these small river networks continue to support Atlantic salmon. Elsewhere, extinction of mussels from several rivers and upstream of dams has been linked to loss of appropriate host fish (Kat & Davis, 1984; Watters, 1996). In stream networks where mussel populations occur upstream of a dam (e.g. headwaters of rivers Ulla and Miño, Figure 4), maintenance of healthy resident trout populations is the only alternative for providing the opportunity for the biotic interaction to occur between parasite and host.

Strategies for concurrent management of host fish and mussel populations are important to implement because recruitment of mussels may be regulated by the density of both mussels and fish (Arvidsson, Karlsson, & Österling, 2012; Haag & Warren, 1998; Strayer et al., 2004). Efforts are underway in Europe and North America to recover unionoid populations through captive breeding (Gum, Lange, & Geist, 2011) and habitat management (Cope et al., 2003; Layzer & Scott, 2006). However, captive breeding efforts might yield greater benefit if integrated with simultaneous restoration of host fish populations in targeted watersheds with sufficient connectivity between habitats to maintain the biotic interaction over time. Our results indicate that conservation of biotic interactions must accommodate a sufficiently large spatial extent to facilitate successful reproduction of host fish, parasitism and subsequent dispersal and recruitment of juvenile mussels into suitable habitats.

As a final point, although mussels and their host fish are commonly considered a parasite–host interaction, one might imagine how conservation of migratory hosts that exhibit ontogenetic habitat changes would enable widespread dispersal of mussels, yielding numerous aggregations of adult mussels in a river network. The long life and filter feeding habit of freshwater mussels in aggregations would provide a secondary benefit to the host fish by improving water quality and clarity. If the ecosystem effect of the filter feeding mussels were large enough, it could enhance future spawning success of host fish, which in turn would produce more potential hosts for future parasitism. Thus, a mussel–host fish system could be viewed as a positive interaction that may have potential to result in recruitment and facilitation cascades (Halpern, Silliman, Olden, Brunno, & Bertness, 2007) comparable to a trophic cascade. We suggest that conservation focused on facilitating biotic interactions such as these could benefit the focal biota, the broader aquatic community with which they occur and the river ecosystem that supports them.

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