Revised: 27 May 2021

Freshwater Biology WILEY

# DOI: 10.1111/fwb.13788

# ORIGINAL ARTICLE

# Landscape features and study design affect elements of metacommunity structure for stream fishes across the eastern U.S.A.

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# Abstract

- 1. Metacommunity ecology includes connectivity in the investigation of local and regional processes to understand community assembly. The elements of metacommunity structure (EMS) framework classifies metacommunities into categorical archetypes based on patterns of three metrics indexing  $\beta$  diversity: coherence, turnover, and boundary clumping. Although the EMS framework is most commonly used to classify metacommunity types, an elements-based approach of examining how factors affect each specific continuous EMS variable could provide a more mechanistic understanding of how metacommunities are structured at the landscape scale. Moreover, few studies have sought to quantify how methodological issues such as number and spacing of local communities affect observed outcomes of EMS-based analyses.
- 2. Using a large dataset of stream fish occurrences in the eastern U.S.A., we used mixed effects models to investigate how (1) landscape-scale variables and (2) methodological issues such as number and location of sampling sites affect coherence, turnover, and boundary clumping individually; as well as (3) how landscape-scale variables influence overall metacommunity patterns derived from the EMS framework.
- 3. Coherence, turnover, and boundary clumping were related to temperature, density of dams, developed land use, and γ diversity. Interestingly, distance among sampled sites in metacommunities negatively affected turnover, and the number of sampling sites positively affected all three variables. Elevation affected overall observed metacommunity patterns, with metacommunities transitioning from Clementsian to clumped species loss patterns with increasing elevation.
- 4. Our results suggest that metacommunity structure is affected by both natural and anthropogenic landscape-scale variables. Observed metacommunity properties are also influenced by sampling density and site location within the catchment. Accounting for important natural, anthropogenic, and methodological issues will be critical for improving the inferential power of metacommunity analyses to begin understanding which landscape-scale variables should be the focus of conservation and management of fish communities at a catchment scale.

# KEYWORDS

anthropogenic effects,  $\beta$  diversity, boundary clumping, catchment, coherence, metacommunity, turnover

# 1 | INTRODUCTION

Metacommunity theory incorporates local and regional processes to explain community assembly (Leibold et al., 2004; Logue et al., 2011; Tonkin et al., 2018). In a metacommunity context,  $\beta$  diversity is characterised by coherence, turnover, and boundary clumping-the elements of metacommunity structure (EMS: Leibold & Mikkelson, 2002). Given a site-by-species matrix of incidences, coherence represents a site where a species is absent that is surrounded by sites where the species is present, termed an embedded absence. Coherence also indicates how species distributions are influenced by the same environmental gradient (Presley, 2020). Turnover represents the number of times species replace one another along some gradient, and boundary clumping represents the degree of distinct species groupings within the metacommunity. Ecologists use positive and negative outcomes of significance tests from coherence, turnover, and boundary clumping to assign a categorical metacommunity structure (Leibold & Mikkelson, 2002; Presley et al., 2010). Each metacommunity type represents a hypothesis for how community structure is shaped. The use of additional modelling can provide information on how dispersal among local communities and local conditions such as environmental factors and species interactions influence community structure along environmental and landscape gradients (Erős et al., 2017). This commonly used classification approach allows ecologists to simultaneously compare hypotheses of community assembly instead of analysing each hypothesis independently (Gascón et al., 2016; Marcilio-Silva et al., 2017).

Many studies have used the traditional EMS approach of categorising metacommunities to investigate community structure (Brasil et al., 2017; Dallas & Presley, 2014; Heino, Nokela, et al., 2015; Henriques-Silva et al., 2013; Murray-Stoker & Murray-Stoker, 2020; Tonkin et al., 2016). However, there has been some discussion on the validity of the EMS approach in terms of how coherence, turnover, and boundary clumping are calculated and subsequently used to assign a categorical metacommunity pattern. First, Schmera et al., (2018) argue that turnover and nestedness are not opposing patterns, but their calculations of turnover and nestedness were completed without showing evidence of coherence first and used a calculation for nestedness (richness-difference) that used a different gradient than the calculations for range turnover. However, the EMS definition of turnover is slightly different than the multitude of other  $\beta$  diversity measures because range turnover from the EMS framework uses species range as a unit whereas the other calculations use species occurrences (Presley, 2020). Second, the EMS framework uses reciprocal averaging to reorder sites into a latent gradient to be comparable to one another for analysis. This approach has also been criticised (Schmera et al., 2018), although Presley et al., (2019) points out that opting for researcher-defined gradients instead of using

reciprocal averaging would affect Type I and II error rates in the series of significance tests on the EMS metrics used to categorise metacommunity types. Regardless of how the debate will be settled, these potential discrepancies in how the elements are calculated to assign metacommunity types suggest that there is value in understanding the factors affecting the quantitative elements themselves, rather than using them to assign categorical metacommunity types. Few studies have investigated the environmental factors that affect coherence, turnover, and boundary clumping in an EMS framework. An elements-based approach of examining how environmental drivers relate to each specific EMS could provide a more mechanistic understanding of how metacommunities are structured at the landscape scale.

Large-extent studies allow for mechanistic exploration of the landscape-scale patterns of metacommunity elements because researchers can partition the study region into many metacommunities occurring along key gradients of connectivity, climate, land cover, and  $\gamma$  diversity (Dias et al., 2017; Record et al., 2021). Large datasets of organism occurrence have been used to infer metacommunity processes in a variety of systems (García-Girón et al., 2020; fHenriques-Silva et al., 2013; Muneepeerakul et al., 2008; Murray-Stoker & Murray-Stoker, 2020). At regional scales, both environmental and dispersal drivers have been shown to impact community assembly (Chase, 2014; Meynard et al., 2013). However, while landscape scale analyses using EMS and  $\beta$  diversity have provided insight into which patterns can be detected, the mechanisms driving these patterns have been much less explored (Dümmer et al., 2016; Murray-Stoker & Murray-Stoker, 2020; Rocha et al., 2018; Specziár et al., 2018; Vazquez et al., 2019). For example, several studies have identified landscape-scale metacommunity patterns using EMS without quantitatively investigating their drivers (Brasil et al., 2017; Henriques-Silva et al., 2013; Presley et al., 2011). Those studies that have investigated landscape drivers of metacommunity patterns using EMS have done so over only one or two catchments (Brasil et al., 2017; Fernandes et al., 2014; Tonkin, Shah, et al., 2017). Many other studies have quantified landscape drivers of  $\beta$  diversity metrics without focusing on how those results relate to the metacommunity framework (Dala-Corte et al., 2019; Edge et al., 2017; Krynak et al., 2019). Meanwhile, landscape-scale studies of  $\alpha$  diversity, species occurrence, and population processes have demonstrated the importance of land cover and connectivity on biotic processes (Allan, 2004; Duarte et al., 2018; Lansac-Tôha et al., 2020). In fact, a recent review implicated the similarities between metacommunity and landscape ecology and the need to better integrate concepts and practices within both (Almeida-Gomes et al., 2020). Exploring the landscape-scale drivers of coherence, turnover, and boundary clumping at large spatial extents will help link mechanisms and VILEY

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large-scale analysis of community assembly, making the connection between metacommunity and landscape ecology.

Attributes of study design may affect observed  $\beta$  diversity and metacommunity analysis results, but there has been little discussion in the metacommunity literature regarding how number and density of sampled sites affect outcomes of metacommunity analyses (Heino et al., 2015). The number of local communities sampled within a metacommunity affects calculations of the three EMS metrics. However, although this outcome is mathematically obvious, no study has shown with field-collected data how differences in the number of local communities will impact the outcome of analyses comparing multiple metacommunities (Patrick & Yuan, 2019). More locations in a metacommunity may increase the likelihood of capturing the entire regional species pool and quantifying true spatial gradients where species can be gained or lost individually or in larger numbers (Troia & McManamay, 2017). Moreover, the distance among sampling sites may also affect the quantified effect of connectivity on coherence, turnover, and boundary clumping by allowing researchers to observe finer-scale patterns along key gradients. Because the metacommunity framework accounts for dispersal of organisms among local communities, randomly selecting sites within the metacommunity may give misleading results due to the changing order of sites in the matrix and distance between those sites. Understanding how factors involving number and distance between sampling sites affect quantified relationships between landscape-scale metacommunity drivers will help to better inform and contextualise inference.

Riverine fishes provide a unique study system for understanding landscape scale drivers of metacommunity properties for several reasons (Altermatt, 2013). First, the linear dendritic structure of river networks restricts longitudinal movement of fishes (Brown & Swan, 2010; Tonkin et al., 2018). Because unassisted overland dispersal is not possible, fish communities may be proximal in Euclidean space, but highly separated in network distance, creating a unique spatial framework to disentangle that relative importance of local and regional factors in structuring metacommunities (Tonkin, Altermatt, et al., 2017). Second, catchments are arranged hierarchically where small catchments are nested within larger catchments separated by overland boundaries or oceans. This structure creates real and discrete spatial units for delineating metacommunities as experimental units in large-scale analyses, which can help to overcome issues of setting arbitrary and unrealistic boundaries of metacommunities (Jelinski & Wu, 1996; Patrick & Yuan, 2019).

In this study, we quantified landscape-scale drivers of stream fish metacommunities in 189 catchments of the eastern U.S.A. We sought to accomplish two objectives: (1) to quantify effects of landscapescale variables on coherence, turnover, and boundary clumping as well as the overall patterns assigned through analysis of the EMS variables; and (2) to identify spatial clumping and hotspots for metacommunity patterns. Because of our large spatial extent, visualising coherence, turnover, and boundary clumping over our study area allowed us to identify regions where there was a significant grouping of high or low values. This approach provided a complementary option for visualising spatial patterns. We hypothesise (1) a negative influence of urbanisation and agriculture on coherence, turnover, and boundary clumping (Table 1). Changes in land use often cause extirpation of specialist species and replacement of cosmopolitan species affecting the elements of metacommunity structure (Olden et al., 2006; Scott & Helfman, 2001). Connectivity barriers such as dams impact the ability of fishes to move within the catchment. We hypothesise that (2) the reduced connectivity and changes in hydrology and instream habitat in catchments with many dams will produce more distinct fish assemblages across the catchment (Poff & Hart. 2002). The result of these affects should be decreased coherence, turnover, and boundary clumping (Table 1). Because headwater stream fish assemblages are often represented as nested subsets of richer downstream assemblages, we hypothesise (3) the changes in elevation and temperature within a catchment will have a negative relationship with coherence, turnover, and boundary clumping because in our study system, headwater streams are generally at a higher elevation with cooler water temperature and are often more isolated than downstream reaches (Brown et al., 2011; Midway & Peoples, 2019). We lastly hypothesise (4) a positive relationship between fluvial distance among local communities, number of local communities, and  $\gamma$  diversity and coherence, turnover, and boundary clumping (Table 1). Including these variables at the forefront of our models will give better insight into how each are shaping metacommunity properties in addition to environmental variables. Due to the dendritic nature of catchments, using fluvial distance among sites will give more biologically relevant results compared to using Euclidean distance in our analyses (Tonkin, Altermatt, et al., 2017). We treated sampling locations (hereon referred to as local communities) as distinct local communities within a metacommunity for each catchment. We quantified spatial patterns for coherence, turnover, and boundary clumping using Moran's I, and visualised these patterns using hotspot analysis. We then used mixed-effects regression models to quantify effects of landscape-scale variables on coherence, turnover, and boundary clumping individually.

# 2 | METHODS

# 2.1 | Study area and spatial scale

Our study area encompassed 12 states in the eastern U.S.A. (Figure 1). This region offers elevational gradients where rivers generally originate in montane regions, and flow east across the coastal plain. Because of our large extent and fluvial discontinuity by oceans, major river systems are disconnected from one another along the river network. Over 22,000 small and large commercial dams occur in the study area. Forest land use dominates our study area (54%), followed by agriculture (16%), urbanisation (11%), and wetlands (7%).

Rivers are hierarchical, with catchments of decreasing size nested in larger drainage basins. In the U.S.A., rivers are categorised by hydrologic unit codes (HUCs), which increase in length as catchment areas become smaller. For example, HUC6 catchments are nested within HUC4 catchments etc. Using catchment boundaries

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**TABLE 1** Landscape-scale variables used in the generalised linear mixed model and linear mixed model to predict the elements of metacommunity structure

Variable	Definition	Source	Range; Average	C Hypothesis	T Hypothesis	BC Hypothesis
Developed (% coverage)	Average percent developed landcover calculated from four developed classes	2011 NLCD (Homer et al., 2015)	(0.022–50.97); 11.35	+	+	-
Agriculture (% coverage)	Average percent crop/ pasture/hay land use per catchment	2011 NLCD (Homer et al., 2015)	(0-51.67); 15.82	+	+	-
Dams	Number of dams in each catchment	NID-2017 USACE	(0–536); 86.13	+	+	+
Temperature (°C)	Average min temperature per catchment	World Climate Data (Hijmans et al., 2005)	(-7.51-18.18); 3.62	-	-	-
Elevation (m above sea level)	Average elevation per catchment	DEM (USGS, N, 2017)	(19.38–980.96); 288.41	-	_	-
Distance among sites (km)	Average distance among sites in each catchment	NA	(4.24–151.71); 63.94	+	+	+
Species richness	Regional species richness for each metacommunity	Fish dataset	(6-77); 38.16	+	+	+
Number of sites	Number of local communities within each metacommunity	Fish dataset	(9–403); 72.28	+	+	+
Sampling effort	Average number communities sampled within each metacommunity	Fish dataset	(1-2.51); 1.33	NE	NE	NE

*Note*: C = coherence, T = turnover, and BC = boundary clumping; (+) hypothesises a positive relationship, (–) hypothesises a negative relationship, (NE) hypothesises no effect.

as discrete spatial units is common in broad-scale studies in aquatic ecology (Guo & Olden, 2014; Patrick & Brown, 2018; Peoples et al., 2018). We used HUC8 catchments, which have approximate areas of  $3,500-4,000 \text{ km}^2$  (Seaber et al., 1987). For the purposes of this study, we treated each sampling location as a local community and each HUC8 catchment as a separate metacommunity and experimental unit within our models. This scale represents the finest scale at which our data can be partitioned into multiple metacommunities that contain 15 or more local communities.

# 2.2 | Fish dataset

We analysed a dataset of contemporary (mid 1990s to present) stream fish occurrence records (presence-absence records) compiled from community sampling by state resource management agencies. Records were subjected to stringent quality control before being included in our dataset, and were only included if: (1) researchers sampled at least 20–30 times mean stream width, a minimum distance required to sufficiently characterise species richness at a site (Barbour et al., 1999); (2) sampling and species identification were completed by professional biologists; (3) sampling was designed to characterise whole assemblages and was not directed at a single species or only game species. This dataset has been used in previous research investigating questions requiring large-extent occurrence data (Midway et al., 2015, 2016; Peoples & Midway, 2018; Wagner & Midway, 2014) (Figure 1). The dataset totals 139,184 sites and 262 fish species. Sites were coarsened to the segment scale, the most appropriate scale for modelling stream fish occurrence (Benda et al., 2004). Streams are hierarchically organised with microhabitats nested within pool/riffle systems and pool/riffle systems together combine to form stream reaches (Frissell et al., 1986). Fish occurrences were pooled for segments with multiple sites or sampling occasions. At this large extent, using occurrence data allows us to avoid introducing bias from number of individuals collected and area sampled (Chao et al., 2005). Although we cannot rule out fish assemblages being temporally dynamic at some sites, we expect that given the relatively short time over which sampling took place, many sites are unlikely to have changed assemblages. Furthermore, any assemblage changes are likely to be inconsequential relative to the spatial scale extent of the study.

# 2.3 | Calculating EMS patterns

Following standard analyses for calculating EMS, we first used the *vegan* package (Oksanen et al., 2015) in R version 3.5.1 (R Core



FIGURE 1 Extent of study area on the eastern U.S.A. Grey polygons represent hydrologic unit code 8 catchments (metacommunities) and dots represent an individual survey site of stream fish incidence data (local communities). Map insets show two regions within the study extent zoomed in to show spatial coverage of local communities

Team, 2019) to ordinate the site-by-species occurrence matrix, which reorders sites with similar species closer together. We used reciprocal averaging to minimise embedded absences of a species range, determine nestedness or high turnover, and define species boundaries without a priori knowledge of environmental gradients (Leibold & Mikkelson, 2002; Willig et al., 2011). We assigned metacommunity patterns after calculating coherence, turnover, and boundary clumping using the metacommunity function in the metacom package (Dallas, 2018). Coherence and turnover calculations resulted in discrete numbers of embedded absences and replacements per metacommunity, respectively. We then compared observed coherence and turnover calculations to a simulated mean to determine statistical significance ( $\alpha = 0.05$ ). Simulated means were drawn from a fixed-row, fixed-column null matrix with 999 simulations (Dallas, 2018). We used Morisita's Index (MI) to represent boundary clumping; MI is a continuous variable that includes information about species representation in different samples in combination with total number of species (Morisita, 1971). MI estimates typically range

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around 1.0, with estimates significantly greater than 1.0 indicating a more clumped species distribution (i.e., unique species grouping) and MI significantly less than 1.0 indicating an over-dispersed species distribution (Leibold & Mikkelson, 2002). Significance testing of MI estimates was done with a Chi-squared test (Hoagland & Collins, 1997). We determined overall metacommunity pattern using positive, negative or non-significance of coherence, turnover, and boundary clumping as in Figure 2a (Leibold & Mikkelson, 2002; Presley et al., 2010). We acknowledge that downsides exist for using the traditional EMS approach (Schmera et al., 2018), but ordering sites by a latent gradient allows us to use a mechanistic approach in quantifying metacommunity assembly (Presley et al., 2019).

### Independent variables 2.4

We calculated independent variables indexing landscape-scale mechanisms hypothesised to affect coherence, turnover, and



**FIGURE 2** (a) Adapted from Henriques-Silva et al., (2013), this graphic represents how coherence, turnover, and boundary clumping assign a metacommunity structure. Coherence represents the number of embedded absences, turnover the number of replacements, and boundary clumping is calculated from Morisita's Index showing the degree of specific species groupings within a metacommunity. Coherence is tested first where a metacommunity with positive coherence results in the testing of turnover. A combination of the turnover and boundary clumping results determine which metacommunity structure is assigned. Quasi structures represent not significant (NS) turnover with the (+) and (-) showing the turnover value leaning towards the positive or negative direction. Site by species matrices show an idealised version of what the metacommunity would look like. Colours surrounding metacommunity structure types correspond to those in. (b) The elements of metacommunity structure (EMS) patterns on the eastern U.S.A. stream fish after calculating coherence, turnover, and boundary clumping in hydrologic unit code 8 catchments with at least 15 local communities. Seven different structures were observed

boundary clumping using ArcMap GIS 10.6 (ESRI, 2018). We reclassified land cover data from the 2011 National Land Cover Dataset (Homer et al., 2015) into three categories (developed, forested, and agriculture). Developed landcover was the combined percentage of open space, low, medium, and high developed area, forested landcover was the combined percent of deciduous, evergreen, and mixed forests, and agriculture was the combined percentage of hay/pasture and cultivated crops. We used the National Inventory of Dams to calculate dam density in each HUC8. We used the National Elevation Dataset to calculate average elevation (USGS, N, 2017), and World Climate Dataset to calculate average maximum water temperature (Hijmans et al., 2005). We calculated and averaged distance among sites (DAS) along the fluvial network using an origin/destination cost matrix in ArcMap, in which both upstream and downstream directions are equal (Table 1). While rarefication of site numbers and DAS address potential impacts on metacommunity sampling, we think deriving effect estimates for these variables is important and each should be at the forefront of our models to understand their impacts instead of rarifying and placing the variables in the model background.

# 2.5 | Statistical analyses

We used mixed effects regression models to quantify effects of landscape-scale variables on coherence, turnover, and boundary clumping. Prior to analyses, we scaled independent variables (Table 1) to a mean of zero and standard deviation of one. We screened for collinearity using Pearson correlation and variance inflation factor, with cutoff values of r > 0.6 and variance inflation factor >2.0. Forest cover was correlated with numerous independent variables and removed from analyses. Model forms varied due to the distribution of response variables and different link functions used, but independent variables were the same for all models. Because coherence and turnover followed an overdispersed Poisson distribution, we used a negative binomial generalised linear mixed model using glmmTMB package (Magnusson et al., 2017). Because MI was continuous and right skewed, the values were log-transformed prior to analysis to improve normality and we modelled MI using a linear mixed model in the Ime4 package (Bates et al., 2007). To account for differences in catchment size that may affect response variables, we used catchment area as an offset for coherence and turnover models. We also included the number of times each segment was sampled as a covariate in each model to account for uneven sampling effort. We used HUC4 catchments as a random intercept in each model to account for spatial nestedness of HUC8s within HUC4s. This approach accounts for spatial autocorrelation within connected fluvial networks; in this region, HUC4s are separated by oceans and are therefore spatially independent for the purposes of studying stream fish metacommunities. Finally, we calculated conditional  $(R_c^2)$ and marginal  $(R_m^2)$   $R^2$  values for each model using the MuMIn package (Barton & Barton, 2015). Marginal  $R^2$  values represent variation explained by fixed effects alone, and conditional R<sup>2</sup> values represent variance explained by both fixed and random effects.

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We used mixed-effects logistic regression to quantify effects of landscape variables (Table 1) on metacommunity types determined from analysing coherence, turnover, and boundary clumping. Because metacommunity types represent a discrete categorical variable, we used multinomial logistic regression in the *lme4* package to quantify effects of landscape-scale variables on metacommunity patterns, and marginal and conditional  $R^2$  values were calculated. In this model, we used only the four most common metacommunity patterns: Clementsian (70 metacommunities), quasi-Clementsian (37), clumped species loss (30), and quasi-clumped species loss (41). For significant variables in this model, we used a post hoc Tukey test to compare variable means among metacommunity types.

Finally, we used spatial analyses to investigate spatial structuring of metacommunity types and each EMS. First, we used Moran's *I* to examine spatial autocorrelation in our study area. Moran's *I* values range from -1.0 to +1.0, in which a positive value represents spatial clumping, and negative values represent spatial dispersion (Getis & Ord, 2010). We then used optimised hot spot analysis to identify locations of significant spatial clumping or dispersion (Ord & Getis, 1995).

# 3 | RESULTS

Gamma diversity in each catchment ranged from six to 77 with a mean of 38 species. Coherence ranged from four to 7,470 embedded absences per metacommunity, with an average of 592. Turnover ranged from 18 to 846,000 replacements per metacommunity, with an average of 44,789. Boundary clumping (MI) ranged from 0.99 to 55.82, with an average of 5.72. We observed seven metacommunity patterns where Clementsian, quasi-Clementsian, clumped

species loss, and quasi-clumped species loss were the most common (Figure 2b).

Coherence ( $R_m^2 = 0.33$ ;  $R_c^2 = 0.35$ ), turnover ( $R_m^2 = 0.68$ ;  $R_c^2 = 0.70$ ), and boundary clumping ( $R_m^2 = 0.45$ ;  $R_c^2 = 0.66$ ) were all affected significantly by landscape scale variables (Figure 3; Table S1). Dam density positively affected coherence and turnover density, while DAS negatively affected coherence and turnover in each metacommunity. Percent developed land use positively affected MI, while dam density negatively affected MI. Gamma diversity positively affected coherence and turnover. Number of sample locations in each metacommunity positively affected all three EMS variables, while temperature negatively affected all three EMS variables (Figure 3, Table S1).

Only elevation was significant in the multinomial logistic regression predicting categorical metacommunity types ( $R_m^2 = 0.12$ ;  $R_c^2 = 0.12$ ). The  $R^2$  values for this model were much lower compared to our  $R^2$  values in the mixed effect models above. Post hoc comparisons showed that elevation was higher for clumped species loss and quasi-Clementsian metacommunities, relative to Clementsian metacommunities (Figure 4).

Spatial analyses showed significant clumping for coherence, turnover, and boundary clumping (p < 0.0001 for all; Figure 5). High and low coherence density concentrated in the New England and South Atlantic Gulf Regions, respectively, with hot spots found in the New England Region. High and low turnover density concentrated in southern New England/eastern Mid-Atlantic Regions and south-eastern U.S.A., respectively, with a hotspot in New England and cold spot in Southern Mid-Atlantic Regions. High and low MI concentrated in Ohio/Mid-Atlantic and South Atlantic Gulf Regions, respectively, with a hot spot detected in the Ohio/Mid-Atlantic Region (Figure 5).



**FIGURE 3** Results from generalised linear mixed model and linear mixed model for influence of landscape-scale variables on coherence (a), turnover (b), and boundary clumping (c) individually. Squares represent the parameter estimate and bars represent the 95% confidence intervals. Confidence intervals not overlapping zero show the direction of the influence for the corresponding landscape-scale variable. Grey bars are to allow for easy viewing across each pane. DAS is distance among sites

FIGURE 4 Average elevation in metres within each metacommunity pattern for the four most common metacommunity patterns observed on the eastern U.S.A. A metacommunity was delineated as a hydrologic unit code 8 catchment. Letters show significance between structures. Clumped species loss occurs at a higher elevation compared to Clementsian patterns



### 4 DISCUSSION

Understanding metacommunity structure beyond the local scale provides broader inference on the factors that structure communities (Brown et al., 2011). We used a mechanistic approach to explore potential relationships among landscape-scale variables and metacommunity properties. Our results demonstrate the importance of dispersal and abiotic factors in determining community composition, with numerous landscape-scale factors affecting coherence, turnover, and boundary clumping as well as the categorical metacommunity patterns they contribute to. Moreover, study design attributes affected the EMS variables, indicating that number of sampling locations and site locations and proximities in the catchment should be accounted for when designing EMS studies or applying the EMS framework to data that were not collected with that purpose.

In support of our first hypothesis, anthropogenic land development positively affected how many unique species groupings occurred within metacommunities. Urbanised landscapes have been associated with a variety of changes to stream habitats including increased nutrient input, sedimentation, runoff, and channelisation (Allan, 2004). Decreases in species richness associated with increased urban land use has been documented for fish communities across the globe (Edge et al., 2017; Tóth et al., 2019; Wang et al., 2001). Even if regional species pools are similar, unique species groupings can still be observed in metacommunities because of interspecific differences in tolerance to urbanisation (Utz et al., 2010), which is a

similar notion to why urbanisation could impact turnover (Johnson et al., 2013). Interestingly, embedded absences and replacements showed no relationship with developed land cover. Some studies have shown that urbanised habitats have communities that are similar to one another, but are different from those in forested areas, suggesting an increased turnover at the urbanisation forest boundary (Ortega-Álvarez & MacGregor-Fors, 2009; Sreekar et al., 2017). Disturbances including urbanisation or drought can impact available habitat decreasing  $\beta$  diversity between sites where habitat filtering favours those species that can withstand the disturbance conditions (Chase, 2007; Picazo et al., 2012). Anthropogenically developed land cover is diverse, containing mixtures of low-level suburban development to high-intensity urban development; these land cover types interact with the underlying geophysical template across the landscape (Deweber et al., 2019). Including a mixture of specific types of development has been a useful way of quantifying effects of developed land cover (Wang et al., 2001), although such an approach would not be appropriate at the spatial extent of our study because they are strongly correlated across a large spatial extent. However, future studies that are more regionally focused may benefit from considering more specific land cover variables to further tease out potential anthropogenic influences on metacommunity properties.

Dam density positively affected coherence and turnover, and negatively affected boundary clumping. These findings contrast with our second hypothesis that decreased connectivity would isolate upstream communities and cause more unique communities. Instead,

FIGURE 5 Metacommunity stream fish spatial patterns observed in each hydrologic unit code 8 catchment on the eastern U.S.A. The left column shows the distribution of coherence, turnover, and boundary clumping and the right column shows hotspot analysis. Moran's I spatial autocorrelation values for each element are shown (all show significant clumping with p < 0.0001)

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this result highlights the effect of taxonomic homogenisation-the process by which communities become more similar (Rahel, 2000). Homogenisation can occur from either establishment of non-native species and/or loss of specialist species due to environmental alterations, human movement of species, etc. (Olden & Poff, 2004; Scott & Helfman, 2001). Stream fish communities across the eastern U.S.A. have experienced significant homogenisation due to non-native species introductions, and this process is correlated with numerous natural and anthropogenic factors (Peoples et al., 2020). Habitat alterations to rivers caused by dams can facilitate establishment of non-native species (Clavero & Hermoso, 2011) and contribute to taxonomic homogenisation of riverine fish communities (Poff et al., 2007). Moreover, the novel impounded habitats produced by dams often serve as a source for new introduced species that replace the lost riverine specialists (Johnson et al., 2008). These relationships corresponding to dam impacts are intuitive, as impoundment of rivers are consequential alterations to riverine systems globally by altering numerous interconnected mechanisms including hydrology, temperature, and habitat diversity (Hitchman et al., 2018; Liermann et al., 2012; McManamay et al., 2015; Poff et al., 2007; Wang et al., 2011). The positive relationship between dam density and embedded absences may suggest decreases in specialist species and community discontinuity caused by dispersal limitation. Increased turnover suggests more species replacements within the metacommunity, and homogenisation could be taking place through the replacement of many specialist species by one or a few generalist species.

In support of our third hypothesis, we found that temperature negatively affected coherence, turnover, and boundary clumping. Embedded absences decreased with increasing temperature, probably reflecting a pattern of increasing temperature from headwaters to downstream. We observed decreased turnover and boundary clumping with increasing temperature because similar species assemblages can occur in neighbouring downstream communities as species numbers approach the regional species pool. Previous work demonstrated warming rivers increased dominant species and increased replacement of northern cold-water species by southern warm-water species (Maire et al., 2019). Community compositional changes from warming rivers could be revealed in metacommunities by observing shifts in coherence, turnover, and boundary clumping as warm water species move into new habitat due to changing climate (Buisson et al., 2013; Domisch et al., 2011; Scott & Helfman, 2001). We can consider temperature a potential proxy variable for elevation and riparian cover, because of the close relationship between these variables and stream temperature. Temperature was the single abiotic landscape scale variable impacting metacommunities from natural temperature changes along the headwater to mainstem gradient.

In support of our fourth hypothesis, we found that  $\gamma$  diversity positively affected coherence and turnover. The relationship between  $\gamma$  and  $\beta$  diversity is affected by many factors (Crist & Veech, 2006; Maloufi et al., 2016). In metacommunities with high  $\gamma$  diversity, habitat heterogeneity and connectivity will probably cause increasing community differentiation as distance among local

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communities increases (Gianuca et al., 2017; Koleff & Gaston, 2002). Studies have identified both positive and negative turnover-driven relationships between  $\gamma$  and  $\beta$  diversity (Maloufi et al., 2016; Patrick & Brown, 2018). This relationship can be non-linear (Gering & Crist, 2002) and can be heavily impacted by species dispersal capabilities (Gianuca et al., 2017). For stream fishes, increased  $\gamma$  diversity can cause more turnover because species cannot inhabit all possible niche spaces available. As regional scale increases, larger-scale filters operate on community assembly causing a smaller subset of the regional species pool within local communities (Jackson et al., 2001).

Study design choices impacted analyses of coherence, turnover, and boundary clumping. The number of local communities sampled within a metacommunity was positively associated with coherence. turnover, and boundary clumping. Increasing the number of sampled communities can provide insight into transitions among more distant communities, which have an increased likelihood of having a distinct assemblage within the metacommunity, similar to how lakes in close proximity have similar communities, but those furthest removed have very different assemblages (Olden et al., 2001). Increased sampling density can affect observed patterns of  $\beta$  diversity by decreasing the probability that local communities with rare species will be excluded (Schroeder & Jenkins, 2018). We also found a negative relationship between distance among sites and turnover. These results are similar to Thompson et al., (2017), who showed how inclusion of variable connectivity among sites within a metacommunity can interact with species' dispersal modes to affect metacommunity properties. Metacommunity analyses are contextualised by a variety of methodological choices including spatial extent and scale, as well as sampling intensity and site positions within the catchment (Declerck et al., 2011; Heino, Melo, et al., 2015; Meynard et al., 2013). For example, conducting analyses at a large spatial extent and relatively coarse resolution may have contributed to many metacommunities being classified as Clementsian, a niche-based structure (Viana & Chase, 2019). Moreover, resampling methods have recently been presented for dealing with arbitrary delineation of spatial units defining metacommunity boundaries and uneven sampling within those units (Patrick & Yuan, 2019). While our choice of the HUC8 scale is reasonable given the life history and overland dispersal limitation of the stream fish species in the region, a logical next step will be to examine the effect of spatial scale choice on metacommunity properties. Moreover, whether by resampling or incorporating into the models as offsets or covariates, uneven sampling and distance among sites must be accounted for in large-scale metacommunity analysis. More biological significance was represented with distance among sites in our models because fluvial distance was measured between sites instead of using Euclidean distance, which can greatly underestimate the distance between sites due to the dendritic nature of catchments in our study extent. Understanding the comparative trade-offs of method choices in affecting outcomes of metacommunity analyses will help to refine analytical procedures.

Clementsian and clumped species loss metacommunities that are characterised by nestedness and high boundary clumping were the most common metacommunity types in our study area. These WILEY Freshwater Biology

metacommunity types are among the most commonly observed patterns in a diversity of systems (Brasil et al., 2017; Erős et al., 2017; Heino et al., 2017; Henriques-Silva et al., 2013). Turnover rates represent the major difference between these two metacommunity types; Clementsian metacommunities have high  $\beta$  diversity and clumped species loss metacommunities have low  $\beta$  diversity, with quasi structures in-between (Heino, Soininen, et al., 2015). Accordingly, our results support the hypothesis that turnover strength plays an important role in mediating the effects of landscape-scale variables in structuring metacommunities (Presley et al., 2010). Outside the metacommunity framework,  $\beta$  diversity literature often examines drivers of turnover without investigating how turnover impacts larger metacommunity properties. For example, studies may focus on how environmental heterogeneity drives turnover and nestedness components of  $\beta$  diversity, and turnover may increase over environmental gradients such as aquatic vegetation density, suggesting species-specific responses to habitat complexity (Cunha et al., 2019). Thus, the research focus is directed toward how habitat affects turnover instead of understanding turnover in the context of organism dispersal, which would begin to incorporate the metacommunity framework. Future studies investigating how landscape-scale variables affect metacommunities through turnover will help to better contextualise results of large-scale community ecology studies.

Elevation increased the likelihood of a clumped species loss metacommunity. We observed a continuum where higher elevation metacommunities were more likely to be classified as clumped species loss, and lower elevation metacommunities were more likely to be classified as Clementsian. Headwater streams generally have distinct species assemblages compared to communities downstream due to decreased connectivity (Finn et al., 2011; Henriques-Silva et al., 2013; Meyer et al., 2007). In much of the study region, catchments are separated by a fall line delineating upland ecoregions from coastal plains. This boundary can also represent a distinct barrier in which streams above the fall line are generally less connected to one another than streams below the fall line (Hupp, 2000; Rohde et al., 2009). Clementsian patterns can result from habitat heterogeneity increasing species richness and increasing changes in land cover creating distinct assemblages in downstream communities (Vörösmarty et al., 2010). Interestingly, López-González et al. (2012) also observed a positive effect of elevation on the likelihood of observing clumped species loss metacommunities of bats in Mexico. The explained variance in our multinomial logistic regression model was very low compared to the explained variance for our models investigating individual continuous metrics, suggesting that modelling each EMS may provide an informative alternative approach for examining the mechanisms that drive metacommunity properties across the landscape. Considering coherence, turnover, and boundary clumping together, elevation was the only landscape-scale variable that explained differences among archetypical metacommunities, but examining each EMS individually showed the influence of other landscape scale variables, excluding elevation.

Metacommunity theory incorporates local and regional processes in understanding community assembly and is thus a modern standard bearer for understanding processes across the landscape. Large extent, multi-metacommunity studies represent an important next step for integrating metacommunity concepts with similar ecological sub-disciplines (Lansac-Tôha et al., 2020). In doing so, these approaches improve our ability to link mechanism with metacommunity properties across large spatial extents and across spatial scales. Our novel approach to using coherence, turnover, and boundary clumping individually suggest that landscape scale variables influence metacommunity properties. Many of these variables occur along natural gradients of elevation, temperature,  $\gamma$  diversity, and fluvial connectivity. However, we also show that anthropogenic changes on the landscape such as hydrologic and land cover alterations influence metacommunity properties by affecting distributions of turnover and nestedness. Another important observation is that inherent characteristics of the dataset have important bearing on observed metacommunity properties. Simply increasing the number of sampled local communities and/or the distance among them can affect metacommunity interpretations. As ecology moves into the era of big data to answer broad questions, accounting for these important natural, anthropogenic, and methodological issues will be critical for improving the inferential power of metacommunity approaches.

## ACKNOWLEDGMENTS

We thank the numerous agency and university employees who contributed to the dataset. We thank T. Wagner for facilitating access to the dataset. We would also like to thank Blake Lytle and Patricia Carbajales-Dale of the Clemson Center for Geospatial Technologies for providing crucial help with large scale GIS calculations. L.S. is supported by the Department of Biological Sciences at Clemson University. This work was supported in part by the USDA/NIFA, under project number SC-1700599, and represents technical contribution number 6985 of the Clemson Experiment Station.

# CONFLICT OF INTEREST

No conflict of interest.

# DATA AVAILABILITY STATEMENT

Data are available from the authors upon a reasonable request.

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# SUPPORTING INFORMATION

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

How to cite this article: Stoczynski, L., Brown, B. L., Midway, S. R., & Peoples, B. K.. Landscape features and study design affect elements of metacommunity structure for stream fishes across the eastern U.S.A. *Freshw Biol.* 2021;66:1736-1750. https://doi.org/10.1111/fwb.13788

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