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Temporal trajectories in metacommunity structure: Insights from interdisciplinary research in intermittent streams

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Abstract

Metacommunity ecology represents a framework for identifying linkages between environmental heterogeneity, spatial processes, and local communities of organisms. Despite advancements in metacommunity theory, there remains a need to understand temporal dynamics of multi-taxa metacommunities in variable ecosystems such as intermittent streams. We present a review of literature, three recent conceptual models, and a case study regarding metacommunity temporal dynamics in intermittent streams. The literature review revealed that the cumulative number of studies addressing temporal dynamics in aquatic metacommunities steadily increased between 2012 and 2020. Intermittent streams were the fourth-most commonly studied ecosystem and interdisciplinary studies involving multiple taxa were the third-most common taxonomic focus. The most common analytical method was variation partitioning, and analysis of beta diversity components surpassed both distance decay and elements of metacommunity structure as the second-most used method from 2018 to 2020. Three recent conceptual models describing metacommunity dynamics in intermittent streams predict: (a) higher local species richness (i.e., alpha diversity) during rewetting and wet hydrologic phases, (b) stronger effects of dispersal over environmental sorting during the rewetting and wet phases, and (c) emergence of primarily nested structures during the wet hydrologic phase. When tested in a case study focused on microbes, aquatic invertebrates, and fishes, each of these predictions were partially, but not completely supported. Our results reveal expanding interest in temporal aspects of aquatic metacommunity structure and highlight how research in intermittent streams is poised to simultaneously advance basic metacommunity ecology and applied conservation biology through continued refinement of new and existing conceptual syntheses.

This article is categorized under:

Water and Life > Nature of Freshwater Ecosystems
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KEYWORDS

biodiversity, community ecology, metacommunity, nonperennial, river, stream

1 | INTRODUCTION

The term "metacommunity" was introduced by Gilpin and Hanski (1991) to describe a set of local communities existing within discrete patches and composed of multiple species, with each local community linked to other communities through dispersal. This concept was later formally implemented in a model that explicitly linked spatial heterogeneity among mosaics of habitat patches with species interactions (Wilson, 1992). From these beginnings, metacommunity theory emerged as multispecies extensions of foundations in metapopulation theory (Hanski & Gaggiotti, 2004; Hanski & Gilpin, 1997), and formal reviews of metacommunity theory are provided by Leibold et al. (2004), Holyoak, Leibold, and Holt (2005), and Leibold and Chase (2017). There is now growing interest in applying metacommunity ecology analytical methods (Box 1) as a means of improving our understanding of the relative roles of environmental versus spatial variables in structuring communities (reviewed by Logue et al., 2011), particularly in the context of addressing biodiversity conservation and management challenges (Cid et al., 2020; Holyoak, Caspi, & Redosh, 2020).

BOX 1 Methods in metacommunity ecology

Applied metacommunity theory has focused largely on the four typologies described by Leibold et al. (2004): species sorting, mass effects, patch-dynamics, and neutral model. The species sorting typology emphasizes matches between environmental templates and species traits, mass effects emphasizes dispersal-mediated persistence of species even among patches that do not match traits, patch-dynamics emphasizes trade-offs in competition and colonization, and the neutral model suggests habitat templates and species traits are irrelevant to community structure. A statistical method based on variation partitioning and useful for identifying major underlying typologies was developed by Cottenie (2005) and has since been widely implemented (Figure 1a). A second approach involves the use of species-by-site incidence matrices and the three elements of metacommunity structure: coherence, species turnover, and boundary clumping (reviewed by Leibold & Mikkelson, 2002). The decision tree of Presley et al. (2010) can be used to assign idealized patterns, including random (i.e., no pattern) or checkerboard (i.e., species exclusions) gradients versus nested subsets, Clementsian, Gleasonian, and evenly spaced gradients (Figure 1b). A third approach described by Logue and Lindström (2008) is based on work by Chase et al. (2005) and the concept of distance decay, or negative correlations among pairwise measures of community similarity, environmental gradient distance (dissimilarity), and geographic distance (Figure 1c). Most recently, the use of beta diversity components (reviewed by Legendre, 2014) were introduced as indices that might be used to infer metacommunity structuring mechanisms (Figure 1d), though these concepts are still being refined (Datry et al., 2016; Ruhí, Datry, & Sabo, 2017).

Application of metacommunity theory to intermittent streams and their biota might provide predictive capability regarding ecological responses to future declines in streamflow. More than half of Earth's streams experience natural drying or temporary cessation of flow (i.e., intermittent flow), and the number of intermittent streams is increasing because of human alteration to hydrologic cycles (Datry, Larned, & Tockner, 2014). In some temperate stream systems, annual flow disruptions are caused by declines in the water table due to a combination of porous bedrock below streams, high temperatures, and low precipitation, particularly during summer months (Xenopoulous et al., 2005). These natural streamflow disturbances reduce suitable habitat and dispersal opportunities for stream biota, and thus operate to filter species occurrence through interactions with species physiological tolerances and life histories (Jackson, Peres-Neto, & Olden, 2001; Jaeger, Olden, & Pelland, 2014; Stanley, Fisher, & Grimm, 1997). In fact, temporary cessation of flow is a fundamental factor in shaping intermittent stream communities (Acuña et al., 2014; Fazi, Vazquez, Casamayor, Amalfitano, & Butturini, 2013; Larned, Datry, Arscott, & Tockner, 2010; Sabater, Timoner, Borrego, & Acuña, 2016; Townshed, 1989). However, intermittent flow is not always a natural phenomenon. In areas with high levels of anthropogenic groundwater extraction, depletion of groundwater can cause historically perennial streams to become intermittent, threatening aquatic biodiversity in the process (Larned et al., 2010; Perkin et al., 2017; Ruhi, Olden, & Sabo, 2016). Metacommunity theory is particularly applicable to describing ecological patterns in intermittent stream systems where fluvial connectivity and patch occupancy are dynamic in space and time (Driver & Hoeinghaus, 2016a; Larned et al., 2010; Winemiller, Flecker, & Hoeinghaus, 2010). A recent focus on the dynamic nature of metacommunities represents a regime shift from the historical focus on purely spatial patterns in metacommunities (Cañedo-Argüelles et al., 2020; Castillo-Escrivà, Mesquita-Joanes, & Rueda, 2020; Holyoak et al., 2020).

The goal of this study was to review concepts and applications of metacommunity theory in intermittent streams. Our first objective was to review a cross-section of peer-reviewed literature to assess the prevalence and timing of studies focusing on temporal fluctuations in metacommunities, as well as the major systems, taxonomic groups, and analytical methods included. We developed an annotated bibliography based on this review that can be used by readers interested in becoming familiar with the state of the science. Our second objective was to select existing theoretical or conceptual frameworks illustrating predictions for temporal aspects of metacommunities in intermittent streams. This collection of concepts can be used for hypothesis development and study design for future research regarding temporal dynamics of metacommunities in intermittent streams. Our third objective was to apply the predictions from the conceptual models to a case study of biodiversity research in a typical intermittent stream. This case study represents just one potential application of the information compiled in this review to help advance understanding of the ecology of intermittent streams.

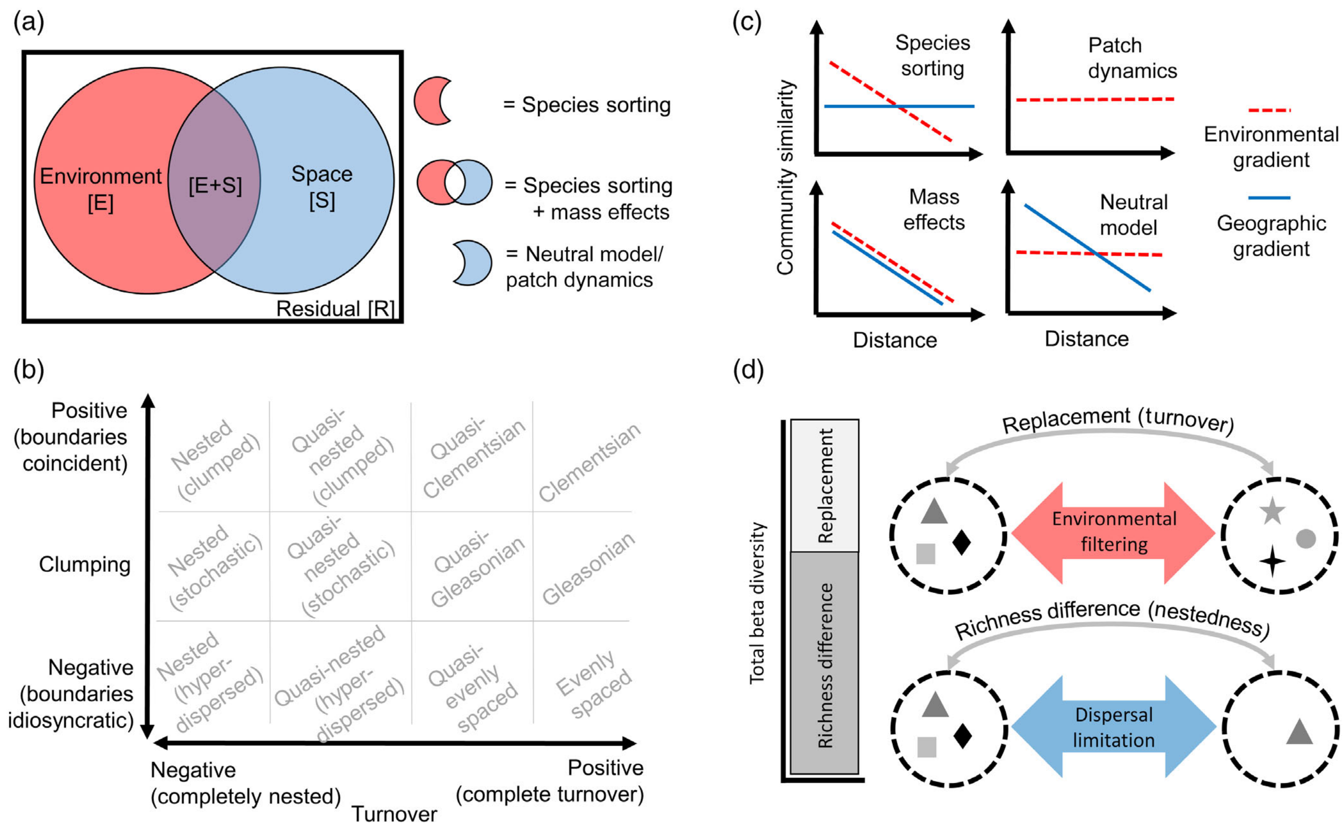

FIGURE 1 Approaches to quantifying metacommunity structures. (a) Cottenie (2005) developed a decision tree based on variation partitioning that assesses contributions by environment ([E]), space ([S]), pure environment (i.e., conditioned by space, [E|S]), and pure space (i.e., conditioned by environment, [S|E]) components and assigns dominate metacommunity typologies. (b) Presley, Higgins, and Willig (2010) provided a decision tree based on the elements of metacommunity structure (coherence, turnover, and boundary clumping; defined by Leibold & Mikkelson, 2002) that classifies metacommunities according to 14 idealized structures. Two idealized structures characterized by non-coherence (random and checkerboard) are not shown here. (c) Logue and Lindström (2008) developed a framework used to assign metacommunity structures based on distance decay, or negative correlations between pairwise measures of community similarity, environmental distance (dissimilarity), and geographic distance. (d) Datry, Bonada, and Heino (2016) noted that the two components of beta diversity (i.e., richness difference or nestedness and replacement or turnover) could be used to infer metacommunity structuring mechanisms such that predominantly nested metacommunities emerge from dispersal limitation while metacommunities with greater turnover emerge from environmental filtering

2 | REVIEW OF TEMPORAL DYNAMICS IN AQUATIC METACOMMUNITIES

Temporal dynamics and trajectories in metacommunity structures represent an emerging emphasis in the field of ecology. We reviewed literature on the topic by conducting an Advanced Search of ISI Web of Science (Thomson Reuters, New York) to retrieve articles on both of the topics "metacommunity" and "temporal" and at least one of the topics "stream," "river," "intermittent," or "aquatic" [search structure was "TS = ("metacommunity" AND "temporal" AND ("stream" OR 'river' OR 'intermittent' OR 'aquatic')"]. We reviewed the 103 articles returned from this search and classified each study regarding (a) whether or not it directly addressed temporal dynamics, (b) the primary ecosystem type studied, (c) the focal taxonomic group(s), and (d) the primary analytical method used to quantify metacommunity structure. We present a summary of the data here and a table detailing the full results (Appendix S1, Table S1). Of the 103 studies reviewed, the most common focal taxa included aquatic invertebrates ($n = 30$), fishes ($n = 16$), studies involving multiple taxa ($n = 11$), zooplankton ($n = 10$), and microbes ($n = 9$; Figure 2a). Fifty-nine studies (57%) directly addressed temporal dynamics in metacommunities and the cumulative number of these studies increased linearly between 2012 and 2016 before accelerating between 2017 and 2020 (Figure 2b). The cumulative number of studies assessing intermittent streams increased in a step-wise fashion, including increasing from 0 to 2 in 2010, from 2 to 9 between 2016 and 2017, and from 9 to 11 in 2020. Other major ecosystem types in which temporal dynamics of metacommunities were studied included perennial streams ($n = 31$), river floodplains ($n = 22$), and perennial lakes and ponds ($n = 13$). Among studies empirically quantifying metacommunity structure, variation partitioning was the most common analysis ($n = 33$ studies), followed by beta diversity and its components ($n = 16$), distance decay ($n = 10$), and the elements of metacommunity structure ($n = 6$). The temporal trajectory of analyses showed that variation partitioning increased in a pattern concomitant with the total number of studies assessing temporal dynamics, distance decay analyses emerged in 2011 and increased linearly, elements of metacommunity analyses emerged in 2014 and increased linearly, and beta diversity analyses emerged in 2015 and surpassed both distance decay and elements of metacommunity structure between 2016 and 2020 (Figure 2c). Studies reviewing metacommunity concepts included three with a general focus on aquatic ecosystems (Bohonak & Jenkins, 2003; Heino et al., 2015a; Stendera et al., 2012), two focused on lotic ecosystems in particular (Erős, 2017; Winemiller et al., 2010), and three focused specifically on intermittent streams (Datry et al., 2016; Larned et al., 2010; Leigh et al., 2016a).

Our review highlights an increasing interest in aquatic metacommunity temporal dynamics with a primary focus on aquatic invertebrates and involving a shifting set of analytical approaches. The earliest review article returned by our search was a review of aquatic invertebrate dispersal published at the beginning of the emergence of metacommunity

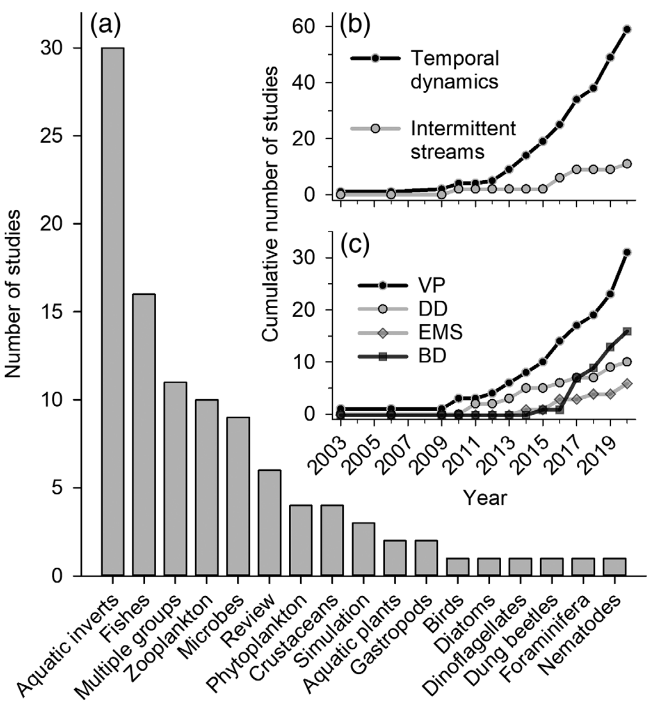

FIGURE 2 Results from a review of 103 studies on the topic of temporal dynamics in aquatic metacommunities illustrating (a) the distribution of studies across different taxa, (b) a rise in considerations of temporal dynamics through time, including in intermittent streams, and (c) temporal trajectories of the methods used to quantify metacommunity structure, including variation partitioning (VP), distance decay (DD), elements of metacommunity structure (EMS), and beta diversity components (BD)

studies (Bohonak & Jenkins, 2003), and a continued emphasis on aquatic invertebrates was still apparent 17 years later. Fishes were the next most studied group ($n = 16$ studies), followed by interdisciplinary studies involving multiple taxa ($n = 11$). Approximately half of the interdisciplinary studies included temporal dynamics ($n = 6$), and these studies focused on perennial streams (Da Silva, Lansac-Tôha, Lansac-Tôha, Sales, & de Sousa Rocha, 2021; Lansac-Tôha et al., 2019; Tonkin et al., 2018), river floodplains (Padial et al., 2014), intermittent ponds (Galvez et al., 2020), and intermittent streams (Datry et al., 2016). Even within the narrow set of interdisciplinary studies, a variety of analytical methods was used, including variation partitioning (Da Silva et al., 2021; Galvez et al., 2020; Padial et al., 2014), elements of metacommunity structure (Tonkin et al., 2018), and beta diversity components (Lansac-Tôha et al., 2019). Logue et al. (2011) previously reviewed empirical approaches to metacommunities and focused on variation partitioning and elements of metacommunity structure. Our results suggest that in the time since that review, distance decay and beta diversity emerged as two increasingly used methods for quantifying metacommunities, particularly in the context of temporal dynamics. Furthermore, improvements in the application of variation partitioning have occurred in the years since development of the model by Cottenie (2005), including treatment of typologies not as mutually exclusive but as existing along continua (Logue et al., 2011), caution regarding the use of spatial factors as direct measures of dispersal (Peres-Neto, Leibold, & Dray, 2012), and improved treatment of Type 1 error (Clappe, Dray, & Peres-Neto, 2018). Finally, although too new to appear in our review of literature, we are aware of at least two other recently developed alternative methods for quantifying metacommunities. These include the internal structure of metacommunities developed by Leibold et al. (2020) and the dispersal-niche continuum index developed by Vilmi et al. (2020). The general pattern of inclusion of new analytical frameworks highlighted by our review combined with recent calls for new methods to analyze intermittent streams (Heino, Melo, et al., 2015a) suggest these new methods might be applied to systems such as intermittent streams to expand our understanding of metacommunity dynamics.

3 | TEMPORAL METACOMMUNITY APPLICATIONS IN INTERMITTENT STREAMS

Emerging evidence for multiple taxonomic groups suggests metacommunity dynamics in intermittent streams may be predictable. Heino et al. (2015b) reviewed metacommunity ecology research applied to freshwater ecosystems and emphasized a need for greater focus on temporal fluxes in dynamic systems such as intermittent streams. Since then, studies addressing the dynamics of metacommunities in intermittent streams have focused on ostracods (De Campos, da Conceição, Martens, & Higuti, 2019), terrestrial athropods (Sánchez-Montoya et al., 2020), aquatic macroinvertebrates (Sarremejane et al., 2017), and fishes (Leonidas et al., 2020; Rodrigues-Filho et al., 2020). Although studies historically focused on a single taxonomic group during investigation, interdisciplinary research is also increasing through both integrative reviews of single taxon studies and development of multitaxa studies. As an example of the former, three single-taxon investigations of Prokaryotes (Romaní et al., 2017), aquatic invertebrates (Boulton, 2003), and fishes (Driver & Hoeinghaus, 2016b) can be simultaneously considered to reveal a unifying theme. Specifically, across these taxa there is a pattern of greatest alpha diversity during rewetting and wet hydrologic phases, lowest alpha diversity during dry or drying periods, and increases in alpha diversity that scale with body size such that smaller organisms respond more rapidly to changes in hydrologic phase (Figure 3a). Similarly, Sarremejane et al. (2017) conducted an integrative assessment of the relative roles of environmental versus dispersal mechanisms on aquatic invertebrate metacommunities across hydrologic phases in intermittent streams and presented a conceptual model that posits greater contribution by spatial mechanisms during rewetting and wet phases (Figure 3b). Finally, Datry et al. (2016) reviewed mechanisms that structure metacommunities in intermittent streams and developed a conceptual model that posits nested metacommunities should be most prevalent during wet periods, while species turnover patterns should dominate during drying, dry, and rewetting hydrologic phases (Figure 3c). The extent to which these models apply to multiple taxonomic groups should be explored through interdisciplinary research endeavors characterized by experts on multiple taxa collaborating within an integrative framework. The challenges related to taxonomic expertise that arise with multi-taxa studies can be overcome through interdisciplinary studies (Box 2). Indeed, our review of literature revealed that 11% of the included studies simultaneously assessed multiple taxonomic groups (e.g., De Bie et al., 2012; Henriques-Silva et al., 2019; Tonkin et al., 2018) and intermittent streams are one of many research frontiers that will benefit from interdisciplinary approaches to metacommunity ecology.

BOX 2 Interdisciplinary research broadens taxonomic perspectives

Community ecologists depend on either first-hand knowledge of particular taxonomic groups or must collaborate with taxonomic specialists to apply the basics of metacommunity ecology (Gotelli, 2004). This is, in part, because taxonomies are increasingly understood at complex levels that necessitate expertise within organismal groups. A suggested alternative to collaboration is the use of “recognizable taxonomic units” by “parataxonomists” that lack the expertise to identify organisms with high resolution (Beattie & Oliver, 1994). But this concept has proven to be contentious (Brower, 1995; Oliver & Beattie, 1997). A related concept is that of “taxonomic sufficiency,” which posits that organisms only need to be identified to a taxonomic resolution that is necessary to detect ecological patterns (Ellis, 1985). This approach also raises criticism (Maurer, 2000; Terlizzi, Bevilacqua, Fraschetti, & Boero, 2003). Clearly, the most comprehensive treatment of questions of taxonomic resolution within community ecology is to recruit taxonomic specialists as collaborators through interdisciplinary research. However, the challenge of achieving the highest level of taxonomic resolution might still persist. For large-bodied organisms with long histories of study (e.g., fishes), taxonomies are more likely to be completely defined compared with smaller, more diverse, and perhaps lesser studied organisms (e.g., aquatic invertebrates). Among very small organisms (e.g., microbes), the highest taxonomic resolution achievable might be based on “operational taxonomic units” derived through molecular sequencing. Thus, one central challenge to multitaxa interdisciplinary studies in community ecology is differences in the ability to study and make accurate comparisons among organisms with vastly different sizes, morphologies, and hypothesized phylogenetic relationships.

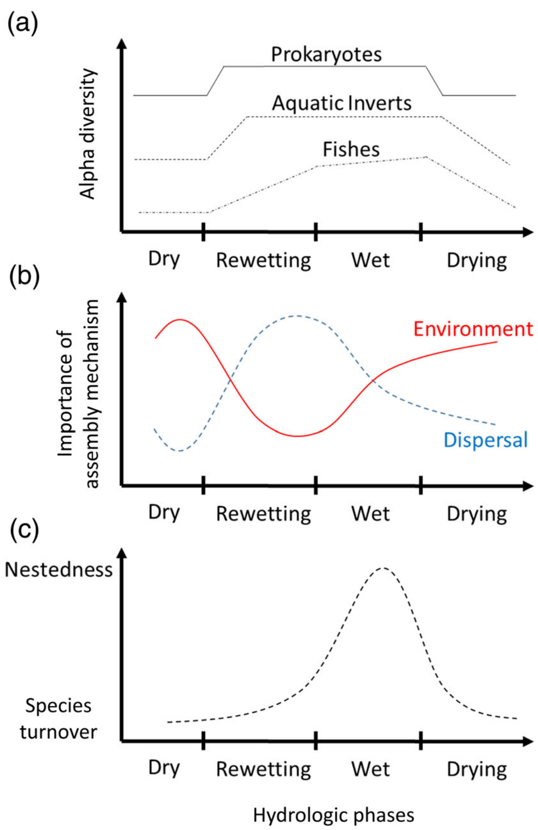

FIGURE 3 Emerging themes in metacommunity structure across hydrologic phases in intermittent streams. (a) Temporal patterns in alpha diversity predicted for prokaryotes (Romaní et al., 2017), aquatic invertebrates (Boulton, 2003), and fishes (Driver & Hoeinghaus, 2016b) across dry, rewetting, wet, and drying hydrologic phases. Note that rates of alpha diversity increase (presumably through recolonization) scale with organism body size. (b) Relative influences by environmental and spatial (i.e., presumably dispersal) variables on metacommunity structure based on the conceptual model developed by Sarremejane et al. (2017). (c) Temporal change in nestedness versus species turnover structures across hydrologic phases based on the conceptual model developed by Datry et al. (2016)

4 | LITTLE CREEK CASE STUDY

We tracked temporal trajectories in metacommunity structure for water microbes, aquatic invertebrates, fishes, and cutaneous microbiomes on the surface of fishes in Little Creek, Tennessee. Little Creek (LC) is a second-order,

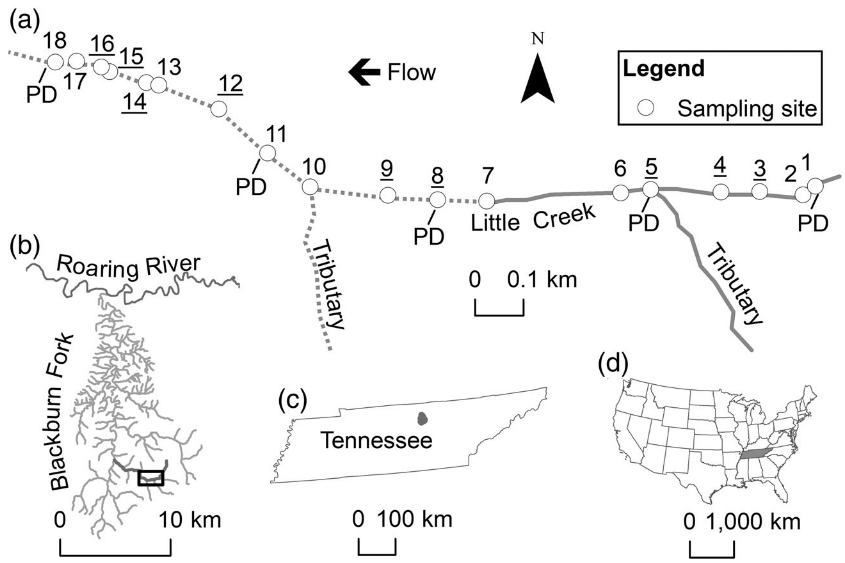

FIGURE 4 Study area map illustrating (a) sites (numbered circles) where fishes, invertebrates, and water microbes were sampled during 2016 and 2017. Invertebrates were sampled at a subset of sites (underlined numbers) and five pressure transducers (PD) were deployed to measure water level and temperature fluctuations at perennial (solid lines) and intermittent (dotted lines) reaches of stream. (b) Little Creek is a tributary to Blackburn Fork in the Roaring River basin in (c) north-central Tennessee in (d) the southeast United States

intermittent stream located in the humid subtropical climate zone of the southeast United States (Figure 4). The catchment for this reach of LC includes upstream urban land uses associated with the city of Cookeville, Tennessee (Perkin, Murphy, Murray, Gibbs, & Gebhard, 2019) and pasture land uses in closer proximity on the Shipley Farm Complex surrounding the stream (Wells et al., 2017). An intact riparian corridor exists along the length of the study reach and buffers LC from the effects of nearby pasture land uses. Consequently, instream habitats, when wetted, are comparable to similarly sized streams across the southeast United States (Gebhard et al., 2017). Ephemeral flow patterns in Little Creek consist of drying at the downstream extent (Figure 5) but continued flow at the upstream extent (Curtis, Gebhard, & Perkin, 2018; Data S1). This pattern is consistent with streams across the region and is caused by percolation of water through permeable soils except where shallow bedrock sandstone layers occur beneath streams (Mayfield, 1986). Our sampling was distributed among rewetting (December 2016), wet (April 2017), and drying (October 2017) hydrologic phases.

4.1 | Aquatic metacommunities

We surveyed aquatic biodiversity to understand the impacts of stream intermittency on metacommunity structure. We identified aquatic macroinvertebrates at the family level, fishes at the species level, and microbiota suspended in the stream water (water microbes hereafter) and on the cutaneous surface of fishes (cutaneous microbiome hereafter) using operational taxonomic units (OTUs; see Appendix S2 for detailed methods). We collected 14 fish species, 50 invertebrate families, 34 Indicator OTUs for water microbes, and 75 Indicator OTUs for cutaneous microbes. Alpha diversity values followed a general pattern of increase between rewetting and wet hydrologic phases and decrease between wet and drying hydrologic phases for microbes (Figure 6a) and aquatic invertebrates (Figure 6b) but not fishes (Figure 6c) nor cutaneous microbes (Appendix S2). Thus, results from the Little Creek case study only matched predictions shown in Figure 3a for some, but not all, of the taxonomic groups investigated.

4.2 | Quantifying metacommunities

We used the variation partitioning (VP) decision tree from Cottenie (2005) and the elements of metacommunity structure (EMS) framework presented by Presley et al. (2010) to quantify metacommunities for each taxonomic group and

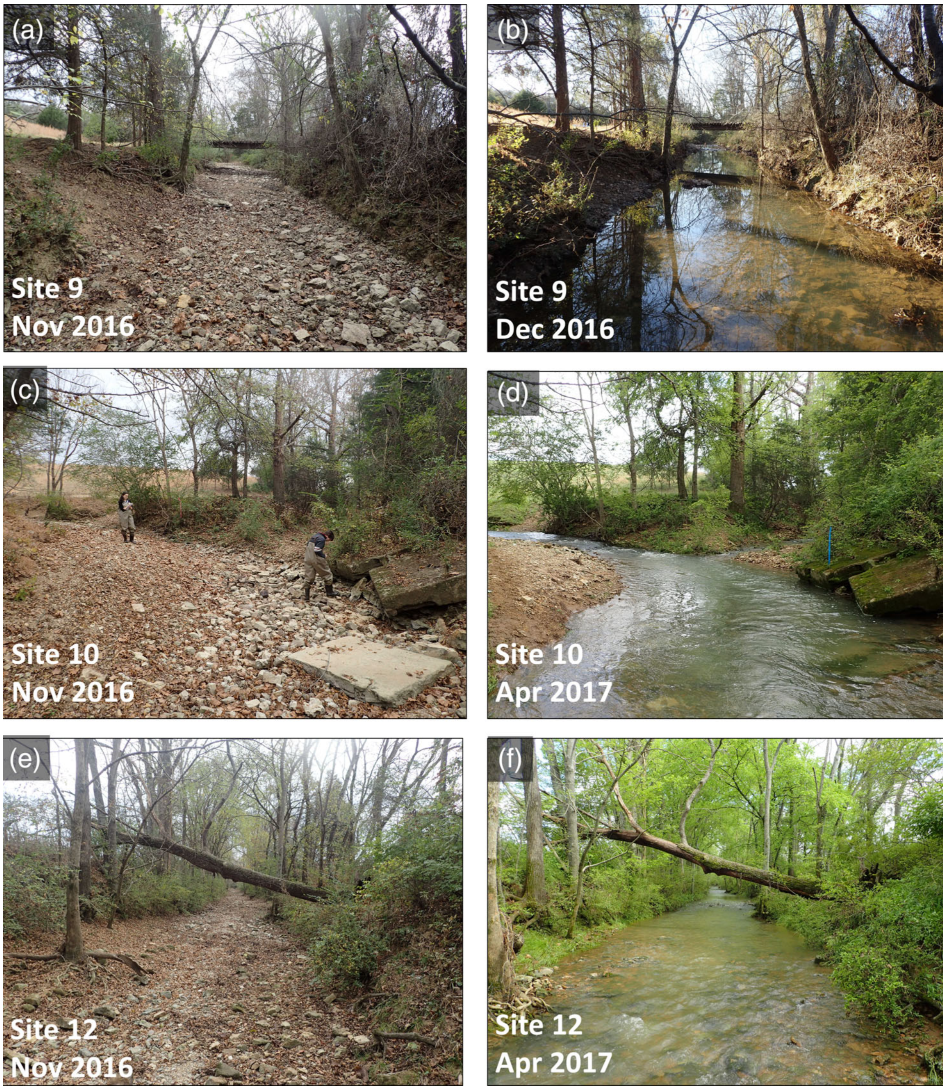

FIGURE 5 Photographs of three sampling sites during initial dry phase in November 2016 (a, c, e), rewetting phase in December 2016 (b), and wet phase in April 2017 (d, f)

each hydrologic phase separately. Based on VP, the water microbe metacommunity structure could not be determined during any phase, invertebrate metacommunity structure followed a pattern of species sorting during rewetting but could not be determined during the remaining periods, and fish metacommunity structure followed a species sorting pattern across all hydrologic phases (Appendix S2). Based on EMS, we found water microbes, aquatic invertebrates, and fishes showed temporal variation in metacommunity structure and generally shifted toward consistent turnover across hydrologic phases (Figure 7a). Cutaneous microbiome metacommunity structures for all species shifted toward increasingly nested structures during the wet hydrologic phase, and then back toward turnover during the drying phase (Figure 7b). The general increase in the number and strength of spatial correlates explaining metacommunity structure for invertebrates, fishes, and cutaneous microbiomes during rewetting and wet phases matched the predictions shown in Figure 3b. Moreover, synchronized shifts toward greater nesting during the wet hydrologic phase for invertebrates and cutaneous microbiomes matched predictions from the conceptual model shown in Figure 3c.

5 | SYNTHESIS AND FUTURE DIRECTIONS

The origins of metacommunity theory emphasized spatially distributed communities linked through dispersal (Leibold et al., 2004). Early works on the theory focused on measures of community structure, niche concepts, and spatial

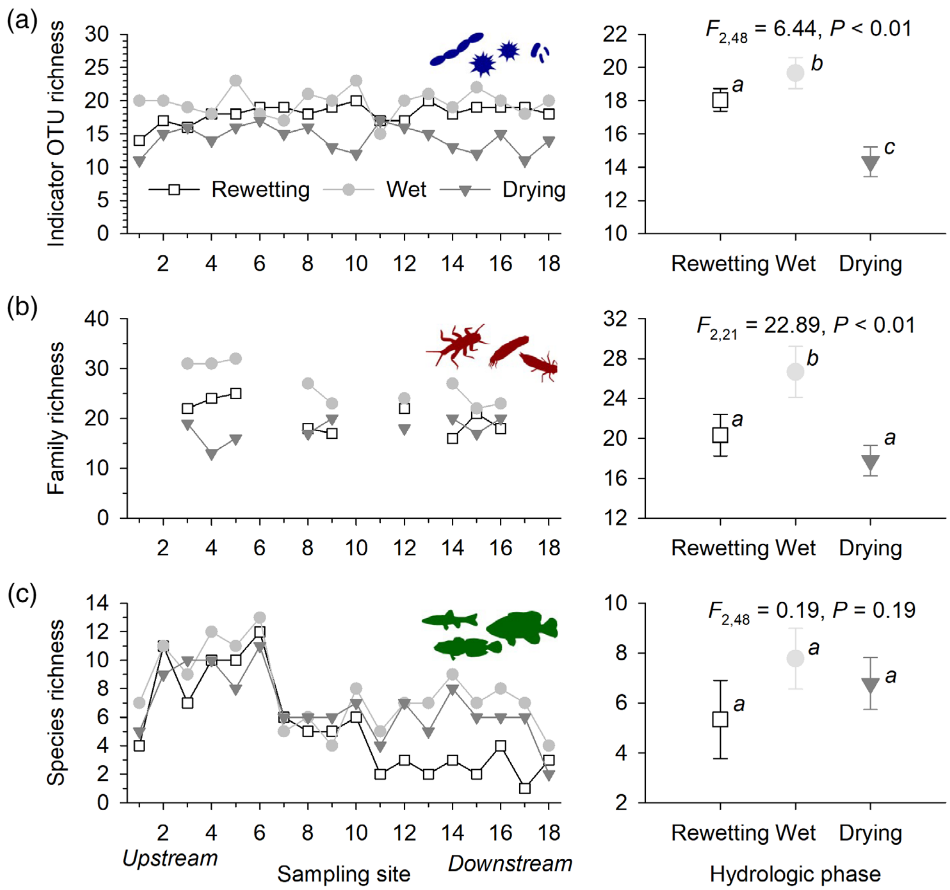

FIGURE 6 Spatiotemporal patterns in (a) water microbe richness, (b) invertebrate family richness, and (c) fish species richness at 18 sites sampled during rewetting (white boxes), wet (gray circles), and drying (dark triangles) hydrologic phases in Little Creek, Tennessee. Sites are arranged from upstream (left) to downstream (right). Invertebrates were only sampled at nine locations. Plots in the right column show means and 95% confidence intervals as well as results from repeated measures analysis of variance and pairwise comparisons (indicated as letters representing differences among means)

proxies for dispersal (Cadotte, 2006; Chase, 2005), and research on these topics continues (Gansfort, Fontaneto, & Zhai, 2020; Tonkin et al., 2018). However, dispersal and the processes that create and maintain environmental heterogeneity are temporally dynamic and there is increasing recognition that temporal aspects of metacommunities require more attention (Holyoak et al., 2020). Recent evidence points to context-dependencies surrounding the temporal scales influencing abiotic and biotic components of metacommunities (Castillo-Escrivà et al., 2020). Highly dynamic systems have emerged as testing grounds for assessing context-dependencies, and intermittent streams are increasingly recognized as useful study systems (Leonidas et al., 2020; Sánchez-Montoya et al., 2020). As an example, the case study of Little Creek highlighted the issue of context-dependencies by revealing concepts developed in other systems showed partial, but not complete, ability to predict metacommunity patterns. Advancing toward an integrative theory of metacommunity ecology first requires understanding where and when theoretical expectations do not hold, and then developing research to address these areas (Brown, Sokol, Skelton, & Tornwall, 2017). Advancement will ultimately come from either refining metacommunity theory, improving the methods used to test theory, or perhaps both (Leibold & Chase, 2017).

Future research in intermittent streams can advance metacommunity ecology theory by addressing research needs identified in our review. Predicting patterns for multiple taxa requires spanning taxonomic boundaries and is best explored through functional traits such as demography, life history, and ecophysiology. Functional traits are increasingly recognized as useful for understanding environmental regulation of communities, and recent trait-based approaches to metacommunity ecology in intermittent streams provide a foundation on which future research can be built (Cañedo-Argüelles et al., 2015; Leigh et al., 2016b; Rogosch & Olden, 2019). Of particular value will be studies that

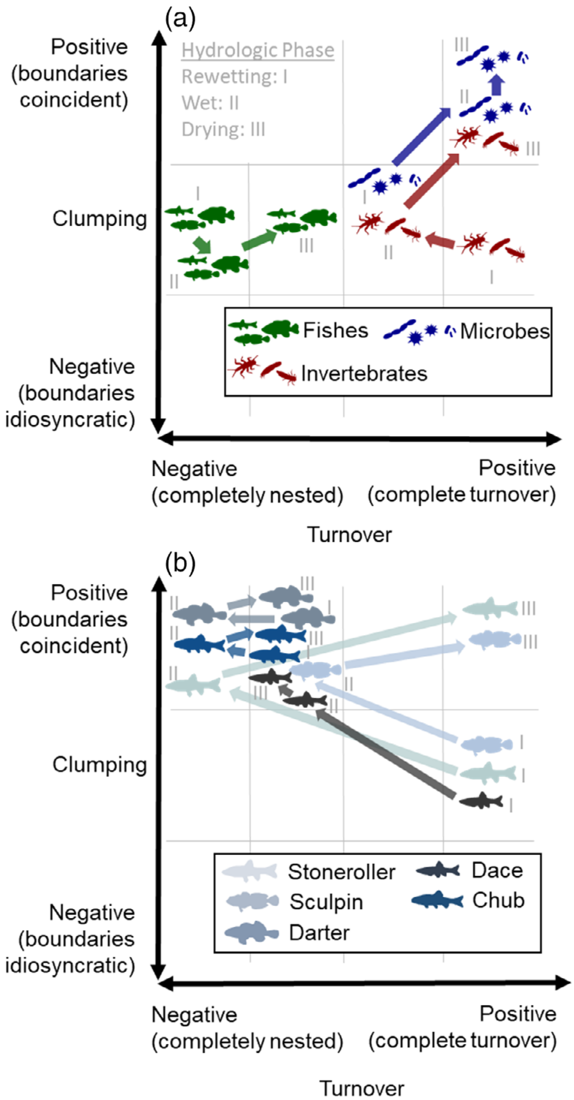

FIGURE 7 Temporal trajectories for metacommunity structures for (a) water microbe, invertebrate, and fish metacommunities and (b) cutaneous microbiome metacommunities on the skin surface of five fish species sampled during rewetting (December 2016), wet (April 2017), and drying (October 2017) hydrologic phases. For both panels, gray lines define 12 grid cells representing metacommunity structures described by Presley et al. (2010) and shown in Figure 1b. Arrows and roman numerals next to symbols indicate trajectories among hydrologic phases, starting with the rewetting phase (I), then the wet phase (II), then the drying phase (III)

contrast trait-based processes in intermittent streams with recently documented patterns in other dynamic systems (e.g., floodplains; De Campos, Lansac-Tôha, da Conceição, Martens, & Higuti, 2018) or highly connected aquatic systems (e.g., lakes; Vilmi, Tolonen, Karjalainen, & Heino, 2017). Development of improved methods used for measuring or approximating dispersal is another focal area for future research (Cid et al., 2020). Recent work in intermittent streams suggests improving applied metacommunity theory will come from development of alternative spatial proxies for dispersal (Tonkin et al., 2018), traits describing dispersal mode (Cañedo-Argüelles et al., 2015), or directly observing dispersal (Hedden & Gido, 2020). Similarly, research incorporating a greater variety of taxa is needed to assess questions of scale in metacommunity ecology, particularly taxa with varying body size (De Bie et al., 2012; Soininen, Heino, & Wang, 2018). Our review revealed that aquatic invertebrates have so far dominated research in intermittent stream metacommunity ecology, but the Little Creek case study highlighted that patterns observed for these taxa do not uniformly apply to organisms with larger (fishes) or smaller (bacteria) body sizes, life spans, life cycles, or that may or may not share dispersal modes with invertebrates. Finally, inclusion of multiple temporal scales in assessments of metacommunity ecology will reveal the pace and tempo of community dynamics. Intermittent streams provide the opportunity to assess multiple temporal scales because water levels fluctuate on scales ranging from daily to annual cycles. Although formal assessments of temporal scale on metacommunity investigations exist for aquatic systems such as perennial lakes (Benito, Fritz, Steinitz-Kannan, Vélez, & McGlue, 2018) and streams (Castillo-Escrivà et al., 2020), this remains a prime area for research in intermittent streams. Additional further research directions for intermittent streams are provided in earlier reviews conducted by Datry et al. (2016), Leigh, Boulton, et al. (2016a), and Cid et al. (2020).

6 | CONCLUSION

Understanding the ecological impacts of intermittency is essential for predicting stream biodiversity responses and setting water management goals in areas where intermittency is expected to increase in prevalence (Eng, Wolock, & Dettinger, 2015; Reynolds, Shafroth, & Poff, 2015; Ruhi et al., 2016). Such predictions are possible through application of theoretical frameworks such as metacommunity theory, but past applications of the theory focused on: (a) spatial patterns over temporal dynamics, (b) a single taxonomic group (pointed out in Fattorini, Dennis, & Cook, 2011; Henriques-Silva et al., 2019), (c) terrestrial or perennial stream ecosystems (reviewed by Datry et al., 2016; Heino, Melo, et al., 2015a), and (d) a subset of possible typologies (reviewed by Brown et al., 2017). We reviewed the current state of the science and discovered that recent conceptual models provided some predictive ability in a previously unstudied system, but there is still additional work to be done in pursuit of a unified theoretical framework. Closing the gaps in knowledge regarding biodiversity response to intermittency will ultimately require interdisciplinary research spanning taxonomic boundaries, assessing multiple spatiotemporal scales, and incorporating new tools for measuring structural (e.g., connectivity) and functional (e.g., traits) aspects of metacommunities (Sabater et al., 2016; Tonkin et al., 2018). Once multitaxa patterns and predictions of metacommunity structure in intermittent streams are uncovered, they can ultimately be used to inform biodiversity survey designs (Mazor, Stein, Ode, & Schiff, 2014; Stubbington et al., 2018) and policies governing protection of these ecosystems (Acuña et al., 2014; Colvin et al., 2019; Fattorini et al., 2011; Leigh, Boulton, et al., 2016a).

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AUTHOR CONTRIBUTIONS
Joshuah Perkin: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; writing-original draft; writing-review & editing. **Isabel Papraniku:** Conceptualization; data curation; formal analysis; investigation; methodology; writing-original draft; writing-review & editing. **W Gibbs:** Conceptualization; data curation; formal analysis; investigation; methodology; writing-original draft; writing-review & editing. **David Hoeinghaus:** Conceptualization; investigation; methodology; writing-original draft; writing-review &-editing. **Donald Walker:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; supervision; writing-original draft; writing-review & editing.

CONFLICT OF INTEREST
The authors have declared no conflicts of interest for this article.

DATA AVAILABILITY STATEMENT
High-throughput DNA sequencing data are available on GenBank (accession number PRJNA599353). All other data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

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

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