

Remaining populations of an upland stream fish persist in refugia defined by habitat features at multiple scales

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Abstract

Aim: Conserving stream biota could require strategies that preserve habitats conveying resistance to ecological impacts of changing land use and climate. Retrospective analyses of species' responses to anthropogenic disturbances can inform such strategies. We developed a hierarchical framework to contrast environmental conditions underlying persistence versus extirpation of an imperilled stream fish, Candy Darter (*Etheostoma osburni*), over decades of changing land use. The decline of *E. osburni* may broadly represent the challenge of conserving sensitive freshwater species in intensively used upland environments.

Location: New River drainage, Appalachian Mountains, USA.

Methods: We surveyed fish and habitat in historically occupied sites to identify population refugia, and used multivariate and spatial analyses to address three questions: (a) what are the environmental correlates of refugia? (b) are the pathways by which land use impacts instream habitat constrained by catchment- and/or segment-scale features? and (c) are *E. osburni* distributional dynamics spatially structured and explained by fine sediment and warm stream temperatures?

Results: We confirmed a recently localized distribution similar to other upland species, marked by at least seven extirpations from streams throughout *E. osburni*'s southern range. Catchment-scale features primarily constrained land use and finer-scale habitat, leading to either extirpations or population-supporting refugia defined by features at multiple scales. Refugium habitats contained cooler temperatures and less fine sediment. Rare mismatches between persistence and habitat suitability were explained by network location, suggesting unmeasured environmental gradients and/or dispersal contributed to distributional dynamics.

Main conclusions: We provided insight at multiple spatial scales into how aquatic species' distributions become fragmented and localized. Our results demonstrate that natural landscape heterogeneity imparts spatially variable resistance of sensitive species to intensive land uses. By recognizing the scale-specific features that buffer populations from extirpation, conservation strategies could be tailored to protect naturally occurring refugium habitats and focus restoration in systems where such habitats are broadly lacking.

KEYWORDS

Candy Darter, distributional dynamics, ecological resistance, *Etheostoma osburni*, fine sediment, land use, multiple stressors, stream temperature

1 | INTRODUCTION

Understanding the factors maintaining suitable stream habitats is crucial for conserving sensitive biota, especially in intensively used landscapes (Weijters, Janse, Alkemade, & Verhoeven, 2009). Existing frameworks recognize stream habitats are hierarchically organized from catchment to microhabitat spatial scales (Frissell, Liss, Warren, & Hurley, 1986). Within this hierarchy, physical heterogeneity is created by interactions among broad- and fine-scale phenomena, giving rise to sets of filtering mechanisms collectively determining local biotic composition (Poff, 1997). Insight into dynamics at any single scale may be gained by examining the context imposed, and uniqueness provided, at broader and finer spatial scales, respectively (Poole, 2002).

The hierarchal organization of stream habitat often causes the effects of regional land use disturbance to propagate through spatial scales before impacting local habitat and biota (Burdon, McIntosh, & Harding, 2013; Isaak & Hubert, 2001; Maloney & Weller, 2011). Alternatively, sensitive biota may persist within marginal landscapes because of the insulating effects of intermediate-scale features including unique channel geomorphology, groundwater inputs, deep pools and riparian cover (Sponseller, Benfield, & Valett, 2001; Torgersen, Price, Li, & McIntosh, 1999; Walters, Leigh, Freeman, Freeman, & Pringle, 2003). Knowing which intermediate-scale habitat features propagate or offset land use signals could help managers assess the potential for intensively used landscapes to support sensitive populations.

Many imperilled stream fishes have recently fragmented, localized distributions resulting from decades of insufficient recruitment and lost population connectivity (Schlosser & Angermeier, 1995). Land use change can facilitate this process and frequently culminates in generalists or cosmopolitan species replacing resource specialists. Moreover, many specialized fishes are restricted to upland regions (Hoagstrom, Ung, & Taylor, 2014), further heightening imperilment risks (Pritt & Frimpong, 2010). For example, 38% of imperilled North American freshwater fishes are both narrowly distributed and threatened by habitat degradation (Jelks et al., 2008). Fine sediment and stream warming are two suspected primary local stressors as both generally increase with intensified land use (Poole & Berman, 2001; Scott, Helfman, McTammany, Benfield, & Bolstad, 2002), yet knowledge of the individual and combined effects of these stressors is overwhelmingly limited to sportfishes (Kemp, Sear, Collins, Naden, & Jones, 2011; Lynch et al., 2016). Insight into specific impacts of land use on upland fishes is especially germane to conservation given these impacts will be compounded by future climate (Martinuzzi et al., 2014; Staudt et al., 2013).

One approach to resisting the impacts of future land use and climate is proactively restoring ecosystems that support sensitive species (Stein et al., 2013). It may be untenable, however, to implement restorative actions at broad spatial scales encompassing entire ecosystems (e.g., reforesting entire catchments). Therefore, resistance-building strategies may instead target more manageable features that mitigate specific stressors including warming water and sediment loading (Folke et al., 2010). For example, stream temperatures can rapidly respond to shading provided by local riparian cover (Moore, Spittlehouse, & Story, 2005). Strategically deciding which local features to restore, augment, or preserve may be informed by retrospectively examining distributional changes of sensitive biota following historical disturbances, given these changes reflect underlying population dynamics. For example, a multi-decadal investigation by Harig and Fausch (2002) discovered deep pools were a key local habitat for translocated Cutthroat Trout (*Oncorhynchus clarkii*), a finding that currently guides conservation within the context of multiple regional stressors (Haak & Williams, 2012).

We developed a conceptual framework to examine distributional changes of an imperilled upland stream fish, Candy Darter (*Etheostoma osburni*, Hubbs & Trautman), over multiple decades. The region's complex topography, conducive to refugia and heterogeneous land use history, make this context ideal for investigating biotic outcomes following intensive land use disturbance. We specifically asked, (a) what are the environmental correlates of refugia? (b) are the pathways by which land use impacts instream habitat constrained by catchment- and/or segment-scale features? and (c) are *E. osburni* distributional dynamics spatially structured and explained by fine sediment and warm stream temperatures?

1.1 | Hierarchical resistance framework

Our framework organized our investigation and may serve as a useful guide for other investigations into mechanisms underpinning distributional changes of stream biota. We integrated concepts from other hierarchical frameworks depicting the creation and maintenance of stream habitat (*Hierarchical Patch Dynamics*; Poole, 2002), the matriculating impacts of land use disturbance on streams (*Land-Cover Cascades*; Burcher, Valett, & Benfield, 2007), the scales at which management actions can interrupt regional disturbances (*Multi-scale Resilience*; Folke et al., 2010), and how multi-scale factors create environmental incompatibilities with species traits (*Landscape Filters*; Poff, 1997).

We hypothesized the effects of catchment-wide land use could be either propagated or offset at catchment (broadest) and segment (intermediate) spatial scales before affecting instream habitats (finest) and populations. We depict alternative outcomes of

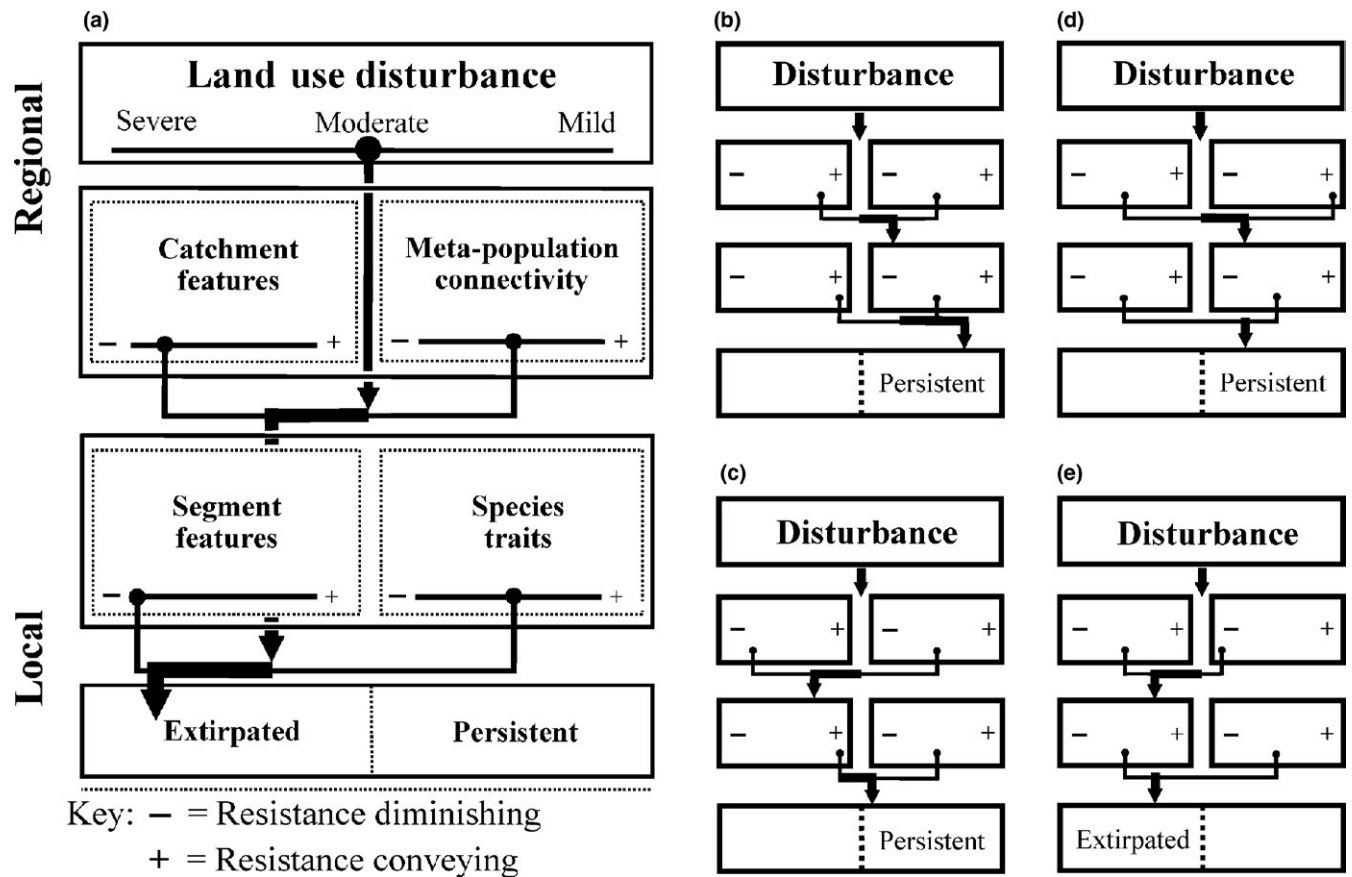


FIGURE 1 A conceptual framework depicting how physical and biotic factors (rectangles) at catchment and segment scales could interact with top-down land use disturbance signals (black arrows) to affect the persistence of a stream fish population. Minus signs (left positioning) and plus signs (right positioning) within factors indicate whether factors diminish or convey population resistance, respectively. (a) Resistance-diminishing catchment and segment environmental features propagate effects of a moderate land use disturbance leading to extirpation. (b) A population persists in a broad refugium shaped by resistance-conveying catchment and segment features. (c) Disturbance is first propagated by catchment features and then offset by segment features, allowing a population to persist in a local refugium. (d) High metapopulation connectivity maintains a population despite land use disturbance. (e) Absence of metapopulation connectivity prevents individuals from recolonizing a site

land use disturbance with a set of hypothetical impact pathways. First, instream habitat could be solely influenced by *upstream catchment pathways* (i.e., influential catchment features not apparent in segment features). Alternatively, catchment-scale features could indirectly influence instream habitat via corresponding segment features (*propagating pathways*, Figure 1a). For example, intensive segment riparian land uses are unlikely to reduce the rates at which heat and fine sediment accumulate downstream in catchments with intensive land uses (Jones et al., 2001). This impact pathway would likely diminish the resistance of a local population at multiple scales. Similarly, catchments and segments may be less amenable to, and/or have habitats that are less impacted by, intensive land uses, causing features at both scales to jointly convey resistance to populations (Figure 1b). We default to the term *resistance* when referring to persistent populations in changing landscapes but recognize persistence could also reflect *resilient* (recovered) habitat and populations following disturbance (Lake, 2000).

In contrast to propagating pathways, segment-scale features may offset signals originating at catchment scales (*offsetting*

segment pathways). These segment features may mitigate disturbance signals originating from intensive catchment land uses, thereby contributing to local refugia within mostly degraded catchments (Figure 1c). For example, particularly steep channel segments can limit siltation and preserve critical habitat for benthic biota (Walters, Leigh, & Bearden, 2003). Conversely, intensive near-stream land uses could impact instream habitat causing localized absences in catchments that are otherwise suitable (pathway not shown in Figure 1).

Biotic factors could also affect population resistance at multiple spatial scales. Within a catchment, frequent dispersal from neighbouring populations could enable a population to persist in suboptimal habitat (Figure 1d), or degraded corridor habitat could inhibit recolonization (Figure 1e; Albanese, Angermeier, & Peterson, 2009). These pathways may be particularly important given dispersal ability, corridor suitability and network topology may influence stream fish responses to changing bioclimatic conditions (Comte & Grenouillet, 2015). Finally, species with certain traits may be especially sensitive to habitat changes linked to land use disturbance, including species

with benthic, visual or coolwater dependencies, invertivory or limited mobility (Kirsch & Peterson, 2014; Scott, 2006).

2 | METHODS

2.1 | Study area

Our study occurred in the New River drainage (NRD), a northwardly draining system within the Appalachian Mountains of the eastern United States (Figure 2). Surveys were restricted to the historical range of *E. osburni* in the Appalachian Plateau (AP) and Valley and Ridge (VR) physiographic provinces. The AP is a more northern high-elevation province, typically underlain by clastic and shale geology. Located south and east of the AP, the VR comprises a mosaic of sedimentary rocks, creating steep continuous ridges separated by wide unconfined valleys (Messinger & Hughes, 2000). Mixed-deciduous forest would predominate the area, but European settlers (c. post-1750) cleared many valleys. Most remaining forests were subsequently logged (c.1880–c.1920), resulting in extensive wildfires, erosion and impacts to fish populations (Goldsborough & Clark, 1908). Current land uses include regrown forests (73%), agriculture (15%; namely, pasture) and urban development (7%).

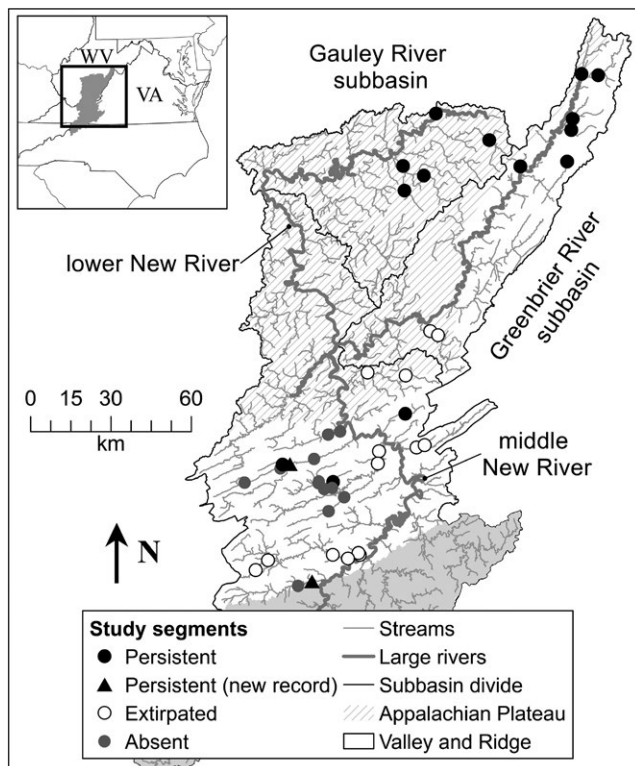


FIGURE 2 Stream segments (study sites; $n = 42$) sampled for *Etheostoma osburni* in 2012 within the New River drainage, Virginia and West Virginia, USA. Map projection: Universal Transverse Mercator, zone 17 N

2.2 | Focal species

Etheostoma osburni is a non-game fish endemic to the NRD that was recently proposed as "Endangered" under the Endangered Species Act (U.S. Federal Register 83: 58747–58754). The species is a member of a rich upland fish fauna concentrated in the temperate and subtropical regions of the south-eastern United States, a hotspot for freshwater biodiversity and imperilment (Burkhead, 2012). Sparse early surveys (1885–1964) documented *E. osburni* in several stream types, indicating its distribution before European settlement was wider than its current distribution suggests (Jenkins & Burkhead, 1994). However, recent absences of *E. osburni* from numerous streams suggest it has declined, especially in its southern range. *Etheostoma osburni* possess traits conferring low resistance to anthropogenic disturbance, including a narrow geographical range and specialized resource needs. Moreover, as a small benthic fish, it may be a poor disperser, sensitizing it to degraded corridor habitat and other constraints on colonization (Schlosser & Angermeier, 1995). Similar traits are shared by many other upland fish species (Hoagstrom et al., 2014).

2.3 | Site selection

Study sites were within 2nd–5th Strahler-order streams; most had records of *E. osburni* presence (Figure 2; Table S1 has collection dates and site abbreviations). We avoided areas inundated by Bluestone Lake reservoir and downstream sections of some tributaries to the New, Gauley and Greenbrier rivers where extirpations may have resulted from Variegate Darter (*E. varietum*), a recently introduced competitor capable of hybridizing with *E. osburni*. We also surveyed sites in seven streams without historical records in *E. osburni*'s southern range, where unknown localized populations would provide the greatest insight into refugium-forming habitats. These seven streams were within (five) or adjacent to (two) catchments with historical (pre-1970) records.

We determined *E. osburni* presence-absence within a stream segment (site), the length of stream between two consecutive tributary confluences (mean \pm SD segment length = 4.1 ± 3.7 km). We surveyed one segment in streams with recent (post-1970) records (13 streams, 13 segments). We surveyed two segments in streams with only historical records (14 streams, 27 segments) in case declining populations were more patchily distributed. The exception was STN1, an adventitious stream with a historical record, where we surveyed only one segment due to its short length. If available, we selected segments overlapping previous collection localities. We randomly selected two segments of the same order in streams without historical records. Overall, we conducted a range-wide survey based on available records of *E. osburni*.

2.4 | Fish and habitat surveys

We surveyed 42 segments during May–July, 2012. We limited surveys to riffles, where *E. osburni* spends most of its life (Dunn &

Angermeier, 2016). Within each segment, we randomly selected three geographical coordinates within 300 m of a road or trail and sampled the closest riffle to each coordinate twice to limit imperfect detection (i.e., three riffles per segment). At the base of each riffle, two crewmembers held a 1.5-m × 3-m seine with 5-mm bar mesh and a double-weighted leadline. Beginning 3 m upstream of the seine, a third crewmember electrofished (Smith-Root LR-24 backpack, pulsed direct current) downstream while disturbing the substrate (one kick-seine). We repeated kick-seines along transects perpendicular to flow until the entire riffle was sampled. The estimated probability of failing to detect *E. osburni* within an occupied segment was <1% (C. Dunn, unpublished data). Individuals were widely distributed within occupied segments (84% of riffles), indicating segments were an appropriate spatial grain to examine relationships between habitat and population persistence.

After fish sampling, we estimated the means of five habitat variables in each sampled riffle. First, five equally spaced transects perpendicular to flow were placed in each riffle. Next, we recorded wetted-channel width and identified seven equidistant points along each transect to record stream depth, water-column velocity at 60% depth (Marsh–McBirney model 2000 flow meter), intermediate-axis width of a randomly selected substrate particle, and two visually estimated descriptors of fine sediment within the 0.5-m² area surrounding each point. Embeddedness was the average percentage of coarse substrates vertically covered by fine sediment;

silt-cover was the percentage of substrate-surface area covered by silt. Percentages for both descriptors were categorized as 0 = ≤5%, 1 = 6%–25%, 2 = 26%–50%, 3 = 51%–75% and 4 = 76%–100%. Finally, all 105 habitat observations were averaged within each segment to represent segment-wide riffle characteristics.

We also recorded hourly water temperatures in each stream in spring (1 March–31 May 2012) and summer (1 June–31 August 2012) with submersible temperature loggers (Hobo Pendant or Tidbit v2, Onset Computer Corporation, Pocasset, MA). Loggers were placed in well-mixed flowing water in each segment. Appendix S1 describes details of logger deployment and procedures for predicting missing temperatures.

2.5 | Organization of data analyses

Our analyses follow the hierarchical framework presented above. We first used principal component analysis (PCA) and partial redundancy analysis (pRDA) to broadly investigate the correlates of refugia and pathways through which catchment- and segment-scale features influence instream habitat (i.e., temperatures and riffle habitat variables). Next, we used logistic regression to test whether two potential local stressors ultimately affected persistence and whether distributional patterns were spatially organized. These analyses collectively allowed us to gauge which impact pathways shaped distributional patterns (Figure 1).

TABLE 1 Groupings and data sources for environmental variables used in multivariate analyses. Appendix S2 has references for data sources

Variable	Data source
Segment-scale features	
Channel slope (m/km)	30-m ² NED; NHDPlus V2
Channel width (m)	Field measurement
Carbonate geology (% in 50-m buffer)	Nicholson et al. (2007), Dicken et al. (2008)
Clastic geology (% in 50-m buffer)	Nicholson et al. (2007), Dicken et al. (2008)
Riparian agriculture (% in 30-m buffer) ^a	2011 NLCD
Riparian developed (% in 30-m buffer) ^a	2011 NLCD
Riparian forested (% in 30-m buffer) ^a	2011 NLCD
Abiotic catchment features	
Mean catchment elevation (m)	30-m ² NED
Catchment area (km ²)	NHDPlus V2
Mean catchment hillslope (degrees)	30-m ² NED
Carbonate geology (%) (Weathering sensitive)	Nicholson et al. (2007), Dicken et al. (2008)
Clastic geology (%) (Weathering resistant)	Nicholson et al. (2007), Dicken et al. (2008)
Catchment land use ^a	
Catchment agriculture (%)	2011 NLCD
Catchment developed (%)	2011 NLCD
Catchment forested (%)	2011 NLCD

Note. NED: National Elevation Dataset; NHDPlus V2: National Hydrography Dataset Plus version 2; NLCD: National Land Cover Dataset.

^aAggregated and categorized from 16 possible land cover classes.

2.6 | Multi-scale correlates of refugia and impact pathways

We first visualized the similarity of instream habitats among segments via PCA. We standardized the means of seven instream variables within each segment: spring mean daily temperature (SPMDT), summer mean daily maximum temperature (SMDMX), depth, embeddedness, silt-cover, substrate size and velocity (Table S2). To gain insight into relationships between instream habitats and broader-scale features, we computed nonparametric correlations between the first two PCA axes (68% of variation) and three variable groups: catchment land use, abiotic catchment features and segment-scale features (Table 1). With the exception of channel width, all features were quantified remotely via a GIS (see Tables S3–S4 and Appendix S2 for details and data sources). All catchment features were calculated from the total area upslope of the lowermost point in each segment, and included percentages for 2011 primary land uses (agricultural, developed, forested) and surficial geology (carbonate, clastic), mean elevation, mean hillslope (topography) and catchment area. Segment-scale features included descriptors of channel geomorphology (mean width, slope) and percentages of riparian land use (30 m) and surficial geology (50 m) on each streamside.

Following PCA, we used pRDA to examine the pathways through which catchment- and segment-scale features govern instream habitat. Before pRDA, channel slope, elevation and catchment area were square-root-transformed to improve linearity. Partial RDA is a constrained ordination that partitioned instream-habitat variation into five components: (1–3) variation solely explained by each of the three variable groups, (4) covariation among variable groups and (5) unexplained variation (Peres-Neto, Legendre, Dray, & Borcard, 2006). We reasoned that (a) catchment land use and abiotic features that solely explained variation in instream habitat supported *upstream catchment pathways*; (b) covariation between catchment and segment features supported *indirect propagating pathways* (Figures 1–5b); and (c) variation solely explained by segment features represented *offsetting segment pathways* (e.g., Figure 1c). We suspected habitat shaped mostly by catchment features would result in extensive refugia, whereas offsetting pathways may promote local refugia coinciding with resistance-conveying segments.

Each variable group comprised a parsimonious set of predictors explaining instream-habitat variation. Eight of 15 original variables were retained after removing highly collinear variables ($r \geq |0.70|$), and those without sufficient explanatory ability during stepwise selection (p -values ≤ 0.10). We used package “vegan” (Oksanen et al., 2015) for all multivariate analyses within Program R (R Core Team, 2017).

2.7 | Effects of temperature, fine sediment and space on persistence

We hypothesized warm temperatures and fine sediment would negatively affect *E. osburni* persistence. We selected two thermal metrics representing alternative hypothesized impacts on fitness:

SPMDT represented temperatures during its spawning season, while SMDMX represented potentially heightened metabolic costs near its thermal tolerance. High collinearity between silt-cover and embeddedness ($r = 0.75$) precluded us from using both fine-sediment metrics. Therefore, we retained embeddedness because it better reflects substrate complexity needed for cover, spawning and foraging.

Variation in population connectivity among sites could also contribute to distributional change. However, population connectivity cannot be measured directly from distributional data without knowing whether intervening, unsampled segments are occupied. As a potential surrogate for population connectivity, we used distance-based eigenvector mapping (DBEM) to produce spatial eigenvectors, which represent the proximities of sites to one another along dispersal corridors within the fluvial network (Griffith & Peres-Neto, 2006). Moreover, including spatial eigenvectors in models can guard against overconfidence in apparent effects of environmental variables if environmental gradients are spatially correlated with the fluvial network (i.e., minimize type 1 error).

We followed procedures outlined by Griffith and Peres-Neto (2006) to develop spatial eigenvectors. We first measured the pairwise fluvial distances among sites; distances were converted into a connectivity matrix by defining neighbouring sites as those within a fluvial distance of 253 km. This distance directly or indirectly linked all sites, thereby maintaining an intact network necessary for DBEM. A randomization procedure with 999 replicates indicated presences and absences were spatially autocorrelated (Moran's $I = 0.21$, $p < 0.01$). Therefore, we used DBEM to convert the connectivity matrix into spatial eigenvectors and then retained the first two eigenvectors as spatial covariates in models.

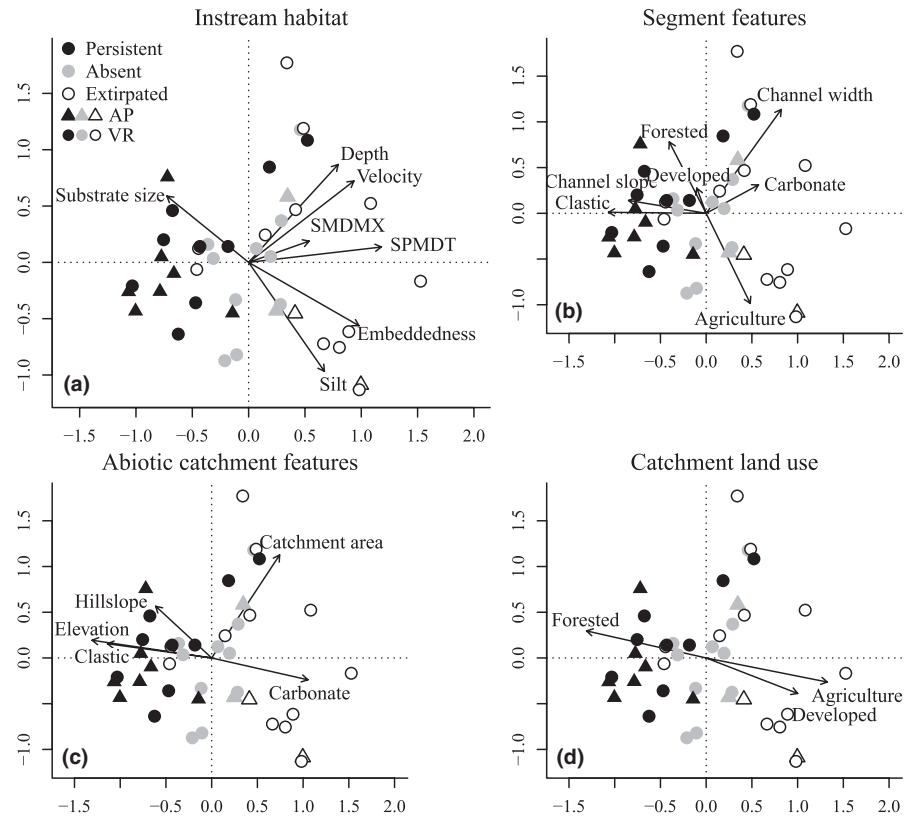
We used logistic regression and an information-theoretic approach to quantify the relative support of models explaining *E. osburni*'s distribution. Competing models were ranked by Akaike's information criterion corrected for small sample size (AICc), a metric for relative model fit penalized by model complexity (Hobbs & Hilborn, 2006). The 15 candidate models were limited to four predictors to prevent over-parameterization. Finally, to assess model performance, we also report the mean area under the receiver operating curve (AUC) of each model via sevenfold cross-validation (Manel, Williams, & Ormerod, 2001); values of 0.5 and 1.0 correspond to random and perfect predictive ability, respectively.

3 | RESULTS

3.1 | Current distribution

We detected *E. osburni* in all 11 northern-range segments but in only 5 of 31 segments in the southern range (Figure 2). We discovered *E. osburni* in two new segments: a single individual in WLF2, potentially sourced from LVA1 located only 1 km upstream, and 30 individuals in CRP1, indicating an undocumented population at the southern edge of the species' range. These occurrences collectively

FIGURE 3 Principal component analysis of instream habitats within study segments (plotted points; $n = 42$) across the range of *Etheostoma osburni* in the New River drainage, USA. Axes 1 (horizontal) and 2 (vertical) explained 43.2% and 24.8% of variation, respectively. Arrows represent non-parametric correlation coefficients between axes and environmental variables. (a) Instream habitat; (b) segment features; (c) abiotic catchment features; (d) catchment land use. AP: Appalachian Plateau; VR: Valley and Ridge; SMDMX: summer mean daily maximum stream temperature; SPMDT: spring mean daily stream temperature



revealed a fragmented distribution with refugia varying in size from subbasins to potentially single segments.

3.2 | Environmental correlates of refugia

The PCA revealed the main gradients in instream habitats among segments (Figure 3a; Table 2). Principal component 1 (PC1, horizontal axis) explained 43.3% of variation and likely represented increasing habitat degradation towards the southern range (right side of Figure 3a is most impacted). Positively loaded segments on PC1 were warmer, more embedded and contained finer substrates and faster water velocities, likely due to greater summer baseflows in many southern VR streams. Principal component 2 (vertical axis) explained 24.8% of variation and reflected greater water depths and less silt-cover.

Axes were highly correlated with features at broader spatial scales (Table 2). Positively loaded segments on PC1 (more degraded) had more agricultural (Figure 3b,d) and developed land (Figure 3d), had carbonate rather than clastic geology (Figures 3b,c), and occurred at lower elevations with more subdued topography (hillslope) (Figure 3c) and less steeply sloped stream channels (Figures 3b). High correlations between PC2 and catchment area ($r = 0.83$; Figure 3c) and channel width ($r = 0.81$; Figure 3b) indicated this axis represented stream size. Overall, *E. osburni* populations persisted in less-degraded segments (negatively loaded on PC1) concentrated in its northern range throughout the Gauley and Greenbrier river subbasins. However, three of five occupied southern-range segments were also negatively loaded on PC1, signalling *E. osburni* mainly

persisted in geographically rare refugia with features more similar to those of northern-range segments.

3.3 | Transmission of catchment disturbance to instream habitat

Partial RDA revealed the main pathways through which catchment features influenced instream habitat (Figure 4; Table 2). Catchment land use, abiotic catchment features and segment features collectively explained 54.2% of instream-habitat variation after adjusting for the number of variables in each group (63.1% of raw variation). Catchment land use primarily covaried with abiotic catchment features (independent = 5.2%, covarying = 18.7%), confirming that catchment features provided a physical template amenable to specific land uses. Although 20.7% of variation was explained solely by upstream catchments, more variation (30.2%) was explained by indirect propagating pathways, demonstrating instream habitat is jointly constrained by segment and catchment features. In contrast, segment features only independently explained 3.3% of variation (i.e., offsetting segment pathways). These findings indicate *E. osburni*'s recently localized distribution was primarily shaped by the two propagating pathways: (a) extirpations following the transmission of impacts from land use disturbance via resistance-diminishing features (Figure 1a) and (b) persistence in refugia defined by features conveying resistance to populations at multiple scales (Figure 1b). This interpretation was further supported by a t test (agricultural land use) and nonparametric MANOVAs (abiotic catchment features, segment features; Anderson, 2001), which collectively found variable groups

Variable	Present	Absent	PC1	PC2
Instream habitat				
Spring mean daily temperature (°C)	11.7 (0.3)	14.0 (0.2)	0.99	0.11
Summer mean daily maximum temperature (°C)	22.5 (0.4)	23.1 (0.3)	0.94	0.33
Mean riffle depth (cm)	13.6 (1.0)	17.1 (1.1)	0.67	0.74
Mean riffle velocity (m/s)	0.28 (0.03)	0.38 (0.02)	0.79	0.61
Mean riffle substrate size (cm)	10.0 (0.8)	7.7 (0.5)	-0.78	0.63
Mean riffle embeddedness index (0–4)	0.4 (0.1)	1.0 (0.1)	0.87	-0.50
Mean riffle silt-cover index (0–4)	0.2 (0.0)	0.5 (0.1)	0.57	-0.82
Segment-scale features				
Channel slope (m/km) ^{ab}	11.0 (1.7)	8.0 (0.7)	-0.99	0.16
Channel width (m) ^{ab}	8.0 (1.1)	10.1 (1.1)	0.59	0.81
Carbonate geology (% in 50-m buffer) ^a	4.4 (3.0)	37.2 (8.1)	0.88	0.48
Clastic geology (% in 50-m buffer) ^{ab}	52.0 (10.6)	2.7 (1.9)	-1.00	0.01
Riparian agriculture (% in 30-m buffer) ^{ab}	8.6 (4.3)	26.6 (4.4)	0.44	-0.90
Riparian developed (% in 30-m buffer)	20.4 (5.3)	13.2 (1.8)	-0.35	0.94
Riparian forested (% in 30-m buffer) ^a	71.0 (6.5)	60.2 (4.0)	-0.46	0.89
Abiotic catchment features				
Mean catchment elevation (m above sea level) ^{ab}	971.1 (21.5)	784.3 (12.7)	-0.99	0.15
Catchment area (km ²) ^{ab}	159.8 (33.3)	252.8 (45.3)	0.55	0.83
Mean catchment hillslope (degrees) ^{ab}	13.6 (0.4)	12.0 (0.7)	-0.73	0.67
Carbonate geology (%) ^a	5.5 (2.5)	25.8 (4.4)	0.98	-0.22
Clastic geology (%) ^a	55.4 (5.7)	21.7 (3.3)	-0.99	0.14
Catchment land use				
Catchment agriculture (%) ^{ab}	8.6 (2.4)	28.8 (3.7)	0.98	-0.20
Catchment developed (%) ^a	3.0 (0.3)	4.8 (0.5)	0.93	-0.36
Catchment forested (%) ^a	86.3 (2.5)	65.6 (4.0)	-0.98	0.22

^aVariables explaining significant variation in scores from PC1 and PC2 via a permutation test ($p \leq 0.10$) using package “vegan” (Oksanen et al., 2015). ^bVariables retained for partial redundancy analysis following stepwise selection using package “vegan” (Oksanen et al., 2015).

TABLE 2 Means \pm (standard errors) of environmental variables describing stream segments in the New River drainage, USA, where *Etheostoma osburni* was either present or absent. Instream-habitat variables were responses used in multivariate analyses. Values under principal components (PC) 1 and 2 are permutation-based correlation coefficients between the first two PC axes and environmental variables. Bolded values highlight the axis with the higher correlation coefficient

in pRDA differed significantly between segments where *E. osburni* was present versus absent ($p \leq 0.10$).

3.4 | Local and spatial predictors of persistence

Population persistence was inversely related to temperature and embeddedness, and sensitive to a site's location within the fluvial network (Table 3). The two top models were similarly supported and had identical model structures except for thermal metrics (SPMDT, $w_1 = 0.42$; SMDMX, $w_2 = 0.37$), which reflects uncertainty into

specific negative effects of warm temperatures on *E. osburni* fitness. Both of these models, however, were far more supported than the intercept-only model ($w_{14, null} = <0.01$) and performed well during cross-validation ($AUC \geq 0.90$; Manel et al., 2001). Given the similarity of the two best-supported models, we highlight the top model, indicating population persistence was impacted by SPMDT ($\hat{\beta} = -1.17$, 1.02, 90% confidence interval [CI90]), embeddedness ($\hat{\beta} = -4.77$, 4.12 CI90) and two spatial covariates. The maximum rate of change in predicted presence along an SPMDT gradient occurred at 13.9°C; the probability of presence decreased from 0.90 ± 0.03 CI90 at 12°C

to 0.21 ± 0.13 CI90 at 15°C (Figure 5a). Similarly, the maximum rate of change in predicted presence for embeddedness occurred at 0.97 or approximately 25% riffle embeddedness (Figure 5b).

Spatial covariates indicated population persistence was spatially structured by latent processes or features. Interpreting spatial

covariates is not straightforward because multiple non-mutually exclusive factors can contribute to spatial patterns. The first spatial covariate (hereafter "SP1"; $\hat{\beta} = -3.80$, 5.02 CI90) is geographically interpretable, with sites in northern and eastern portions of the Gauley and Greenbrier river subbasins having the highest probability of presence and sites in the southern range having the lowest. High occupancy of *E. osburni* within the Gauley (100% of sites) and Greenbrier (80% of sites) subbasins suggests populations persist in unsampled, intervening segments within these two subbasins; therefore, SP1 could reflect greater population connectivity in the northern range. Additionally or alternatively, SP1 could reflect important broad environmental gradients. The multivariate correlation between distance matrices for spatial eigenvectors and all broad environmental variables was low ($r = 0.05$), assessed via a Mantel test, but the first spatial covariate had higher correlations with some variables: mean catchment elevation ($r = -0.72$), land use ($r = 0.50$ for agriculture; $r = -0.45$ for forest), and geology ($r = -0.55$ for clastic; $r = 0.33$ for carbonate). The second spatial covariate ($\hat{\beta} = -5.65$, 5.23 CI90) did not strongly reflect any measured broad environmental gradients (most strongly correlated with elevation, $r = -0.28$).

Regardless of the factors represented by spatial covariates, their inclusion removed spatial autocorrelation (Moran's $I = -0.04$, $p = 0.82$), improved cross-validation (Table 3) and imposed a spatial context on predictions. For example, an optimal spatial location counterbalanced negative effects of warm temperatures and embeddedness on persistence (Figure 5c,d). Comparisons between predictions from spatially explicit models and those using identical median scores for spatial covariates (i.e., controlling for space) indicated LWA2, SEC1 and SEC2 were unoccupied spatially suboptimal segments containing suitable spring temperatures and low embeddedness (Figure 5a,b). In contrast, *E. osburni* persisted in two

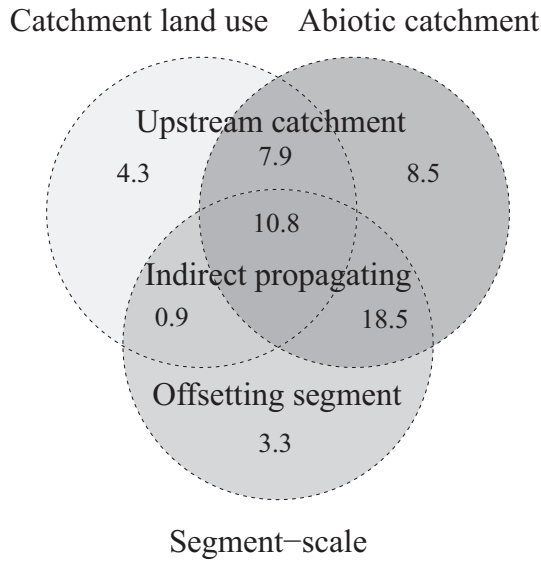


FIGURE 4 Venn diagram showing adjusted variation in instream habitats (summing to 54.2%) partitioned by catchment land use, abiotic catchment- and segment-scale features via partial redundancy analysis. Instream habitats were measured in 42 segments in the New River drainage, USA. "Upstream catchment" pathways represent influential catchment features not apparent in segments. "Indirect propagating" represents pathways where catchment land use and/or abiotic catchment features constrain segment features and instream habitat. "Offsetting segment" pathways represent variation solely explained at the segment scale

TABLE 3 Akaike's information criterion (AICc) of models with effects of stream temperature, substrate embeddedness (EMB) and/or two spatial covariates (SP) on *Etheostoma osburni* presence in 42 stream segments in the New River drainage, USA. ΔAICc is the difference between top- and lower-ranked models (i). Model weight (W_i) is the probability of a model being the best-supported model. Evidence ratio (W_1/W_i) is the number of times the top-ranked model is better supported over lower-ranked models. Area under the curve (AUC) is a threshold-independent measure of cross-validation predictive ability (0.5 AUC = random, 1.0 AUC = perfect)

Rank	Model components	LL	ΔAICc	W_i	W_1/W_i	AUC
1	SPMDT + EMB + SP1 + SP2	-7.1	0.00	0.42	1.0	0.97
2	SMDMX + EMB + SP1 + SP2	-7.2	0.24	0.37	1.1	0.96
3	EMB + SP1 + SP2	-9.7	2.55	0.12	3.6	0.91
4	SPMDT + SP1 + SP2	-10.6	4.45	0.05	9.2	0.95
5	SPMDT + SMDMX + SP1 + SP2	-10.3	6.45	0.02	25.2	0.95
6	SPMDT + EMB	-13.3	7.25	0.01	37.4	0.95
7	SPMDT + SMDMX + EMB	-12.9	8.90	<0.01	85.8	0.95
8	SPMDT + SMDMX	-14.2	9.15	<0.01	96.8	0.91
9	SPMDT	-15.4	9.24	<0.01	101.5	0.88
10	SP1 + SP2	-15.2	11.11	<0.01	258.4	0.84
11	SMDMX + SP1 + SP2	-14.2	11.53	<0.01	319.3	0.83
12	SMDMX + EMB	-19.8	20.31	<0.01	>1,000	0.83
13	EMB	-21.1	20.61	<0.01	>1,000	0.76
14	Intercept-only (null)	-27.9	32.02	<0.01	>1,000	0.50
15	SMDMX	-27.2	32.78	<0.01	>1,000	0.75

Note. LL: log likelihood; SMDMX: summer mean daily maximum temperature; SPMDT: spring mean daily temperature.

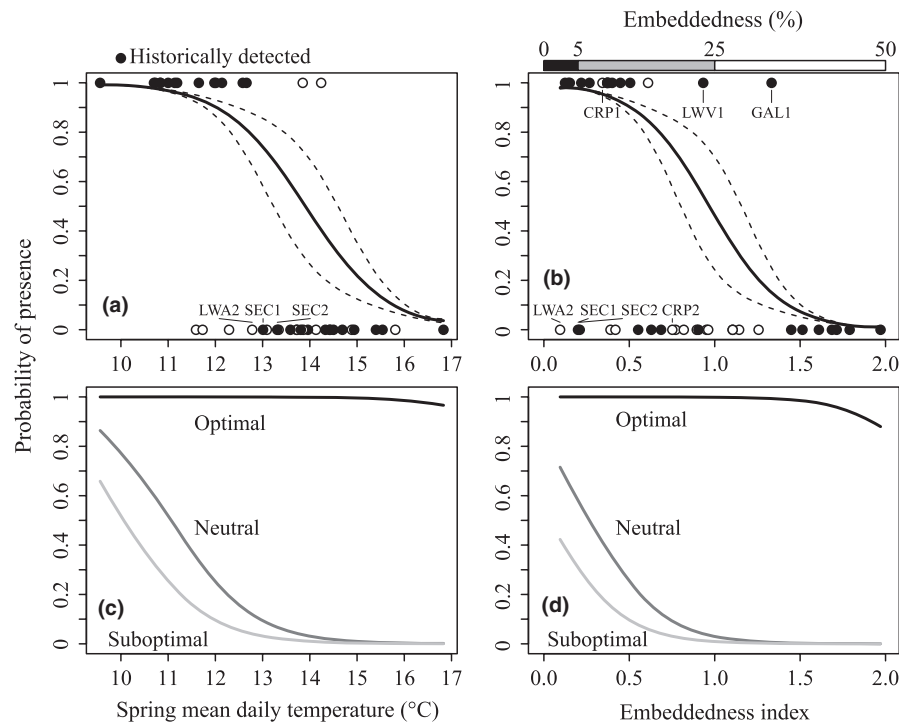


FIGURE 5 Predicted probabilities, with 90% confidence intervals, of *Etheostoma osburni* presence along (a) temperature and (b) embeddedness gradients in the New River drainage, USA. The upper horizontal axis (b) presents the range in percentage embeddedness encompassed by categories of the embeddedness index (0–2 shown). Presences and absences in segments ($n = 42$) were plotted at 1 and 0, respectively. Filled and open circles represent segments where *E. osburni* was either documented or not documented by historical surveys, respectively. Panels c–d demonstrate the influence of spatial location on probabilities across temperature (c) and embeddedness (d) gradients at the 75th (“optimal” spatial context), 50th (“neutral” spatial context) and 25th (“suboptimal” spatial context) percentiles of two spatial covariates. We added codes for sites referenced in the main text.

spatially optimal locations in the Gauley River subbasin, GAL1 and LWV1, with high embeddedness (Figure 5b, Table S5).

4 | DISCUSSION

We documented probable extirpations of *E. osburni* from at least seven streams in the species’ southern range. This fragmented, localized distributional pattern is consistent with many other sensitive stream species’ distributions, and we hypothesize these patterns result from at least three interacting phenomena: (a) spatial variation in landscape features, (b) propagation of regional land use impacts to instream habitat via indirect pathways and (c) insufficient corridor habitat to facilitate recolonization following disturbance-mediated extirpation.

4.1 | Multi-scale correlates of refugia and impact pathways

The distribution of catchment-wide abiotic features, including high elevations, rugged topography and clastic geology, seemed to govern the locations and variable sizes of refugia. These same features coincided with northern-range *E. osburni* populations and with most of the isolated populations in its southern range. High covariation

with catchment land use indicates abiotic catchment features may initially influence population persistence by mediating the extent, intensity and duration of intensive land uses through time. For example, *E. osburni* was extirpated from catchments with more intensive agriculture and, to a lesser extent, urban development, which were enabled by amenable physical features, such as lower elevations and subdued topography associated with carbonate geology (Hack, 1957). Agriculture in these catchments (28.8%) exceeded levels that have impacted other upland fishes in the region [10%–20% non-forest (Sutherland, Meyer, & Gardiner, 2002); 12% agriculture (Hudy, Thieling, Gillespie, & Smith, 2008)]. Similarly fragmented distributions of North American (Utz, Hilderbrand, & Raesly, 2010), South American (Dala-Corte et al., 2016) and European fishes (Marzin, Verdonschot, & Pont, 2013) collectively underscore the sensitivity of upland stream communities to intensive land uses.

Impacts of catchment land use disturbance appeared to transfer to instream habitat primarily via indirect propagating pathways (Figure 1a). Multi-scale habitat relationships indicated several segment features potentially contributed to impact pathways, including easily weathered carbonate geology, which enables streamside pasture in low-relief valleys and channel widening in deforested unconfined channels (Hack, 1957). Rather than being subjected to the effects of a chronic *press* disturbance from agriculture (*sensu* Lake, 2000), many currently forested catchments with

resistance-conveying features were mainly exposed to an intense, but short-term, pulse disturbance from historical logging. Resistance-conveying features such as rugged topography and weathering-resistant clastic geology typically promote steep stream channels (Hack, 1957), which can limit fine-sediment deposition (Montgomery & Buffington, 1997) and afford access to high-elevation thermal refugia (Isaak & Rieman, 2013). Together, such features contribute to extensive habitat suitability for *E. osburni*, which may have enabled populations to resist shorter-term pulse disturbances (Figure 1b).

Unfortunately, no historical habitat data are available, beyond cursory descriptions, to more definitively demonstrate these impact and resistance pathways. However, unlike entirely static interpretations of land use disturbance impacts, which can be confounded by covariation with abiotic features (Allan, 2004), our retrospective investigation revealed that even intensive land uses operating within the context of abiotic features can result in distributional change. Generalizing our results, along with those from similar snapshot investigations (e.g., Jones, Helfman, Harper, & Bolstad, 1999; Sutherland et al., 2002; Walser & Bart, 1999), would benefit from additional retrospective investigations into distributional changes of upland fishes in areas with variable land use disturbance histories.

4.2 | Instream predictors of persistence

Ours is one of the first studies to link temporal distributional changes for a non-game fish with field-measured stream temperatures. Segments not supporting *E. osburni* were on average 1.6°C warmer in spring and had 0.6°C higher summer mean daily maxima (Table 2). Warmer temperatures in many of these segments partly reflect natural conditions that once supported populations at lower elevations and latitudes. However, agriculture could have also warmed stream temperatures by increasing surface run-off and solar exposure (Poole & Berman, 2001; Trimble & Mendel, 1995). Our models could not confidently determine which thermal metric was more influential. Because virtually nothing is known about of *E. osburni*'s thermal ecology, we cannot discount any of several temperature-related hypotheses potentially explaining *E. osburni*'s decline, including summer exceedances of thermal tolerances, mis-timed spring spawning (Krabbenhoft, Platania, & Turner, 2014), diminished performance at specific life stages (Turschwell, Balcombe, Steel, Sheldon, & Peterson, 2017) and interspecific interactions (Lawrence et al., 2014). Broader knowledge of how warming temperatures impact the fitness of stream fishes would help clarify how temperature contributed to the declines of *E. osburni* and other imperilled upland fishes. This knowledge may become increasingly valuable in regions experiencing warming temperatures, including ours, where streams are warming 0.028°C annually (Rice & Jastram, 2015).

Stream biota can be exposed locally to multiple stressors symptomatic of regional disturbances (Townsend, Uhlmann, & Matthaei, 2008). Our top models were consistent with this pattern and also included a negative effect of embeddedness, which can impact biota in several ways (Kemp et al., 2011; Wood & Armitage, 1997). Like many other upland fishes, *E. osburni* possesses several biotic traits

potentially sensitizing it to fine sediment. For example, invertivory and lithophilous spawning could cause sensitivity to diminished substrate complexity across multiple life stages, or embedded substrates could reflect high levels of suspended fine sediment, which can diminish the foraging efficiencies of upland fishes (Zamor & Grossman, 2007). Overall, our observations at finer scales provided rare insight into distributional fragmentation and suggest the localized distributions of other upland stream species could reflect multiple local stressors.

4.3 | Potential factors spatially structuring populations

Inclusion of spatial covariates in our models partly explained rare mismatches between instream-habitat suitability and population persistence. For example, *E. osburni* persisted in two spatially optimal northern locations (GAL1, LWV1) in the Gauley River subbasin despite high embeddedness. Persistence in these segments could reflect an extinction debt (sensu Jackson & Sax, 2010), latent influences of environmental gradients (Peres-Neto & Legendre, 2010) and/or metapopulation connectivity (Figure 1d; Dunham & Rieman, 1999). Although we cannot discount the two former factors, genetic analysis indicates recent dispersal among respective *E. osburni* subpopulations within the Gauley and Greenbrier river subbasins (Gibson, 2017). This corroborates estimated effects of spatial covariates and suggests varying dispersal rates across the species' range contributed to population persistence.

Spatial covariates also explained multiple absences in southern-range segments with suitable habitat but spatially suboptimal locations. This pattern may have also resulted from latent environmental gradients, an inability to recolonize sites (Albanese et al., 2009; Figure 1e) or both. For example, southern-range segments in large corridor streams (catchments $\geq 100 \text{ km}^2$) were warmer ($\bar{x}_{\text{SPMDT}} = 14.3^\circ\text{C} \pm 0.2 \text{ SE}$, $n = 18$) and more embedded ($\bar{x}_{\text{emb.index}} = 0.9 \pm 0.1 \text{ SE}$) than those in the northern range ($\bar{x}_{\text{SPMDT}} = 11.8^\circ\text{C} \pm 0.4 \text{ SE}$; $\bar{x}_{\text{emb.index}} = 0.4 \pm 0.1 \text{ SE}$, $n = 10$). Diminished corridor habitat could further isolate remaining southern populations, thereby potentially limiting recolonization. If distributional patterns arose from spatially variable population connectivity, translocation may be a necessary resistance-building strategy to mitigate diminished dispersal (Olden, Kennard, Lawler, & Poff, 2011).

4.4 | Introduced species as potential stressors

The replacement of specialized endemics by more generalized, and often introduced, species frequently contributes to biotic homogenization (Scott, 2006; Walters, Leigh, & Bearden, 2003). We could not fully investigate potential contributions of introduced species to *E. osburni*'s decline because we avoided the *E. osburni*-*E. varium* hybrid zone, where these impacts might be strongest. During *post hoc* evaluation, the best-supported models with terms for other introduced darter richness detected by our sampling (maximum = three species; $\hat{\beta}_{\text{richness}} = -1.35$, 1.78 CI90; $\Delta\text{AICc} = 3.06$)

and introduced darter density (maximum = 58 fish/100 m²; $\hat{\beta}_{\text{density}} = -0.06$, 0.18 CI90; $\Delta\text{AICc} = 4.79$) were not supported. However, these models do not reflect potential effects from >50 other introduced fishes within the NRD. For example, introduced species have interrupted the dispersal of other stream-dependent fishes in larger mainstem corridors (Kovach et al., 2017; Labbe & Fausch, 2000). Moreover, the regional prevalence of degraded areas could mediate propagule pressure of more generalized competitors and predators on upland refugia (Lapointe, Thorson, & Angermeier, 2012), thereby leading to deleterious interactions at local scales (Merriam & Petty, 2016). Intensive catchment-wide land uses often improve habitat suitability for thermally and fine-sediment-tolerant species (Scott, 2006). Indeed, retrospective analyses by Hitt and Roberts (2012) and Buckwalter, Frimpong, Angermeier, and Barney (2018) in the NRD documented replacements of specialized upland natives with more generalized fishes; both studies implicated land use in these dynamics. Future research could extend our approach to examine whether multi-scale physical features and community dynamics jointly exacerbate or reduce effects of catchment-wide, top-down disturbances.

4.5 | Unique segment-scale contributions to local refugia

Although finer-scale features were primarily constrained by catchment features, 3.3% of adjusted instream-habitat variation was solely explained at segment scales, suggesting segment features can independently contribute to local refugia. This may help explain the unexpected persistence of *E. osburni* within Cripple Creek (CRP) given the stream's agricultural (34%) catchment. Moreover, *E. osburni* was restricted to the lowermost segment (CRP1), suggesting persistence coincided with unique segment-scale features (Sedell, Reeves, Hauer, Stanford, & Hawkins, 1990; Figure 1c). Temperatures in unoccupied (CRP2) versus occupied segments were comparable and notably warm (SPMDT > 14°C), but riffles in CRP1 had far less fine sediment (0.3 embeddedness index in CRP1 vs. 0.8 in CRP2, Figure 5b). More riparian forest cover could potentially be a source of segment-scale resistance in CRP1 (80% forested in CRP1 vs. 50.5% in CRP2), which may have helped maintain suitable habitat by limiting insolation and filtering fine sediment from run-off (Jones et al., 1999; Sponseller et al., 2001).

Discovering the population in CRP1 also demonstrated the conservation benefits of examining distributional changes at multiple spatial scales. Segment-scale features may decouple normally correlated local stressors, offering rare insights into the effect of each stressor. For example, CRP1 demonstrated *E. osburni* can persist in warm streams if embeddedness is low, thereby suggesting a compensatory mechanism. Moreover, CRP is apparently the only agricultural catchment (>12%) where *E. osburni* persists (exempting WLF). Consequently, CRP1 presents a unique opportunity to examine fitness consequences of local stressors in situ, especially if compared to conditions in non-occupied CRP segments and in less agricultural catchments. In turn, this knowledge may help identify segments

capable of supporting populations and provide realistic reference criteria for habitat restoration in intensively used landscapes. Finally, persistence of *E. osburni* in CRP1 underscored the need to better document existing distributions of sensitive biota, which may reveal unknown dimensions of habitat suitability not easily measured via landscape-scale analyses.

5 | CONCLUSION

Land use is an important factor influencing the distributions of stream biota (Allan, 2004). However, investigations into distributional dynamics often overlook the indirect pathways through which land use disturbance either impacts or, just as importantly, fails to impact populations. Here, certain catchment and nested segment features were subjected to prolonged intensive land uses that likely compromised two local habitat variables important for *E. osburni* persistence: cool stream temperatures and unembedded substrates. Cool stream temperatures will become increasingly rare as air temperatures rise (McDonnell et al., 2015), further threatening *E. osburni* and upland stream biota worldwide. However, our results indicate limiting effects of more manageable stressors (e.g., sediment loading) and potentially maintaining population connectivity may be viable strategies for resisting impacts of warming streams.

Conservation practitioners may benefit from our organizational framework in other cases where species distributions have become fragmented and localized. Retrospective analyses of distributional dynamics can reveal the primary scales through which features convey biotic resistance, and the variability of these relationships across a species' range. In turn, this knowledge could inform conservation strategies. For example, strategies may emphasize preserving population connectivity throughout broad refugia spanning multiple catchments, or opt to further insulate a single catchment refugium from introduced species. Alternatively, attempting to counterbalance impacts of regional disturbances with local resistance-building features may be the most appropriate strategy in catchments amenable to prolonged intensive land uses. Ultimately, the localization of species' distributions is a complex long-term process. By extension, conserving stream biota is equally complex but may be aided by clearer insights into the pathways through which anthropogenic disturbances impact stream habitats.

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DATA ACCESSIBILITY

All data are provided in Tables S2–S4.

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BIOSKETCH

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Author contributions: Both authors designed this study. C.G.D collected and analysed data, and led writing. P.L.A. co-wrote and edited the manuscript.

SUPPORTING INFORMATION

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

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