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## ARTICLE

# Isolation controls reestablishment mechanisms and post-drying community structure in an intermittent stream

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**Abstract**

Biota in disturbance-prone landscapes have evolved a variety of strategies to persist long term, either locally (*resistance*) or by regional recolonization (*resilience*). Habitat fragmentation and isolation can limit the availability of recolonization pathways, and thus the dynamics of post-disturbance community reestablishment. However, empirical studies on how isolation may control the mechanisms that enable community recovery remain scarce. Here, we studied a pristine intermittent stream (Chalone Creek, Pinnacles National Park, California) to understand how isolation (distance from a perennial pool) alters invertebrate community recolonization after drying. We monitored benthic invertebrate reestablishment during the rewetting phase along a ~2-km gradient of isolation, using mesh traps that selected for specific recolonization pathways (i.e., drift, flying, swimming/crawling, and vertical migration from the hyporheic). We collected daily emigration samples, surveyed the reestablished benthic community after 6 weeks, and compared assemblages across trap types and sites. We found that isolation mediated migration dynamics by delaying peak vertical migration from the hyporheic by ca. 1 day on average per 250 m of dry streambed. The relative importance of reestablishment mechanisms varied longitudinally—with more resistance strategists (up to 99.3% of encountered individuals) in the upstream reaches, and increased drift and aerial dispersers in the more fragmented habitats (up to 17.2% and 18%, respectively). Resistance strategists persisting in the hyporheic dominated overall (88.2% of individuals, ranging 52.9%–99.3% across sites), but notably most of these organisms subsequently outmigrated downstream (85.6% on average, ranging 52.1%–96% across sites). Thus, contrary to conventional wisdom, resistance strategists largely contributed to downstream resilience as well as to local community recovery. Finally, increased isolation was associated with a general decrease in benthic invertebrate diversity, and up to

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a 3-fold increase in the relative abundance of drought-resistant stoneflies. Our results advance the notion that understanding spatial context is key to predicting post-disturbance community dynamics. Considering the interaction between disturbance and fragmentation may help inform conservation in ecosystems that are subject to novel environmental regimes.

#### KEYWORDS

dispersal, disturbance, dormancy, invertebrates, resilience, resistance, stress

## INTRODUCTION

Organisms in disturbance-prone environments have developed a wide range of life history, behavioral, and morphological adaptations that can facilitate population persistence over time (e.g., Allison & Martiny, 2008; Lytle & Poff, 2004; Meyer, 2016). These strategies fall along axes that facilitate resistance (i.e., the ability to persist through a disturbance) and resilience (i.e., the ability to recolonize following a disturbance) (e.g., Lake, 2013). While these traits may sustain populations in well-connected ecosystems, habitat fragmentation could eliminate recolonization pathways and hinder ecological rescue (Fahrig, 2003; McRae et al., 2012), or decrease resistance success by lengthening or intensifying stressful conditions (Oliver et al., 2015). Habitat isolation caused by natural or anthropogenically induced decreases in habitat connectivity may alter the relative importance of different reestablishment strategies (e.g., Perkin et al., 2015; Warneke et al., 2021). However, empirical evidence documenting the effects of isolation on post-disturbance community recovery remains scarce (Fahrig et al., 2019; Fletcher Jr et al., 2018).

Habitat connectivity and organismal dispersal are key determinants of community stability in heterogeneous landscapes (Patrick et al., 2021; Wang et al., 2019). While habitat fragmentation tends to disrupt population dynamics in a multitude of ecosystems globally (Haddad et al., 2015), effects are often variable and context dependent (see arguments in Fahrig et al., 2019; Fletcher Jr et al., 2018). For instance, theoretical work has indicated that extinction risk of populations may depend on the relative degree of disturbance (habitat destruction) and fragmentation; however, these risks may be ameliorated if dispersal strength of organisms and refuge availability remain high (Liao et al. 2015). In forested systems, the interactive effects of habitat destruction and fragmentation on seed dispersal are generally detrimental to populations, but responses are often species-specific (Kirika et al., 2008). Conversely, habitat fragmentation may facilitate spatially asynchronous responses to disturbance in marine and other “open” systems, lowering

metapopulation-wide extinction risk (König et al., 2019; Yeager et al., 2020). The spatial extent and predictability of a given disturbance may also impact the relative fitness of resilience and resistance traits (e.g., dispersing in space vs. “time”) (Buoro & Carlson, 2014; Sarremejane et al., 2020), thus influencing the speed and trajectory of community recovery.

Studying community recovery is particularly important for systems that undergo frequent stress or disturbance—such as intermittent streams characterized by periodic flow cessation, drying, and rewetting cycles (Datry et al., 2017). During drying, habitats within a stream network often become disconnected as waters recede. As such, migratory dynamics that rely on the presence of wetted pathways can be disrupted (Brooks et al., 2020). Additionally, habitat contraction and eventual fragmentation during flow cessation increases stress in multiple ways—for example, by raising water temperature, reducing dissolved oxygen level and water quality, and increasing organismal density and associated biotic interactions (Woelfle-Erskine et al., 2017). Individual populations might experience varying levels of mortality associated with drying (Sarremejane et al., 2021), but impacts at the watershed level can be buffered by an influx of propagules from source populations once waters return (Gauthier et al., 2021). In this vein, the position of perennial refuges within the stream network may influence reestablishment dynamics (Magoulick & Kobza, 2003), and sites located immediately downstream of refuges could recover faster than those separated by long stretches of dry streambed. Because intermittent streams are periodically disturbed and habitats experience varying degrees of isolation as distance from perennial waters increases, they might serve as a model system to explore how the interaction of disturbance and fragmentation alters community reestablishment.

Benthic macroinvertebrates use four primary reestablishment pathways in streams: aerial colonization via flight, downstream migration via drift, upstream locomotion, and vertical migration from subsurface interstitial spaces (Merritt & Cummins, 1996). In their classic experiment, Williams and Hynes (1976) sought to

quantify the relative contribution of these four pathways by placing traps that selectively sampled each recolonization mechanism. Their results indicated that downstream drift acted as the primary driver of macroinvertebrate population reestablishment. However, their study system was a perennial, forested stream where periodic disturbance was not a defining feature of the hydrologic regime. Subsequent work highlighted the complexity of reestablishment dynamics in streams, with colonization patterns varying among species (Cañedo-Argüelles et al., 2015; Lancaster & Downes, 2017a), body size (Principe & Del Corigliano, 2006), and habitat use (Carvalho & Uieda, 2006; Lancaster & Downes, 2017b). Additionally, dispersal success often relies on both the presence of wetted migratory pathways and the hydrologic conditions of the receiving systems (Brooks et al., 2020). Finally, hyporheic refuges can facilitate the local persistence of individuals or even entire populations when surface waters dry; however, empirical evidence suggests that the importance of the hyporheic zone as a refuge may vary longitudinally along a stream network (Dole-Olivier, 2011; Stubbington, 2012). Understanding how habitat isolation may alter the relative importance of each reestablishment mechanism (or combinations thereof) would help predict how stream communities will fare under more variable, warmer hydroclimates—which are poised to increase both local drying stress and regional fragmentation levels (Jaeger et al., 2014).

Here, we sought to examine how the relative importance of different recolonization mechanisms following a seasonal drying event are mediated by habitat isolation (i.e., downstream distance from the closest perennial waters and a putative source of propagules). To this end, we designed a field experiment where we placed traps that allow a specific recolonization pathway (i.e., vertical migration from the hyporheic, upstream or downstream dispersal, and aerial migration), representing both resilience (dispersal pathways) and resistance (use of hyporheic refuges) strategies. We replicated these sets of traps along a longitudinal gradient of habitat isolation (distance from a perennial pool) during the rewetting period of a pristine intermittent stream. We hypothesized that drying disturbance and habitat fragmentation interact and alter the relative importance of resistance and resilience recolonization strategies (e.g., Oliver et al., 2015) (see Figure 1a for hypothesized relationships).

In particular, we predicted that: (1) Different recolonization mechanisms would contribute to benthic community reestablishment at each site, with vertical migration from the hyporheic (resistance strategists) increasing in relative importance as isolation increases, and resilience strategists either remaining constant (aerial, crawlers/swimmers) or decreasing (drifters)—

contrasting with perennial systems as distance from the perennial source of propagule increases and dispersal becomes more difficult (Figure 1a); (2) These differential patterns in dominant recolonization mechanism and immigration/emigration rates would be associated with dissimilarity in community composition across the reach; (3) The rewetting front would promote vertical migration of invertebrates from hyporheic habitats, and these patterns would propagate spatially and temporally (sensu Dole-Olivier, 2011); and finally, (4) Each site would act as both an importer and exporter of individuals, but the relative rates of immigration and emigration would vary longitudinally along the stream, with emigration rates increasing downstream as more organisms may use resistance strategies and eventually leave the local habitat. By examining how habitat connectivity may alter the relative contribution of different mechanisms that allow communities to bounce back after disturbance, we aim to identify patterns that might be generalizable across systems and scales of disturbance.

## METHODS

### Study site

Our experiment was conducted in the West Fork of Chalone Creek at Pinnacles National Park, California, United States (Figure 1). The Amah Mutsun and Chalone peoples were inhabitants and stewards of the land now occupied by Pinnacles until they were supplanted by European missionaries and settlers. Modern descendants of these tribes still work to maintain the eco-cultural heritage of their ancestors on these lands. The park is characterized by a semi-arid Mediterranean climate with an average precipitation of 420 mm that predominantly falls from December to March. Pinnacles National Park sits on the Pinnacles fault, and breccia formations dominate the landscape. Tectonic activity at the park has given rise to numerous talus caves and underground springs that remain wetted year-round. Surface flow intermittency is common at Pinnacles, and streams tend to flow only between December and April. Only ~1% of the total stream network length remains wetted during a typical dry season (T. Apgar and A. Ruhi, unpublished data; Bogan & Carlson, 2018). The West Fork of Chalone Creek runs for 2471 m from Balconies Cave (36.5002° N, 121.2011° W) to the confluence with the main stem of Chalone Creek (36.5016° N, 121.1808° W) with a gradient of 30.35 m/km. Balconies Cave is perennially wetted, and opportunistic sampling and observations suggest it might act as a source of recolonization propagules within the

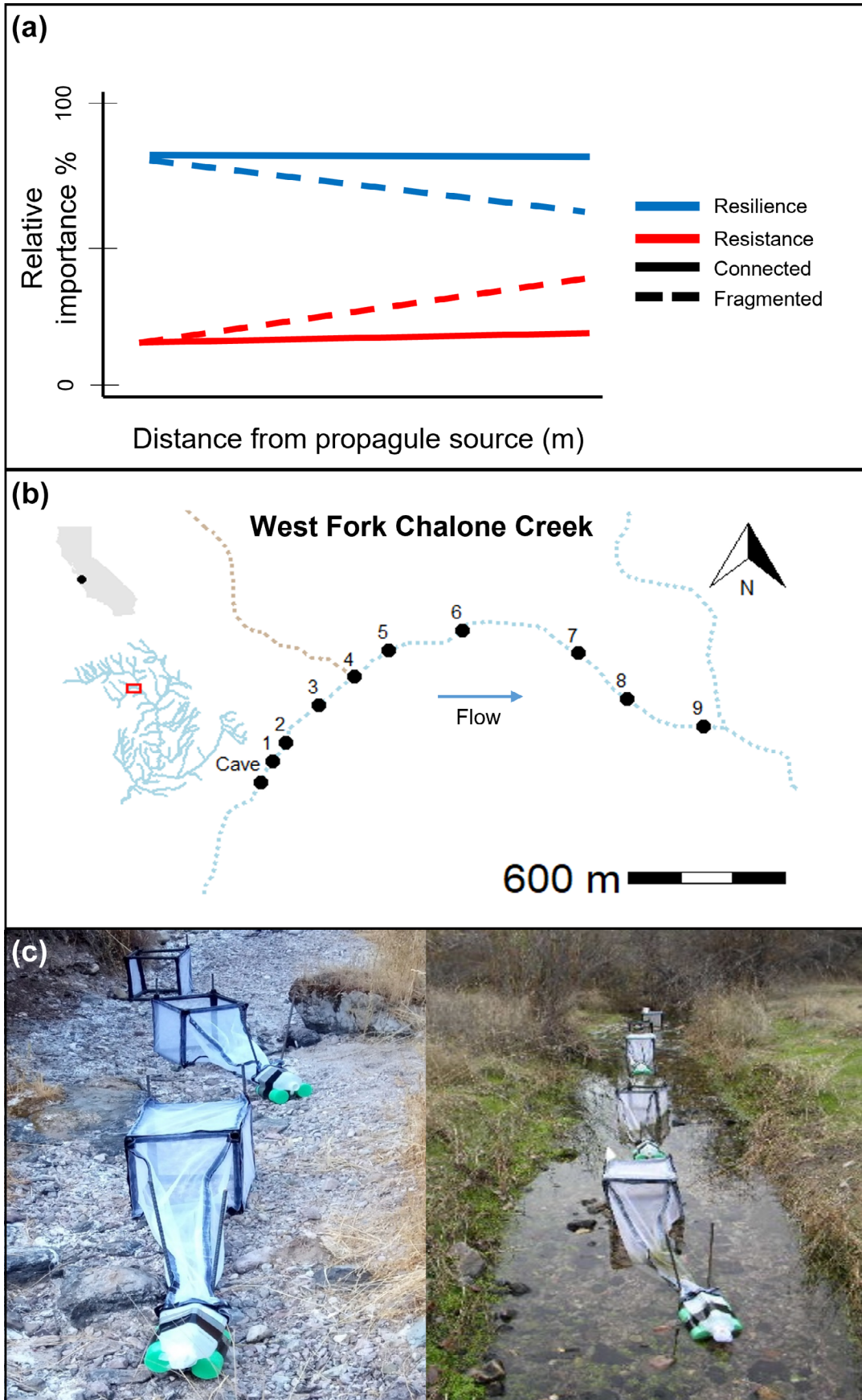


FIGURE 1 Legend on next page.



system. Our sample reach was 2231 m in length and started approximately 100 m downstream from the cave (Figure 1, Appendix S1: Table S1). This stretch of the West Fork dries annually. Macroinvertebrate communities have been continually monitored at Chalone Creek since 2015, and patterns of both larval and adult stonefly (Plecoptera) diversity have been documented—with 16 species present at the park (Bogan & Carlson, 2018). Additionally, some stream reaches within Pinnacles maintain high water tables even while dry—facilitating hyporheic migration and allowing taxa more traditionally associated with perennial systems to persist (Merritt & Cummins, 1996). Groundwater monitoring in downstream sections of Chalone Creek developed by the U.S. Geological Survey recently revealed that the water table is relatively shallow (0–10 m), and strongly variable across seasons (Scheiderich et al., 2022).

## Experimental design

To examine the contribution of reestablishment mechanisms following a seasonal drought, we designed, built, and deployed a series of traps on the dry streambed that selectively favor a given re-colonization pathway. Each trap was a  $33 \times 33 \times 33$  cm cube constructed with 0.5 in diameter PVC pipe and 500  $\mu$ m polyester mesh netting. The traps were anchored to the substrate with rebar stakes. All traps were open on the bottom to allow for benthic recolonization of the natural substrates found on the streambed. In addition, the aerial trap (trap A) was open facing up (to allow recolonization via flying); the crawling trap (trap C) was open facing downstream (to allow recolonization via swimming and/or crawling); and the drift trap (type D) was open facing upstream (to allow recolonization via drift). Finally, the hyporheic trap (type H) was only open on the bottom—this trap examined the unique contribution of vertical migration from the hyporheic. Additionally, we included a control trap (trap E) that was open on the top, upstream, and downstream sides, but not on the lateral sides (Appendix S1: Figure S1). Traps that were closed on the downstream side (i.e., the aerial, hyporheic, and drift traps) were fitted with a 1.2 m conical mesh tail that fed

into a 0.5-gallon plastic container with a 3 cm diameter opening. The container was attached to a 16 cm floatation device that kept the opening above water and limit upstream colonization. The tail apparatus prevented debris from clogging the trap and allowed organisms to leave the trap in the direction of flow (similarly to the other two trap types) (Figure 1, Appendix S1: Figure S1). We documented rates of outmigration by collecting organisms leaving the hyporheic trap through this opening (see next section and Appendix S1: Figure S1).

The traps were deployed at nine sites along the 2230-meter-long stream reach. Sites were labeled 1 through 9, with site 1 being located  $\sim$ 100 m downstream of the perennially wetted Balconies Cave, and site 9 about 2.3 km downstream (Figure 1). Sites were not equidistant (mean distance = 279 m, SD = 119 m); instead, they were placed at slightly increasing distances to maximize resolution near the propagule source. Final locations were refined based on similarities between substrate size, canopy cover, and slope (Appendix S1: Table S2). As stream width was relatively narrow, traps were placed in a line within the stream channel 2 m apart from each other. However, the traps were staggered within the channel to not obstruct flow into the next trap downstream. Trap order was random at each site, except for the hyporheic trap which was always placed in the most downstream position to facilitate collection of organisms migrating out of each reach. There were no effects of trap order on resultant community assemblages (ANOVA for trap placement  $p = 0.542$ ).

Traps were deployed between 20 November 2019 and 23 November 2019, after a long dry period (163 days) and prior to flow resumption. Rewetting of West Fork Chalone Creek was progressive, controlled by small rain episodes that lifted the groundwater table. Shallow surface water (but minimal surface flow) returned at the most upstream habitat (site 1) on November 27. On December 1st, after a rain event, surface water levels increased at site 1 and a rewetting front formed and arrived at site 6. By the next day (December 2) at 1:17 PM, the rewetting front arrived at the end of the study reach, and all sites (1–9) were inundated and flowing (see video downloadable via Zenodo; Fournier et al., 2022c). After full rewetting, there was one

**FIGURE 1** (a) Conceptual diagram showing the hypothesized relative importance of resilience (recolonization) and resistance strategies to benthic community reestablishment in a non-fragmented (solid) and fragmented (dashed) model system. We expect fragmentation to increase the relative contribution of resistance strategists while decreasing the contribution of resilience to reestablishment because dispersal-related mechanisms (e.g., drift, flight) may be constrained by fragmentation (here depicted as distance from the nearest propagule source). (b) Experimental sites (1–9) on the West fork of Chalone Creek (Pinnacles National Park, California), and their relative positions in the Chalone Creek watershed and the state of California. (c) Photos of the deployed sets of traps at one of our experimental sites prior to flow resumption, on 23 November (Site 8), and after flow resumption, on 21 December (Site 9).

non-scouring discharge event on December 4th (Appendix S1: Figures S2, S3), which caused a significant amount of debris to collect around the traps. Debris was cleaned, and all traps were fully operational within <1 week. As this event occurred relatively early into our experiment, we believe that the impact of the debris ultimately did not affect final community composition. No additional incidences occurred after this event. All traps were sampled and removed ~6 weeks after full rewetting, on January 13 to 15 (see next section). We also measured mean water velocity and depth in the microhabitats where traps had been placed to track synchrony in streamflow fluctuations across sites (Appendix S1: Figures S2, S3).

### Invertebrate sample collection and processing

Invertebrates were sampled two-fold: (i) a single, final sample from the developed benthic community after the 6-week long trap deployment; and (ii) from the net that collected outmigrant flux from the hyporheic daily for five weeks until the end of the deployment period. Specifically, (i) on January 13–15, around six weeks after rewetting (seven after deployment), we sampled the benthic invertebrate community by removing the mesh on the downstream side and placing a 500  $\mu\text{m}$  mesh size surber sampler immediately downstream of the trap. The substrate within the 33  $\times$  33 cm trap area was disturbed thoroughly by hand allowing dislodged materials to be collected in the surber sampler. All samples were stored in 98% ethanol for processing. Additionally, (ii) we sampled the flux of organisms outmigrating from hyporheic traps daily at all sites, via a 500  $\mu\text{m}$  mesh size net secured with a rubber band over the opening in the tail section of hyporheic traps. Each day, the net was collected, placed into a bottle of 98% ethanol, and replaced with a new piece of net. Samples were processed over the last 4 weeks of the deployment for the period when all traps were inundated and collecting (12 December 2019 to 13 January 2020; 32 days total).

All samples were cleaned and processed by removing and counting all invertebrates. For benthic samples, up to 100 Plecoptera individuals (the most common taxa by far) per trap sample were randomly selected by swirling the specimens in a gridded petri dish and removing all individuals within sequential cells. These individuals were identified to genus level and measured from their head to the terminal tip of their abdomen. All remaining invertebrates were identified to order level. For outmigrant samples,

organisms were picked from the net, identified to order level, and counted.

### Data analysis

To test whether the contributions of reestablishment pathways changed across the longitudinal section, we used analysis of covariance (ANCOVA) with trap type as a predictor and longitudinal distance from the perennial water source as a covariate. Prior to analysis, data were examined for assumptions of normality, homogeneity of variances, and linearity. We excluded the control trap from these analyses, as organisms encountered in these traps did not represent a specific migratory pathway.

To test if flow intermittency would create longitudinal patterns in community structure, we first visualized community dissimilarity via a non-metric multidimensional scaling (NMDS). To this end, we used the Hellinger transformation and Bray–Curtis dissimilarity index on the abundance by site matrix. We then ran a permutational multivariate analysis of variance (PERMANOVA) and centroid goodness of fit tests to determine if assemblages in close proximity to the potential source of propagules might differ from those at increasing distances. For NMDS and PERMANOVA we used the R “vegan” package (Oksanen et al., 2007) in R version 4.0.5 (R Core Team, 2021).

To explore how rates of outmigration changed over time and across sites, we fitted multivariate autoregressive state-space (MARSS) models using the R “MARSS” package (Holmes et al., 2014). MARSS models are a useful expansion of MAR time-series models, and incorporate observation error—an advantage as ignoring observation error can alter inferences (Knappe & de Valpine, 2012). In this case, we used them to assess the magnitude of fluctuations in outmigrant flux at each site and examine spatial structure across sites. MARSS model structure in the matrix form is as follows:

$$X_t = BX_{t-1} + U + W_t, \text{ where } W_t \sim MVN(0, Q) \quad (1)$$

$$Y_t = ZX_t + V_t, \text{ where } V_t \sim MVN(0, R), \quad (2)$$

where Equation (1) is the state process and Equation (2) is the observation process. Data enter the model in Equation (2), where  $Y_t$  is our abundance data (one time series per site).  $X_t$  are the true (“hidden”) states of outmigrant flux at each site, and  $Z$  is an identity matrix that connects observations to states. In turn, in state process (Equation 1)  $B$  is an interaction matrix that captures both density-dependent effects at a given site and

potential interactions across sites (further described below), and  $U$  captures long-term trends in outmigrant flux. Finally,  $W_t$  and  $V_t$  are error terms for the state and observation model respectively.  $W_t$  was drawn from a multivariate normal distribution of mean 0 and variance/covariance  $Q$  (see next paragraph for  $Q$  structures). Similarly,  $V_t$  was drawn from a multivariate normal distribution of mean 0 the variance/covariance matrix  $R$ , assumed to be consistent and uncorrelated across sites (“diagonal and equal”).

We constructed candidate models representing different hypotheses around  $U$  (overall trends in outmigrant flux across the 6 weeks),  $B$  (directional interactions between outmigrant flux across sites), and  $Q$  (stochastic variation in outmigrant flux). Specifically, our models specified three permutations of  $U$ : (1)  $U$  estimated as a single value for all sites, (2)  $U$  values allowed to differ across sites, and (3)  $U$  set as zero (i.e., no deterministic trends). In models that did not estimate  $U$ , we specified 5 options for the  $B$  matrix: (1) a  $B$  matrix where site interactions were all allowed and consistent across sites and pairs of sites (i.e., shared diagonal and off-diagonal value), (2) outmigration at one site influenced its immediate downstream neighbor, (3) outmigration at one site influenced up to two sites downstream, (4) outmigration at one site influenced up to three sites downstream, and (5) a blocked matrix where sites 1, 2, and 3 interacted among themselves, sites 4, 5, and 6 interacted among themselves, and sites 7, 8, and 9 also interacted among themselves (but no interactions were allowed between site clusters). All  $B$  matrices allowed for density-dependence, or stability of flux around its mean value, captured in the diagonal parameters. In turn, for the  $Q$  matrix we tested models where: (1) process error variances (diagonal values) were shared between sites, and covariances among sites (off-diagonal values) were set to zero; (2) variances were independent among sites and covariances were set to zero; (3) variances and covariances were shared across sites; (4) a blocked matrix similar to that described above (for  $B$ ), in which sites were grouped in three clusters and shared variances and covariances within each cluster (but not among them); and finally (5) an unconstrained matrix in which all parameters were estimated independently. This nested strategy delivered a total of 35 models that were assessed for convergence and ranked according to their Akaike Information Criterion corrected for small sample sizes ( $AIC_c$ ). Prior to analyses, data were natural  $\log(x + 1)$  transformed. Models were fitted using maximum likelihood estimation and a Kalman expectation–maximization algorithm. Model coefficients were evaluated based on bootstrapped 95% confidence intervals (CIs). We evaluated model diagnostics by

examining normality and autocorrelation (ACF) in model residuals.

To explore migration dynamics, we calculated and compared cumulative emigration and immigration at each site. We quantified emigration as the sum of all individuals encountered in every daily outmigrant sample at each site. Immigration was calculated at each site by first subtracting the number of individuals encountered in the hyporheic trap (H) at that site (as all trap types were open on the bottom) from each of the remaining traps, and then summing the hyporheic-adjusted values for aerial (A), crawling/swimming (C), and drift (D), with the hyporheic values (H), following the equation:

$$\text{Immigration per site} = (A - H) + (C - H) + (D - H) + H, \quad (3)$$

where each letter represents the cumulative abundance of organisms in the relevant trap. We then used Theil-Sen median-based regressions (R package “mblm” Komsta & Komsta, 2013) to examine if emigration and immigration rates changed monotonically with increasing distance from the water source (Balconies Cave). Theil-Sen approaches are less sensitive to outliers and more robust than simple linear regression (Fernandes & Leblanc, 2005).

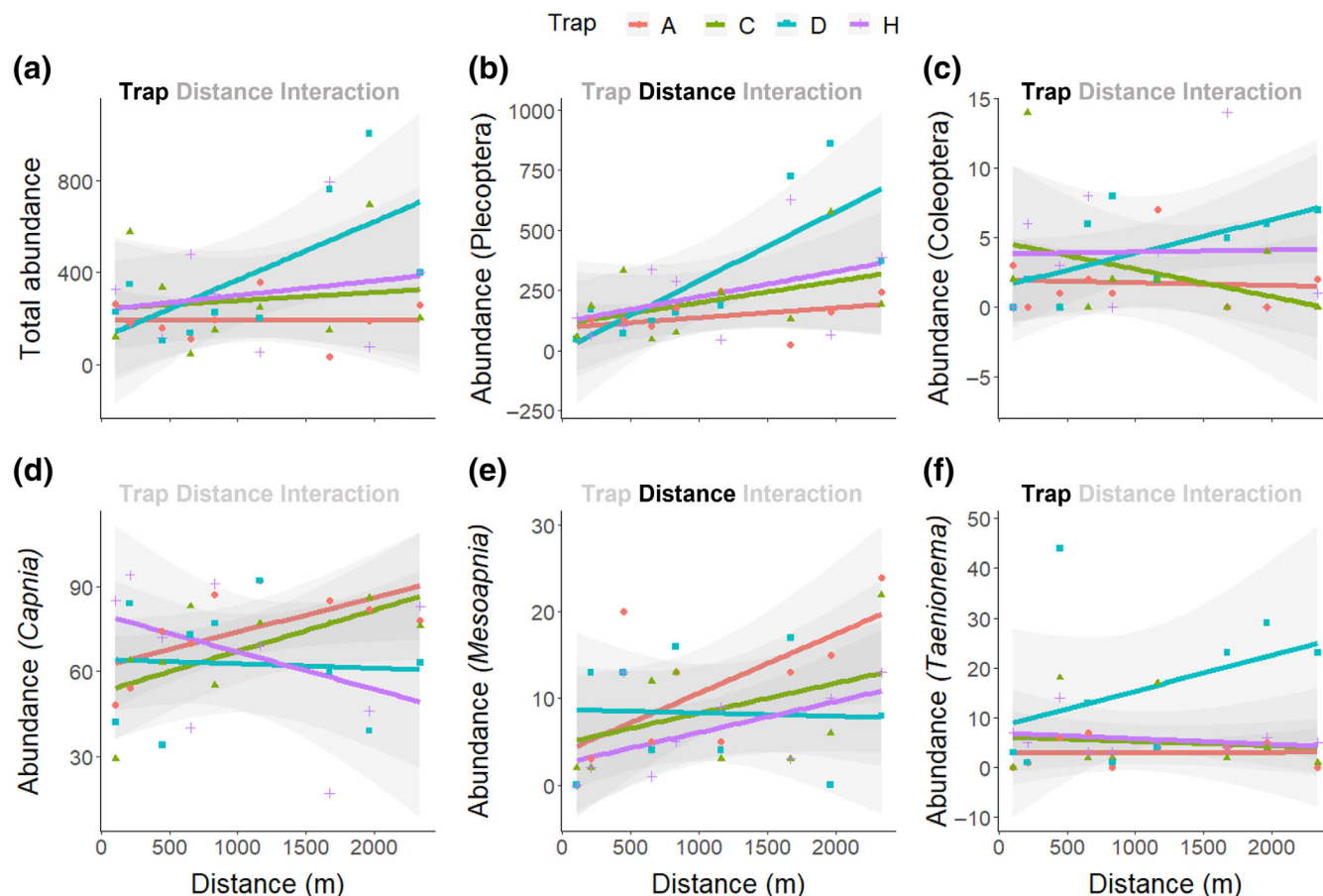
## RESULTS

Across all samples, we collected and processed 57,309 invertebrates representing seven insect orders and several groups of non-insects including mollusks and Collembola. From that total, 39,773 (69.4%) were immature stages (nymphs) of stoneflies (Plecoptera) (Appendix S1: Tables S1, S3). Among Plecoptera, we encountered 7 genera: *Capnia*, *Mesocapnia*, *Bolshecapnia*, *Taenionema*, *Sweltsa*, *Baumanella*, and *Nemoura*. Each of these taxa have been previously documented at the National Park (Bogan & Carlson, 2018).

### Pathways of community reestablishment

When examining the final (6-week) benthic community, we found that trap type was a significant predictor of total macroinvertebrate abundance ( $F_{3,28} = 3.398$ ,  $p = 0.031$ ). In particular, more individuals had colonized via aerial dispersal than vertically migrated from the hyporheic and remained in the local patch. These patterns were true in general for the combination of all taxa and specifically





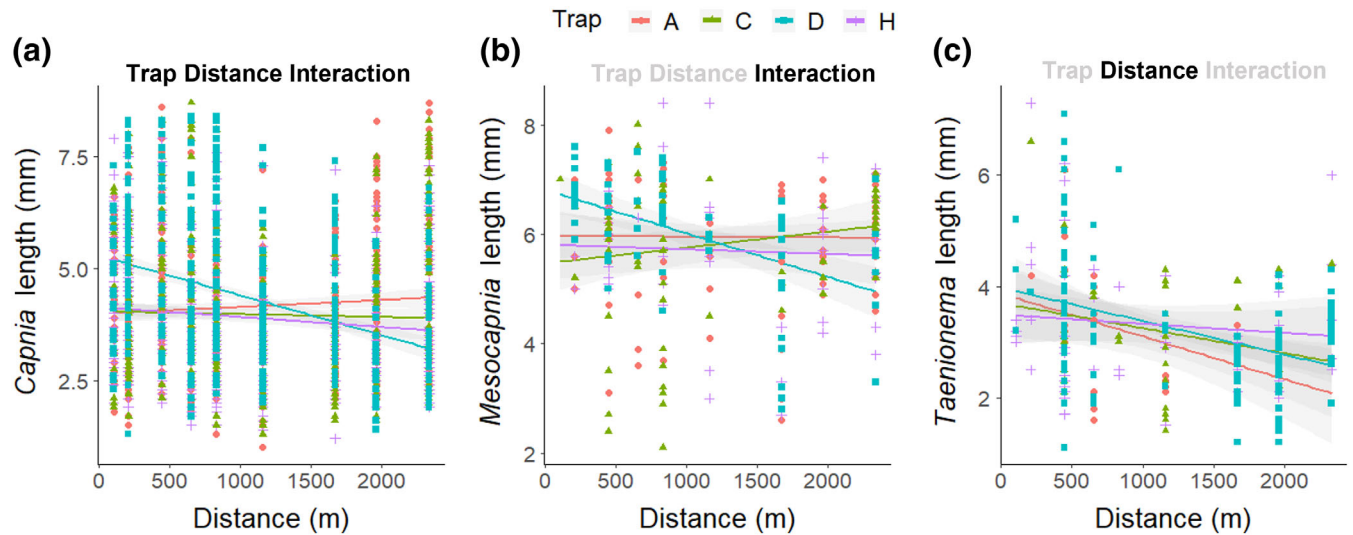
**FIGURE 2** Invertebrate abundance per trap by distance from the perennial waters. Plots show: (a) all invertebrates pooled, (b) Plecoptera, (c) Coleoptera and the Plecoptera genera, (d) *Capnia*, (e) *Mesocapnia*, and (f) *Taenionema*. Bands represent standard error. Significant factors in the ANCOVA (i.e., *Trap*, *Distance*, or the *Interaction* term) are bolded.

for Coleoptera abundance ( $F_{3,28} = 3.736$ ,  $p = 0.022$ ) (Figure 2, Appendix S1: Table S6, Figure S2). Additionally, we found distance from a water source was a driver of total Plecoptera abundance with downstream sites having higher abundances than less fragmented sites ( $F_{1,28} = 10.231$ ,  $p = 0.003$ ). Among Plecoptera genera, we found that *Taenionema* primarily used drift as a reestablishment mechanism ( $F_{3,28} = 3.804$ ,  $p = 0.021$ ), and *Mesocapnia* abundance increased with distance from the cave ( $F_{1,28} = 5.782$ ,  $p = 0.023$ ). We also found that organismal size varied by trap for *Capnia* and *Baumanella* ( $F_{3,2433} = 11.93$ ,  $F_{3,52} = 7.863$ ,  $p < 0.001$ ), and by distance for *Capnia*, *Bolshecapnia*, *Baumanella*, and *Taenionema* (all tests  $p < 0.05$ , see Appendix S1: Table S6). We found an interactive effect of trap type and distance on *Capnia* and *Mesocapnia* size ( $F_{3,2433} = 29.21$  and  $F_{3,297} = 6.819$  respectively,  $p < 0.001$ ), with larger individuals using drift as a recolonization pathway closer to the cave while switching to aerial dispersal at greater distances (Figure 3, Appendix S1: Table S6). While we documented notable differences in recolonization pathways along the gradient of isolation (prediction 1), we did not find that the relative importance of hyporheic migration increased; nor that the

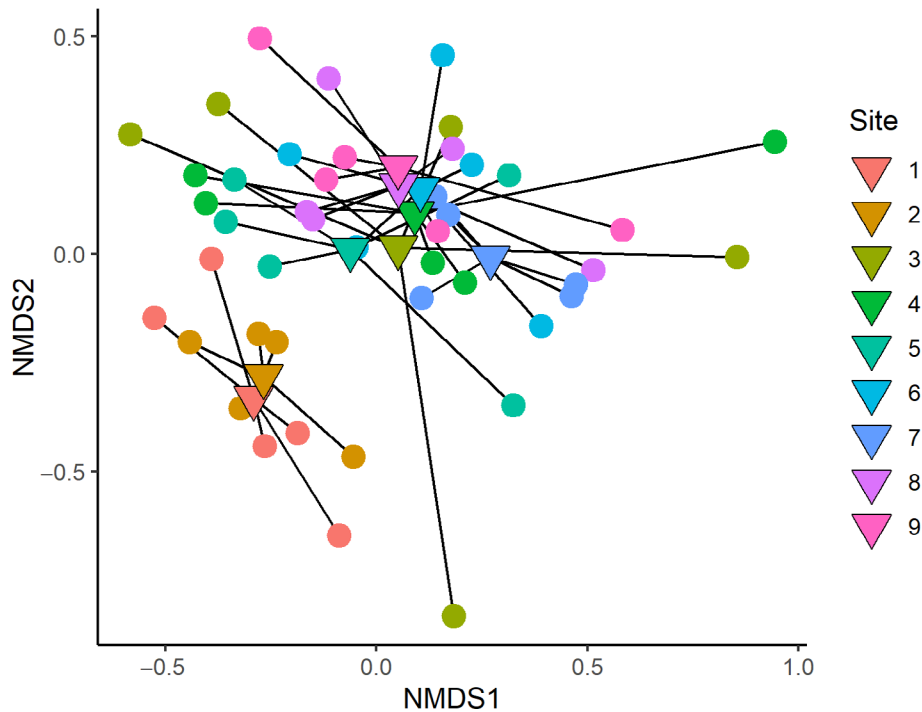
contribution of resilience strategies decreased at downstream sites.

## Habitat isolation and community structure

We found that communities at sites 1 and 2 (those nearest to the perennial water source) were significantly dissimilar from all other sites (maximum Bray–Curtis dissimilarity score for sites 1 and 2: 55.7% and 40.1%,  $F_{1,28}$ ,  $p = 0.001$ ) (Figure 4). However, we found that communities were not dissimilar among trap types ( $F_{1,35}$ ,  $p = 0.102$ ), nor was there an interactive effect between site and trap type. Upstream sites also had higher taxonomic diversity than downstream sites (Shannon index: mean for site 1: 1.28, mean for site 9: 0.26,  $F_{1,28} = 10.063$ ,  $p = 0.003$ ; Simpson index: mean for site 1: 6.49, mean for site 9: 1.11,  $F_{1,28} = 5.605$ ,  $p = 0.025$ ). These diversity and dissimilarity patterns were driven largely by the dominance of Plecoptera at more fragmented sites (Appendix S1: Table S6) and support our expectation that fragmentation would govern variation in community composition along the stream (prediction 2).



**FIGURE 3** Organismal length per trap by distance from the perennial waters, for: (a) *Capnia*, (b) *Mesocapnia*, and (c) *Taenionema*. Bands represent standard error. Significant factors in the ANCOVA (i.e., *Trap*, *Distance*, or the *Interaction* term) are bolded.

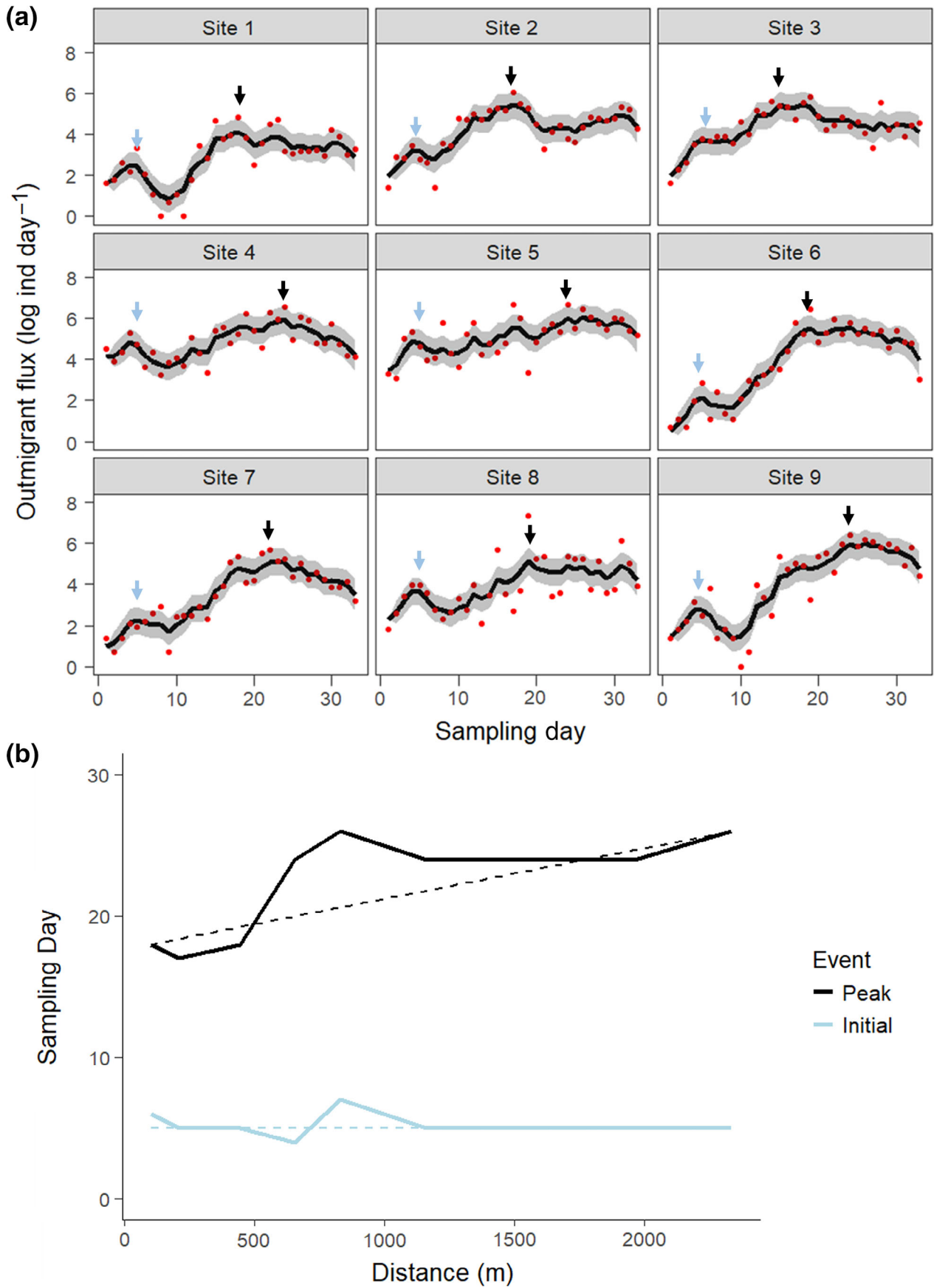


**FIGURE 4** Non-metric multidimensional scaling (NMDS) showing Bray-Curtis Dissimilarity patterns of invertebrate communities that had developed in all traps and sites, after the 6-week deployment. Centroid distance for 1 and 2 (the closest to the water source) compared to all other sites (3–9) was significant  $p = 0.036$ . The 2-D stress value was 0.204. Circles represent communities encountered within each trap, while triangles represent the centroid for the communities at that site.

### Outmigration

The time-series models (MARSS) on daily outmigration flux for the entire community showed that outmigration at each site affected its neighbor site immediately downstream, while also showing some density-dependent effects for each site (i.e., fluctuations around the mean

in the *B* matrix) (Figure 5, Appendix S1: Table S4). Bootstrapped parameter estimates for our off-diagonal *B* parameter were slightly positive (0.033) and CIs did not overlap zero confirming that outmigration at one site had a positive, significant influence on the immediate downstream site following a 1-day lag. In turn, the positive *Q* parameters for variance and covariance (variance:



**FIGURE 5** Legend on next page.

0.0587, covariance: 0.0509; neither including zero in their 95% CI's) indicated that sites fluctuated stochastically—with these fluctuations being shared among sites (Appendix S1: Table S5). Additionally, when we examined the recovered MARSS states (i.e., fluctuations in outmigrant flux free of observation error) across sites, we found that the date of absolute peak outmigration increased by up to 8 days (from 19 to 27 days) across the whole stream reach, as distance from the perennial water source increased. This trend represents an average increase of 0.37 days of delay per 100 m of fragmentation (95% CI: 0.16 to 0.5 days; Thiel-Sen test  $p = 0.003$ ) (Figure 5). Notably, we also observed a small short-lived pulse in outmigrant flux at most sites shortly after full rewetting occurred (ranging from ~5–8 days). However, no longitudinal trend was observed in this case (Thiel-Sen test  $p > 0.999$ ). Overall, we found strong support for our prediction that rewetting would drive migration from the hyporheic zone, and that these patterns would propagate spatially with isolation (prediction 3).

### Immigration and emigration fluxes

Vertical migrants from the hyporheic zone accounted for 88.2% of all individuals (range across sites: 52.9%–99.3%). However, 85.6% of the organisms that used this strategy did not remain local, but instead continued to drift downstream after migration from the hyporheic (range across sites: 52%–96%; Figure 6). Accordingly, when examining these patterns across the longitudinal gradient, we found that emigration was higher than immigration at all sites (Figure 6). However, the net flux of migrants was nearly 0 at site 7. This pattern largely resulted from a spike of migrants in the drift trap. Throughout the study reach, both immigration (ranging from 263 individuals at site 1 to 662 at site 9; with a peak of 2029 at site 7) and emigration (ranging 1025 individuals at site 1 to 5199 at site 9; with a peak of 7871 at site 5) trended upward with distance from a water source. In particular, immigration increased on average 28.7 individuals every 100 m (Theil-Sen 95% CI: 16.4–71.8 individuals per 100 m of fragmentation,  $p = 0.003$ ), while emigration increased on average by 84.1 individuals every 100 m (Theil-Sen 95% CI: 3.2–285.4

individuals per 100 m,  $p = 0.039$ ). Here, our predictions that resistance strategists might also migrate downstream, and that emigration rates would increase throughout the study area were supported; however, immigration also increased downstream—rather than remaining flat (prediction 4).

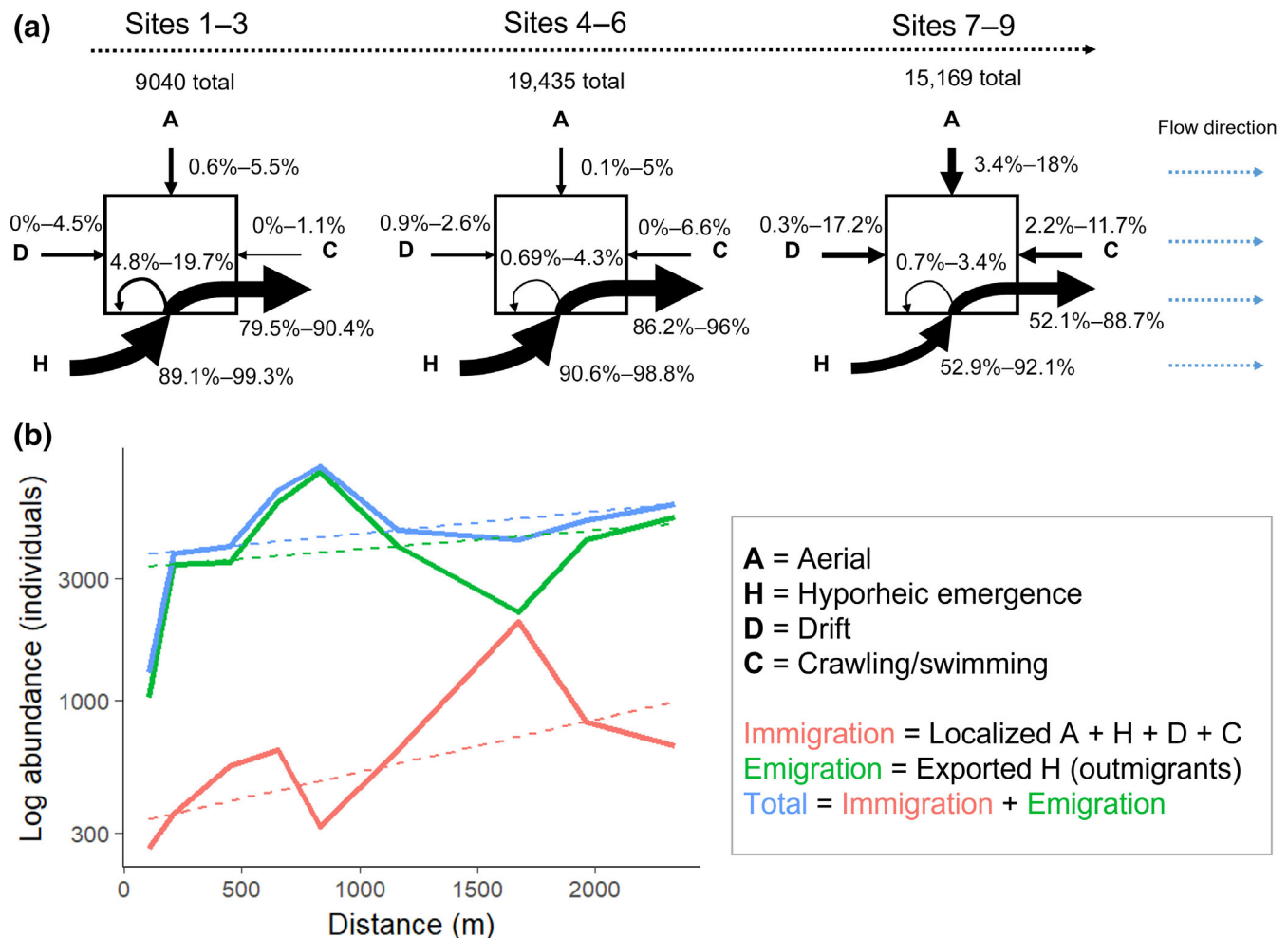
## DISCUSSION

Ecological research has long focused on understanding how disturbance and habitat fragmentation structure communities (e.g., Resh et al., 1988). An important knowledge gap relates to how spatial and environmental context may influence post-disturbance community reestablishment—potentially altering temporal responses by mediating source-sink dynamics (Lloyd et al., 2005). Here, we investigated the interaction between disturbance and spatial structure experimentally by examining a pristine intermittent stream that spanned a gradient of habitat isolation (i.e., increasing distance from perennial waters). We found that: (i) isolation altered the relative importance of recolonization mechanisms, but vertical migration from the hyporheic was paramount and most organisms migrated to downstream habitat; (ii) these processes generated a spatial pattern in community composition/structure along the axis of stream fragmentation; and (iii) the progressive rewetting pulse drove vertical migration of invertebrates from their refuges in the hyporheic to the streambed. Our results confirm that isolation influences post-disturbance recovery and advance the notion that resistance and resilience strategies may be non-mutually exclusive.

### Migration dynamics and post-drying reestablishment

Migration is an integral component of population persistence in disturbed or patchy ecosystems (e.g., Townsend, 1989). Our study quantified both immigration (through organisms captured in our traps) and emigration fluxes (as the sum of local individuals emerging from the benthos and attempting to drift downstream), and we observed distinct spatial patterns for both processes. Organisms vertically

**FIGURE 5** (a) Temporal patterns of daily outmigrant flux, as modeled via multivariate autoregressive state-space (MARSS) models (states  $\pm$  confidence intervals). The “hidden” states (free of observation error) are shown in black, while raw observations are shown in red. Outmigration flux data was collected for over a month (starting on 12 December 2019 and through the end of the experiment). Black arrows show the day of peak hyporheic migration, light blue arrows show the day when the initial pulse took place. (b) Relationship between distance from the perennial waters and day of initial pulse and peak outmigration (solid lines). Data were analyzed via median-based regression (Theil-Sen, see dashed lines) to assess monotonic trends. Day of peak hyporheic migration was significantly influenced by distance from a perennial source ( $p = 0.003$ ), but the initial pulse was not ( $p > 0.99$ ).



**FIGURE 6** (a) Summary of the relative importance of each recolonization pathway (with percentage ranges) along our study stream (sites were grouped in three longitudinal clusters for simplicity). Arrows and values represent the relative range of inputs and outputs at each site; the total abundance of invertebrates is also shown. Migration from the hyporheic was paramount (53%–99% of the total contributions), but most organisms migrating vertically subsequently left the local habitat (outward arrow) and therefore contributed to downstream recovery, rather than staying and contributing to “local” recovery (inward curving arrow). (b) Summary of log-adjusted abundance comparing immigration (via adjusted trap counts), emigration (via the sum of all encountered outmigrants), and the sum of immigration and emigration (total) across all sites by distance from a perennial water source. Dashed lines are fitted median-based regressions (Theil-Sen method) showing overall slope. All three pathways (Immigration, Emigration, and Total) were significantly influenced by distance from a water source ( $p < 0.05$ ).

migrating from the hyporheic comprised most individuals encountered at each site (Figure 6). However, nearly all sites (i.e., all except site 7) were strong net exporters, as organisms that emerged from the hyporheic zone then attempted to emigrate downstream. Though the total number of all migrants increased longitudinally along the fragmentation gradient, downstream sites imported a higher proportion of individuals relative to upstream locations. The unidirectional nature of flow in riverine systems imposes constraints on migration—facilitating downstream dispersal (Ward, 1989). Typically, upstream reaches subsidize downstream habitats by exporting propagules and enabling longitudinal resource transfer (e.g., MacDonald & Coe, 2007; Resh et al., 1992).

The steady accumulation of drifting migrants at downstream sites, coupled with the difficulty of upstream dispersal, likely explains patterns in our study reach, which may continue to change temporally (propagating downstream) as succession advances.

Our study also highlights that resistance and resilience strategies are not binary—but a spectrum (Cohen & Levin, 1987). Within our study, we observed that most migrants encountered at each site employed a resistance strategy (i.e., hyporheic migration) to persist through the dry period, and then repopulated downstream reaches via a resilience strategy (i.e., downstream dispersal). While classical studies often attributed macroinvertebrate reestablishment success primarily to dispersal capabilities



(e.g., Williams & Hynes, 1976), our study shows that resistance within the hyporheic zone might be more important than previously understood (Stubbington & Datry, 2013; Vander Vorste et al., 2016). Accordingly, macroinvertebrate populations in intermittent systems might exemplify the dual importance of dispersal in space and dispersal in time (Buoro & Carlson, 2014; Venable & Lawlor, 1980). Indeed, in plant ecology dispersal-dormancy relationships (e.g., seed banks) have long been studied to understand population persistence in heterogeneous or unpredictable environments (e.g., Leigh et al., 2016; Venable & Brown, 1988). Evolutionary trade-offs may exist that favor dispersal through either space or time (e.g., long-lived plant species tend to have wider-dispersed seeds that are less capable of dormancy) (Chen et al., 2020; Rees, 1993); however, in our case a combination of the two likely decreased extinction risk of species over-summering in hyporheic refugia (as in Snyder, 2006). Because most resistance strategists drifted and rescued downstream habitats, our results illustrate the need to integrate spatio-temporal scales when studying post-disturbance community recovery.

Outmigration patterns analyzed via time-series (MARSS) models showed that the rewetting front elicited vertical migration from the hyporheic, with fluxes at each site predicting downstream outmigration rates (Figure 5). Although models that incorporated interactions between a given site and its immediate downstream neighbor ranked the highest, models that incorporated longer influences (two to three sites downstream) received similar support—suggesting that 1 to 3-day lags are plausible (Appendix S1: Table S4). We note here that outmigration was monitored via hyporheic traps that were closed on their upstream side, and thus did not collect drift from upstream traps. Therefore, the observed wave effect may not be explained by the same individuals traveling downstream, but rather by lagged-synchronized fluctuations in vertical migration and subsequent emigration across sites. These results agree with outmigration and emergence being primarily governed by flow cues (Dole-Olivier, 2011), and the fact that the rewetting front sequentially moved along the stream section. The observation that process error variances and covariances were shared among sites indicates that stochastic fluctuations in outmigration rates were consistent throughout the stream (e.g., due to coordinated fluctuations in flow or temperature, Dole-Olivier, 2011; Vander Vorste et al., 2016). In summary, the lingering effects of isolation were evident in the spatial structure that our models recovered, as well as in the lagged patterns of outmigration observed along the stream. Thus, we add to growing evidence that fragmentation alters the dynamics of both resilient and resistant strategists, and it may diminish the capacity of

communities to persist long-term in the face of severe disturbance regimes (Laurance & Curran, 2008).

## Isolation mediates disturbance response and community composition

We observed that patterns of reestablishment contributing to localized recovery diverged from observations of reach-level processes. Previous work showed that drift is crucial to sustaining macroinvertebrate populations (e.g., Townsend & Hildrew, 1976; Williams & Hynes, 1976; but see Vander Vorste et al., 2016). However, our traps captured fewer drifting organisms than previous theory would suggest. Indeed, our experiment highlighted the importance of vertical migration from the hyporheic (i.e., resistance strategists). Despite this, these organisms tended to not remain local and most vertical outmigrants subsequently dispersed downstream. While drifting organisms did not contribute highly to local recovery, the outflux of resistance strategists at each site indicates that drift is likely highly influential across the network. However, as our study reach only spanned approximately two kilometers, we are unable to determine where propagules exiting our reach ultimately colonized. As organisms continue to drift downstream, the relatively low contribution of drift to each individual site in our study area might not reflect its net importance to broader metapopulation structure.

Additionally, we observed distinct taxa and size-specific patterns across the stream reach. In our case, Plecoptera abundance increased with distance from the perennially-wetted habitat. Plecoptera are often pioneer taxa in intermittent systems like Chalone Creek, recolonizing benthic habitats quickly after seasonal (winter) rewetting (Bogan & Carlson, 2018; Merritt & Cummins, 1996). Their nymphs can use the hyporheic zone during the dry phase, migrating vertically upon surface flow resumption (Rahman et al., 2021) and emerging as flying adults shortly after (Ruhi, personal observation). A particular stonefly genus, *Taenionema*, primarily used drift-based dispersal. This genus is known to inhabit both perennial and intermittent reaches (Bogan & Carlson, 2018), and thus might benefit from multiple pathways. Notably, we observed size-based patterns within Plecoptera genera, where larger individuals used drift-based dispersal in upstream reaches but switched to aerial dispersal downstream. Passive dispersal, like drift, is more difficult in fragmented systems, and previous work has shown that passive dispersal limitation is more pronounced for larger bodied organisms (De Bie et al., 2012). Additionally, larger-bodied organisms might be better suited to use active

forms of dispersal. Indeed, larger-bodied taxa (and taxa with higher relative thoracic mass) have higher aerial dispersal abilities (Lancaster & Downes, 2013) and tend to occupy more habitat patches across a landscape (Hoffsten, 2004). Among aquatically dispersing organisms, larger-bodied individuals might more readily control their movement within flowing waters. Despite the primacy of vertical migration from the hyporheic among all encountered individuals, examination of insect orders contributing to local recovery (i.e., organisms encountered in the final trap sample as opposed to in the emigration samples) indicates aerial dispersal was the primary driver of local reestablishment. Flying insects can colonize stream habitats quickly after rewetting (Bogan & Boersma, 2012; Ruhí et al., 2013), and taxa with increased flight capabilities (like most Coleoptera) can disperse greater distances than organisms that require in-stream dispersal (Merritt & Cummins, 1996). Additionally, phenotypic traits such as adult body size, wing size, and relative thoracic mass may also influence dispersal ability (Lancaster & Downes, 2013).

In addition to controlling the mechanisms that enable invertebrate community reestablishment, habitat isolation also influenced the composition and structure of the re-established community. In particular, communities near the perennial water source were dissimilar from communities in the isolated communities further downstream, and biodiversity declined sharply along the longitudinal axis of the stream (Figure 4). We contend that these patterns are governed by two factors. First, the perennially wetted Balconies Cave likely acts as a source population for drying-sensitive taxa, and these populations can more readily establish within habitats in close proximity. Supporting this idea, sites 1 and 2 contained taxa that are commonly associated with perennial systems and were absent from less connected sites (e.g., *Sweltsa* spp.; Merritt & Cummins, 1996). These organisms might represent migrants from hydrologically stable habitats whose dispersal capacities were limited by distance. Second, the rewetting front, though largely synchronous, caused upstream sites to have surface water up to 5 days earlier than some at greater distances from the perennial section. Our outmigrant sampling indicates that peak hyporheic migration occurred earlier in upstream reaches that wetted first (Figure 5). Additionally, unmeasured subsurface flow between the first cluster of sites might explain similar timing in peak hyporheic migration in the absence of surface flow connection. Among immature stages of stream insects, dispersal success requires wetted migratory pathways (Brooks et al., 2020). Previous studies showed that recolonization rates can be governed by the length of time a habitat is suitable (Peres-Neto, 2004), and that migration from the hyporheic is related to

hydroperiod length (Whiles & Goldowitz, 2001). Accordingly, slightly earlier rewetting may have facilitated the migration of resilience strategists and may have given resistance strategists longer to emerge from the hyporheic zone. Adding to ongoing debates on the role of habitat fragmentation on biodiversity (Fahrig et al., 2019; Fletcher Jr et al., 2018), our study shows that habitat fragmentation has a strong potential to alter both the dynamics and structure of the re-establishing communities.

## Synthesis, future directions, and conclusions

Flow regimes in general, and drying regimes in particular, act as environmental filters that influence structure of whole stream communities and the ecosystem processes that depend upon them (Datry et al., 2017; Palmer & Ruhí, 2019). In the complex habitat mosaic of intermittent streams, resistance and resilience traits often enable population recovery following flow resumption (Bogan et al., 2017). However, even these adaptations have limits. For example, intensified drought regimes can lead invertebrate communities to a “novel” state (Bogan & Lytle, 2011), altering their community trait combinations and overall functional diversity levels (Leigh et al., 2019). Severe drought often decreases system-wide connectivity, impacting access and use of refuges even when these exist in the riverscape (Doretto et al., 2020; Sarremejane et al., 2021). While the spatial aspects of fragmentation are the subject of substantial scrutiny, disrupted temporal dynamics have received relatively less attention in the literature (Auffret et al., 2015). In our study, we observed spatially structured lags in rates of outmigration and drift. If habitat isolation causes a delay in post-disturbance recovery of some, but not all organisms, phenological mismatches can emerge (Renner & Zohner, 2018), potentially increasing the risk of co-extinctions if lags are long enough (Hagen et al., 2012). Overall, our work shows that intensified seasonal and suprasedonal droughts may affect stream biodiversity via the interactive effects of local drying stress and network-level habitat isolation—and these impacts may be best anticipated by focusing not only in spatial patterns, but also in disrupted temporal dynamics.

Our study showed a clear interaction between drying and isolation on post-drying invertebrate community recovery, but several unaccounted factors could have also influenced community dynamics. First, the timeframe of our experiment intentionally captures a system in flux. We observed distinct temporal patterns in migration

dynamics wherein upstream sites represented more successional advanced communities than downstream sites. However, as the stream remains wetted, downstream communities might continue to accrue species and become more homogenous to upstream sites. Experiments or monitoring efforts over longer time frames could assess whether mid-term communities (e.g., those present when the stream recedes and fragments again) preserve the differences that can be observed shortly after rewetting. Second, we were unable to account for lateral migration into the traps through subsurface interstitial spaces. While this type of movement is unlikely to alter our observed patterns, additional levels of subsurface sampling (e.g., across lateral gradients and depth profiles) might provide valuable insights on variation in the quality of hyporheic refugia (Dole-Olivier, 2011). Finally, multi-year droughts, earlier or stronger rewetting fronts (e.g., scouring floods that dislodge resistance forms), or interannual hydrologic variation in winter wet periods and summer conditions could alter the observed community patterns (e.g., Power et al., 2008). Examining if the mechanisms driving the reported interaction between drying and fragmentation are consistent across climates, water years, or geologies (e.g., in systems with a less porous streambed), would allow testing the transferability of our findings to other ecosystems.

Intermittent streams offer a unique opportunity to examine how biological communities recover after periodic, spatially correlated disturbance that occur along natural gradients of habitat isolation (Hwan & Carlson, 2016). Here, we developed a large-scale field experiment that revealed how (and why) spatial fragmentation controls post-drying community recovery. Our results show that habitat isolation alters the relative importance of the mechanisms that allow for post-drying recovery, with storage effects likely having a paramount, under-appreciated contribution—and with their benefits propagating downstream. As human activities continue to degrade natural ecosystems globally and across spatio-temporal scales (e.g., Palmer et al., 2008), it is critical that we assess the impacts of disturbance and isolation jointly—with close attention to their interaction.

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#### CONFLICT OF INTEREST

The authors declare no conflict of interest.

#### DATA AVAILABILITY STATEMENT

Data (Fournier et al., 2022a) are available in Dryad at <https://doi.org/10.6078/D1SM5H>. Supporting code (Fournier et al., 2022b) is available in Zenodo at <https://doi.org/10.5281/zenodo.6261393>.

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## SUPPORTING INFORMATION

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

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