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Stream fish colonization but not persistence varies regionally across a large North American river basin

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ABSTRACT

Many species have distributions that span distinctly different physiographic regions, and effective conservation of such taxa will require a full accounting of all factors that potentially influence populations. Ecologists recognize effects of physiographic differences in topography, geology and climate on local habitat configurations, and thus the relevance of landscape heterogeneity to species distributions and abundances. However, research is lacking that examines how physiography affects the processes underlying metapopulation dynamics. We used data describing occupancy dynamics of stream fishes to evaluate evidence that physiography influences rates at which individual taxa persist in or colonize stream reaches under different flow conditions. Using periodic survey data from a stream fish assemblage in a large river basin that encompasses multiple physiographic regions, we fit multi-species dynamic occupancy models. Our modeling results suggested that stream fish colonization but not persistence was strongly governed by physiography, with estimated colonization rates considerably higher in Coastal Plain streams than in Piedmont and Blue Ridge systems. Like colonization, persistence was positively related to an index of stream flow magnitude, but the relationship between flow and persistence did not depend on physiography. Understanding the relative importance of colonization and persistence, and how one or both processes may change across the landscape, is critical information for the conservation of broadly distributed taxa, and conservation strategies explicitly accounting for spatial variation in these processes are likely to be more successful for such taxa.

1. Introduction

Ecologists and managers are interested in the processes that regulate species distributions and abundances, in part so that they can anticipate how populations and communities will respond to environmental changes and management actions (Clark et al., 2001). In the case of water resource management, ecologists frequently consider the stream flow regime to be a 'master variable' influencing ecological processes (Power et al., 1995; Poff et al., 1997), and consequently have focused on quantifying biotic responses to changes in stream flow characteristics (e.g., Galbraith et al., 2010; Atkinson et al., 2014). Conservation practitioners often give limited consideration to spatial variation in such regulating processes because species of concern typically experience relatively homogeneous environmental conditions within restricted ranges produced by the combination of specific habitat requirements and diminished habitat availability. However, the conservation community knows less about how more broadly distributed organisms are affected by spatial heterogeneity in population responses to environmental variation.

Many species have distributions that span distinctly different physiographic regions. Ecologists recognize effects of physiographic differences in topography, geology, and climate on local habitat configurations, and thus the relevance of landscape heterogeneity to species distributions, abundances (Swanson et al., 1988), and metapopulation processes (i.e., colonization, extinction; Hanski, 1999). Therefore, a broadly distributed species might respond differently in different physiographic regions to the same environmental change, implying that the most effective management or conservation actions could also differ across physiographic regions (Whittingham et al., 2007; McAlpine et al., 2008). Physiographic influences could thus be particularly

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relevant to maintaining common species (Watson and Watson, 2015; Frimpong, 2018) found over wide geographic ranges, as well as more broadly but patchily distributed imperiled species.

Studies conducted across different environments have demonstrated physiographic or spatial effects on population state responses (e.g., abundance, occurrence, composite indices) of broadly distributed aquatic and terrestrial taxa. For example, occurrence models for organisms such as farmland birds (Whittingham et al., 2007), koalas (McAlpine et al., 2008), greater sage-grouse (Dzialak et al., 2013), and stream fishes (Wenger and Olden, 2012) that were developed in one particular area poorly predicted occurrence in other areas. In freshwater systems, ecologists have reported physiographic variation in the effects of urbanization on invertebrates and fishes (Morgan and Cushman, 2005; Stanfield and Kilgour, 2006; Goetz and Fiske, 2008; Cuffney et al., 2010; Utz et al., 2009, 2010), and have also provided evidence that stream flow characteristics and their influence on snapshot measures of fish assemblages vary among physiographic regions (Knight et al., 2012, 2014). Yet, to our knowledge, researchers have not explicitly examined how physiography affects the vital rates that determine metapopulation dynamics.

Here, we address physiographic influence on metapopulation dynamics using stream fishes as model organisms. Even though habitat for stream fishes typically exists as a continuum, rather than as sharply-defined patches, individual stream reaches have proven to be useful units for estimating species occupancy and turnover rates in relation to a variety of covariates (Gotelli and Taylor, 1999; Peterson and Shea, 2015). We have similarly examined occupancy dynamics to evaluate how physiography may influence rates at which individual taxa persist in or colonize stream reaches under different flow conditions. To do this, we fit multi-species dynamic occupancy models (MacKenzie et al., 2006; Royle and Kéry, 2007) to periodic survey data for a suite of fish species occurring across a large river basin that encompasses multiple physiographic regions. Previous work demonstrated that seasonal stream flow and species traits can strongly influence metapopulation dynamics of fishes (Peterson and Shea, 2015; Shea et al., 2015). Thus, we considered three hypotheses: (1) that rates of persistence or colonization differ between physiographic regions; (2) that the effects of stream flow on metapopulation rates differ between physiographic regions; and (3) that effects of physiography on persistence or colonization rates vary in relation to fluvial specialization, a species-specific characteristic produced by a combination of biological traits. To test the possibility that apparent physiographic effects might be the result of correlations between physiography and other influential site-level characteristics, we also modeled occupancy dynamics in relation to two site-specific covariates, watershed size and connectivity. We thus evaluated the magnitude of physiography relative to other site-level effects in influencing persistence and colonization of widely-distributed fish species. Finally, we considered conservation consequences of observed regional differences in metapopulation rates.

2. Methods

2.1. Study area

The Apalachicola-Chattahoochee-Flint (ACF) Basin is a large (~51,000 km^2) river drainage covering portions of Georgia, Florida, and Alabama in the southeastern United States (Fig. 1). The basin is noted for both high freshwater biodiversity and conflicts over water resource allocation. > 100 described freshwater fishes are found in the ACF Basin, of which approximately 10% are endemic, in addition to high mussel and crayfish diversity (Couch et al., 1996; Abell et al., 2000; Brim Box and Williams, 2000; Elliot et al., 2014). Water resource management in the ACF Basin is challenging because it must ensure sufficient water quantity and quality for resident freshwater and estuarine biota while simultaneously meeting the water demands of a rapidly expanding population in metropolitan Atlanta, Georgia, as well as extensive irrigated agriculture in the lower basin. Climatic changes also threaten to intensify water resource conflicts in the ACF Basin, as forecasts project amplified variability that could increase the frequency of both floods and droughts (Ficke et al., 2007; Carter et al., 2014). Largely as a result of habitat and hydrologic alteration, 17 freshwater fishes in the ACF Basin are currently listed as of conservation concern by the State of Georgia, and one species is listed as threatened under the U.S. Endangered Species Act. Many of these fishes primarily inhabit tributary streams, as do many imperiled freshwater fishes globally, prompting efforts to quantify factors that influence species viability in relation to changing stream conditions.

Like many large eastern North American watersheds, the ACF Basin encompasses multiple physiographic provinces. The northern half overlays portions of the Blue Ridge and Piedmont physiographic provinces, whereas the southern half is exclusively within the Coastal Plain province (Fig. 1). The northern and southern halves of the basin are divided by the Fall Line, a narrow but sharp geological boundary separating an upland region underlain with generally resistant igneous and metamorphic crystalline rocks, from the Coastal Plain region characterized by softer sedimentary rock (Garrity and Soller, 2009; Elliot et al., 2014). For many rivers in this area of the continent the Fall Line creates a set of contrasting fluvial environments. Coastal Plain streams below the Fall Line are characterized by relatively low channel slopes, reduced channel confinement, and reduced flow permanence (i.e., elevated frequency of channel drying events). In comparison, upland streams above the Fall Line tend to have steeper slopes as well as higher degrees of confinement and flow permanence (Elliot et al., 2014).

2.2. Fish surveys

Between 2011 and 2016, we sampled fishes at 40 wadeable sites distributed across six sub-watersheds (Fig. 1; Supplementary material, Table S1) selected to represent the diversity of small-stream habitats across the ACF Basin. Sampled reaches were heterogeneous and typically consisted of pool-run-riffle sequences, and we attempted to sample with equal consistency and efficiency in each habitat type within each sample reach. We sampled each site at least twice (range = 2–9 samples; mean = 5.6; Supplementary material, Table S1) and sampling events occurred twice each year, once during the spring (generally May–June) and again during the fall (generally September), with the lone exception being 2011, when sampling was initiated during the fall (resulting in 11 possible sampling events over the six years). Due to funding constraints, sampling intensity declined after fall 2013, but we had no evidence that persistence or colonization rates changed relative to the earlier sampling period. During sampling, we captured fishes by backpack electroshocking or disturbing streambed substrates, or both, to encourage fish movement downstream into a seine (2.4-m × 1.8-m, 3.175-mm mesh). We also used seine hauls in low flow areas. Capture methods varied among sites and sampling events depending on local habitat structure and streamflow. Captured individuals were identified to species and counted, although we collapsed count data into binary detection data in our models (see Section 2.5.2). At least one sampling event at every site involved sampling multiple reaches to enable estimation of detection probabilities, although we recognize that detection may be underestimated from spatial replicates when species occurrences are naturally uneven across adjacent stream reaches. We isolated reaches by setting block nets or by using natural features (e.g., cascades) that restricted fish movement. Among all sampling events, reach lengths (46.9 ± 12.7 m; mean ± SD) and sampling times (33.5 ± 18.9 min) were generally similar. When we observed sites that were completely dry during sampling events, we assumed that all possible taxa were absent.

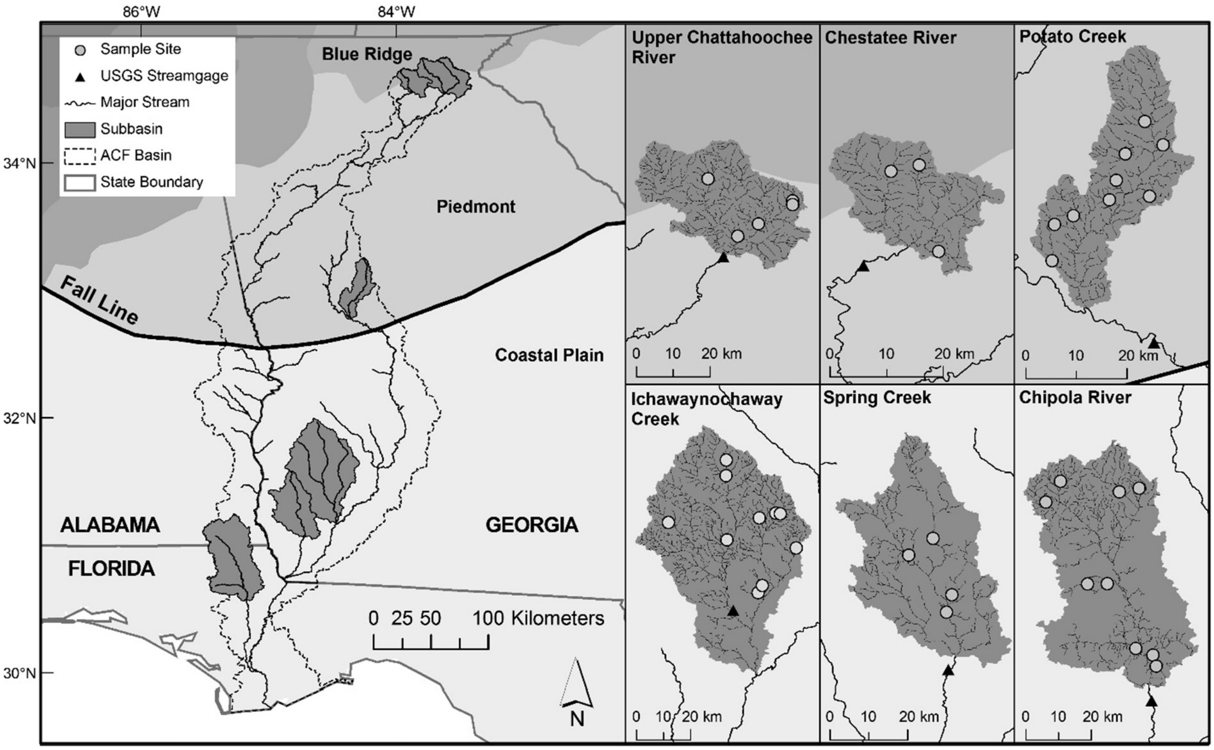

Fig. 1. Map of Apalachicola-Chattahoochee-Flint (ACF) River Basin in Georgia, Alabama, and Florida, southeastern United States. Fish sampling occurred in shaded sub-watersheds. Circles in insets depict sampling locations and triangles are locations of USGS streamgages used for flow calculations.

2.3. Focal taxa

For our analysis, we considered only those detected taxa that were broadly distributed above and below the Fall Line in the ACF Basin. This focus on broadly distributed taxa eliminated the possibility that any differences in metapopulation rates attributed to physiography actually reflected taxonomic differences among geographically-separated assemblages. Each taxon included in our analysis was detected at least once at two or more sites above and below the Fall Line. We assigned distributions for each taxon on the basis of species accounts (Etnier and Starnes, 1993; Boschung Jr and Mayden, 2004; Straight et al., 2009; Page and Burr, 2011) and unpublished survey data (Straight et al., 2009). Recognizing that the requirement of some species for flowing-water habitats could influence their response to changing flow conditions, we assigned each taxon to one of two groups: fluvial specialists (FS) that require flowing-water habitats for at least some portion of their life cycle (Kinsolving and Bain, 1993; Travnichek et al., 1995), or habitat generalists (HG) that do not depend on flowing water (Etnier and Starnes, 1993; Boschung Jr and Mayden, 2004; Freeman and Marcinek, 2006).

2.4. Flow calculations

We estimated an index of relative flow magnitude (hereafter flow index) to relate hydrology to stream fish metapopulation dynamics. Flow indices were calculated for the intervals between sampling events and were based on stream flow data from nearby USGS streamgages. We used daily average flows from six different USGS streamgages, each one of which was downstream of all sampling sites in the respective sub-watershed where the streamgage was located (Fig. 1; Supplementary material, Table S2). We considered flows during two intervals each year: spring (March 1 to June 30) and summer (July 1 to September 30). First, we estimated median flows for individual site × sampling date combinations using daily average flows for the interval between the beginning of the season when sampling was performed and the actual date of sampling. When sampling was not conducted at a given site or when sampling fell outside our defined seasons, we used flow time series spanning the entire sampling season (e.g., March 1 to June 30 for July samples) to estimate interval median flows. Thus, within each sub-watershed, interval median flows potentially varied among sites as a function of sampling date but were identical for sites sampled on the same date as well as for sites that were not sampled during particular seasons. We focused on flows immediately preceding sampling because hydrologic conditions during this time most likely exert the greatest influence on stream fish occurrence via recent colonization and persistence processes (Peterson and Shea, 2015; Shea et al., 2015).

Because upstream drainage areas associated with each site varied by more than two orders of magnitude (range = 6–734 km^2; Supplementary material, Table S1), we standardized interval median flow estimates to generate interval flow indices that were comparable among all sites. To do this, we used only those years preceding sampling (i.e., 2010 and earlier) with complete flow records (i.e., January 1 to December 31; February 29 data omitted; range = 53–87 years; Supplementary material, Table S2) to calculate period-of-record mean values for seasonal median flows (spring and summer) at each streamgage. Interval-specific median flows were divided by these long-term means to generate interval flow indices. For example, a flow index of 2.5 indicated an interval median flow 250% greater than seasonal average median flows, whereas a flow index of 0.5 indicated interval median flows that were only 50% of average median flows.

2.5. Modeling approach

We used a hierarchical representation of dynamic multi-species occupancy models (MacKenzie et al., 2003, 2006; Royle and Kéry, 2007) to relate flow to stream fish metapopulation dynamics (e.g., Peterson and Shea, 2015; Shea et al., 2015). This approach estimates colonization and persistence probabilities as functions of specified covariates while allowing for incomplete detection. Dynamic occupancy models rely on a pair of linked sub-models to produce estimates of relevant probabilities; the coupled sub-models include a state process model that reflects temporal changes in taxa occurrence and an observation model that accounts for the imperfect observation of taxa during sampling events.

2.5.1. State process sub-model

We defined an initial occurrence state for each taxon, z_{1j} (i.e., true presence or absence) as a Bernoulli random variable with a value of 1 if taxon j occurred during time 1, and a corresponding value of 0 if the taxon was truly absent:

$$z_{1j} \sim \text{Bernoulli}\,(\varphi_{1j})$$

where φ_{1j} was the initial occupancy probability for taxon j. We assumed that φ_{1j} was constant across all sites $i = 1, 2, \ldots, 40$ for each taxon j. Subsequent to the initial sampling event, we modeled temporal changes in occupancy exclusively on the basis of local colonization and persistence processes. We defined local colonization (γ_{tij}) as the probability that a site i unoccupied by taxon j at time t was occupied at time $t + 1$. Likewise, we defined local persistence (Φ_{tij}) as the probability that a site i occupied by taxon j at time t remained occupied over the interval between t and $t + 1$. Thus, we modeled occurrence states subsequent to the initial sampling event as other Bernoulli random variables conditional on previous occurrence states:

$$z_{t+1ij} \mid z_{tij} \sim \text{Bernoulli}\,\{z_{tij} \times \Phi_{tij} + [1 - z_{tij}] \times \gamma_{tij}\}$$

Colonization and persistence probabilities were modeled as functions of different covariates using the logit link:

$$\text{logit}(\gamma_{tij} \text{ or } \Phi_{tij}) = b0 + \boldsymbol{B} \times \boldsymbol{X_{ijt}} + \epsilon_i + \epsilon_j + \epsilon_t$$

where $b0$ was the intercept (community-wide mean across taxa), $\boldsymbol{B}$ was a vector representing parameter values for different covariates $\boldsymbol{X_{ijt}}$, and ϵ terms were random effects representing variation among sites (ϵ_i), taxa (ϵ_j), and sampling intervals (ϵ_t) in mean probabilities of these processes (MacKenzie et al., 2003).

We evaluated different site-, taxon-, and interval-specific covariates in our colonization and persistence models. In all models, we included a binary season variable (spring = 1; fall = 0) reflecting the timing of an individual sampling event and meant to account for different time spans from fall to spring samples (7–8 months between events) compared with spring to fall samples (4–5 months between events). To test our hypotheses that physiography influenced community-wide metapopulation rates, or the effects of stream flow magnitude on those rates, we included physiographic region (coded as 1 or 0, for sites above or below the Fall Line), flow index, and a flow index × physiographic region interaction in colonization and persistence models. We grouped Piedmont and Blue Ridge sites (i.e., above the Fall Line) because preliminary analyses suggested relationships between metapopulation process rates and flow indices were not significantly different between the two regions, and to provide approximately equal sample sizes above ($n = 17$ sites) and below ($n = 23$ sites) the Fall Line. To test our third hypothesis, that metapopulation rates and physiographic influences differed between fluvial specialist and habitat generalist species, we included a binary species-level covariate (FS = 1; HG = 0) as a main effect and as a fluvial specialization × physiographic region interaction in models for persistence and colonization.

We also evaluated the possibility that two other site-specific covariates, watershed size and connectivity, influenced metapopulation rates the same as or more strongly than physiography. We expected larger streams to generally, but not always, support larger fish populations and thus to have higher rates of persistence than smaller streams. Conversely, we expected streams with generally low connectivity to larger segments within the same watershed to have lower colonization rates than larger streams with higher connectivity (Gorman, 1986; Osborne and Wiley, 1992). We used watershed size, measured as the upstream drainage area at each site (centered and scaled so that mean = 0 and SD = 1; range: −0.50–5.11), as a proxy for stream size in models for persistence and colonization. To test for effects of site-level connectivity within the stream network, we used downstream link magnitude (i.e., the link magnitude of the nearest downstream segment; also centered and scaled) as a measure of connection to a larger segment (Peterson and Shea, 2015).

As in the physiography model, we included the site-level covariates watershed size and connectivity as fixed effects and in interactions with both flow index and fluvial specialization in models for persistence and colonization. Effects of the different site-level covariates were examined by fitting three separate models that differed only on the basis of which site-level covariate was included. Finally, we fit a composite covariate model including only those site-level variables, and interactions, from the three single-covariate models for which 95% credible intervals on the regression parameter estimates did not overlap zero (e.g., Kanno et al., 2015). We used this process in an effort to limit the number of estimated parameters in any single model and to facilitate evaluation of covariate effects relative to one another.

2.5.2. Observation sub-model

We used an observation sub-model to account for the imperfect detection of taxa during sampling events because it is rare that all species are detected during ecological sampling (Bayley and Peterson, 2001; Price and Peterson, 2010), and misleading conclusions can be drawn from analyses that fail to account for imperfect detection when it exists (Kéry and Schmidt, 2008). We relied on our spatially replicated surveys at each site to formally distinguish between taxon absence and non-detection, modeling our binary detection data y_{tikj} as a Bernoulli random variable:

$$y_{tikj} \sim \text{Bernoulli}\,(z_{tij} \times p_{tij})$$

where y_{tikj} was the observed detection (=1) or non-detection (=0) of taxon j in reach k at site i and time t. In this sub-model, p_{tij} was the probability of detecting taxon j at site i and time t, given that taxon j was actually present (i.e., $z_{tij} = 1$). Similar to colonization and persistence probabilities, we modeled detection probability using the logit link:

$$\text{logit}(p_{tij}) = b0 + \epsilon_i + \epsilon_j + \epsilon_t$$

where $b0$ was the intercept (community-wide mean across taxa), and ϵ terms were random effects representing variation among sites (ϵ_i), taxa (ϵ_j), and sampling events (ϵ_t) in mean detection probability, including, e.g., variation among sites in use of electrofishing and seining. Although detection can vary as a function of covariates, our focus was not on explaining this variability with fixed effects, but rather in allowing flexibility in detection so as not to bias estimates of fixed effects on colonization and persistence.

2.6. Model fitting and interpretation

We fit all models using a Bayesian framework implemented with the Markov chain Monte Carlo (MCMC) software JAGS (Plummer, 2003) using package 'R2jags' (Su and Yajima, 2015) in R version 3.2.4 (R Core Team, 2015) (see Supplementary material, Appendix A for composite model JAGS code). We used Jeffery's priors (mean = 0 and SD = 1.643; uninformative on the logit scale) for colonization, persistence, and detection covariates. For all model fitting, posterior distributions of model parameters were estimated by taking every fourth sample from 16,000 iterations of three chains after discarding 4000 burn-in iterations. We assessed model convergence using the Brooks-Gelman-Rubin statistic ($\hat{R}$; Brooks and Gelman, 1998) and by visually inspecting parameter trace plots to ensure adequate mixing among chains. Finally, we used a Bayesian P-value based on the Freeman-Tukey measure of discrepancy to assess model fit, following Kéry and Schaub (2012). This discrepancy metric considered the difference between the observed and

Table 1

Focal taxa considered in an analysis of physiographic and other covariate effects on metapopulation dynamics in streams of a large U.S. river basin. Distributions of all taxa include the Coastal Plain (CP) physiographic region below the Fall Line, and Piedmont (P) and Blue Ridge (BR) physiographic regions above the Fall Line (FL). Detections are the number of site × sampling event combinations with taxon detections. Fluvial specialization indicates the degree of dependence on flowing water conditions for life cycle completion: FS, fluvial specialist; HG, habitat generalist.

Taxon	Common name	Family	Distribution	Detections below FL	Detections above FL	Fluvial spec.
Cyprinella venusta	Blacktail shiner	Cyprinidae	CP, P, BR	27/116 23%	4/117 3%	FS
Hybopsis sp. cf. *H. winchelli*	Clear chub	Cyprinidae	CP, P, BR	5/116 4%	34/117 29%	FS
Notemigonus crysoleucas	Golden shiner	Cyprinidae	CP, P, BR	13/116 11%	7/117 6%	HG
Notropis cummingsae	Dusky shiner	Cyprinidae	CP, P	23/116 20%	6/63 10%	FS
Notropis longirostris	Longnose shiner	Cyprinidae	CP, P, BR	21/116 18%	10/117 9%	FS
Notropis texanus	Weed shiner	Cyprinidae	CP, P	86/116 74%	15/63 24%	FS
Minytrema melanops	Spotted sucker	Catostomidae	CP, P, BR	29/116 25%	4/117 3%	FS
Ameiurus natalis	Yellow bullhead	Ictaluridae	CP, P, BR	15/116 13%	12/117 10%	HG
Noturus leptacanthus	Speckled madtom	Ictaluridae	CP, P	63/116 54%	9/63 14%	FS
Esox americanus	Redfin pickerel	Esocidae	CP, P	76/116 66%	10/63 16%	HG
Gambusia sp.	Mosquitofish	Poeciliidae	CP, P, BR	84/116 72%	45/117 38%	HG
Lepomis auritus	Redbreast sunfish	Centrarchidae	CP, P, BR	84/116 72%	78/117 67%	HG
Lepomis cyanellus	Green sunfish	Centrarchidae	CP, P, BR	11/116 9%	20/117 17%	HG
Lepomis gulosus	Warmouth	Centrarchidae	CP, P, BR	51/116 44%	17/117 15%	HG
Lepomis macrochirus	Bluegill	Centrarchidae	CP, P, BR	82/116 71%	72/117 62%	HG
Lepomis microlophus	Redear sunfish	Centrarchidae	CP, P	29/116 25%	11/63 17%	HG
Lepomis punctatus × *miniatus*	Spotted sunfish	Centrarchidae	CP, P	94/116 81%	22/63 35%	HG
Micropterus salmoides	Largemouth bass	Centrarchidae	CP, P, BR	47/116 41%	45/117 38%	HG
Percina nigrofasciata	Blackbanded darter	Percidae	CP, P, BR	84/116 72%	109/117 93%	FS

(model-based) expected number of taxa detected in each survey, and compared it with the same difference calculated for a replicate data set simulated using persistence, colonization, and detection estimates at each MCMC iteration. The Bayesian *P*-value was the proportion of summed discrepancy values for the simulated data that exceeded the same for the observed data; a value of 0.5 indicated a lack of bias, whereas extreme values (i.e., < 0.05 or > 0.95) indicated consistent bias in model estimates.

3. Results

3.1. Survey summary – fishes

We detected 19 taxa across 233 total site × sampling date combinations that met our criteria of widespread distribution and were therefore included in our analysis (Table 1). Observed richness of these 19 taxa during a single site × sampling date combination was a maximum of 15, averaged 6.3 ± 3.7 (mean ± SD) taxa across all possible combinations, and was generally higher below the Fall Line (8.0 ± 3.5) than above (4.5 ± 2.9; Supplementary material, Fig. S1). Collectively, the 19 taxa represented seven different families, although the majority was either Centrarchidae (37%) or Cyprinidae (32%). Fluvial specialists (5 of 8 were cyprinids) comprised 42% of the taxa, while the others were habitat generalists (7 of 11 were centrarchids). While all taxa were detected at multiple sites above and below the Fall Line, the relative abundances of focal taxa exhibited considerable variation among sites.

3.2. Survey summary – hydrology

The initiation of sampling coincided with a relatively severe basin-wide drought, but was followed by generally high-flow conditions in 2013 and 2014 (Supplementary material, Fig. S2). We observed spatially patchy wet and dry conditions between summer 2014 and spring 2016 before a moderate drought occurred in summer 2016 (Supplementary material, Fig. S2). As a result of these variable hydrologic conditions, our flow index estimates ranged between 0.00 and 7.25.

3.3. Model results

All models converged ($\widehat{R} \leq 1.05$ for all estimated model parameters) and overall model fit, while slightly biased, was adequate based on computed Bayesian *P*-values (range = 0.823–0.832; e.g., Supplementary material, Fig. S3). Taxon-level differences in detection were apparent, as was some differentiation among sites (Supplementary material, Fig. S4), but parameter estimates for mean detection and random effects were similar among all models (which we expected because the models had identical structures for detection). The models with single site-level covariates (physiography, drainage area, and connectivity) all showed positive effects of flow index on colonization and persistence (Supplementary material, Table S3). Additionally, physiography, drainage area, and fluvial specialization were all significant in colonization models, and the flow index × drainage area interaction was positive in the persistence model. Neither the site-level measure of connectivity nor any of the other covariate interactions had non-zero parameter estimates (i.e., no overlap with zero within 95% credible interval) for effects on stream fish colonization or persistence probabilities. We thus focused on results for the composite model that included the variables supported by the single site-level covariate models.

3.3.1. Colonization

Our composite model results supported the hypothesis that physiography is a factor of primary importance to stream fish colonization, at least among the group of covariates we considered in this analysis. Model results indicated that colonization rates varied by physiographic location, being higher in streams below the Fall Line than in streams above the Fall Line (Table 2). The fluvial specialization characteristic appeared similarly important to colonization, and flow index also had a positive, non-zero effect on colonization rates (Table 2). Watershed size did not appear to influence colonization (Table 2), leaving physiography as the only significant site-specific covariate in our composite model. Thus, our models suggested that stream fish colonization rates in the ACF Basin are highest for habitat generalists in Coastal Plain streams (i.e., below the Fall Line) during high-flow conditions (Fig. 2). Random effect estimates from our composite model revealed variation in colonization rates among taxa, sites, and, to a lesser extent, sampling intervals (Table 2); this means certain taxa and sites were more or less likely to be associated with colonization events (Supplementary

Table 2

Parameter estimates for colonization, persistence, and detection probabilities based on composite model fitting. All values are on a logit scale. Random effect estimates are mean variances. Lower and upper values are 95% credible interval bounds. DA = scaled and centered site-specific drainage area.

Parameter	Estimate	SD	Lower	Upper
Colonization				
Fixed effects				
Intercept	−1.05	0.70	−2.46	0.27
Flow index	0.29	0.14	0.03	0.57
Above fall line	−2.58	0.62	−3.83	−1.41
DA	0.29	0.28	−0.26	0.85
Fluvial specialist	−2.11	0.81	−3.69	−0.42
Random effects				
Taxon	3.44	1.67	1.43	7.62
Site	2.38	0.97	1.05	4.78
Interval	0.88	2.39	0.03	3.42
Persistence				
Fixed effects				
Intercept	1.94	0.66	0.63	3.30
Flow index	1.13	0.48	0.32	2.19
DA	0.57	0.71	−0.71	2.13
Flow index × DA	1.20	0.73	−0.08	2.82
Random effects				
Taxon	1.08	0.87	0.09	3.34
Site	9.50	5.18	3.32	22.46
Interval	0.27	0.48	0.00	1.45
Detection				
Fixed effects				
Intercept	0.50	0.37	−0.21	1.23
Random effects				
Taxon	2.36	0.99	1.14	4.81
Site	0.47	0.16	0.23	0.87
Event	0.01	0.01	0.00	0.04

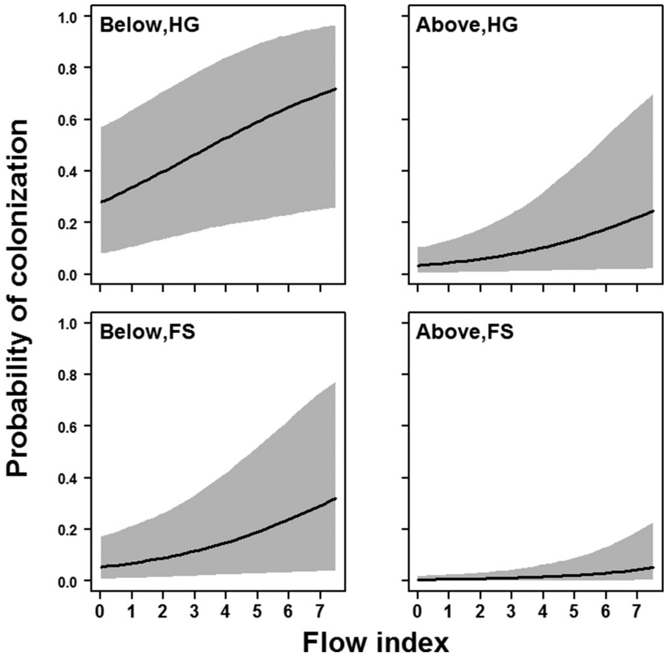

Fig. 2. Estimated mean colonization probabilities as a function of composite model covariates. Mean values (black line) and the 95% credible intervals (grey polygon) are plotted for each combination of physiography (above or below the Fall Line) and fluvial specialization (HG = habitat generalist; FS = fluvial specialist). All mean values and credible intervals based on mean watershed drainage area (71.5 km^2).

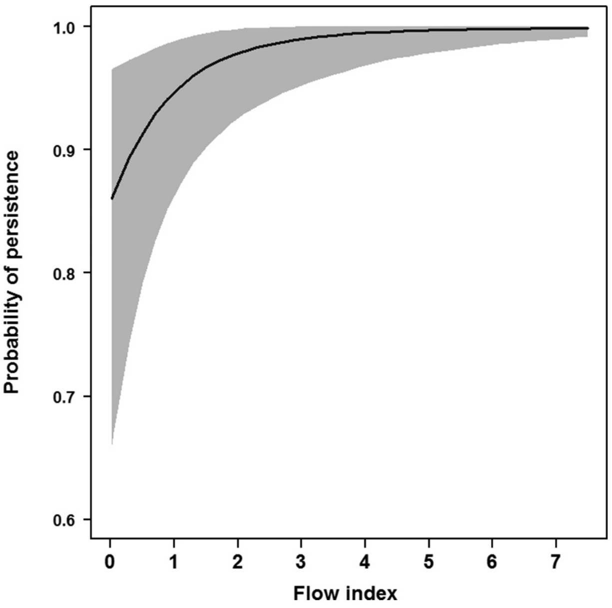

Fig. 3. Estimated mean persistence probability as a function of composite model covariates. Mean value (black line) and the 95% credible interval (grey polygon) are both plotted. Mean value and credible interval based on mean watershed drainage area (71.5 km^2). Note difference between *y*-axis values here and in Fig. 2.

material, Fig. S5).

3.3.2. *Persistence*

Similar to colonization results, our fitted composite persistence model suggested that stream fish persistence increased with flow index (Fig. 3). It appears that a given change in flow index affected persistence more strongly than colonization; i.e., the mean flow parameter estimate is 3.9 times greater for persistence than it is for colonization (Table 2). However, the certainty of this conclusion is limited by overlap in 95% credible intervals for the flow parameter estimates (Table 2). Interestingly, we did not find strong evidence that site-level covariates (including physiography) had substantial effects on persistence rates. Site-level covariate model results suggested that the positive effect of flow on persistence was stronger in larger streams than it was in smaller streams, but the flow × drainage area interaction was not statistically significant in our fitted composite model (Table 2). Random effect estimates in the composite model indicated that persistence rates varied considerably among sites and less so among taxa and intervals (Supplementary material, Fig. S6).

4. Discussion

Conservation practitioners and policy developers can benefit from understanding the spatial generality of relationships between organisms and drivers of metapopulation dynamics. By using a dynamic occupancy modeling framework, our study is one of the first to quantitatively examine the relationship between metapopulation processes of broadly distributed taxa and environmental conditions, specifically landscape heterogeneity produced by topographic, geologic, and climatic variation at the scale of physiographic regions. Our results suggest that stream fish colonization but not persistence is strongly governed by physiography, with estimated colonization rates considerably higher in Coastal Plain streams than in upland systems above the Fall Line in a large southeastern U.S. river basin. Because we restricted our analysis to taxa occurring in both Coastal Plain and upland streams, our results imply that stream fish colonization in the ACF Basin is governed by fundamental differences between physiographic regions, whereas persistence appears comparatively uniform across the basin. Given the importance of colonization to metapopulation dynamics, we argue that it would be useful to consider physiographic influences in the management and conservation of these stream fishes, as well as other broadly distributed taxa. Region-specific conservation and management plans that reflect heterogeneity in metapopulation processes may be most successful at promoting sustained population and community viability.

Our observation that colonization rates were higher in Coastal Plain streams than in upland systems is consistent with our finding that site-level species richness was generally greater in Coastal Plain streams. There are several possible explanations for the disparity in colonization rates. Colonization by mobile stream fishes may be facilitated by a lack of hydrodynamic barriers to upstream movement (sensu Grossman et al., 2010), especially at high flow, in unconfined, low-gradient Coastal Plain streams. This explanation is supported by studies demonstrating the influence of hydraulic or habitat characteristics that may result from particular physiographies. For example, high water velocities may constrain the distribution of species with low swimming capacities, and increasing water depth may impede fish movement (Jackson et al., 2001; Grossman et al., 2010). We are not aware of studies that have examined movement differences of the same stream fish species in different types of channels, but some case studies support our observations of elevated colonization rates in Coastal Plain streams. For instance, Sheldon and Meffe (1995) observed rapid (days-weeks) recolonization of defaunated pools by fishes in streams with similar gradients and substrates to our Coastal Plain systems. In contrast, Albanese et al. (2009) reported relatively slow rates of colonization by stream fishes in higher-gradient mountain streams. We suggest that future attempts to examine fish movement across a range of stream channel forms would be valuable, as they would offer a more explicit test of the hypothesis that movement capacity is influenced by induced spatial dependence, or true gradients, in hydraulic and habitat features imposed by physiographic constraints (Borcard et al., 2011). We also note that the extent of natural (e.g., waterfalls) and anthropogenic barriers (including unmapped, small dams and relatively impassable culverts at road crossings) may differ between upland and Coastal Plain stream systems, resulting in differences in fish colonization rates. Such a difference could contribute to our failure to find an effect of downstream link magnitude on colonization if, for example, some sites with high downstream link magnitude values are isolated by barriers.

Another possible explanation for higher colonization rates in Coastal Plain systems is that stream fish populations are locally adapted to prevailing hydrologic regimes. If, for example, Coastal Plain populations experience more frequent drying and rewetting sequences, then there could be selection for traits that confer enhanced colonization capabilities relative to populations above the Fall Line, where streams are less likely to approach drying conditions. In support of this hypothesis, Bennett et al. (2016) report two of three stream fishes studied exhibit higher fecundity, a trait associated with a periodic life history strategy (Winemiller and Rose, 1992), at sites with hydrologic characteristics (greater seasonality, lower variability) that theoretically favor selection of periodic traits. Likewise, studies of blacktail shiner (*Cyprinella venusta*) populations in Gulf Coastal Plain streams in the U.S. provide compelling evidence that intraspecific variation in egg size is linked to stream flow patterns; results support the hypothesis that large egg size is favored in areas with higher mean annual runoff (Heins and Baker, 1987, 2017; Machado et al., 2002). This local adaptation hypothesis is not necessarily exclusive of the hydrodynamic barrier hypothesis. However, our failure to find support for a physiographic difference in the effect of flows on colonization probability argues against the latter hypothesis, assuming such a barrier would increase with stream flow and particularly in higher gradient streams.

Beyond the possibility of locally adapted populations and physiographic differences that facilitate or constrain fish movement, there are other potential explanations for our observation that colonization varies across space. First, a larger population at the regional scale must translate into a larger number of potential colonists. Therefore, colonization rates should be higher in regions with larger populations than in regions where population sizes are smaller. We observed considerable variability in abundance in taxa among sites, and detections were more likely in Coastal Plain streams than in upland streams for 16 of the 19 taxa included in our analysis, so we cannot rule out the possibility that colonization was higher in Coastal Plain streams as a result of larger populations in the region. Secondly, differences in stream network topology and position have been cited as influencing population dynamics, with colonization and persistence rates both increasing with complexity of branch connections (Grant, 2011; Seymour and Altermatt, 2014) and proximity to mainstream segments (Hitt and Angermeier, 2008, 2011). Further explaining the variation in colonization above and below the Fall Line may require examining network topology across our study extent, especially as measures of topology have been shown to vary at similar regional scales (Betz et al., 2010).

Finally, there may be spatial variation we did not capture with our site-level covariates that could manifest as differences in a particular characteristic across the landscape or as autocorrelation among sampled sites. Variation in land use is inevitable at spatial scales as large as the ACF Basin, and different responses by freshwater populations and communities are commonly attributed to different land use patterns (Allan, 2004). We considered including broad land use classes (i.e., agricultural, forested, urban) as a site-level covariate, but they were either strongly correlated with our binary physiography variable or, in the case of urban land cover, not statistically significant predictors of colonization or persistence rates. As an illustration of the existing correlation, sites above the Fall Line have much less agricultural land cover (19.9 ± 11.8%, $n = 17$; mean ± SD) than Coastal Plain sites (35.2 ± 14.1%, $n = 23$). This correlation precluded our ability to include land use as a covariate in models that also included our binary physiography variable, as well as our ability to distinguish between land use and physiographic effects. Similarly, preliminary analyses using three spatial eigenvectors identified by Moran's eigenvector maps method (Dray et al., 2006) as site-level covariates describing spatial structure among our sampling sites suggested that the only eigenvector that significantly influenced colonization and persistence rates represented a longitudinal gradient, which was also strongly correlated with our binary physiography variable. These correlations represent sources of uncertainty in our conclusion that physiographic differences are driving observed spatial differences in colonization rates, but we argue that explanation is most ecologically plausible given the potential for physiographic constraints to produce network topologies along with hydraulic and habitat conditions that influence stream fish movements and evolutionary histories.

Differences in colonization probabilities across physiographic regions, as we found, are potentially important to conservation, even in the absence of regional differences in environmental effects on metapopulation rates. This is because colonization defines population resilience. To illustrate this idea, we consider a scenario analogous to our model results in which an environmental factor (e.g., stream flow) affects population persistence and colonization identically across regions, but in which only colonization differs between regions. Managers concerned with the effect of this environmental factor on a suite of species might reasonably examine changes in species occurrence or richness across sites representing a gradient in that factor, rather than collect data through time as would be needed to analyze occupancy dynamics. Suppose, specifically, that the environmental factor of interest lowers species persistence equally in two regions in which colonization rates differ. One can then use an incidence function $\gamma/(\gamma + (1 - \Phi))$, where γ and Φ are colonization and persistence probabilities, respectively (Hanski, 1994), to determine the expected proportion of sites occupied at equilibrium. This calculated expected occupancy shows steeper decline relative to the baseline or undisturbed condition in the region where colonization is lower (Fig. 4). This implies that the commonly used analysis of proportional changes in a

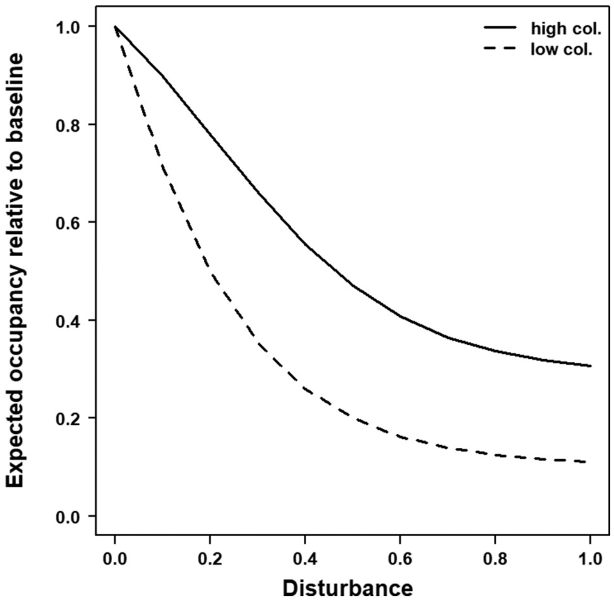

Fig. 4. Differences in equilibrium occupancy across a gradient in an environmental factor (‘Disturbance’) for populations in two regions, one with high (solid line) and one with low (dashed line) colonization probabilities. Equilibrium occupancy is defined as $\gamma/(\gamma + (1 - \Phi))$, where γ and Φ are colonization and persistence probabilities, respectively (Hanski, 1994). In this example, persistence declines identically with disturbance in both regions, ranging from 0.92 to 0.08 as ‘Disturbance’ increases from 0 to 1. Colonization, however, is lower in one region (0.03) than the other (0.30). The plotted response variable is expected occupancy as a proportion of the baseline value (i.e., when ‘Disturbance’ is 0), and shows a greater relative decline in one region driven solely by lower colonization.

population state (e.g., probability of species occurrence, species richness) across an environmental gradient in different physiographic regions could lead to the conclusion that the environmental factor acts more strongly on vital rates such as reproduction or survival in one region than the other, when in fact the effect is identical. Rather, the relative difference in population state along the environmental gradient is the outcome of differential colonization rates.

Similarly, inherent differences among species groups in colonization rates, as we found for habitat generalist and fluvial specialist fishes, could lead to an erroneous conclusion of differential sensitivity to an environmental factor. It is not clear, however, what mechanism(s) may explain our finding that habitat generalists were generally better colonizers than fluvial specialists. We did observe that, among the fishes included in our analysis, the habitat generalists were generally larger than the fluvial specialists. Stream fish species or individuals with larger body size have been hypothesized to move more than smaller-bodied individuals or species, either due to higher energetic requirements (Gatz Jr and Adams, 1994; Aparicio and de Sostoa, 1999) or to larger home range sizes (Minns, 1995). However, empirical studies of the influence of body size on fish movement appear to be equivocal, with some studies finding positive relationships between body size and dispersal or colonization (e.g., Niemi et al., 1990; Minns, 1995; Radinger and Wolter, 2014; Shea et al., 2015) and others reporting weak or no relationships (e.g., Taylor and Warren Jr, 2001; Albanese et al., 2004, 2009). Beyond body size, there are other traits that could confer different colonization capabilities to stream fishes and that may be components of a biological trait syndrome that clearly distinguishes fluvial specialists from habitat generalists. For example, mobility (Albanese et al., 2009), spawning modes (Shea et al., 2015), and locomotion morphologies (Peterson and Shea, 2015) have all been shown to influence streamfish colonization or occurrence. Additionally, it is plausible that fecundity, and thus propagule abundance, correlates positively with colonization (Hitt and Roberts, 2012), and we did observe that habitat generalists in our analysis tended to be more fecund than fluvial specialists, based on available fecundity data (Frimpong and Angermeier, 2009). Finally, we note that other studies (e.g., Mims and Olden, 2013; Perkin et al., 2017) have also observed differences in streamfish colonization or occurrence as a function of life history strategies defined by Winemiller and Rose (1992), categorizations that are similar to our fluvial specialization characteristic in that they are defined by a combination of specific biological traits. Regardless of the mechanism, our results suggest that habitat generalists have higher colonization rates than fluvial specialists, which could help to explain previous findings that fluvial specialists, but not habitat generalists, show lower species richness with increased flow alteration (Freeman and Marcinek, 2006; Kanno and Vokoun, 2010).

4.1. Temporally dynamic rate approaches in conservation

The dynamic occupancy modeling framework we used, which is one example of a rates approach in flow-ecology studies (Wheeler et al., 2017), offers several benefits over studies that rely on state responses (e.g., occurrence, species richness) that are not repeatedly measured over time or that, when repeatedly collected over time, are treated independently. First, rates approaches can provide insight into the metapopulation processes underlying observed changes in community assemblages and biodiversity (McGill et al., 2017). As illustrated by our equilibrium occupancy calculations (Fig. 4), misleading conclusions about metapopulation processes can result when analytical approaches do not involve explicit estimation of these processes. In spite of this, most of the previous studies we know of that examined physiographic influences on freshwater biota have used state responses. Rates approaches like the one used here may offer a demographically mechanistic basis for evaluating environment × physiography interactions. For example, Utz et al. (2009, 2010) reported that invertebrate and fish responses to urbanization differed between the Coastal Plain and Piedmont physiographic regions in the mid-Atlantic United States but, based on their use of state responses, they could not identify the metapopulation processes underlying observed biotic changes. Our model results (higher fish colonization rates in Coastal Plain compared to Piedmont streams) represent a plausible demographic hypothesis for the results observed by Utz et al. (2009, 2010). In fact, this hypothesis is supported by a related study where macroinvertebrate densities recovered more quickly in Coastal Plain than in Piedmont streams, suggesting higher colonization rates below the Fall Line (Utz and Hilderbrand, 2011).

Beyond providing insight into how and when assemblages change, the multi-species approach we applied permits community-wide inference while also improving estimates for all taxa, even those that were rarely observed, by virtue of ‘borrowing’ information from the most commonly detected taxa (Zipkin et al., 2009, 2010). Additionally, although we have demonstrated application of this modeling approach using stream fishes, we note that its use is far less constrained by taxonomy than by data availability since temporally repeated species detection data at periodically surveyed sites are required for implementation. We acknowledge that such data are relatively rare, particularly over large geographic areas, due to financial and logistical constraints. Nonetheless, dynamic occupancy models have been applied to stream fishes (e.g., Peterson and Shea, 2015; Shea et al., 2015), amphibians (e.g., Adams et al., 2013; Kroll et al., 2015), birds (e.g., Ruiz-Gutiérrez et al., 2010; Broms et al., 2016), and some mammals like koalas (Santika et al., 2014), although other taxonomic groups (e.g., reptiles) are also likely to be appropriate targets. We also note that extensions have been incorporated to similar modeling approaches that allow for temporal changes in habitat suitability, e.g., changes between flowing and dry riverine habitats (Matthews and Marsh-Matthews, 2003; Falke et al., 2012).

4.2. Management and conservation implications

In general, our study suggests that conservation outcomes for some taxa can be maximized by adopting region-specific approaches. For example, in our study system, it may be desirable to focus on maintaining high persistence rates when managing streams above the Fall Line since replacement of lost species via colonization is unlikely to occur very quickly. In contrast, conservation efforts for Coastal Plain streams could focus on maintaining and facilitating colonization since replacement of extirpated species can occur more rapidly than in upland sites. While some actions (e.g., limiting water withdrawals, maintaining minimum flow levels) are likely beneficial in both regions, other effective strategies would depend on location. For example, conservation efforts above the Fall Line would likely be aided by examining the influence of various local habitat characteristics on persistence given broad differences in persistence among sites, whereas identification and removal of barriers that limit habitat connectivity via fish movement may prove more valuable in Coastal Plain systems.

Effective conservation of broadly distributed taxa like the suite of stream fishes examined here will require a full accounting of all factors that potentially influence populations. While ecologists recognize that physiographic heterogeneity can produce spatial variation in local habitat characteristics, the potential influence of physiography on population dynamics remains largely unexamined, especially with respect to metapopulation processes that underpin observed changes in commonly measured state variables like species occurrence and richness. Understanding the relative importance of colonization and persistence, and how one or both processes may change across the landscape, is critical information for the conservation of broadly distributed taxa, and we echo earlier arguments (Gotelli and Taylor, 1999) that conservation strategies explicitly accounting for spatial variation in these processes are likely to be more successful for such taxa.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2018.04.023.

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