Received: 20 December 2022 | Revised: 18 January 2023 | Accepted: 19 January 2023
DOI: 10.1111/eff.12705

ORIGINAL RESEARCH

Ecology of FRESHWATER FISH WILEY

Stabilising effects of karstic groundwater on stream fish communities

Nathaniel P. Hitt[1] | **Karli M. Rogers**[1] | **Karmann G. Kessler**[1] | **Martin A. Briggs**[2] | **Jennifer H. Fair**[3]

[1]Eastern Ecological Science Center, U.S. Geological Survey, Kearneysville, West Virginia, USA

[2]Observing Systems Division, U.S. Geological Survey, Hydrologic Remote Sensing Branch, Storrs, Connecticut, USA

[3]Eastern Ecological Science Center, U.S. Geological Survey, Turners Falls, Massachusetts, USA

Correspondence
Nathaniel P. Hitt, U.S. Geological Survey, Eastern Ecological Science Center, Kearneysville, West Virginia, USA.
Email: nhitt@usgs.gov

Funding information
U.S. Geological Survey

Abstract

Although groundwater exchange processes are known to modulate atmospheric influences on stream temperature and flow, the implications for ecological stability are poorly understood. Here, we evaluated temporal change in stream fish communities across a gradient of groundwater influence defined by karst terrain (carbonate parent materials) within the Potomac River basin of eastern North America. We surveyed 12 sites in 2022 that had been sampled 29–30 years previously with similar methods. We also collected stream temperature data from each site and used the regression slope of the air-water temperature relationship to index stream thermal sensitivity and groundwater exchange processes. Sites in karst terrain exhibited strong groundwater controls on stream temperature, and fish communities were more stable over time in these locations than elsewhere. However, stream thermal sensitivity was a stronger predictor of species persistence than the spatial distribution of karst terrain in contributing areas, highlighting the ecological importance of local variation in groundwater discharge processes. The presence of calcium precipitates (marl) in stream substrates was associated with low thermal sensitivity and ecological stability over time, and we suggest such visible features may be a useful indicator of climate change refugia in stream ecosystems.

KEYWORDS
colonisation, extirpation, fish community, groundwater, karst, streams

1 | INTRODUCTION

A central goal of ecology is to understand why biological communities change over time (Connell & Sousa, 1983), and this line of research is necessary to predict how ecosystems and ecosystem services will respond to contemporary climate change. Conceptual models have described species colonisation and extinction dynamics based on habitat size and proximity to source populations (MacArthur & Wilson, 1967), resource availability and habitat patch configurations (Dunning et al., 1992), and environmental disturbances and dispersal dynamics (Leibold et al., 2004). Stability of habitat conditions is often assumed to stabilise ecological communities over time (Van Meerbeek et al., 2021), but this assumption is rarely tested with empirical data.

Hydrological events have a fundamental role in stream fish colonisation and extinction dynamics. Floods can produce debris flows that extirpate local fish populations (Roghair et al., 2002) or scour stream substrates reducing egg survival and juvenile abundance (Hitt et al., 2020; Kanno et al., 2016). In contrast, low flows can fragment stream fish populations into isolated pools that increase competition and predation pressures (Harvey & Stewart, 1991; Propst et al., 2008) or eliminate fish populations if refugia are unavailable (Magoulick & Kobza, 2003). Flow regimes are also closely tied to stream fish life history strategies, as observed in response to natural flow variation (Mims & Olden, 2012), drought and low-flow conditions (Perkin et al., 2015), and flow regulation from impoundments (McManamay & Frimpong, 2015; Olden et al., 2006). Precipitation and stream flows are becoming increasingly variable and less predictable with contemporary climate change (Hammond et al., 2022; Milly et al., 2008; Zhao et al., 2016), and this motivates research to understand the risks to freshwater fish populations and communities (Kovach et al., 2019).

Groundwater exchange processes have important moderating effects on stream flow and temperature (Kaandorp et al., 2019; Winter, 2007), and this affects the quality and connectivity of fish habitat (Kurylyk et al., 2014; Meisner et al., 1988). Streams flowing over shallow unconfined aquifers constrained by near-surface bedrock exhibit more seasonal dewatering and more thermal sensitivity to air temperature than streams connected to deeper groundwater sources (Briggs et al., 2022). Moreover, a continental-scale study demonstrated that streams dominated by shallow groundwater sources are warming in significantly greater proportion than streams fed by deeper groundwater sources, particularly over summer months (Hare et al., 2021). Thermal buffering and cooling of channel water by groundwater is predicted to provide refugia from climate warming and extreme warm events in some locations (Kaandorp et al., 2019; Kelleher et al., 2012; Snyder et al., 2015) as influenced by source aquifer hydraulic properties, flowpath depth, and recharge dynamics (Sullivan et al., 2021).

Karst terrain presents a challenge for understanding ecological effects of climate change in streams. On one hand, extensive dissolution and fracture of carbonate bedrock in karst terrain generate large aquifers with extensive groundwater-surface water connectivity that can stabilise flow and temperature in receiving streams (Kresic, 2013; White, 1977; White & Reich, 1970). On the other hand, conduit-type groundwater flow paths can produce relatively rapid streamflow responses to rainfall (Jones, 1997; White, 1969). Complicating the matter, carbonate aquifers typically contain a combination of conduit-type and fracture-type flow paths (Bonacci et al., 2009; Shuster & White, 1971), and discharge from karst springs can exhibit a combination of fast and slow responses to precipitation (Chang et al., 2015; Shirafkan et al., 2021). Moreover, springs in karst terrain can exhibit distinct geochemical signatures reflecting differences in groundwater flow paths and parent materials (Vesper & Herman, 2020), and dye-tracing experiments in karst terrain have revealed preferential groundwater flow paths through complex networks of faults superimposed on conduit-type and fracture-type flow paths (Kozar et al., 1991). Thermal sensitivity, defined here as the response of stream temperature to changes in air temperature, also indicates that streams influenced by fracture-type groundwater flow paths are less sensitive to atmospheric conditions than streams influenced by conduit-type groundwater flow paths (O'Driscoll & DeWalle, 2006; Shuster & White, 1971).

Ecological research has shown effects of karst terrain on taxonomic and functional attributes of stream fish communities. Magoulick et al. (2021) observed less seasonal variation in fish communities within karst-influenced streams than in streams dominated by runoff sources. Coulter and Galarowicz (2015) reported a sharp transition from warmwater to coldwater fish communities where karst groundwater entered a stream from a cave outlet. Kollaus et al. (2015) attributed karst groundwater to the stability of stream fish communities over time in an urbanising landscape, suggesting stabilised flow and thermal conditions relative to non-karst streams elsewhere. Moreover, stream fishes in karst terrain exhibit equilibrium-type life history strategies that capitalise on stable environmental conditions (Hitt et al., 2022; Magoulick et al., 2021). However, the temporal stability of ecological responses is not well understood.

Here, we evaluated effects of groundwater discharge on stream fish communities by quantifying temporal change in community composition in the presence and absence of karst terrain. We expected that streamflow and temperature associated with groundwater in karst terrain would promote temporal stability of fish communities, and we evaluated stream thermal sensitivity to air temperature as an index of groundwater exchange processes. We also contrasted effects of groundwater and karst terrain to effects of upstream basin area and elevation given their importance for stream fish community composition (Roberts & Hitt, 2010).

2 | METHODS

2.1 | Study area

We evaluated stream fish communities within the Ridge and Valley physiographic region of Potomac River basin in eastern North America (Figure 1). The region is contained by the Blue Ridge mountains to the east and the Appalachian Plateau to the west. Geological features include a series of ridges and valleys oriented southwest to northeast with resistant sandstones and conglomerates comprising the ridges and erosive limestones and shales comprising the valley floor (Evans et al., 2016). The region is primarily forested along the ridgelines while the valley consists of agriculture and forest cover with limited areas of urban development (Irani & Claggett, 2010).

Karst terrain is a major feature of the valley floor within this region (Weary & Doctor, 2014) including numerous sinkholes and caves characteristic of karst geology (Dasher, 2012; Doctor & Doctor, 2012; Jones, 1997). Groundwater flow paths in this region exhibit combinations of conduit-type and fracture-type systems, with preferential flow paths following major faults (Evaldi et al., 2009; Kozar et al., 1991; McCoy & Kozar, 2008). Water chemistry of springs and streams in this region also indicates differences due to carbonate rock type (limestone and dolomite; Vesper & Herman, 2020), aquifer depth (Vesper et al., 2009), and groundwater flow path complexity (conduit- or fracture-type; Shuster & White, 1971). Marl substrates occur in some streams within the

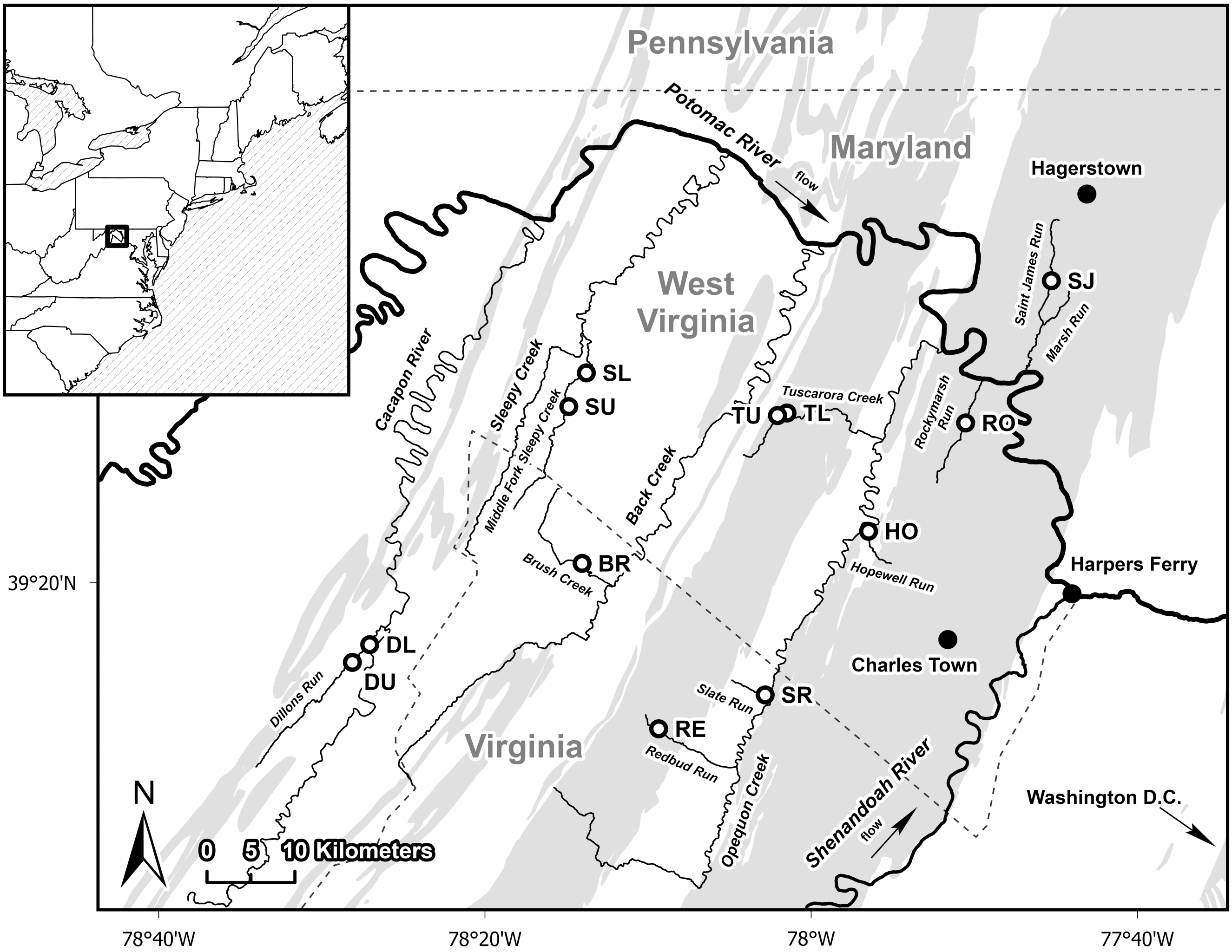

FIGURE 1 Map of study site locations in the Potomac River basin in eastern North America. Codes for sample sites (open circles) are defined in Table 1. Karst terrain (grey regions) was delineated by Weary and Doctor (2014).

study region (Hubbard et al., 1985) due to the precipitation of calcium carbonate as groundwater emerges into stream channels (Ford & Pedley, 1996).

2.2 | Fish data

During summer 2022, we resurveyed stream fish communities in 12 sites that were sampled by USEPA (2000) (*n* = 11) or Snyder et al. (2003) (*n* = 1) in 1993 or 1994, yielding a 29 to 30 year timespan for analysis (Table 1). The goal of the USEPA study was to assess the ecological condition of streams across the mid-Atlantic highland region of eastern North America (Herlihy et al., 2000), and the fish data have also been used to model species occurrence (Rashleigh et al., 2005) and to evaluate fish dispersal dynamics (Hitt & Angermeier, 2008, 2011). Likewise, the goal of the Snyder et al.'s (2003) study was to identify relationships between land use, environmental quality, and fish community composition. However, Snyder et al. (2003) encompassed a smaller study area (Opequon Creek watershed) than the USEPA study which included sites across the eastern United States. Site location coordinates are given in Appendix S1.

Both studies surveyed stream fishes using standard backpack electrofishing techniques within an area defined as 40 times the mean wetted width (McCormick & Hughes, 2000). USEPA (2000) collected fish from a single-pass electrofishing survey, and we limited data from Snyder et al. (2003) to a single pass for comparability. We repeated these methods in each site. All fish surveys were conducted during baseflow conditions between April and September (Table 1). We identified individuals to the species level using a taxonomic key (Jenkins & Burkhead, 1994) and released them, and we preserved a few individuals for taxonomic identification in the laboratory. We excluded age-0 fish, and we incorporated several changes into the USEPA (2000) fish data based on zoogeographic considerations described in Hitt (2007). Our fish sampling protocols were approved by US Geological Survey IACUC review (study #2021-06L) and state scientific collection permits in West Virginia, Maryland, and Virginia.

2.3 | Environmental covariates

For each site, we calculated elevation, upstream basin area, and percent karst terrain within surficial watersheds using the USGS Stream Stats Batch Processor v5.3.04 and ArcGIS Pro 2.9.2. Karst terrain was defined by Weary and Doctor (2014) from state geological maps. We estimated mean wetted stream width within fish sampling areas as the average of 11 evenly spaced transects perpendicular to the channel (Lazorchak et al., 2000). We also measured stream temperature at each site at 30-min increments from June 1 to August 31, 2022 (92 days) using Onset ProV2 gages within perforated PVC cases mounted to substrate. Temperature gages were co-located with fish sampling sites with the exception that the Hopewell Run gage was located approximately 1 km upstream from the fish sampling area. We inspected raw data plots for temperature spikes and anomalies indicating dewatering (Sowder & Steel, 2012), and we observed none.

We estimated the thermal sensitivity for each site from the linear regression slope of the daily mean air-water temperature relationship (Kelleher et al., 2012; Snyder et al., 2015; Wissler et al., 2022). Air temperature data were collected from a geographically centralised weather station (Eastern West Virginia Regional Airport, GHCND:USW00013734) and adjusted to expected air temperatures for each site based on a lapse rate of 9.8°C per km of elevation change (Stull, 1988). We interpreted thermal sensitivity values <0.45 as groundwater-controlled sites following Kelleher et al. (2012). We also noted the presence or absence of marl substrates within the fish sampling area in each site.

2.4 | Statistical analysis

We quantified fish community structure using nonmetric multidimensional scaling (NMS). We excluded the rarest species from analysis by omitting taxa with <20 individuals in the dataset. Alternative levels of rare taxa exclusion had little effect on observed ordination patterns (results not shown). We applied *ln*-transformations to the abundance data and fit a 2-dimensional NMS ordination from Bray-Curtis distances. We then represented temporal change in community composition as the length of the vector in the 2-dimensional NMS space between the first and second sampling period for each site, and we evaluated the convex hull of the ordination space defined for time periods and thermal sensitivity levels. Prior studies have used this approach to address similar research questions (Matthews & Matthews, 2016; Morrill et al., 2022). We used functions in the R package "vegan" version 2.6-2 (Oksanen et al., 2022) to fit the NMS model.

We also evaluated temporal change by tabulating the proportion of species exhibiting colonisation, extirpation, or persistence in each site and evaluating environmental covariates using beta regression techniques. Rates of colonisation, extirpation, and persistence were expressed as the proportion of the cumulative number of fish species observed within sites. Beta regression techniques are appropriate for this analysis because the response variables are expressed as proportional data (Douma & Weedon, 2019). We applied a *ln*-transformation to continuous covariates (elevation, basin size, thermal sensitivity), and we applied an arcsine-square root transformation to a proportional covariate (proportion of watershed in karst terrain; Weary & Doctor, 2014). We scaled environmental covariates to a mean of 0 and standard deviation of 1 to facilitate comparison. We fit beta-regression models with probit links using functions in R package "betareg" version 3-1.4 (Cribari-Neto & Zeileis, 2010). Environmental covariates from the first survey period were not collected in most cases, precluding empirical analysis of physical habitat change over time. We conducted all analyses in R version 4.2.1 (R Core Team, 2022).

3 | RESULTS

Sample sites ranged in elevation from 112 to 269 m above sea level (mean = 182 m), upstream watershed size ranged from 373 to 5400 ha (mean = 2664 ha), and wetted stream width ranged from 2.2

TABLE 1 Study site information. Karst % gives the per cent of karst terrain in the upstream watershed (Weary & Doctor, 2014). Geographic coordinates are given in Appendix S1.

Site code	Site name	State	First survey	Second survey	Elevation (m)	Basin size (ha)	Wetted width (m)	Karst %
BR	Brush Creek	VA	5/3/1994	7/22/2022	195	5096	5.5	0.0
DL	Dillons Creek, lower	WV	5/19/1993	8/3/2022	249	4876	6.4	29.3
DU	Dillons Creek, upper	WV	4/14/1994	8/3/2022	269	4590	5.6	31.1
HO	Hopewell Run	WV	9/28/1993	9/27/2022	120	3142	4.4	78.6
RE	Redbud Run	VA	6/2/1993	8/1/2022	218	632	3.3	100.0
RO	Rocky Marsh Run	WV	4/15/1994	7/20/2022	125	3255	5.2	100.0
SJ	Saint James Run	MD	6/1/1994	8/2/2022	149	985	3.7	100.0
SR	Slate Run	VA	6/1/1993	8/1/2022	145	373	2.2	0.0
SL	Sleepy Creek, lower	WV	4/15/1994	8/4/2022	215	5400	8.0	0.0
SU	Sleepy Creek, upper	WV	5/18/1993	8/5/2022	230	4228	7.2	0.0
TL	Tuscarora Creek, lower	WV	5/17/1993	8/17/2022	169	1408	3.8	49.8
TU	Tuscarora Creek, upper	WV	4/15/1994	8/17/2022	174	1016	2.9	48.5

to 8.0 m (mean = 4.9 m; Table 1). Karst terrain encompassed the entire upstream watersheds for 3 sites (Redbud Run, Rocky Marsh Run, Saint James Run) and 79% of the Hopewell Run site (Table 1). Conversely, karst terrain was absent from watersheds for 4 sites (Brush Creek, Slate Run, Sleepy Creek lower, Sleep Creek upper) and comprised less than half of the Dillons Creek watershed (Table 1). The Tuscarora Creek sites were located over karst terrain (Figure 1), but approximately half of their watersheds were not underlain by karst (Table 1). We observed marl precipitates in sites where karst terrain comprised at least 79% of the upstream watershed (Redbud Run, Rocky Marsh Run, Saint James Run, Hopewell Run; Appendix S2).

Stream temperatures measured at 30-min timesteps ranged from 12.4 to 28.8°C during the sampling period (June 1–August 31, 2022), with the minimum observed in Redbud Run and the maximum observed in the Sleepy Creek lower site (Table 2). Daily mean air temperatures at the Martinsburg weather station ranged from 17.5 to 28.1°C, and site-specific adjustments ranged from −1.02°C at a higher elevation site (Dillons Creek upper site, elevation 269 m) to +0.44°C at a lower elevation site (Hopewell Run, elevation 120 m). Thermal sensitivities ranged from 0.32 to 0.58 with Redbud Run as the least sensitive site and Sleepy Creek lower as the most sensitive site (Figure 2; Table 2). Four sites showed thermal sensitivities <0.45 indicative of groundwater-controlled thermal regimes (Kelleher et al., 2012) with the remaining 8 sites showing stronger atmospheric controls on stream temperature (Figure 2; Table 2). Linear model R^2 values ranged from .67 to .80 across sites (mean = 0.73). Thermal sensitivity was associated with site elevation (positive), basin size (positive), and the percent karst terrain within watersheds (negative; Appendix S3).

The fish dataset included 5854 individuals from 37 species and 8 taxonomic families (Table 3; Appendix S4). Among surveys, species richness ranged from 3 (Redbud Run in 1993 and 2022) to 20 (Dillons Creek lower in 2022) with an average of 10.8 species per survey (Table 3). Among sites, cumulative species richness was greatest in the Sleepy Creek lower site (25 species) and included at least 10 species for most sites (Table 4). Total abundance was greatest within Leusciscidae (51% of all individuals), followed by Cottidae (21% of all individuals) and Percidae (18% of all individuals). In contrast, Anguillidae and Salmonidae each were represented by a single species and cumulatively comprised less than 1% of all observed individuals (Table 3).

Blacknose dace (*Rhinichthys atratulus*) was the most abundant species in the dataset (25% of all individuals), followed by fantail darter (*Etheostoma flabellare*, 15% of all individuals), Blue Ridge sculpin (*Cottus caeruleomentum*, 11% of all individuals), pearl dace (*Margariscus margarita*, 8% of all individuals), and bluntnose minnow (*Pimephales notatus*, 5% of all individuals). Other species comprised less than 5% of the individuals in the dataset. Tessellated darter (*Etheostoma olmstedi*), river chub (*Nocomis micropogon*), and rainbow trout (*Oncorhynchus mykiss*) were the rarest species, each represented by a single individual in the dataset (Table 3).

Species richness varied over time in 8 of the 12 sample sites, of which 6 increased and 2 decreased (Table 4). We observed the largest gain in species richness in the Dillons Creek lower site with the addition of 10 species. In contrast, the Sleepy Creek lower site and Slate Run each lost 2 species over time (Table 4). Sites showing no change in species richness included low-richness sites (i.e., Redbud Run and Tuscarora Creek lower site) and high-richness sites (i.e., Sleepy Creek lower site and Dillons Creek upper site; Table 4). We observed 3 species in the second survey but not the first (i.e., apparent colonisations): rainbow darter (*Etheostoma caeruleum*), spottail shiner (*Notropis hudsonius*), and river chub. In contrast, we observed 5 species in the first survey but not the second (i.e., apparent extirpations): golden redhorse (*Moxostoma erythrurum*), comely shiner (*Notropis amoenus*), swallowtail shiner (*Notropis procne*), tessellated darter, and rainbow trout.

Colonisation and extirpation rates varied among species (Table 3). Green sunfish (*Lepomis cyanellus*) exhibited the largest colonisation trend with new occurrences in 7 sites (58%) that were unoccupied during the first survey (Table 3). Largemouth bass (*Micropterus salmoides*), Potomac sculpin (*Cottus girardi*), and yellow bullhead (*Ameiurus natalis*) also were observed in at least 4 sites that

TABLE 2 Stream temperature summaries by site in degrees Celsius. Minimum, maximum, mean, and standard deviations are calculated from 30-min increment data collected during summer 2022 (June 1–August 31). Thermal sensitivity is expressed as the regression slope for daily mean air and water temperatures during summer 2022 (see Figure 2). Site codes are defined in Table 1.

Site code	Minimum	Maximum	Mean	Standard deviation	Thermal sensitivity
BR	16.1	26.5	21.5	2.04	0.55
DL	15.5	27.3	21.5	2.17	0.57
DU	15.4	26.5	21.1	2.00	0.55
HO	15.9	25.2	20.2	1.67	0.36
RE	12.4	22.4	16.6	2.02	0.32
RO	14.4	23.5	19.0	1.79	0.35
SJ	13.5	24.6	19.5	2.09	0.44
SR	15.4	26.4	21.0	1.78	0.58
SL	17.2	28.8	22.5	2.17	0.49
SU	16.3	27.1	21.7	2.03	0.56
TL	15.4	26.6	20.7	2.17	0.50
TU	16.8	28.5	22.5	2.30	0.56

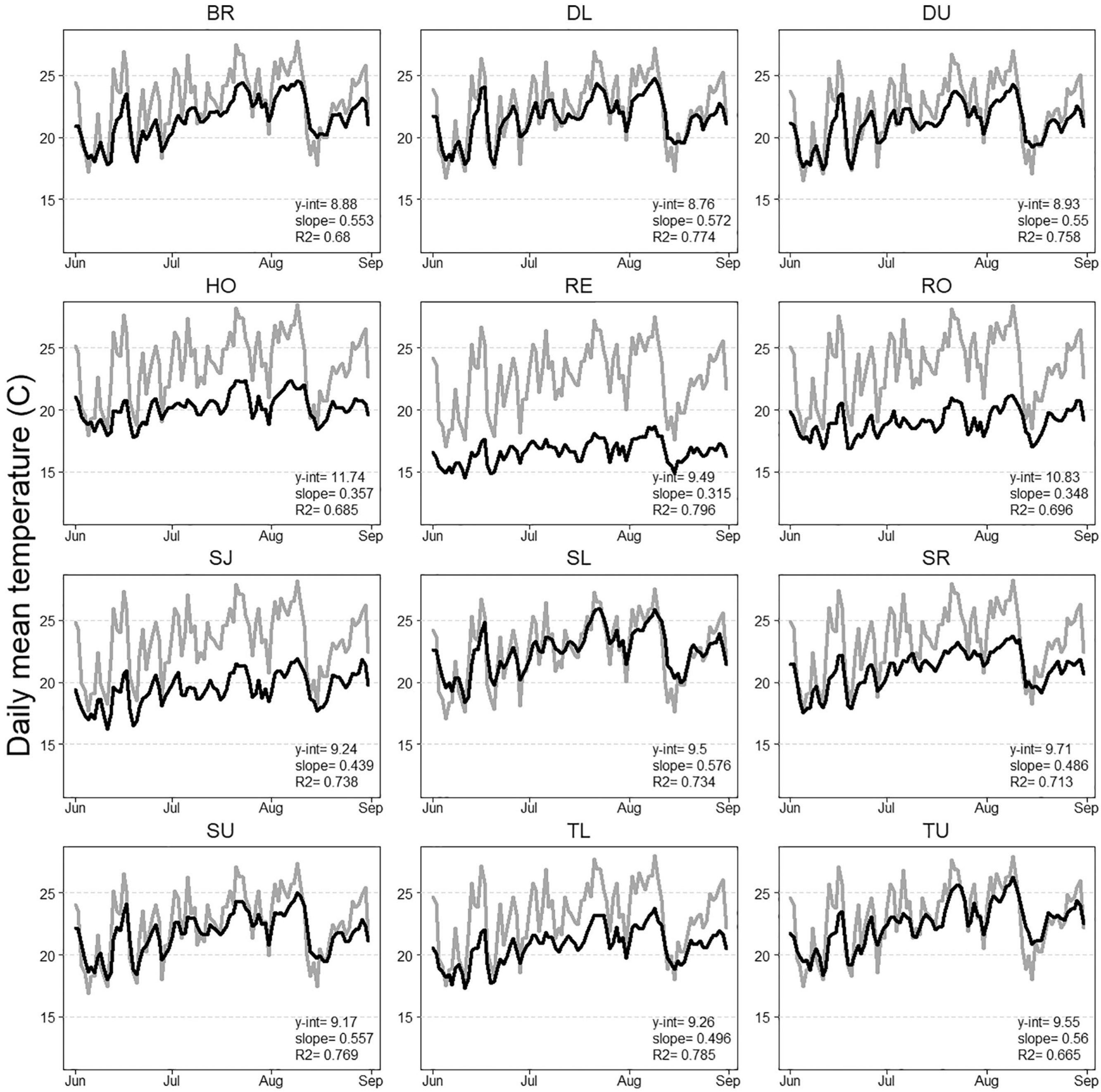

FIGURE 2 Daily mean air temperatures (grey) and water temperatures (black) for sample sites from June 1–August 31, 2022, including linear regression model coefficients and R^2 values. Site codes are given in Table 1, and geographic coordinates are given in Appendix S1.

were unoccupied during the initial surveys (Table 3). Centrarchid and Leuciscid fishes showed the largest extirpation trends: rock bass (*Ambloplites rupestris*), redbreast sunfish (*Lepomis auritus*), smallmouth bass (*Micropterus dolomieu*), spotfin shiner (*Cyprinella spiloptera*), and swallowtail shiner (*Notropis procne*); each was observed in 3 sites during the first survey but not the second. Blacknose dace, fantail darter, and white sucker (*Catostomus commersonii*) exhibited the greatest persistence over time, with each species observed during both survey periods in at least 9 of the 12 sites (75%) (Table 3). American eel (*Anguilla rostrata*) also was observed during both time periods in Hopewell Run (Figure 1).

Rates of species colonisation, extirpation, and persistence varied among sites (Table 4). Colonisation rates averaged 0.27 among sites and ranged from 0 (no species gained in Redbud Run) to 0.55 with 12 species gained in the Dillons Run lower site. Extirpation rates averaged 0.17 across sites and ranged from 0 to 0.90 with the loss of 8 species in the Sleepy Creek upper site. Persistence rates averaged 0.56 across sites and ranged from 0.36 (8 of 22 species persisting in the Dillions Run lower site) to 1.0 with persistence of 3 species in Redbud Run (Table 4). Considered in aggregate among sites, colonisation rates exceeded extirpation rates (Wilcoxon test, $p = .08$), and persistence rates exceeded

TABLE 3 Species abundances observed during 1993–1994 and 2022. Species codes are plotted in Figure 3a

Family	Scientific name	Common name	Species code	Abundance	Temporal change		
					+	−	=
Anguillidae	*Anguilla rostrata*	American eel	ANRO	2	0 (0.00)	0 (0.00)	1 (0.08)
Catostomidae	*Catostomus commersonii*	White sucker	CACO	133	2 (0.17)	0 (0.00)	9 (0.75)
	Erimyzon oblongus	Creek chubsucker	EROB	8	0 (0.00)	2 (0.17)	1 (0.08)
	Hypentelium nigricans	Northern hog sucker	HYNI	34	3 (0.25)	0 (0.00)	2 (0.17)
	Moxostoma erythrurum	Golden redhorse	MOER*	2	0 (0.00)	1 (0.08)	0 (0.00)
Centrarchidae	*Ambloplites rupestris*	Rock bass	AMRU*	94	0 (0.00)	3 (0.25)	3 (0.25)
	Lepomis auritus	Redbreast sunfish	LEAU	31	0 (0.00)	3 (0.25)	2 (0.17)
	Lepomis cyanellus	Green sunfish	LECY*	124	7 (0.58)	0 (0.00)	4 (0.33)
	Lepomis gibbosus	Pumpkinseed	LEGI	29	2 (0.17)	2 (0.17)	0 (0.00)
	Lepomis macrochirus	Bluegill	LEMA	71	2 (0.17)	2 (0.17)	2 (0.17)
	Micropterus dolomieu	Smallmouth bass	MIDO*	13	0 (0.00)	3 (0.25)	1 (0.08)
	Micropterus salmoides	Largemouth bass	MISA*	29	5 (0.42)	0 (0.00)	1 (0.08)
Cottidae	*Cottus caeruleomentum*	Blue Ridge sculpin	COCA	671	1 (0.08)	1 (0.08)	6 (0.5)
	Cottus girardi	Potomac sculpin	COGI	388	4 (0.33)	1 (0.08)	1 (0.08)
	Cottus sp. cf. *girardi*	Checkered sculpin	COSP	154	0 (0.00)	0 (0.00)	1 (0.08)
Ictaluridae	*Ameiurus natalis*	Yellow bullhead	AMNA	31	4 (0.33)	0 (0.00)	1 (0.08)
	Noturus insignis	Margined madtom	NOIN	24	3 (0.25)	0 (0.00)	1 (0.08)
Leuciscidae	*Campostoma anomalum*	Central stoneroller	CAAN	153	1 (0.08)	0 (0.00)	5 (0.42)
	Cyprinella spiloptera	Spotfin shiner	CYSP	21	1 (0.08)	3 (0.25)	1 (0.08)
	Luxilus cornutus	Common shiner	LUCO	3	1 (0.08)	2 (0.17)	0 (0.00)
	Margariscus margarita	Pearl dace	MAMA	516	0 (0.00)	1 (0.08)	4 (0.33)
	Nocomis micropogon	River chub	NOMI	1	1 (0.08)	0 (0.00)	0 (0.00)
	Notemigonus crysoleucas	Golden shiner	NOCR	17	1 (0.08)	1 (0.08)	0 (0.00)
	Notropis amoenus	Comely shiner	NOAM	2	0 (0.00)	1 (0.08)	0 (0.00)
	Notropis buccatus	Silverjaw minnow	NOBU	40	0 (0.00)	2 (0.17)	1 (0.08)
	Notropis hudsonius	Spottail shiner	NOHU	31	1 (0.08)	0 (0.00)	0 (0.00)
	Notropis procne	Swallowtail shiner	NOPR	15	0 (0.00)	3 (0.25)	0 (0.00)
	Pimephales notatus	Bluntnose minnow	PINO*	278	2 (0.17)	1 (0.08)	4 (0.33)
	Rhinichthys atratulus	Blacknose dace	RHAT	1471	3 (0.25)	0 (0.00)	9 (0.75)
	Rhinichthys cataractae	Longnose dace	RHCA	139	3 (0.25)	0 (0.00)	3 (0.25)
	Semotilus atromaculatus	Creek chub	SEAT	208	3 (0.25)	0 (0.00)	4 (0.33)
	Semotilus corporalis	Fallfish	SECO	72	0 (0.00)	0 (0.00)	2 (0.17)
Percidae	*Etheostoma blennioides*	Greenside darter	ETBL*	139	1 (0.08)	0 (0.00)	5 (0.42)
	Etheostoma caeruleum	Rainbow darter	ETCA*	45	3 (0.25)	0 (0.00)	0 (0.00)
	Etheostoma flabellare	Fantail darter	ETFL	863	1 (0.08)	0 (0.00)	11 (0.92)
	Etheostoma olmstedi	Tessellated darter	ETOL	1	0 (0.00)	1 (0.08)	0 (0.00)
Salmonidae	*Oncorhynchus mykiss*	Rainbow trout	ONMY*	1	0 (0.00)	1 (0.08)	0 (0.00)

Note: Species considered non-native in the Potomac River basin are indicated with *. Abundance is the number of individuals observed during both time periods. Temporal change is expressed as the number of sites where species showed colonisation (+), extirpation (−), or persistence (=). Proportions of sites are given in parentheses.

rates of immigration or extirpation (Wilcoxon test, $p < .001$, respectively).

A 2-dimensional NMS ordination represented spatial and temporal variation in fish community composition (stress = 0.15; Figure 3). Species space in the ordination was defined primarily by a gradient between Checkered sculpin (*Cottus* sp. cf. *girardi*; COSP) and fallfish (*Semotilus corporalis*; SECO) on axis 1 and between silver shiner (*Notropis buccatus*; NOBU) and Centrarchid species on axis 2 (bluegill, pumpkinseed sunfish, largemouth bass) (Figure 3a). Survey space in the ordination separated the first surveys from Dillons Creek

TABLE 4 Fish species richness, colonisation, extirpation, and persistence within sample sites. Site codes are defined in Table 1. Rates are expressed as the proportion of the cumulative number of fish species observed within sites. Species richness is given as the number of fish species observed during the first and second surveys with the cumulative total in parentheses.

		Colonisation		Extirpation		Persistence	
Site code	Species richness	Count	Rate	Count	Rate	Count	Rate
BR	10, 17 (18)	8	0.444	1	0.056	9	0.500
DL	10, 20 (22)	12	0.545	2	0.091	8	0.364
DU	18, 18 (23)	5	0.217	5	0.217	13	0.565
HO	14, 19 (22)	8	0.364	3	0.136	11	0.500
RE	3, 3 (3)	0	0.000	0	0.000	3	1.000
RO	6, 7 (8)	2	0.250	1	0.125	5	0.625
SJ	4, 5 (5)	1	0.200	0	0.000	4	0.800
SR	9, 7 (11)	2	0.182	4	0.364	5	0.455
SL	18, 18 (25)	7	0.280	7	0.280	11	0.440
SU	16, 14 (22)	6	0.273	8	0.364	8	0.364
TL	6, 6 (8)	2	0.250	2	0.250	4	0.500
TU	5, 6 (7)	2	0.286	1	0.143	4	0.571

(DL1, DU1) from other surveys along axis 1 and separated the first and second surveys from Slate Run (SR1, SR2) from other surveys along axis 2 (Figure 3b).

Temporal change in fish community composition was associated with the thermal sensitivity of sample sites (Figure 3c,d). Sites exhibiting low thermal sensitivity (<0.45) exhibited shorter distances between surveys in the NMS ordination space than sites with high thermal sensitivities (>0.45) (Wilcoxon test, $p = .004$; Figure 3c). Likewise, the convex hull space occupied by sites with thermal sensitivities >0.45 exhibited more temporal variation than sites with low thermal sensitivity (Figure 3d), indicating that fish communities were more stable over time in sites with stronger groundwater controls on stream temperature. In contrast, sites with high thermal sensitivities (>0.45) exhibited a loss of beta diversity over time, as indicated by the smaller convex hull area of the communities in 2022 than during the first sampling period (Figure 3d). Euclidean distances in NMS space were strongly correlated to Bray-Curtis distances among surveys (Spearman *rho* = .63; results not shown) suggesting statistical robustness of the observed trends.

Beta regression models revealed environmental associations with colonisation, extirpation, and persistence rates across sites (Table 5). Model coefficients showed increasing colonisation with basin size and thermal sensitivity and decreasing colonisation rates with elevation ($p < .001$ respectively; model pseudo-$R^2 = .92$). Extirpation rates decreased with the percent of the watershed in karst terrain ($p < .01$) whereas other covariates were insignificant in this regard (model pseudo-$R^2 = .58$). In contrast, species persistence increased with elevation and decreased with basin size and thermal sensitivity ($p < .01$, respectively; model pseudo-$R^2 = .88$, Table 5). Across models, gains in elevation were associated with increasing species persistence rates and decreasing colonisation rates. Conversely, gains in stream size (as indexed by upstream basin area) were associated with decreasing persistence rates and increasing colonisation rates. Thermal sensitivity was positively associated with species colonisation rates and negatively associated with species persistence rates (Table 5).

4 | DISCUSSION

Our results highlight the importance of groundwater for stream fish community composition. We found that fish communities in sites with the strongest groundwater signals (i.e., thermal sensitivities <0.45) were most stable over time, and these sites were characterised by species persistence rather than colonisation or extirpation. Our results support prior research demonstrating that streams in karst terrain exhibit lower thermal sensitivities than sites lacking karst (Kelleher et al., 2012; O'Driscoll & DeWalle, 2006). Our results also extend prior work by demonstrating that thermal sensitivity was a stronger predictor of species persistence and colonisation rates than the presence of karst terrain, suggesting the ecological importance of local variation in groundwater-surface water interactions. We also observed that sites with marl substrates, which may be controlled by proximal discharge of groundwater supersaturated with carbon dioxide, were more thermally resilient and ecologically stable over time than sites lacking these substrates, suggesting that such features may be a useful visual indicator of climate change refugia in stream ecosystems.

Prior research has shown that stream fish communities are more stable over time in larger rivers than smaller streams (Horowitz, 1978; Schlosser, 1990), and this has been attributed to the relative stability of environmental conditions such as flow and temperature with increasing stream volume (Hynes, 1970). However, we observed the opposite pattern: fish communities in larger sites showed higher colonisation rates and lower persistence rates than in smaller sites (Table 5), and this may indicate increased access to regional species pools or remote resources with increasing stream volume. For instance, stream network connectivity can enable fish dispersal from riverine source populations (Hitt & Angermeier, 2008, 2011) and can provide habitat for life history expression (i.e., feeding, breeding, and refugia; Schlosser, 1991). In our study, Hopewell Run and Slate Run were located <1 km upstream from rivers that more than doubled their flow volume, and Hopewell Run was large enough (i.e., >1000 ha basin size) to support immigrants from riverine source populations

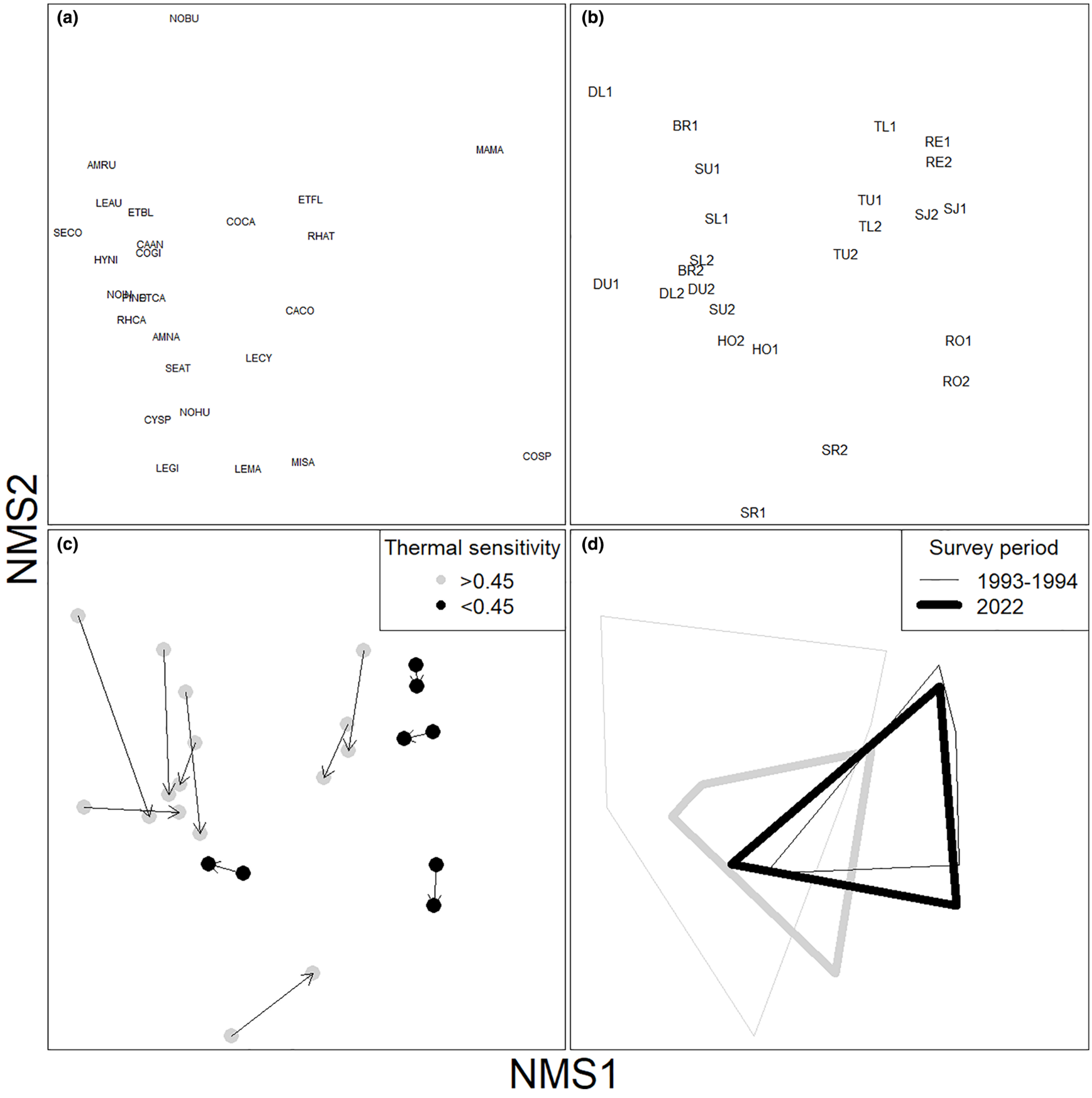

FIGURE 3 Nonmetric multidimensional scaling (NMS) ordination of fish species abundance by species (a) and sites (b). Temporal change in community composition is shown with arrows (c) and convex hulls (d) for sites with low thermal sensitivity (<0.45, black) and high thermal sensitivity (>0.45, grey). Site codes are given in Table 1, thermal sensitivities are given in Table 2, and species codes are given in Table 3.

within this distance (Hitt & Angermeier, 2008). Nonetheless, fish community composition in Hopewell Run was more stable over time than in sites lacking strong groundwater signals (i.e., thermal sensitivity >0.45; Figure 3).

Prior research has shown that stream fish communities within karst terrain are distinct from communities elsewhere in the study area (Hitt et al., 2022), and our analysis further indicates that fish communities in karst terrain are more stable over time. Coulter and Galarowicz (2015) suggested that karst groundwater inputs affect stream fishes by "resetting" habitat conditions along the river continuum to those expected in smaller and colder headwater streams. Ward and Stanford (1983) offered a similar conceptual model regarding the effects of flow regulation in rivers (i.e., serial discontinuity concept). Our results suggest a somewhat different model. Although we expect streams in karst terrain generally to exhibit colder temperatures than expected for a given elevation (Bonacci et al., 2009; Kresic, 2013; O'Driscoll & DeWalle, 2006), we also expect flow stabilisation from karst groundwater inputs would resemble downstream conditions rather than upstream conditions (Hynes, 1970) as reported by Horowitz (1978) and others. As such, we suggest that karst groundwater inputs combine aspects of

TABLE 5 Beta regression models for species colonisation, extirpation, and persistence among sites ($n = 12$). Karst is expressed as the proportion of karst terrain the upstream watershed. Thermal sensitivity (TS) is expressed as the regression slope of the air-water temperature relationship during summer 2022. Covariates were scaled to facilitate comparison.

Response	Covariate	Coefficient	Standard error	z	p
Colonisation	Elevation	−0.48	0.11	−4.45	<.001
	Basin size	0.39	0.09	4.55	<.001
	Karst	0.12	0.12	0.99	.321
	TS	0.62	0.15	4.13	<.001
Extirpation	Elevation	−0.19	0.16	−1.19	.233
	Basin size	0.08	0.14	0.56	.575
	Karst	−0.57	0.22	−2.60	.009
	TS	−0.02	0.23	−0.10	.922
Persistence	Elevation	0.51	0.12	4.19	<.001
	Basin size	−0.32	0.10	−3.32	<.001
	Karst	0.20	0.14	1.45	.148
	TS	−0.54	0.17	−3.20	.001

upstream and downstream conditions with a net effect of stabilising environmental fluctuations. Likewise, Ramírez-García et al. (2023) observed temporal stability of fish communities in a spring-fed lake ecosystem with stable environmental conditions over time, and Kollaus et al. (2015) also reported temporal stability of lotic fish communities in a river system stabilised by karstic groundwater inputs.

The presence of marl substrates in sites with the strongest groundwater signals (i.e., thermal sensitivity < 0.45) suggests its utility for ecological analysis. Vesper et al. (2019) found that calcium precipitation rates in a Virginia stream were greatest during summer conditions characterised by low flows, warm temperatures, and high alkalinity. Our study sites did not represent the warm springs sampled by Vesper et al. (2019), but our results support their assertion that local conditions affect precipitation rates because marl was not present at all sites within karst terrain. Although high calcium concentrations can reduce salmonid egg survival rates (Ketola et al., 1988), sedimentation and limited availability of spawning habitat may be more important limitations than stream temperature for salmonid fish populations in the study area. We therefore interpret the presence of marl as an index of potential thermal refugia in locations that often may benefit from physical habitat restoration (e.g., streambank stabilisation, riparian vegetation). Our results also suggest that the presence or absence of marl could help classify streams as "groundwater stable" or "groundwater flashy" hydrologic classes within karst landscapes (Fox & Magoulick, 2022; Leasure et al., 2016).

Our surveys revealed important species-specific changes over time. We observed immigration of rainbow darter in 3 sites, including a site in karst terrain (Hopewell Run) suggesting the species' physiological tolerance of a wide range of environmental conditions. Rainbow darter is considered non-native within the Potomac River basin due to its rapid colonisation into major tributaries following the first observation in 1977 (Cessna et al., 2014), and our surveys provide additional support for assertion that the species is non-native in the study area. We also observed the apparent extirpation of smallmouth bass in 3 sites (Dillons Creek lower and upper sites, Sleepy Creek lower site) and its persistence in 1 site (Brush Creek). This species shows declining abundance trends in the Potomac River associated with scouring flows during egg incubation and larval development (Hitt et al., 2020), and our survey results suggest that smallmouth bass may be declining due to destabilised flows in headwater tributaries as well. Conversely, we observed the immigration of green sunfish into 7 sites that were unoccupied previously and its persistence within 4 sites (Table 3). Colonisation occurred within small stream sites (e.g., Saint James Run) and large stream sites (Sleepy Creek upper site), indicating the physiological tolerance of this species. Moreover, green sunfish exhibits life history traits associated with equilibrium, opportunistic, and periodic strategies (Hitt et al., 2022), suggesting that such a combination of strategies may facilitate colonisation of stable or dynamic environmental conditions. McCormick et al. (2001) considered green sunfish an indicator of declining ecological integrity in Appalachian streams using data that included the USEPA (2000) records we evaluated (Table 1), but they noted "the paucity of green sunfish" (McCormick et al., 2001: 860) in contrast to our observations.

We found that checkered sculpin was associated with low thermal sensitivity in the community ordination space (Figure 3), consistent with prior research showing the limitation of this species to karst groundwater-dominated streams in the Ridge and Valley portion of the Potomac River basin (Hitt et al., 2021, 2022). Hitt et al. (2022) attributed the patchy distribution of this species to its life history strategy (low fecundity and parental care) that requires stable environmental conditions, and our results indicate the persistence of this species where it occurred (Rocky marsh Run, Figure 1). We also found that pearl dace was associated with low thermal sensitivity sites (<0.45; Figure 3), and it persisted in 4 of the 5 sites where it occurred (Table 3). The exception was the Tuscarora Creek upper site where it was observed in 1994 but not 2022, and this site is in a watershed with a mix of karst and non-karst terrain at equal proportion (Table 1) suggesting a peripheral distribution for pearl dace in locations where karstic groundwater inputs become less important. Our analysis indicated that checkered sculpin and pearl dace indicate streams with strong groundwater inputs, and we suggest that monitoring the distribution and abundance of these species could inform our understanding of groundwater warming (Hare et al., 2021) and groundwater contaminant pathways in karst terrain (Padilla & Vesper, 2018).

We also found that beta diversity decreased over time among sites lacking strong groundwater controls (i.e., thermal sensitivity >0.45; Figure 3d). This pattern does not simply reflect the loss of species richness in non-karst environments because sites with the largest gain in species richness over time (Brush Creek and Dillons Creek lower) were more centrally located in the community ordination space in 2022 than in prior surveys (Figure 3c), indicating the colonisation of common species that occur across a larger proportion of sites (e.g., green sunfish). Such losses of beta diversity may have implications for functional diversity and associated ecosystem services (Mori et al., 2018), and our dataset could be used to evaluate fish species traits in this regard.

Interpretation of our analysis requires consideration of sampling methods and variation in species detection. Although we sampled fish communities using backpack electrofishing as previously implemented (USEPA, 2000), this sampling method includes some level of imperfect detection that can affect inference on temporal trends, particularly for rare species (Reid & Haxton, 2017). However, this is unlikely to bias our analysis because rare species were detected at a similar rate in both survey periods. For instance, the proportion of observed “rare” species (i.e., <20 individuals) observed during surveys was not different between sample periods ($t = 0.26$, $p = .80$), and we excluded rare species from our multivariate analysis. We used the original coordinates to navigate to our sample sites, but in some cases the original coordinates were located off the stream channel. We updated the sample site locations using a straight line to the stream channel, and we recognise that localised differences in microhabitat features may affect the accumulation of fish species with backpack electrofishing methods (Angermeier & Smogor, 1995). We therefore interpret our surveys as samples of reach-scale processes rather than microhabitat-scale processes.

Our study contributes an empirical analysis of the ecological importance of groundwater connectivity to stream ecosystems. We showed that stream fish communities were more stable over time in places with the strongest groundwater signals as quantified by the slope of the linear relation between daily air-water temperature data (June 1–August 31, 2022). Our analysis also indicated the utility of marl substrates as an indicator of persistent groundwater-surface water interactions that may promote ecological resiliency to climate change. Our results also revealed ecological distinctions among streams within karst terrain, consistent with the complex groundwater flow paths known from the study area (Evaldi et al., 2009; Kozar et al., 1991; Vesper & Herman, 2020). Our study provides a temporal perspective within discrete locations sampled previously, but additional sites are needed to evaluate the spatial properties of ecological change over time in the study area. This could be accomplished with longitudinally structured stream fish surveys over time paired with high spatial resolution stream temperature data.

AUTHOR CONTRIBUTIONS

All co-authors developed the conceptual framework and study design; N.H., K.R., and K.K. conducted fieldwork; N.H. led the analysis and manuscript preparation with support from all co-authors.

ACKNOWLEDGEMENTS

We thank S. Faulkner, C. Snyder, D. Doctor, M. Eackles, J. Lamm, T. Woods, F. Vanderbilt, T. O'Connell, S. Phillips, and K. Hyer (U.S. Geological Survey) for assistance with this study. We also thank two anonymous reviewers for helpful comments. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

FUNDING INFORMATION

This work was funded by USGS Chesapeake Bay studies, the USGS Ecosystems Mission Area, the USGS New England Water Science Center, and the USGS Eastern Ecological Science Center.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data collected by the U.S. Geological Survey for this study are available through ScienceBase.gov. Water temperature data are provided at https://doi.org/10.5066/P9LJ8RNN, and fish community data are provided at https://doi.org/10.5066/P92ML1EC and in Appendix S5 (online). Air temperature data are available from the Global Historical Climatology Network daily at https://www.ncei.noaa.gov/.

ORCID

Nathaniel P. Hitt https://orcid.org/0000-0002-1046-4568
Karli M. Rogers https://orcid.org/0000-0002-6188-7405
Karmann G. Kessler https://orcid.org/0000-0001-5681-4909
Martin A. Briggs https://orcid.org/0000-0003-3206-4132
Jennifer H. Fair https://orcid.org/0000-0002-9902-1893

REFERENCES

Angermeier, P. L., & Smogor, R. A. (1995). Estimating number of species and relative abundance in stream-fish communities: Effects of sampling effort and discontinuous spatial distributions. *Canadian Journal of Fisheries and Aquatic Sciences*, *52*, 936–949. https://doi.org/10.1139/f95-093

Bonacci, O., Pipan, T., & Culver, D. C. (2009). A framework for karst ecohydrology. *Environmental Geology*, *56*, 891–900. https://doi.org/10.1007/s00254-008-1189-0

Briggs, M. A., Goodling, P., Johnson, Z. C., Rogers, K. M., Hitt, N. P., Fair, J. B., & Snyder, C. D. (2022). Bedrock depth influences spatial patterns of summer baseflow, temperature, and flow disconnection for mountainous headwater streams. *Hydrology and Earth System Sciences*, *26*, 3989–4011. https://doi.org/10.5194/hess-26-3989-2022

Cessna, J. F., Raesly, R. L., Kilian, J. V., Cincotta, D. A., & Hilderbrand, R. H. (2014). Rapid colonization of the Potomac River drainage by the rainbow darter (*Etheostoma caeruleum*) following introduction. *Northeastern Naturalist*, *21*, 1–11. https://doi.org/10.1656/045.021.0101

Chang, Y., Wu, J., & Liu, L. (2015). Effects of the conduit network on the spring hydrograph of the karst aquifer. *Journal of Hydrology*, *527*, 517–530. https://doi.org/10.1016/j.jhydrol.2015.05.006

Connell, J. H., & Sousa, W. P. (1983). On the evidence needed to judge ecological stability or persistence. *The American Naturalist*, *121*, 789–824. https://doi.org/10.1086/284105

Coulter, A. A., & Galarowicz, T. L. (2015). Fish assemblage and environmental differences upstream and downstream of a cave: A potential reset mechanism. *Environmental Biology of Fishes*, *98*, 1223–1231. https://doi.org/10.1007/s10641-014-0354-4

Cribari-Neto, F., & Zeileis, A. (2010). Beta regression in R. *Journal of Statistical Software*, *34*, 1–24. https://doi.org/10.18637/jss.v034.i02

Dasher, G. R. (2012). The caves and karst of West Virginia. *West Virginia Speleological Survey Bulletin*, *19*, 1–264.

Doctor, D. H., & Doctor, K. Z. (2012). Spatial analysis of geologic and hydrologic features relating to sinkhole occurrence in Jefferson County, West Virginia. *Carbonates and Evaporites*, *27*, 143–152. https://doi.org/10.1007/s13146-012-0098-1

Douma, J. C., & Weedon, J. T. (2019). Analysing continuous proportions in ecology and evolution: A practical introduction to beta and Dirichlet regression. *Methods in Ecology and Evolution*, *10*, 1412–1430. https://doi.org/10.1111/2041-210X.13234

Dunning, J. B., Danielson, B. J., & Pulliam, H. R. (1992). Ecological processes that affect populations in complex landscapes. *Oikos*, *65*, 169–175. https://doi.org/10.2307/3544901

Evaldi, R. D., Paybins, K. S., & Kozar, M. D. (2009). *Hydrogeologic factors affecting base-flow yields in the Jefferson County area, West Virginia, October–November 2007. U.S. Geological Survey Scientific Investigations Report 2009–5145*.

Evans, M. A., Orndorff, R. C., & Henika, W. (2016). Structural geology of the Valley and Ridge Plateaus provinces. Chapter 3. In C. M. Bailey, W. C. Sherwood, S. Eaton, & D. S. Powars (Eds.), *The Geology of Virginia*. Virginia Museum of Natural History Special Publication 18.

Ford, T. D., & Pedley, H. M. (1996). A review of tufa and travertine deposits of the world. *Earth Science Reviews*, *41*, 117–175. https://doi.org/10.1016/S0012-8252(96)00030-X

Fox, J. T., & Magoulick, D. D. (2022). Hydrologic and environmental thresholds in stream fish assemblage structure across flow regimes. *Ecological Indicators*, *144*, 109500. https://doi.org/10.1016/j.ecolind.2022.109500

Hammond, J. C., Simeone, C., Hecht, J. S., Hodgkins, G. A., Lombard, M., McCabe, G., Wolock, D., Wieczorek, M., Olson, C., Caldwell, T., Dudley, R., & Price, A. N. (2022). Going beyond low flows: Streamflow drought deficit and duration illuminate distinct spatiotemporal drought patterns and trends in the U.S. during the last century. *Water Resources Research*, *58*, e2022WR031930. https://doi.org/10.1029/2022WR031930

Hare, D. K., Helton, A. M., Johnson, Z. C., Lane, J. W., & Briggs, M. A. (2021). Continental-scale analysis of shallow and deep groundwater contributions to streams. *Nature Communications*, *12*, 1450. https://doi.org/10.1038/s41467-021-21651-0

Harvey, B. C., & Stewart, A. J. (1991). Fish size and habitat depth relationships in headwater streams. *Oecologia*, *87*, 336–342. https://doi.org/10.1007/BF00634588

Herlihy, A. T., Larsen, D. P., Paulsen, S. G., Urquhart, N. S., & Rosenbaum, B. J. (2000). Designing a spatially balanced, randomized site selection process for regional stream surveys: The EMAP mid-Atlantic pilot study. *Environmental Monitoring and Assessment*, *63*, 95–113. https://doi.org/10.1023/A:1006482025347

Hitt, N. P. (2007). *Effects of stream network topology on fish assemblage structure and bioassessment sensitivity in the mid-Atlantic highlands, USA. PhD Dissertation, Virginia Polytechnic Institute and State University. Blacksburg, VA*.

Hitt, N. P., & Angermeier, P. L. (2008). Evidence for fish dispersal from spatial analysis of stream network topology. *Journal of the North American Benthological Society*, *27*, 304–320. https://doi.org/10.1899/07-096.1

Hitt, N. P., & Angermeier, P. L. (2011). Fish community and bioassessment responses to stream network position. *Journal of the North American Benthological Society*, *30*, 296–309. https://doi.org/10.1899/09-155.1

Hitt, N. P., Kessler, K. G., Macmillan, H. E., Rogers, K. M., & Raesly, R. L. (2021). Comparative morphology of freshwater sculpin inhabiting different environmental conditions in the Chesapeake Bay headwaters. *Environmental Biology of Fishes*, *104*, 309–324. https://doi.org/10.1007/s10641-021-01078-8

Hitt, N. P., Landsman, A. P., & Raesly, R. L. (2022). Life history strategies of stream fishes linked to predictors of hydrologic stability. *Ecology and Evolution*, *12*, e8861. https://doi.org/10.1002/ece3.8861

Hitt, N. P., Rogers, K. M., Kelly, Z. A., Henesy, J., & Mullican, J. E. (2020). Fish life history traits indicate increasing flow stochasticity in an unregulated river. *Ecosphere*, *11*, e03026. https://doi.org/10.1002/ecs2.3026

Horowitz, R. J. (1978). Temporal variability patterns and the distributional patterns of stream fishes. *Ecological Monographs*, *48*, 307–321. https://doi.org/10.2307/2937233

Hubbard, D. A. J., Giannini, W. F., & Lorah, M. M. (1985). Travertine-marl deposits of the Valley and Ridge Province of Virginia - a preliminary report. *Virginia Minerals*, *31*, 1–15.

Hynes, H. B. N. (1970). *The ecology of running waters*. University of Toronto Press.

Irani, F. M., & Claggett, P. R. (2010). *Chesapeake Bay watershed land cover data series. U.S. Geological Survey Data Series 505. Reston, Virginia*. https://doi.org/10.3133/ds505

Jenkins, R. E., & Burkhead, N. M. (1994). *Freshwater Fishes of Virginia*. American Fisheries Society.

Jones, W. K. (1997). *Karst Hydrology Atlas of West Virginia*. Karst Waters Institute, Special Publication 4.

Kaandorp, V. P., Doornenbal, P. J., Kooi, H., Broers, H. P., & de Louw, P. G. B. (2019). Temperature buffering by groundwater in ecologically valuable lowland streams under current and future climate conditions. *Journal of Hydrology X*, *3*, 100031. https://doi.org/10.1016/j.hydroa.2019.100031

Kanno, Y., Pregler, K. C., Hitt, N. P., Letcher, B. H., Hocking, D. J., & Wofford, J. E. B. (2016). Seasonal temperature and precipitation regulate brook trout young-of-the-year abundance and population dynamics. *Freshwater Biology*, *61*, 88–99. https://doi.org/10.1111/fwb.12682

Kelleher, C., Wagener, T., Gooseff, M., McGlynn, B., McGuire, K., & Marshall, L. (2012). Investigating controls on the thermal sensitivity of Pennsylvania streams. *Hydrological Processes*, *26*, 771–785. https://doi.org/10.1002/hyp.8186

Ketola, H. G., Longacre, D., Greulich, A., Phetterplace, L., & Lashomb, R. (1988). High calcium concentration in water increases mortality of salmon and trout eggs. *Progressive Fish-Culturist*, *50*, 129–135. https://doi.org/10.1577/1548-8640

Kollaus, K. A., Behen, K. P. K., Heard, T. C., Hardy, T. B., & Bonner, T. H. (2015). Influence of urbanization on a karst terrain stream and fish community. *Urban Ecosystems*, *18*, 293–320. https://doi.org/10.1007/s11252-014-0384-x

Kovach, R., Dunham, J., Al-Chokhachy, R., Snyder, C., Young, J., Lynch, A., Konrad, C., Jaeger, K., Hitt, N. P., Letcher, B., Rea, A., Sepulveda, A., Pederson, G., Lambert, P., Torgersen, C., Stoker, J., & Muhlfeld, C. (2019). An integrated framework for ecological drought across riverscapes of North America. *BioScience*, *69*, 418–431. https://doi.org/10.1093/biosci/biz040

Kozar, M. D., Hobba, W. A., & Macy, J. A. (1991). *Geohydrology, water availability, and water quality of Jefferson County, West Virginia,* *with emphasis on the carbonate area. U.S. Geological Survey. Water-resources Investigations Report 90–4118*.

Kresic, N. (2013). *Water in Karst: Management, vulnerability, and restoration*. McGraw Hill.

Kurylyk, B. L., MacQuarrie, K. T. B., & Voss, C. I. (2014). Climate change impacts on the temperature and magnitude of groundwater discharge from shallow, unconfined aquifers. *Water Resources Research*, *50*, 3253–3274. https://doi.org/10.1002/2013WR014588

Lazorchak, J. M., Hill, B. H., Averill, D. K., Peck, D. V., & Klemm, D. J. (2000). *Environmental Monitoring and Assessment Program - Surface Waters: Field Operations and Methods for Measuring the Ecological Condition of Non-Wadeable Rivers and Streams*. U.S. Environmental Protection Agency, Cincinnati OH. EPA/620/R-00/007.

Leasure, D. R., Magoulick, D. D., & Longing, S. D. (2016). Natural flow regimes of the Ozark-Ouachita interior highlands region. *River Research and Applications*, *32*, 18–35. https://doi.org/10.1002/rra.2838

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., Holt, R. D., Shurin, J. B., Law, R., Tilman, D., Loreau, M., & Gonzalez, A. (2004). The metacommunity concept: A framework for multi-scale community ecology. *Ecology Letters*, *7*, 601–613. https://doi.org/10.1111/j.1461-0248.2004.00608.x

MacArthur, R. H., & Wilson, E. O. (1967). *The Theory of Island Biogeography*. Princeton University Press. https://doi.org/10.1515/9781400881376

Magoulick, D. D., Dekar, M. P., Hodges, S. W., Scott, M. K., Rabalais, M. R., & Bare, C. M. (2021). Hydrologic variation influences stream fish assemblage dynamics through flow regime and drought. *Scientific Reports*, *11*, 10704. https://doi.org/10.1038/s41598-021-89632-3

Magoulick, D. D., & Kobza, R. M. (2003). The role of refugia for fishes during drought: A review and synthesis. *Freshwater Biology*, *48*, 1186–1198. https://doi.org/10.1046/j.1365-2427.2003.01089.x

Matthews, M. J., & Matthews, E. (2016). Dynamics of an upland stream fish community over 40 years: Trajectories and support for the loose equilibrium concept. *Ecology*, *97*, 706–719. https://doi.org/10.1890/14-2179.1

McCormick, F. H., & Hughes, R. M. (2000). Aquatic Vertebrates. Chapter 10. In J. M. Lazorchak, B. H. Hill, D. K. Averill, D. V. Peck, & D. J. Klemm (Eds.), *Environmental Monitoring and Assessment Program – surface waters: Field operations and methods for measuring the ecological condition of non-wadeable rivers and streams*. US Environmental Protection Agency.

McCormick, F. H., Hughes, R. M., Kaufmann, P. R., Peck, D. V., Stoddard, J. L., & Herlihy, A. T. (2001). Development of an index of biotic integrity for the mid-Atlantic highlands region. *Transactions of the American Fisheries Society*, *130*, 857–877. https://doi.org/10.1577/1548-8659

McCoy, K. J., & Kozar, M. D. (2008). Use of sinkhole and specific capacity distributions to assess vertical gradients in a karst aquifer. *Environmental Geology*, *54*, 921–935. https://doi.org/10.1007/s00254-007-0889-1

McManamay, R. A., & Frimpong, E. A. (2015). Hydrologic filtering of fish life history strategies across the United States: Implications for stream flow alteration. *Ecological Applications*, *25*, 243–263. https://doi.org/10.1890/14-0247.1

Meisner, D. J., Rosenfeld, J. S., & Regier, H. A. (1988). The role of groundwater in the impact of climate warming on stream salmonines. *Fisheries*, *13*, 2–8. https://doi.org/10.1577/1548-8446(1988)013<0002:TROGIT>2.0.CO;2

Milly, P. C. D., Betancourt, J., Falkenmark, M., Hirsch, R. M., Kundzewicz, Z. W., Lettenmaier, D. P., & Stouffer, R. J. (2008). Stationarity is dead: Whither water management? *Science*, *319*, 573–574. https://doi.org/10.1126/science.1151915

Mims, M. C., & Olden, J. D. (2012). Life history theory predicts fish assemblage response to hydrologic regimes. *Ecology*, *93*, 35–45. https://doi.org/10.1890/11-0370.1

Mori, A. S., Isbell, F., & Seidl, R. (2018). Beta diversity, community assembly, and ecosystem functioning. *Trends in Ecology and Evolution*, *33*, 549–564. https://doi.org/10.1016/j.tree.2018.04.012

Morrill, D. P., Connolly, M. H., Adams, G. L., & Adams, S. R. (2022). Fish assemblage shifts in and Ozark river over 80 years amidst a mosaic of forest regeneration and persistent pasture. *Ecology of Freshwater Fish*, *32*. https://doi.org/10.1111/eff.12683

O'Driscoll, M. A., & DeWalle, D. R. (2006). Stream–air temperature relations to classify stream–ground water interactions in a karst setting, central Pennsylvania, USA. *Journal of Hydrology*, *329*, 140–153. https://doi.org/10.1016/j.jhydrol.2006.02.010

Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Solymos, P., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., Evangelista, H., … Weedon, J. (2022). *Vegan: Community Ecology Package. R package version 2.6-2*. https://CRAN.R-project.org/package=vegan

Olden, J. D., LeRoy Poff, N., & Bestgen, K. R. (2006). Life history strategies predict fish invasion and extirpations in the Colorado River basin. *Ecological Monographs*, *76*, 25–40. https://doi.org/10.1890/05-0330

Padilla, I. Y., & Vesper, D. J. (2018). Fate, transport, and exposure of emerging and legacy contaminants in karst systems: State of knowledge and uncertainty. In W. B. White, J. S. Herman, E. K. Herman, & M. Rutigliano (Eds.), *Karst Groundwater Contamination and Public Health* (pp. 33–49). Springer. https://doi.org/10.1007/978-3-319-51070-5_5

Perkin, J. S., Gido, J. B., Cooper, A. R., Turner, T. F., Osborne, M. J., Johnson, E. R., & Mayes, K. B. (2015). Fragmentation and dewatering transform Great Plains stream fish communities. *Ecological Monographs*, *85*, 73–92. https://doi.org/10.1890/14-0121.1

Propst, D. L., Gido, K. B., & Stefferud, J. A. (2008). Natural flow regimes, nonnative fishes, and native fish persistence in arid-land river systems. *Ecological Applications*, *18*, 1236–1252. https://doi.org/10.1890/07-1489.1

R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Ramírez-García, A., Domínguez-Domínguez, O., López-López, E., Moncayo-Estrada, R., & De La Cruz-Agüero, J. (2023). Temporal changes in the fish community structure of a small subtropical spring lake: Decadal and seasonal analysis. *Ecology of Freshwater Fish*, *32*, 53–63. https://doi.org/10.1111/eff.12669

Rashleigh, B., Parmar, R., Johnston, J. M., & Barber, M. C. (2005). Predictive habitat models for the occurrence of stream fishes in the mid-Atlantic highlands. *North American Journal of Fisheries Management*, *25*, 1353–1366. https://doi.org/10.1577/M04-202.1

Reid, S. M., & Haxton, T. J. (2017). Backpack electrofishing effort and imperfect detection: Influence on riverine fish inventories and monitoring. *Journal of Applied Ichthyology*, *33*, 1083–1091. https://doi.org/10.1111/jai.13463

Roberts, J. H., & Hitt, N. P. (2010). Longitudinal structure in temperate stream fish communities: Evaluating conceptual models with temporal data. *American Fisheries Society Symposium*, *73*, 281–299. https://doi.org/10.47886/9781934874141

Roghair, C. N., Dolloff, C. A., & Underwood, M. K. (2002). Response of a brook trout population and instream habitat to a catastrophic flood and debris flow. *Transactions of the American Fisheries Society*, *131*, 718–730. https://doi.org/10.1577/1548-8659(2002)131<0718:ROABTP>2.0.CO;2

Schlosser, I. J. (1990). Environmental variation, life history attributes, and community structure in stream fishes: Implications for environmental management and assessment. *Environmental Management*, *14*, 621–628. https://doi.org/10.1007/BF02394713

Schlosser, I. J. (1991). Stream fish ecology: A landscape perspective. *BioScience*, *41*, 704–712. https://doi.org/10.2307/1311765

Shirafkan, M., Mohammadi, Z., Sivelle, V., & Labat, D. (2021). The effects of exchange flow on the karst spring hydrograph under different flow regimes: A synthetic modeling approach. *Water*, *13*, 1189. https://doi.org/10.3390/w13091189

Shuster, E. T., & White, W. B. (1971). Seasonal fluctuations in the chemistry of limestone springs: A possible means for characterizing carbonate aquifers. *Journal of Hydrology*, *14*, 93–128. https://doi.org/10.1016/0022-1694(71)90001-1

Snyder, C. D., Hitt, N. P., & Young, J. A. (2015). Accounting for the influence of groundwater on thermal sensitivity of headwater streams to climate change. *Ecological Applications*, *25*, 1397–1419. https://doi.org/10.1890/14-1354.1

Snyder, C. D., Young, J. A., Villella, R., & Lemarie, D. P. (2003). Influences of upland and riparian land use patterns on stream biotic integrity. *Landscape Ecology*, *18*, 647–664. https://doi.org/10.1023/B:LAND.0000004178.41511.da

Sowder, C., & Steel, E. A. (2012). A note on the collection and cleaning of water temperature data. *Water*, *4*, 597–606. https://doi.org/10.3390/w4030597

Stull, R. B. (1988). *An Introduction to Boundary Layer Meteorology*. Kluwer Academic Publishers.

Sullivan, C. J., Vokoun, J. C., Helton, A. M., Briggs, M. A., & Kurylyk, B. L. (2021). An ecohydrological typology for thermal refuges in streams and rivers. *Ecohydrology*, *15*, e2295. https://doi.org/10.1002/eco.2295

US Environmental Protection Agency (USEPA). (2000). *Mid-Atlantic highlands streams assessment. EPA-903-R-00-015*. US Environmental Protection Agency Region 3.

Van Meerbeek, K., Jucker, T., & Svenning, J. (2021). Unifying the concepts of stability and resilience in ecology. *Journal of Ecology*, *109*, 3114–3132. https://doi.org/10.1111/1365-2745.13651

Vesper, D. J., Grand, R. V., Ward, K., & Donovan, J. J. (2009). Geochemistry of a spring-dense karst watershed in a complex structural setting, Appalachian Great Valley, West Virginia, USA. *Environmental Geology*, *58*, 667–678. https://doi.org/10.1007/s00254-008-1541-4

Vesper, D. J., & Herman, E. K. (2020). Common spring types in the Valley and Ridge province: There is more than karst. *Environmental and Engineering Geoscience*, *26*, 345–358. https://doi.org/10.2113/EEG-2321

Vesper, D. J., Moore, J. E., & Edenborn, H. M. (2019). Tufa deposition dynamics in a freshwater karstic stream influenced by warm springs. *Aquatic Geochemistry*, *25*, 109–135. https://doi.org/10.1007/s10498-019-09356-9

Ward, J. V., & Stanford, J. A. (1983). The serial discontinuity concept of lotic ecosystems. In T. D. Fontaine & S. M. Bartell (Eds.), *Dynamics of Lotic Ecosystems* (pp. 29–43). Ann Harbor Science.

Weary, D. J., & Doctor, D. H. (2014). *Karst in the United States: A digital map compilation and database. U.S. Geological Survey Open-File Report 2014–1156*. https://doi.org/10.3133/ofr20141156

White, E. L. (1977). Sustained flow in small Appalachian watersheds underlain by carbonate rocks. *Journal of Hydrology*, *32*, 71–86. https://doi.org/10.1016/0022-1694(77)90119-6

White, E. L., & Reich, B. M. (1970). Behavior of annual floods in limestone basins in Pennsylvania. *Journal of Hydrology*, *10*, 193–198. https://doi.org/10.1016/0022-1694(70)90189-7

White, W. B. (1969). Conceptual models for carbonate aquifers. *Ground Water*, *7*, 180–186. https://doi.org/10.1111/j.1745-6584.1969.tb01279.x

Winter, T. C. (2007). The role of ground water in generating streamflow in headwater areas and in maintaining base flow. *Journal of the American Water Resources Association*, *43*, 15–25. https://doi.org/10.1111/j.1752-1688.2007.00003.x

Wissler, A. D., Segura, C., & Bladon, K. D. (2022). Comparing headwater stream thermal sensitivity across two distinct regions in Northern California. *Hydrological Processes*, *36*, e14517. https://doi.org/10.1002/hyp.14517

Zhao, G., Gao, H., & Cuo, L. (2016). Effects of urbanization and climate change on peak flows over the San Antonio River basin, Texas. *Journal of Hydrometeorology*, *17*, 2371–2389. https://doi.org/10.1175/JHM-D-15-0216.1

SUPPORTING INFORMATION

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

How to cite this article: Hitt, N. P., Rogers, K. M., Kessler, K. G., Briggs, M. A., & Fair, J. H. (2023). Stabilising effects of karstic groundwater on stream fish communities. *Ecology of Freshwater Fish*, *00*, 1–14. https://doi.org/10.1111/eff.12705