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Effects of life-history traits on stream fish abundances across spatial scales

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Abstract

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Identifying cross-scale patterns of ecological processes is imperative, especially in hierarchically structured riverine ecosystems. The role of abiotic factors in determining cross-scale spatial structure of stream fish populations and communities is well studied, but less is known about how species traits drive cross-scale patterns. We investigated the role of species traits for explaining autocorrelation of stream fish abundance at spatial scales ranging from local stream reaches to major basins. We calculated intraclass correlation coefficients (ICCs) representing abundance autocorrelation within species (N = 47) at each of five spatial scales. A hierarchical Bayesian regression then modelled ICCs against spatial scale with the resulting regression coefficients modelled as functions of species traits. Finally, we ordinated the scale-byspecies ICC matrix to calculate an overall metric describing species whose abundances were autocorrelated along a gradient of large to small scales, and modelled this metric as a function of species traits. Abundances of most species were autocorrelated at smaller spatial scales. Maximum fecundity had a significant positive relationship with abundance patterns across spatial scales. Species habitat affinities and body forms were significantly associated with overall abundance patterns across spatial scales: populations of upland/lotic-affiliated species adapted to streams with high flow correlated at small (≤10 km²) spatial scales. Lowland/lacustrine species with laterally compressed bodies showed little correlation across scales. The appropriate spatial scale for modelling abundance is determined not only by exogenous (e.g. environmental) factors, but also endogenous factors, like traits. Careful consideration of traits and life history will aid researchers in designing more effective and efficient surveys and analyses.

KEYWORDS

abundance, Bayesian hierarchical model, body shape, fecundity

1 | INTRODUCTION

Issues of spatial scale are fundamental components of ecology (Wiens, 1989), especially in river ecosystems (Cooper, Diehl, Kratz, & Sarnelle, 1998). Ecological patterns are often scale-dependentkey drivers may differ depending on the scale of interest (Soranno et al., 2014), and unique properties may emerge across spatial scales (Heffernan et al., 2014). Identifying drivers of cross-scale patterns provides mechanism to cross-scale inference (Jackson & Fahrig, 2015; McGarigal, Wan, Zeller, Timm, & Cushman, 2016). Stream fishes are ideal for studying cross-scale patterns for two reasons (Hugueny, Oberdorff, & Tedesco, 2010; Olden et al., 2010). First, streams are linear systems that are structured hierarchically across spatial scales (Frissell, Liss, Warren, & Hurley, 1986; Poff, II FY-

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1997). Second, the dendritic network of stream systems creates naturally delineated units (catchments) at discrete spatial scales, restricting fishes to within-system dispersal (Fagan, 2002; Landeiro, Magnusson, Melo, Espirito-Santo, & Bini, 2011). Accordingly, it is well recognised that stream fishes are regulated by factors operating across spatial scales (Fausch, Torgersen, Baxter, & Li, 2002; Jackson, Peres-Neto, & Olden, 2001; Schlosser, 1991). Many studies have sought to characterise spatial structure of freshwater organisms by examining distance decay of spatial autocorrelation in assemblage structure (Leprieur, Beauchard, Hugueny, Grenouillet, & Brosse, 2008; Wilkinson & Edds, 2001) or population parameters of individual species (Earnest, Scott, Schaefer, & Duvernell, 2014; Primmer et al., 2006). However, scale of autocorrelation for other patterns such as stream fish abundance is less studied.

Spatial structure of ecological processes in streams can be driven by endogenous (e.g. species traits), as well as exogenous (e.g. abiotic features) factors (Bonada, Dolédec, & Statzner, 2012). Numerous studies of aquatic organisms have focused on the role of traits on spatial structure of species occurrence (Kneitel, 2018; Radinger & Wolter, 2015), synchrony of recruitment among sites through time (Bret, Bergerot, Capra, Gouraud, & Lamouroux, 2015; Cattanéo, Hugueny, & Lamouroux, 2003; Grenouillet, Hugueny, Carrel, Olivier, & Pont, 2001) and community properties (de Bie et al., 2012; Cañedo-Argüelles et al., 2015; Grönroos et al., 2013). At the population level, most studies have been species-specific and thus have limited utility for generalising across taxa. Multi-species, trait-based studies are less common (Pyper, Mueter, & Peterman, 2005; Ruetz, Trexler, Jordan, Loftus, & Perry, 2005), and mechanistic analyses seeking to identify common patterns among species are even rarer (Chevalier, Laffaille, & Grenouillet, 2014). As a result, the role of species traits on spatial correlation of stream fish abundance remains to be studied.

Traits can be an important endogenous contributor to spatial structure of fish populations and communities. For instance, more mobile species should have larger scales of effect because dispersal can swamp the effect of local processes. This relationship may covary with other traits such as body size and reproductive capability (Jackson & Fahrig, 2012; Miguet, Jackson, Jackson, Martin, & Fahrig, 2016). Additionally, many studies have found grossly different scaling patterns among species for various population parameters. For example, scale of effect for population synchrony of small-bodied Everglades (Florida, USA) fishes occurs at relatively small scales (~10 km), while populations of larger species in the same system synchronise at much larger scales (Chick, Ruetz, & Trexler, 2004; Trexler et al., 2002). Other studies have identified spatial correlation at tens (Bret et al., 2015; Myers, Mertz, & Bridson, 1997) to hundreds of kilometres (Grenouillet et al., 2001; Rook, Hansen, & Gorman, 2012; Tedesco, B., Paugy, D., & Fermon, Y., 2004). This suggest a species-specific (i.e. trait-based) mechanism contributing to patterns of spatial autocorrelation among stream fish populations. However, we know of no study that has examined how species traits affect patterns of spatial structure of stream abundance in the river network hierarchy. Understanding how species traits influence cross-scale patterns of spatial structure represents a step towards

integrating life-history theory into population ecology across spatial scales (Chevalier et al., 2014).

The goal of this study was to identify the role of species traits in determining spatial autocorrelation of stream fish abundance at and across discrete spatial scales. We accomplished this goal by addressing three objectives. First, we used random effects models to quantify the amount of variation in stream fish abundance explained by categorical spatial groupings (autocorrelation of abundance of each species at each scale) of increasing size—ranging from local reaches (i.e. sites, <1 km²), to whole streams (~90 km^2), to progressively larger catchments (up to ~22.000 km²). This variation is represented as intraclass correlation coefficients (ICCs): one ICC per species (N = 47) per spatial scale (N = 5). Second, we used a Bayesian hierarchical approach to estimate regression slopes quantifying change in ICCs with increasing spatial scale. These slopes represent the effect of increasing scale on observed spatial autocorrelation of abundance for each species. In level 2 of this model, we modelled the slopes from level 1 as functions of key species traits (e.g. life history and dispersal) that have been shown to affect other ecological process such as recruitment synchrony (e.g. Chevalier et al., 2014) and community structure (e.g. de Bie et al., 2012), but are yet to be examined for spatial patterns of stream fish abundance. The Bayesian hierarchical approach allowed us to assess cross-scale patterns in magnitude of effect of spatial grouping (scales) on abundance autocorrelation, but did not inform on general patterns of spatial grouping (i.e. whether abundance was autocorrelated at large or small scales). Accordingly, we used ordination to reduce dimensionality in ICCs and then regressed the dominant eigenvector on species traits. This approach complimented the Bayesian analysis in providing inference on aggregate patterns of spatial structure of abundance. Overall, our analyses allowed us to draw inference on the role of endogenous factors affecting the spatial structure of stream fish abundance.

2 | METHODS

2.1 | Fish abundance and trait data

The data used in this study came from an ongoing stream sampling programme conducted by the North Carolina Department of Environment and Natural Resources (NCDENR) Division of Water Resources Biological Assessment Branch. Since 1991, a standardised protocol has been used to sample almost 1,000 stream reaches throughout North Carolina (Figure 1). Sample sites are wadeable 183-m (600 ft.) steam reaches. Reaches are sampled approximately once every five years, mainly between April and June, although some are sampled more frequently. Sampling included backpack electrofishing units (most frequently two units), along with an appropriate number of dip netters based on the stream size. Reaches were sampled using two-pass depletion covering all available habitats; the first pass moved upstream, while the second pass returned downstream. Given the uniform sample size (reach length) and effort (2-pass removal), all sampling units were treated as equal and catch can be directly compared among samples. All individuals were collected and identified to species. Unidentifiable individuals of all sizes were preserved in 10% neutrally buffered



FIGURE 1 Spatialisation of North Carolina used in this study. (a) Location of North Carolina within the eastern USA; (b) locations of study sites (stream reaches); (c) HUC12s; (d) HUC8s; (e) HUC10s; (f) HUC6s

formalin and identified upon return to the laboratory. Additional programmatic details can be found in the Standard Operating Procedures (NCDENR, 2006). Although 175 species were represented in the data, we limited our inference to only those species that had ≥5 records of sampling in 4 or more basins (HUC6s, see below), and which did not have very low detection probabilities (Peoples & Frimpong, 2011); this resulted in n = 47 species (Appendix S1, Table S1).

To represent spatial scales of increasing size (at scales greater than the reach level), we adopted hydrological unit codes (HUCs; Seaber, Kapinos, & Knapp, 1987), which represent nested catchments. Our smallest scale was the reach level (183-m reaches, n = 365), with areas increasing to HUC12 (87 ± 1 km², n = 317), HUC10 (451 ± 10 km², n = 176), HUC8 (3,797 ± 261 km², n = 47) and HUC6 (22,661 \pm 2,362 km², n = 14) (Figure 1). Based on our subsetting, we were left with n = 12,789 samples, where each sample represents a count of unique species for a unique time and study site. All spatial units at the HUC12 level and larger were aggregated from site-level captures. Sampling took place from 1991 to 2016.

2.1.1 | Fish traits

The trait categories of life history, macrohabitat preference and microhabitat preference (Table 1) were extracted from the FishTraits database (Frimpong & Angermeier, 2009). We used principal coordinate analysis (PCoA) of Jaccard dissimilarities (ideal for binary data) to reduce dimensionality in micro- and macrohabtiat preference data (Table 1). Because (a) life history was only represented by four traits, and (b) those traits were correlated with one another (0.51 > r > 0.86), we used only maximum total length and fecundity in subsequent analyses. These variables are hypothesised to have positive relationships with the size of the scale of effect for animals (Jackson & Fahrig, 2015; Miguet et al., 2016). Dispersal capabilities were represented by two morphological ratios that are closely related to mobility (Olden, Poff, & Bestgen, 2008; Poff & Allan, 1995). The first, termed "shape factor,' is the proportion of the maximum body depth to the total length. The second, termed, "swim factor" is the proportion of the depths of the caudal fin and caudal peduncle (Webb & Weihs, 1986). These variables were either obtained from Buckwalter (2016) or measured directly from Jenkins and Burkhead (1994).

2.2 | Quantifying variability within spatial scales

We used a Bayesian hierarchical approach to quantify spatial correlation within species across spatial scales. Our approach is superficially similar to quantifying spatial autocorrelation by examining distance decay of semivariance in some population metric (e.g. abundance or recruitment). However, our approach differs in several key aspects. First, it allowed us to estimate not only scale of effect (a goal of correlogram analysis), but also correlation patterns across discrete scales. Second, the hierarchical approach allowed us to retain error structure to a level 2 model examining the factors that drive those correlations across scales. Finally, the multivariate approach allowed us to assess cross-scale patterns as a whole -WILEY- FRESHWATER FISH

TABLE 1 Twelve species traits used as independent variables inmodels predicting cross-scale patterns of stream fish abundance inNorth Carolina, USA

Group	Variables	Description
Macrohabitat	Lacustrine	Preference for lacustrine (i.e. lakes) habitats
Macrohabitat	Lowland	Preference for lowland streams
Macrohabitat	Upland	Preference for upland streams
Macrohabitat	Montane	Preference for montane streams
Macrohabitat	Large river	Preference for large rivers
Macrohabitat	Small river	Preference for small rivers
Macrohabitat	Springs	Preference for springs
Macrohabitat	Creek	Preference for small streams
Microhabitat	Slow current	Preference for slow current velocity
Microhabitat	Moderate current	Preference for moderate current velocity
Microhabitat	Fast current	Preferences for fast current velocity
Microhabitat	Prefers lotic	Preference for lotic (flowing water) streams
Microhabitat	Prefers Ientic	Preference for lentic (slow water) streams
Life history	Total length	Maximum reported total length
Life history	Fecundity	Maximum reported number of eggs
Life history	Age at maturation	Earliest reported age a sexual maturity
Life history	Maximum lifespan	Maximum reported lifespan
Physiological tolerance	Maximum tempera- ture tolerance	Maximum temperature observed in species' range (see Frimpong & Angermeier, 2009 for calculation)
Swimming ability	Swim factor	Ratio of maximum caudal fin depth to maximum caudal peduncle depth
Swimming ability	Shape factor	Ratio of maximum body depth to total length
Trophic	Trophic level	Mean trophic level obtained from Froese and Pauly (2012)

by quantifying general patterns of ICCs across scales (i.e. whether species abundances were autocorrelated at large or small scales).

To accomplish this, we first quantified the amount of withinspecies variability in abundance at each spatial scale. To do this, we modelled log-transformed abundance (comparable to the transform used in a Poisson model for count data) using random intercept models, in which the random effect represented the focal spatial scale

$$\log\left(\mathbf{y}_{i}\right) = \alpha_{j[i]} + \sigma^{2}$$

where $\log(y_i)$ is the log abundance of sample *i* in *n* samples, $\alpha_{j[i]}$ is the estimated mean log abundance of sample *i* nested in spatial scale

j, and α^2 is the residual variance. We ran the model separately for five spatial scales (*j* = 5): reach, HUC12, HUC10, HUC8 and HUC6. The random intercepts $\alpha_{j/ij}$ were assumed to come from a normal distribution

$$\alpha_{j[i]} \sim N\left(\mu_{\alpha}, \sigma_{\alpha}^{2}\right)$$

with mean abundance μ_{α} and within-species variance σ_{α}^2 To quantify the amount of variability attributable to the spatial scale, we estimated the proportion of within-species variance compared to the total variance, σ^2 , using the intraclass correlation coefficient (ICC),

$$\mathsf{ICC} = \frac{\sigma_{\alpha}^2}{\sigma_{\alpha}^2 + \sigma^2}$$

ICCs are similar to a Pearson correlation coefficient, but they range from 0 to 1, with 0 indicating no detectable variance explained by the random effect, and 1 indicating all the variance in the data can be explained by the random effect. All estimates of ICCs were done using the *Imer* function in the *Ime4* package in R version 3.3.2 (R Development Core Team, 2016).

2.3 | Modelling ICCs

2.3.1 | Bayesian hierarchical beta regression

Once we estimated abundance autocorrelation at each spatial scale (ICCs), we sought to quantify (a) species-specific patterns of ICC change across spatial scales, and (b) how species traits affect those patterns. To do this, we used beta regression—a regression model suited for modelling proportion data (Ferrari & Cribari-Neto, 2004), such as ICC values. We adapted a Bayesian hierarchical model of beta regression and included both random intercepts and slopes for each species (assuming our 47 species are drawn from a larger group of species). The beta regression was modelled as

$$logit (ICC_i) = \alpha_{j[i]} + \beta_{j[i]} \times x_i$$

Species-specific intercepts and slopes were estimated for j = 47 species. The intercepts (α_j) describe the ICC at the site level, and the slopes (β_j) describe the change in ICC with increasing size of spatial scale (i.e. catchment area, km²); x is the log of the mean size of each spatial grouping based on HUCs in North Carolina. Slopes and intercepts were allowed to vary among species and were assumed to come from a multivariate normal (MVN) distribution for the slopes and intercepts and a normal probability distribution for log_e -transformed ϕ_j with mean μ_{ϕ} and variance ω_{ϕ}^2 When modelling the beta distribution, second parameter, φ (precision), is also estimated; however, this was not a parameter of interest in our model, and therefore, we allow it to vary among species but do not further analyse it. The variance-covariance matrix was modelled using the scaled inverse Wishart distribution (Gelman & Hill, 2007). Level 2 of the model was parameterised as follows:

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$$\begin{pmatrix} a_{j} \\ \beta_{j} \end{pmatrix} \sim \mathsf{MVN} \begin{pmatrix} \begin{pmatrix} \gamma_{0}^{\alpha} + \gamma_{1}^{\alpha} \times Z_{\mathsf{TL}} + \gamma_{2}^{\alpha} \times Z_{\mathsf{Macro}} + \gamma_{3}^{\alpha} \times Z_{\mathsf{Fec}} + \gamma_{4}^{\alpha} \times Z_{\mathsf{Shape}} + \gamma_{5}^{\alpha} \times Z_{\mathsf{Micro}} \\ \gamma_{0}^{\beta} + \gamma_{1}^{\beta} \times Z_{\mathsf{TL}} + \gamma_{2}^{\beta} \times Z_{\mathsf{Macro}} + \gamma_{3}^{\beta} \times Z_{\mathsf{Fec}} + \gamma_{4}^{\beta} \times Z_{\mathsf{Shape}} + \gamma_{5}^{\beta} \times Z_{\mathsf{Micro}} \\ \begin{pmatrix} \sigma_{a}^{2} & \rho \sigma_{a} \sigma_{\beta} \\ \rho \sigma_{a} \sigma_{\beta} & \sigma_{\beta}^{2} \end{pmatrix} \end{pmatrix},$$

where γ terms represent level 2 regression coefficients, subscript 0 indicates the intercept, and subscripts 1–5 are the slope coefficients for each predictor, Z. All Z values are species-level predictors for j = 47 species. σ_{α}^2 is the among-species variance for intercepts, and σ_{β}^2 is the among-species variance for slopes. ρ is the between-species correlation. Traits in the hierarchical beta regression were notated as total length (Z_{TL}), macrohabitat (Z_{Macro}), fecundity (Z_{Fec}), shape factor (Z_{Shape}) and microhabitat (Z_{Micro}) (Table 1).

For all hierarchical Bayesian models, three Markov chains were run with each chain beginning with a different random starting value. From a total of 300,000 samples from the posterior distribution, the first 50,000 samples of each chain were discarded, and then, every 3rd sample was retained for a total of 150,000 samples used to characterise the posterior distribution. To assess convergence, we examined the scale reduction factor \hat{R} , a convergence statistic, for each parameter in addition to evaluation of trace plots and plots of posterior distributions. Analyses were completed using JAGS in the *R2jags* package (Plummer, 2013) run within R (R Development Core Team, 2016).

2.3.2 | Relating overall ICC patterns to species traits

The Bayesian hierarchical models inform on the strength of the relationship between within-species abundance autocorrelation with increasing spatial scale, but do not adequately characterise general or aggregate patterns. For example, ICCs of many species had discrete breakpoints at different scales; this information is not fully retained in the slopes. Accordingly, we reduced dimensionality in cross-scale ICC patterns to calculate a metric of general spatial structure across scales. To do so, we first calculated Bray-Curtis distances on the scale-by-species ICC matrix (in which columns were spatial groupings/scales, rows were species, and values were ICCS). We then reduced dimensionality on this matrix using principal coordinate analysis (PCoA), producing eigenvectors representing general patterns of species whose abundance are autocorrelated on a gradient of large to small scales. We then modelled this eigenvector as a function of species traits to understand how traits affect general patterns of spatial autocorrelation of abundance across scales. Prior to analyses, we sought to account for phylogenetic signal in species traits at the family level. To do so, we initially screened traits for family-level differences using analyses of variance (ANOVA). Because traits differed significantly among families (but very weakly and only among a few pairs of families; Appendix S1, Table S2), we used a random effects model to account for this variation. This consisted of modelling each trait as a function of a random intercept of family; the residuals from these models represent trait variation that cannot be explained by within-family differences. While this approach is not as resolute as eigenvector-based methods on phylogenetic distance matrices (Diniz-Filho, Sant'Ana, & Bini, 1998), it is satisfactory at this phylogenetic scale (sensu Mahoney et al., 2015; Marczak, Thompson, & Richardson, 2007). Finally, we used multiple linear regression to relate the ICC eigenvector to species traits. In all analyses, we defined statistical significance as 95% confidence intervals of

Trait vectors



1. Calculate intraclass correlation coefficients (ICCs) using a random effects model for each spatial scale

FIGURE 2 Diagram showing the sequential analyses used in the study

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Lenemie euritue	0	0	0.0	0.5	0.2	0.2
Lepomis auritus -		.9	0.0	0.5	0.3	0.3
The seteres flab allows	0	.0	0.0	0.0	0.7	0.4
Etheostoma nabeliare -	0	.0	0.7	0.0	0.4	0.2
Noturus insignis -		7	0.7	0.5	0.4	0.4
Leponiis macrochirus -	0	./	0.7	0.0	0.3	0.2
Cotostomus commences	0	./	0.7	0.5	0.4	0.3
Catostomus commersonii -	0	./	0.7	0.0	0.0	0.4
Luxilus albeolus	0	./	0.7	0.0	0.4	0.2
Cline sterror for dulaidas	0	.7	0.0	0.5	0.4	0.5
Clinostomus funduloides -		./	0.5	0.3	0.2	0.0
Cyprinella analosiana -	0		0.0	0.4	0.2	0.0
Ameliume alebuseabelus	0	.0	0.0	0.5	0.3	0.2
Ameiurus platycephalus	0	.0	0.5	0.5	0.4	0.4
Chrosomus oreas	0	.0	0.0	0.4	0.2	0.1
Campostoma anomalum -	0	.0	0.6	0.6	0.3	0.0
Micropterus saimoides -	0	.0	0.6	0.5	0.3	0.2
Semotilus atromaculatus -	- 0	.6	0.5	0.4	0.2	0.0
Aphredoderus sayanus -	- 0	.6	0.5	0.4	0.4	0.4
Lepomis gulosus -	- 0	.5	0.4	0.4	0.2	0.1
Hypentelium nigricans -	Q	.5	0.5	0.4	0.0	0.0
Lepomis gibbosus -	0	.5	0.5	0.5	0.2	0.2
Ameiurus natalis -	- 0	.5	0.5	0.3	0.1	0.0
Hybognathus regius -	- 0	.5	0.5	0.4	0.3	0.0
Erimyzon oblongus -	- 0	.5	0.5	0.4	0.2	0.2
Ameiurus nebulosus -	- 0	.5	0.5	0.4	0.2	0.1
Micropterus dolomieu -	- 0	.5	0.5	0.4	0.2	0.2
Enneacanthus gloriosus -	- 0	.5	0.5	0.5	0.6	0.1
Notropis hudsonius -	0	.5	0.5	0.4	0.0	0.0
Lepomis microlophus -	- 0	.5	0.5	0.4	0.2	0.1
Esox americanus -	- 0	.5	0.4	0.4	0.2	0.1
Gambusia holbrooki	0	0.4	0.4	0.3	0.2	0.1
Etheostoma olmstedi -	- 0	.4	0.5	0.3	0.2	0.0
Notemigonus crysoleucas -	- 0	0.4	0.4	0.3	0.2	0.1
Fundulus rathbuni	0	.4	0.4	0.3	0.2	0.1
Esox niger -	- 0	.4	0.4	0.3	0.1	0.0
Umbra pygmaea -	- 0	.4	0.3	0.1	0.0	0.0
Notropis altipinnis -	- 0	.4	0.4	0.2	0.1	0.0
Perca flavescens -	- 0	.4	0.4	0.3	0.2	0.1
Centrarchus macropterus -	- 0	0.4	0.3	0.2	0.1	0.1
Notropis amoenus -	- 0	.3	0.3	0.2	0.1	0.1
Pomoxis nigromaculatus -	- 0	.3	0.2	0.2	0.0	0.1
Ameiurus brunneus -	- 0	.3	0.2	0.1	0.1	0.0
Rhinichthys cataractae -	- 0	.3	0.3	0.2	0.2	0.1
Notropis leuciodus -	0	.3	0.2	0.2	0.1	0.0
Luxilus coccogenis -	- 0	.2	0.2	0.3	0.4	0.2
Cottus bairdii -	0	.2	0.1	0.1	0.0	0.0
Ambloplites rupestris -	0	.0	0.0	0.1	0.0	0.1
	~	1				11100
	S	lie	HUU12	HUCTU	HUC8	HUC6
	0	0.9				

FIGURE 3 ICC estimates by species over five spatial scales. Species are sorted in descending order by site-level ICC. The x-axis is the logarithmic scale of km², with designations (tick marks) for where mean values for each spatial grouping occurs

parameter estimates not overlapping 0. Figure 2 shows the sequential relationship of the steps in our statistical analysis.

RESULTS 3

3.1 | Trends in cross-scale abundance correlation and reducing dimensionality

Random effects models calculated ICCs that were quite variable among species across spatial scales, ranging from 0 to 0.87; mean ICCs (plus standard deviation, s) for all species combined at each scale (from site level to HUC 6) were 0.51 (s = 0.18), 0.48 (s = 0.17), 0.37 (s = 0.16), 0.23 (s = 0.16) and 0.13 (s = 0.14). However, it was clear that ICC values generally declined with increasing scale (Figure 3), with the exception of Centrarchus macropterus (whose ICCs changed little among scales). The first PCoA eigenvector reducing dimensionality of ICCs explained 60% of the variance in ICCs across the five spatial scales. ICCs at all spatial scales were positively correlated with this eigenvector. However, ICCs at the three smallest spatial scales (site, HUC12 and HUC10) were correlated much stronger with

this eigenvector than ICCs at larger scales (Table 2). Accordingly, increases in this eigenvector represent increasing affinities for species abundances to structure at smaller and smaller spatial scales.

3.2 | Effects of traits across spatial scales

PCoA delineated macro- and microhabitat affinities among species that represent a gradient ranging from lentic and lacustrine systems in lowland regions, to lotic systems in upland/montane regions. The first macrohabitat eigenvector described 50% of the variation in species macrohabitat affinities. This variable was negatively correlated with lacustrine and lowland habitats, and positively correlated with montane and upland systems (Table 2). The first microhabitat eigenvector described 62% of the variation in microhabitat affinities among species. This variable was negatively correlated with slow current velocities and lentic microhabitats, and positively correlated with lotic, moderate and fast current velocities (Table 2). These variables were used as independent variables in level 2 of the hierarchical Bayesian model and in multiple linear regression predicting changes in ICCs across spatial scales.

TABLE 2 Correlations between primary eigenvectors and the original data used to calculate them for three principal coordinates analyses on three separate sets of variables: intraclass correlation coefficients (ICC), macrohabitat preferences and microhabitat preferences

Variables	ICC	Macrohabitat eigenvector	Microhabitat eigenvector
Site	0.93	-	-
HUC12	0.95	-	-
HUC10	0.92	-	-
HUC8	0.75	-	-
HUC6	0.59	-	-
Lacustrine	-	-0.73	-
Lowland	-	-0.77	-
Upland	-	0.47	-
Montane	-	0.75	-
Large river	-	-0.31	-
Small river	-	-0.39	-
Springs	-	0.27	-
Creek	-	-0.04	-
Slow current	-	-	-0.71
Moderate current	-	-	0.69
Fast current	-	-	0.67
Prefers lotic	-	-	0.88
Prefers lentic	-	-	-0.69

All hierarchical models converged, which was assessed through visual trace plots and all estimated $\hat{R} < 1.1$. The first level of the hierarchical Bayesian beta regression modelled ICCs by spatial scale

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for each species (Figure 4). Anticipating high interspecific variability in ICCs, the second level of this model estimated effects of species traits on ICC trends across spatial scales. This level revealed fecundity as the only significant predictor of the rate of change in ICCs from small to large spatial scales, having a positive effect (Figure 5).

Multiple linear regression identified macrohabitat affinity and shape factor as significant predictors of aggregate ICCs across spatial scales (0.54 ± 0.23 and 0.09 ± 0.04 respectively). In general, abundances of species that have larger shape factors (longer total length, relative to height; terete or fusiform body shape) and are associated with more upland/lotic systems tend to aggregate at increasingly smaller spatial scales. Likewise, abundances of species that have lower shape factors (generally taller and laterally compressed) and are associated more closely with lowland and lacustrine habitats tended to aggregate at larger spatial scales (if at all). Maximum total length (0.01 \pm 0.04), microhabitat affinity (-0.28 \pm 0.12) and fecundity (0.03 ± 0.04) were not significant predictors of the ICC eigenvectors. Our results were not strongly phylogenetically driven; means were not significantly different (p > 0.05) for some traits, and those with significant (p < 0.05) differences were driven usually by one or two families (Appendix S1, Figure S1).

4 | DISCUSSION

Our results demonstrate the role of endogenous factors in determining spatial structure of stream fish abundance. Cross-scale patterns of abundance were correlated within spatial scales ranging from local sites to large catchments, and the scale of correlation differed significantly as functions of key species indexing species habitat requirements, dispersal ability and life history. Abundances





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FIGURE 5 Effect of log(fecundity) on species-specific beta regression slopes. Points represent species-specific beta regression slopes of ICC over spatial scales with lines representing the 90% credible intervals. The blue solid line represents the hierarchical regression. (Note that the slopes do not perfectly correspond with those from Figure 4 because the hierarchical model uses information from all species and all data points, which results in a small amount of parameter shrinkage towards the means.) The grey polygon indicates the 95% credible interval on the slope

of species in our study system were structured mostly at smaller spatial scales (stream reaches and small catchments), although some species showed little change across scales.

The relationship between abundance correlation and spatial scale varied among species, but was significantly related to species habitat requirements. Abundances of species requiring upland lotic habitats were more correlated at small spatial scales, while species preferring lowland lentic systems showed little correlation at any scale. Furthermore, abundances of stream fishes adapted to upland flow regimes (more fusiform/terete to thrive in habitats of higher flow; e.g., Notropis spp.) were more correlated at increasingly smaller scales. This pattern likely represents the dynamic relative influence of dispersal and local habitat requirements at different positions in the stream network (Brown et al., 2011; Swan & Brown, 2011). For example, the high natural heterogeneity of upland streams can cause site- and stream-specific (i.e. HUC12) effects in population processes that depress dispersal (Cattanéo et al., 2003), despite being mediated by larger-scale climactic processes (Grenouillet et al., 2001; Labbe & Fausch, 2000; Tedesco et al., 2004). Conversely, local habitat features may play less of a role in structuring population processes in lowland streams because they lie in closer fluvial proximity to mainstem rivers, which supply a large number of immigrants to their tributaries, thus structuring population processes through dispersal (Grenouillet, Pont, & Hérissé, 2004; Hitt & Angermeier, 2008). Accordingly, the relative effects of stream network topology may be evident in spatial scaling of stream fish abundance via the traits that determine the distribution of species throughout the stream network.

In addition to habitat requirements, life-history traits also influenced spatial structure of stream fish abundance. Hierarchical Bayesian regression results suggest the relationship between abundance autocorrelation and increasing spatial scale was stronger on species with lower fecundities; these results are in line with life-history theory. Along with generation time and juvenile survivorship, fecundity is a keystone trait in the tri-lateral life-history continuum

model of freshwater fishes (Winemiller, 2005; Winemiller & Rose, 1992). In minimising fecundity, fishes can optimise either juvenile survivorship (the "equilibrium" life-history strategy) or population generation time (the "opportunistic" strategy). Interspecific variation in the life-history continuum has been shown to affect the spatial scaling of large-river fishes in Africa (Tedesco & Hugueny, 2006). However, these were for "periodic" species (optimising fecundity at the expense of the other two traits), which are poorly represented in wadeable streams because they are large-bodied and require predictable variations in abiotic conditions (Mims & Olden, 2012; Olden & Kennard, 2010). Chevalier et al. (2014) found that recruitment of opportunistic strategists (i.e. early maturing serial spawners with small clutch sizes) was more correlated than other life-history strategists. In the present study, the observed relationship represents a shift away from opportunistic strategies from uplands to lowlands. In optimising generation time, opportunistic strategists are ideally adapted for the highly variable abiotic conditions in upland streams (Winemiller, 2005). These results demonstrate that accounting for interspecific variation in species life history can improve our ability to

understanding large-scale spatial patterns in population processes.

Placing our results in the context of other studies of freshwater fishes is difficult; we know of no other study that has examined effects of species traits on scale of effect for stream fish abundance. In fact, a recent meta-analysis Jackson and Fahrig (2015) examined evidence between key species traits and scale of effect for abundances of several vertebrate groups. Although they found little evidence of an effect, no studies were available for fishes-a point that highlights the opportunities for exploring spatial scaling relationships among freshwater fishes. We can, however, relate our work to studies that have sought to understand scale of effect for other aspects of stream fishes. For example, many studies have sought to understand the spatial scale at which population processes such as recruitment synchronise, finding patterns between 50 km (approximately the HUC8 scale; Myers et al., 1997) and 100 km (approximately the HUC6 scale; Cattanéo et al., 2003; Grenouillet et al., 2001; Tedesco et al., 2004). Ours is most similar to Chevalier et al. (2014), who examined how spatial synchrony patterns varied with species traits. However, we studied adult abundance, not recruitment, and our study had no temporal component. The role of dispersal in determining spatial scale of abundance correlation is surely quite different between the two processes and should be studied further in stream fishes.

Similarly, many studies have examined the role of species traits for determining spatial scale of community and metacommunity structure in stream ecosystems (Saito, Soininen, Fonseca-Gessner, & Siqueira, 2015; Strecker et al., 2011). A common finding among these studies is that key traits such as dispersal ability and body size disrupt metacommunity structure by swamping the effects of local variables (de Bie et al., 2012; Grönroos et al., 2013; Padial et al., 2014). Just as meta-communities are homogenised by highly dispersing species (Leibold et al., 2004), we found that abundance autocorrelation of species with high dispersal ability is homogenised at large spatial scales. Like studies of recruitment synchrony, we can only draw limited comparison with these community-level studies. However, our work does touch

on a common theme emerging in the literature: cross-scale patterns in aquatic communities are affected by species traits.

Identifying the spatial scales of effect on abundance autocorrelation provides context for observations across broad spatial extents and helps generate predictions and testable hypotheses for population structure (Tobin, 2004). Large-scale relationships between abundance and distribution have been described for a diversity of taxa (Brown, 1984), although to date much of this work has focused on terrestrial organisms (see Jackson & Fahrig, 2015 for a review). While it might be expected that species abundances are more similar at smaller spatial scales that at larger spatial scales, our study is among the first to quantify this for a diversity of stream fishes. More importantly, the degradation of abundance similarity with increasing scale is heterogeneous among species; some freshwater fish maintained similar abundances at the catchment and basin scale, while others had dissimilar abundances beyond very small areas (HUC12). Species-specific expectations of abundance are not only useful from a management perspective-for example helping to design efficient sampling and conservation programmes-but also help shed light on abundance variability and extirpation risk for sensitive and threatened species.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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