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COMMUNITY ECOLOGY – ORIGINAL RESEARCH

Functional trait sorting increases over succession in metacommunity mosaics of fish assemblages

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Abstract

Metacommunity theory predicts that the relative importance of regional and local processes structuring communities will change over time since initiation of community assembly. Determining effects of these processes on species and trait diversity over succession remains largely unaddressed in metacommunity ecology to date, yet could confer an improved mechanistic understanding of community assembly. To test theoretical predictions of the increasing importance of local processes in structuring communities over successional stages in metacommunities, we evaluated fish species and trait diversity in three pond metacommunities undergoing secondary succession from beaver (*Castor canadensis*) disturbance. Processes influencing taxonomic and trait diversity were contrasted across pond communities of different ages and in reference streams. Counter to predictions, the local environment became less important in structuring communities over succession but did exert a stronger effect on trait sorting. Beta diversity and trait richness declined over succession while there was no influence on species richness or trait dispersion. The trait filtering in older habitats was likely a response to the larger and deeper pond ecosystems characteristic of late succession. In contrast to these observed effects in ponds, the local environment primarily structured species and trait diversity in streams. Analyses of the relative importance of regional and local processes in structuring fish assemblages within each pond metacommunity suggests that habitat age and connectivity were more important than the environment in structuring communities but contributions were region and scale-dependent. Together, these findings highlight that regional and local processes can differentially influence taxonomic and trait diversity in successional metacommunity mosaics.

Keywords Beaver pond · Chronosequence · Diversity-age · Scale-dependence · Secondary succession

Introduction

The mechanisms structuring biological and functional trait diversity operate over both space and time (Chesson 2000; Levin 2000). To predict and explain patterns of diversity over multiple spatial scales, the metacommunity concept invokes regional processes such as species dispersal in addition to local niche-based processes (Leibold et al. 2004). The incorporation of succession into metacommunity studies to explain species and trait diversity remains limited (Sferra et al. 2017; Schiesari et al. 2019), however, despite such temporal scale processes being well-established to influence community structure (Cowles 1899; Alexander et al. 2012). Across landscapes, natural and anthropogenic perturbations create a geographic mosaic of different successional stages maintained by a patchy disturbance regime (Prach and Walker 2011; Meiners et al. 2015). Despite the high frequency of secondary succession operating in contemporary landscapes, the relative importance of regional and local processes in influencing community and trait structure along successional mosaics in metacommunities remains largely unknown.

According to metacommunity theory, the time since local disturbance may mediate community assembly and trait diversity as the relative importance of regional and local processes changes over succession (Mouquet et al.

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2003). Early successional stages are often characterized by high species turnover influenced by both regional (e.g., dispersal), and trait-based (e.g., competition–colonization tradeoffs or growth rate), drivers (Pacala and Rees 1998; Young et al. 2001). In heterogeneous landscapes characterized by low connectivity, dispersal limitation constrains the number of species that arrive to newly disturbed patches effectively limiting species colonization potential during the initial stages of succession (De Bie et al. 2012; Moritz et al. 2013). This scenario places increased importance on priority effects influencing community assembly (Fukami 2015). Priority effects can occur when competition–colonization tradeoffs drive fast local dynamics while limiting immigration (Yu and Wilson 2001). Conversely, late successional stages may be more structured by local species sorting and associated competitive exclusion, with resulting declines in species diversity (Mouquet et al. 2003; Li et al. 2016). During these later stages, dispersal limitation is reduced, invasion resistance is increased (Law and Morton 1996), and there is greater trait convergence (Fukami et al. 2005). Since dispersal is often no longer limiting late in succession, communities can demonstrate colonization failures based upon strong biotic interactions or inadequate resource availability (Inouye and Tilman 1995; Cadotte et al. 2006). In contrast to these successional stage-dependent patterns, high connectivity landscapes often do not experience priority effects or dispersal limitation and are characterized by homogenous communities and trait distributions (Mouquet and Loreau 2003; Howeth and Leibold 2010). Consequently, communities connected by high dispersal rates are likely less sensitive to the local processes mediating succession and may lack distinct assemblages across successional stages.

In low and moderately connected regions, local environmental characteristics that can structure community and trait composition often vary throughout succession with different possible response trajectories (Horn 1974; Pickett et al. 1987). Odum (1969) suggests succession can alter biogeochemical cycling, preventing loss of, or expand the storage of, major nutrients such as nitrogen and phosphorus in both terrestrial and aquatic ecosystems. These environmental shifts over the successional trajectory can influence multiple local processes and have the potential to structure communities and the ecological and life history trait composition of species (Tilman 1993; Mouillot et al. 2013). Subsequent changes in local dynamics may depend on the resource gradients restricting species (Keddy 1992), the exclusion of weaker competitors by stronger ones (Hardin 1960), and the risk of predation and availability of prey refugia (Howeth and Leibold 2010). These processes can lead to the convergence of viable local trait strategies within a successional stage. In contrast, the local niche space along the environmental gradient may promote limiting similarity (MacArthur and Levins 1967; Winemiller 1991) and stabilizing mechanisms (Chesson 2000) that regulate functionally unique species and lead to the divergence of traits within an assemblage. Together, these processes may operate differentially over succession to determine species and trait diversity at each successional stage, with proportional consequences to regional species and trait diversity in the metacommunity.

The relative importance of regional and local processes in structuring species and trait diversity in successional metacommunity mosaics remains empirically unaddressed. The successional trajectories of beaver-formed (*Castor* spp.) ponds offer a model system for testing these diversity responses. The ponds are spatially discrete aquatic patches connected by species dispersal via a stream network in watershed landscapes and vary in their time of formation and thus successional stage to yield metacommunity mosaics (Johnston and Naiman 1990; Brown et al. 2011). The differential effects of pond age on local ecosystem properties is poorly understood, but recent work suggests linear environmental trajectories along chronosequences (Sferra et al. 2017). As ecosystem engineers, beavers can have large effects on the biological, chemical, and physical characteristics of aquatic habitats as they convert streams to ponds from dam construction and initiate secondary succession (Naiman et al. 1988; Rosell et al. 2005). Habitat alterations catalyzed by beaver dams can change local hydrology and increase habitat heterogeneity that correspondingly influences community composition and trophic structure (Wright et al. 2002; Anderson and Rosemond 2007; Smith and Mather 2013). Previous studies demonstrate effects on the diversity of zooplankton (Sferra et al. 2017), macroinvertebrates (Law et al. 2016; Bush et al. 2019), and macrophytes (Ray et al. 2001), and the attributes of fish assemblages (Collen and Gibson 2000). The differential response of fish community and trait composition to the successional stage-dependent environments of beaver ponds remains understudied; however, where earlier work has only compared fish community composition in streams to ponds (Smith and Mather 2013) or to very coarse successional stages (Snodgrass and Meffe 1998; Schlosser and Kallemeyn 2000). Although no work has evaluated ecological and life history traits in fishes across beaver pond successional stages, previous studies assessing effects of low-head dams on stream communities demonstrate influences on trophic and reproductive traits (Helms et al. 2011; Smith et al. 2017). The effect of secondary succession on species and trait diversity in metacommunities may depend on the spatial, temporal, and environmental template maintained by the successional mosaics, but these responses remain unaddressed in any taxonomic group.

To test theoretical predictions of the relative importance of regional and local processes on species and trait diversity over successional stages and within metacommunity mosaics, we evaluated fish assemblages in three beaver pond metacommunities. Processes influencing diversity and composition in pond fish communities of different successional stages were contrasted with reference stream fish communities and were predicted to increase local species and trait richness in ponds following greater local habitat heterogeneity and ecosystem size after dam formation (Smith and Mather 2013). Following theory, we predicted that communities in younger ponds would be structured more by regional effects and consequently would exhibit low species and trait richness and higher beta diversity among communities in the same early successional stage from dispersal limitation (Mouquet et al. 2003; Fukami 2015). During mid-successional stages, local processes were predicted to become more important in structuring communities in increasingly heterogeneous habitats (Ray et al. 2001; Law et al. 2017), and, therefore, species richness would be higher (Mouquet et al. 2003; Sferra et al. 2017), beta diversity would be lower and trait richness would be higher (Purschke et al. 2013) relative to earlier successional stages. The communities located in the oldest ponds were predicted to be primarily structured by local processes, where species richness (Snodgrass and Meffe 1998; Mouquet et al. 2003), beta diversity, and trait richness (Purschke et al. 2013; Li et al. 2016) were hypothesized to decline in these more stable communities that are closer to equilibrium. Finally, the differential importance of these local and regional processes may depend upon the range of successional stages and degree of habitat connectivity represented within each metacommunity through scale-dependent effects (Rolls et al. 2018; Viana and Chase 2019).

Methods

Study system

The study sites included 24 ponds and nine headwater streams distributed among three regional watersheds in the Talladega National Forest in central Alabama, USA (Online Resource 1: Fig. S1). All ponds were actively maintained by North American beaver (*Castor canadensis*) and represented stream-connected habitats that vary in time of formation and thus successional stage. Eight beaver ponds and three upstream reference reaches were located in each of three United States Geological Survey 12-digit hydrologic unit code (HUC-12) watersheds, corresponding to three metacommunities regionally constraining fish dispersal therein. Two metacommunity watersheds drain to the Black Warrior River (HUC-031601130103, hereafter watershed, region, or metacommunity ‘A’, and HUC-031601130401, ‘B’), while the third drains to the Cahaba River (HUC-031502020505, ‘C’). Average air temperature for the duration of the study, May 2016 to February 2017, was 18.86 °C and the total precipitation was 66.01 cm.

To delineate chronosequences, an estimated year of pond formation (pond age) for 16 sites was established using a combination of dendrochronological methods and historical aerial photography analyses previously applied in the study system (Sferra et al. 2017, Online Resource 2). The age of the remaining eight ponds was taken from Sferra et al. (2017).

Species and environment sampling

Fish communities were characterized in the 24 ponds and nine stream reaches over three sampling periods in 2016 and 2017: 13 April–4 June; 28 June–29 August; and 2 October–4 February. In each watershed, three stream sites located upstream of study ponds were selected to represent 100 m of stream habitat and were located at least 100 m above the pond to eliminate any potential pond effects on the fish assemblage.

Each of the three pond fish community surveys consisted of a standardized combination of seine, fyke net, and minnow trap sampling. Four seine (1.2 m × 3.0 m net, 4.76 mm mesh) hauls along the pond perimeter were conducted. One fyke net (0.6 m × 1 m, two 3.7 m wings, 6.35 mm mesh) was deployed in each pond for 12 h from dusk to dawn. Twelve minnow traps with a standardized combination of three aperture widths (25.4 mm, 38.1 mm, and 50.8 mm) to target different fish size classes were also set for 12 h. To capture larger individuals that may be missed utilizing these methods, the ponds were additionally sampled with (1) two single-winged fyke nets connected by a 3.7 m lead and deployed for 12 h during survey two and (2) one daytime 2-h angling session during survey three. Because of drought conditions and associated low water levels that prevented trap and net deployment, two ponds (Pond 8, 22) could not be sampled during the second survey (total precipitation, 2.34 cm; average air temperature, 20.67 °C) and two ponds (1, 8) could not be sampled during the third survey (total precipitation, 8.48 cm; average air temperature, 15.32 °C). Each stream fish community survey consisted of a standardized combination of four seine hauls, the 12-h deployment of six minnow traps with a standardized set of the three apertures, and three 100-m passes of backpack electrofishing with block nets (Smith-Root LR-20; Smith-Root Incorporated, Vancouver, Washington, USA). Low flow conditions prevented sampling of three streams during survey two (upstream of ponds 1, 7, 24) and one stream during survey three (upstream of pond 1). All captured fish from the pond and stream sampling efforts were identified to species using regional references (Mettee et al. 1996; Page and Burr 1997; Boschung and Mayden 2004) and measured to the nearest 0.1 mm (standard length, SL) before being released.

The pond and stream environments were surveyed concurrently with the fish to evaluate pond response to succession. At the deepest location within each pond, conductivity, pH (YSI Model 63; Yellow Springs Instruments, Yellow Springs, OH, USA), dissolved oxygen (YSI Model ProODO), and water depth were measured. Water samples were additionally collected for nutrient analyses from the middle of the water column using a 0.75 m-long 5-L vertical sampler. The area of aquatic vegetation cover of each pond, including macrophytes and semi-aquatic vegetation, was measured with a handheld global positioning system (GPS; Garmin Model eTrex10, Olathe, Kansas, USA) and converted to proportion cover. In spring 2016, the perimeter of each pond was walked once and the area calculated on a GPS for 16 of the study ponds. The area of the remaining eight ponds was acquired from a previous study (Sferra et al. 2017). In the laboratory, pond water was vacuum filtered onto glass fiber filters (Whatman GF/F; GE Healthcare, Tokyo, Japan). From the filtrate, colored dissolved organic carbon (CDOC) was measured using a UV spectrophotometer (Shimadzu UV-1800, Columbia, Maryland, USA) (Cuthbert and Del Giorgio 1992). Total dissolved nitrogen and phosphorus (TDN and TDP) were analyzed from the filtrate using standard spectrophotometric methods after persulfate digestion (Prepas and Rigler 1982; Crumpton et al. 1992). In streams, at the 50-m (halfway) location, conductivity, pH, dissolved oxygen, and water for nutrients were sampled. The stream maximum wetted width and maximum water depth were also measured during each survey. For the nine pond–stream pairs, temperature data loggers (HOBO Pro v2; Onset Computer Corporation, Pocasset, Massachusetts, USA) were placed approximately 15 cm below the water surface in each habitat to monitor water temperature every 12 h. Sites that were not sampled for fish communitites because of drought conditions were also not surveyed for the environment.

Species traits

Ecological, life history, and phylogenetic traits in fishes that may be responsive to dam barriers and successional stage were identified from literature (Helms et al. 2011; Hitt and Roberts 2012; Howeth et al. 2016; Smith et al. 2017). A total of nine traits for study species was acquired from a publicly available online database (FishTraits; Frimpong and Angermeier 2009) and literature (Nelson et al. 2016; Online Resource 3: Table S1). Ecological traits included (1) macrohabitat association (lentic, lotic); (2) temperature tolerance range (sum of maximum and absolute value of minimum temperatures); and (3) trophic guild (herbivore-detritivore, invertivore, invertivore-piscivore, omnivore, and adults do not eat). The life-history traits included (4) body size (maximum total length in cm); (5) fecundity (count of maximum eggs per spawning season, per female); (6) longevity (maximum lifespan in years); (7) reproductive guild (non-guarders and open substratum spawners, non-guarders and brood hiders, guarders and substratum choosers, guarders and nest spawners, and substrate indifferent); and (8) spawning frequency (batch, serial). Phylogenetic relatedness (9) was accounted for following the approach of Grafen (1989) by ranking species according to their family membership (i.e., their degree of derived characters, ordered from most ancient to most derived) from Nelson et al. (2016).

Statistical analyses

To test for the effects of succession on community and trait assembly, study sites were binned into four categories based upon habitat type defined by a previous study of successional stages in this system that showed differences in zooplankton community response (Sferra et al. 2017): (1) streams ($n=9$), (2) age class one ponds (24–39 years; $n=8$), (3) age class two ponds (42–57 years; $n=10$), and (4) age class three ponds (60–70 years; $n=6$).

Local species and trait diversity

To determine whether species and trait diversity differed over succession, the effects of habitat type on local fish richness, beta diversity, functional trait richness, and trait dispersion were tested. Cumulative local fish species richness was calculated from the three surveys. From this data set, beta diversity was measured among all community pairs within a habitat type using the incidence-based Raup–Crick dissimilarity index that determines if beta diversity values are different than what would be expected by chance (Chase et al. 2011). The dissimilarity index was calculated with the "raupcrick" function using the community ecology package 'Vegan' (Oksanen et al. 2013) in the R statistical environment (version 3.4.2; R Foundation for Statistical Computing, Vienna, Austria). Trait richness was obtained using the convex hull volume calculation and represents the multidimensional trait space occupied by each community (Cornwell et al. 2006; Villéger et al. 2008). This index requires a greater number of species than the number of traits tested. For two of the stream sites, trait richness could not be calculated because observed species richness was less than the number of traits. Trait dispersion represents the average distance to the centroid of all the species in a community, when those species are plotted in multidimensional trait space (Laliberté and Legendre 2010). Trait richness and dispersion were evaluated using the nine traits in the data set with the "dbFD" function in the 'FD' package in R (Laliberté and Legendre 2010). Community and trait diversity values were contrasted by the four habitat type categories with a one-way ANOVA. Normality (Shapiro–Wilk), equal variance

(Bartlett), ANOVA, and Tukey's HSD post-hoc tests were performed in R.

In order to test for differences in community composition between habitat type and pond successional stage, permutational multivariate ANOVA and permutational analysis of dispersion using Bray–Curtis distances calculated from average abundance were performed. For the analyses, (1) stream-pond pair communities ($n = 9$ pairs) were contrasted by habitat type, streams and ponds, and (2) the 24 pond communities were binned into the three pond age classes. Analyses were conducted with the "adonis" and "betadisper" functions using 9999 permutations in 'Vegan.' The response of individual taxa to stream versus pond habitat for all 33 study sites, and the three pond age classes for the 24 ponds, were analyzed separately with indicator species tests (Dufrêne and Legendre 1997). An indicator species analysis evaluated the response of each species to habitat type and pond age class based on relative abundance and frequency of occurrence in each category to produce an indicator value (IV). IVs are the percentage score corresponding to a species categorical occurrence, where a score of 100 indicates a perfect categorization. Indicator species analyses were performed in PC-ORD (version 6.08, MjM software, Gleneden Beach, Oregon, USA; McCune and Mefford 2011) using 9999 permutations.

Local environment

To assess differences between the stream environments and the pond environments in the nine stream–pond pairs, standard effect sizes and *t* tests were used for each of the eight environmental variables that were measured in both habitat types and that represented average survey values. These variables included CDOC, conductivity, dissolved oxygen, maximum depth, pH, water temperature ($n = 8$ pairs due to equipment failure), TDN and TDP. Standard effect size was calculated as the difference between the pond mean and the stream mean divided by the mean of the pond and stream standard deviations (Osenberg et al. 1997). To evaluate the response trajectory of environmental variables to pond age, linear regression was applied as informed by modeling a subset of the ponds (Sferra et al. 2017). Each of nine variables, a single measurement of area and the average over three sampling periods of CDOC, conductivity, dissolved oxygen, maximum depth, pH, proportion vegetation cover, TDN, and TDP were modeled as a function of pond age in years. Normality tests (Shapiro–Wilk), linear modelling, and *t* tests were performed in R.

Metacommunity structure

To determine whether local processes become more important in structuring fish community composition and trait dispersion over succession, Mantel tests were used to evaluate correlations between community and trait composition and the environment for streams and each pond age class for all 33 study sites (Douglas and Endler 1982; Allen et al. 2011). For each of the four habitat type categories: (1) Bray–Curtis matrices, calculated from mean species abundance, and (2) trait dispersion matrices, calculated as the Euclidean distances between the trait dispersion site values, were related to the environment. The environmental distance matrices were generated from the pairwise difference of principal component (PCA) axis 1 site scores produced from centered and standardized mean variables, a method which preserves variation in the data set (Borcard et al. 1992). For the stream PCAs, seven variables were used: conductivity, dissolved oxygen, maximum water depth, pH, TDN, TDP, and wetted width. The resulting PCA axis I explained 57% of the environmental variance in streams. For the pond PCAs, eight variables were used: conductivity, dissolved oxygen, maximum depth, pH, pond area, TDN, TDP, and vegetation cover. The resulting PCA axis I explained between 31 and 44% of the environmental variance for the pond age classes.

To test for any metacommunity- and scale-dependent differences in the amount of variation in fish community structure contributed by the local environment, habitat age, and spatial processes among the eight ponds within each of the three regions, partial Mantel tests were performed (Smouse et al. 1986). Community dissimilarity was based upon Bray–Curtis distances calculated from mean species abundance. Environmental distances were generated from the pairwise difference of principal component (PCA) axis 1 site scores using the eight centered and standardized pond environmental variables. The resulting PCA axis I explained between 40 and 43% of the environmental variance within each metacommunity. Temporal distances were based on the pairwise difference in year of pond formation. Hydrologic distance, as a measure of pond connectivity and fish dispersal routes, was calculated as the shortest stream distance between ponds using the Network Analyst/OD Cost Matrix Tool in ArcGIS 10 (Environmental Systems Research Institute, Redlands, California, USA). For each metacommunity, partial Mantel correlations were produced between the community matrix and all pairwise combinations of environmental, temporal and hydrologic distances with each analysis controlling for a different predictor matrix. PCA and Mantel tests used 9999 matrix permutations and were performed in PC-ORD.

Results

Local species and trait diversity

There was an effect of habitat type on local fish species richness (one-way ANOVA, $F_{3,\,29} = 6.81$, $P = 0.001$,

Fig. 1a). Streams supported lower species richness than all three pond age classes, but the pond age classes did not differ from each other (Tukey HSD, streams vs. pond age class 1 $P = 0.001$, streams vs. pond age class 2 $P = 0.020$, streams vs. pond age class 3 $P = 0.037$, pond age class 1 vs. pond age class 2 $P = 0.519$, pond age class 1 vs. pond age class 3 $P = 0.704$, and pond age class 2 vs. pond age class 3 $P = 0.999$). Additionally, there was an effect of habitat type on beta diversity (one-way ANOVA, $F_{3, 119} = 17.00$, $P < 0.001$, Fig. 1b). There was higher species turnover among streams than among ponds within any age class (Tukey HSD, streams vs. pond age class 1 $P = 0.022$, streams vs. pond age class 2 $P < 0.001$, streams vs. pond age class 3 $P = 0.002$, pond age class 1 vs. pond age class 2 $P = 0.005$, pond age class 1 vs. pond age class 3 $P = 0.579$, and pond age class 2 vs. pond age class 3 $P = 0.498$). There was also a significant difference in beta diversity between the first two pond age classes, illustrating an increase in community similarity in mid- to later-successional stages.

Habitat type influenced trait richness (one-way ANOVA, $F_{3, 27} = 5.34$, $P = 0.005$, Fig. 1c). Trait richness was higher in age class 1 ponds relative to streams but marginally declined in the older class 2 and class 3 ponds (Tukey HSD, streams vs. pond age class 1 $P = 0.006$, streams vs. pond age class 2 $P = 0.051$, streams vs. pond age class 3 $P = 0.839$, pond age class 1 vs. pond age class 2 $P = 0.685$, pond age class 1 vs. pond age class 3 $P = 0.085$, and pond age class 2 vs. pond age class 3 $P = 0.408$). The effect of habitat type did not influence trait dispersion (one-way ANOVA, $F_{3, 29} = 1.50$, $P = 0.236$, Fig. 1d).

There was a significant difference in community composition between streams and ponds (PERMANOVA, $F_{1, 17} = 4.70$, $P < 0.001$). Additionally, stream community composition was more variable than pond community

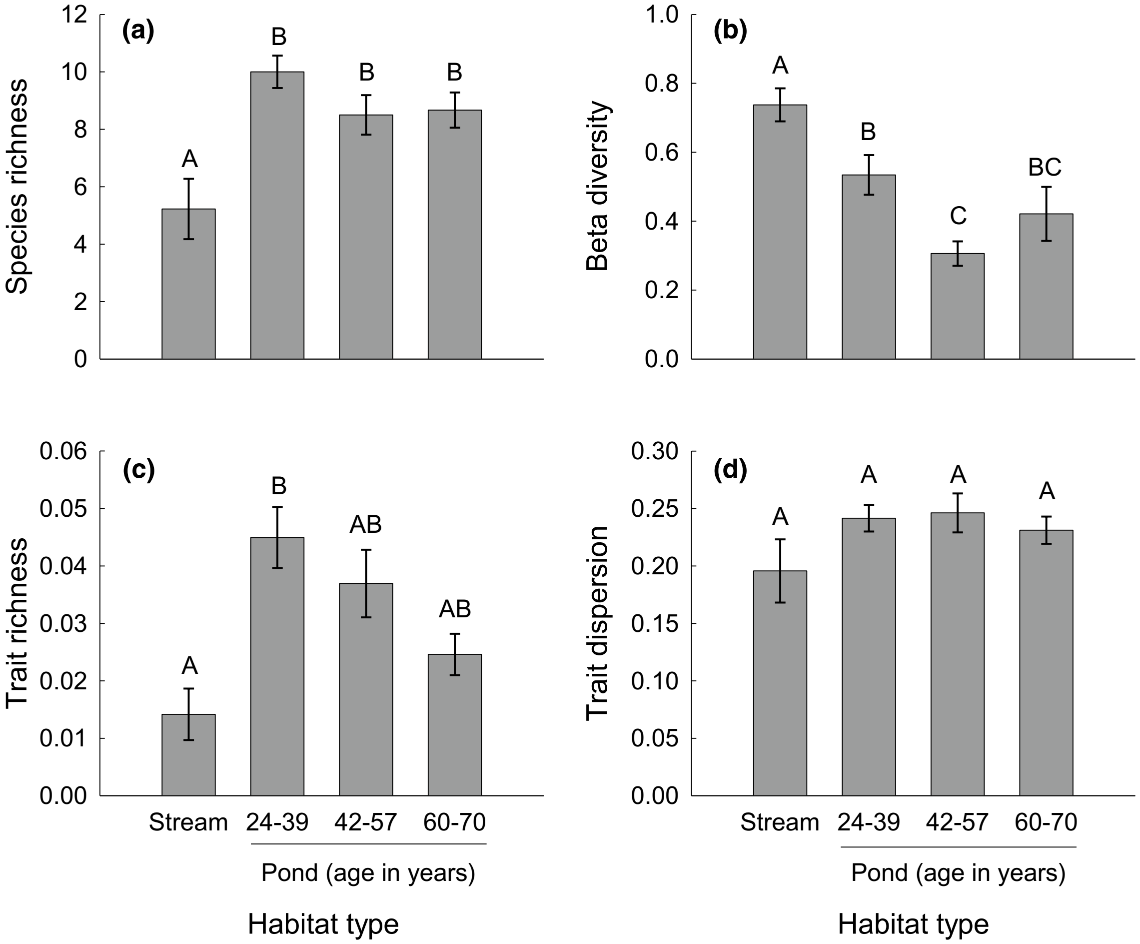

Fig. 1 **a** Species richness, **b** beta diversity, **c** trait richness, and **d** trait dispersion by habitat type. Habitat type includes streams ($n = 9$, except for **c** where $n = 7$) and ponds aggregated by age class, including those 24–39 years of age ($n = 8$), 42–57 years of age ($n = 10$), and 60–70 years of age ($n = 6$). **b** Beta diversity is the Raup–Crick dissimilarity for ponds within the same habitat type. Uppercase letters denote post hoc contrasts for effects of habitat type ($P < 0.05$). Values are mean ± 1 SE

composition (PERMDISP, $F_{1,17}=14.40$, $P=0.002$; average distance to centroid, streams: 0.529, ponds: 0.329). Seven species were indicators of either pond or stream habitat (Online Resource 4: Table S1, Fig. S1). Yellow bullhead (*Ameiurus natalis*), creek chubsucker (*Erimyzon oblongus*), warmouth sunfish (*Lepomis gulosus*), bluegill sunfish (*L. macrochirus*), and dollar sunfish (*L. marginatus*) were associated with ponds, while gulf darter (*Etheostoma swaini*) and creek chub (*Semotilus atromaculatus*) were associated with streams. Although community composition did not differ among the three pond age classes (PERMANOVA, $F_{1,23}=1.40$, $P=0.116$; PERMDISP, $F_{1,23}=0.50$, $P=0.615$), three species were significant indicators of pond age class (Fig. 2, Online Resource 4: Table S2). Blackspotted topminnow (*Fundulus olivaceus*) was an indicator of age class 1 ponds. Warmouth sunfish was an indicator of age class 2 ponds. Spotted bass (*Micropterus punctulatus*) was an indicator of age class 3 ponds.

Local environment

Among regions, ponds ranged from 24 to 70 years of age (Online Resource 5: Table S1). Pond area and maximum water depth significantly increased with the number of years since pond formation (Fig. 3a, b; Online Resource 6: Table S1–S2). No other environmental variables responded to the temporal gradient (all variables $P>0.05$). Ponds were deeper and warmer than streams (Fig. 3c; Online Resource 6: Table S3–S4).

Metacommunity structure

The Mantel tests evaluating the correlation between community composition and trait dispersion with the local environment by habitat type showed a stronger association between these variables in streams than in any of the three pond age classes (Fig. 4). There was a decreasing correlation between community composition and the environment as pond age increased (Fig. 4a). This result indicates that regional processes, such as dispersal, may be more influential in structuring fish communities as ponds become older. While the correlation between trait dispersion and the environment in ponds never exceeded that of streams, it did increase with each pond age class (Fig. 4b). This pattern suggests that trait sorting becomes relatively more important in later successional stages.

The partial Mantel tests determined the relative influence of pond age differences, spatial hydrologic distances, and the local environment on metacommunity structure (Table 1). Mantel correlations for Metacommunity A indicated that pond age most strongly structures fish community composition in the region. In contrast, the lack of any significant temporal, spatial, or environmental predictors

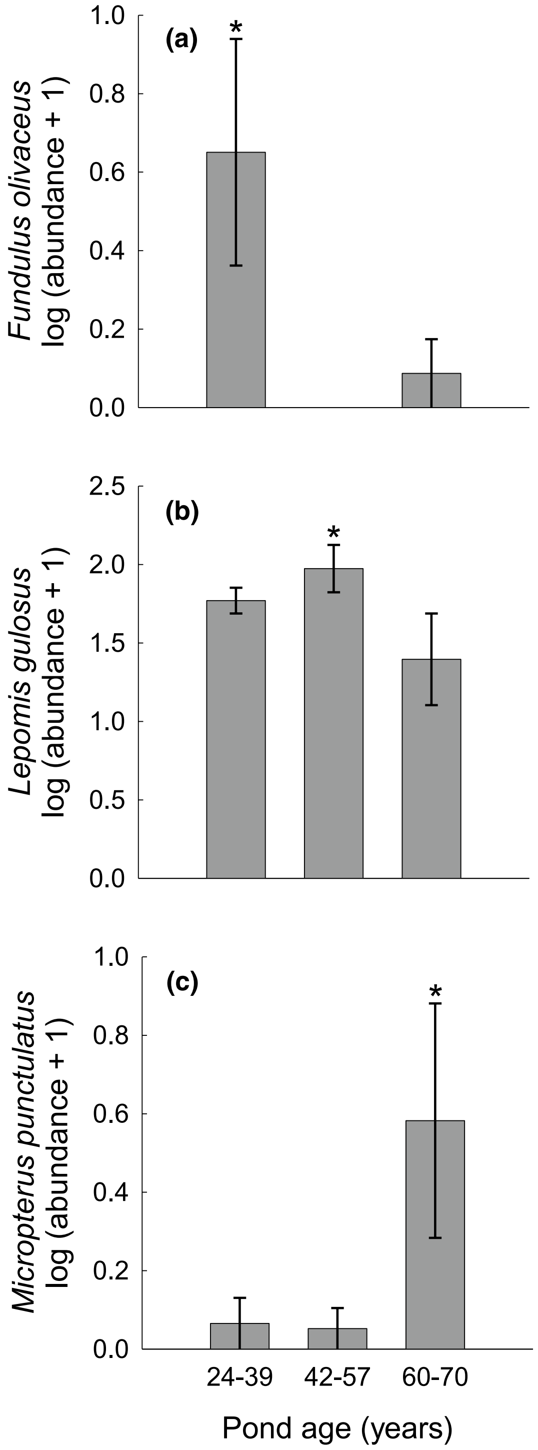

Fig. 2 Densities of indicator species by pond age class. *Fundulus olivaceus*, *Lepomis gulosus*, and *Micropterus punctulatus* density [mean log (abundance + 1) ± SE] over three sampling periods in age class 1 (24–39 years, $n=8$), class 2 (42–57 years, $n=10$), and class 3 (60–70 years, $n=6$) ponds. Asterisks indicate significant indicator species by pond age class ($P<0.05$, Online Resource 4: Table S2)

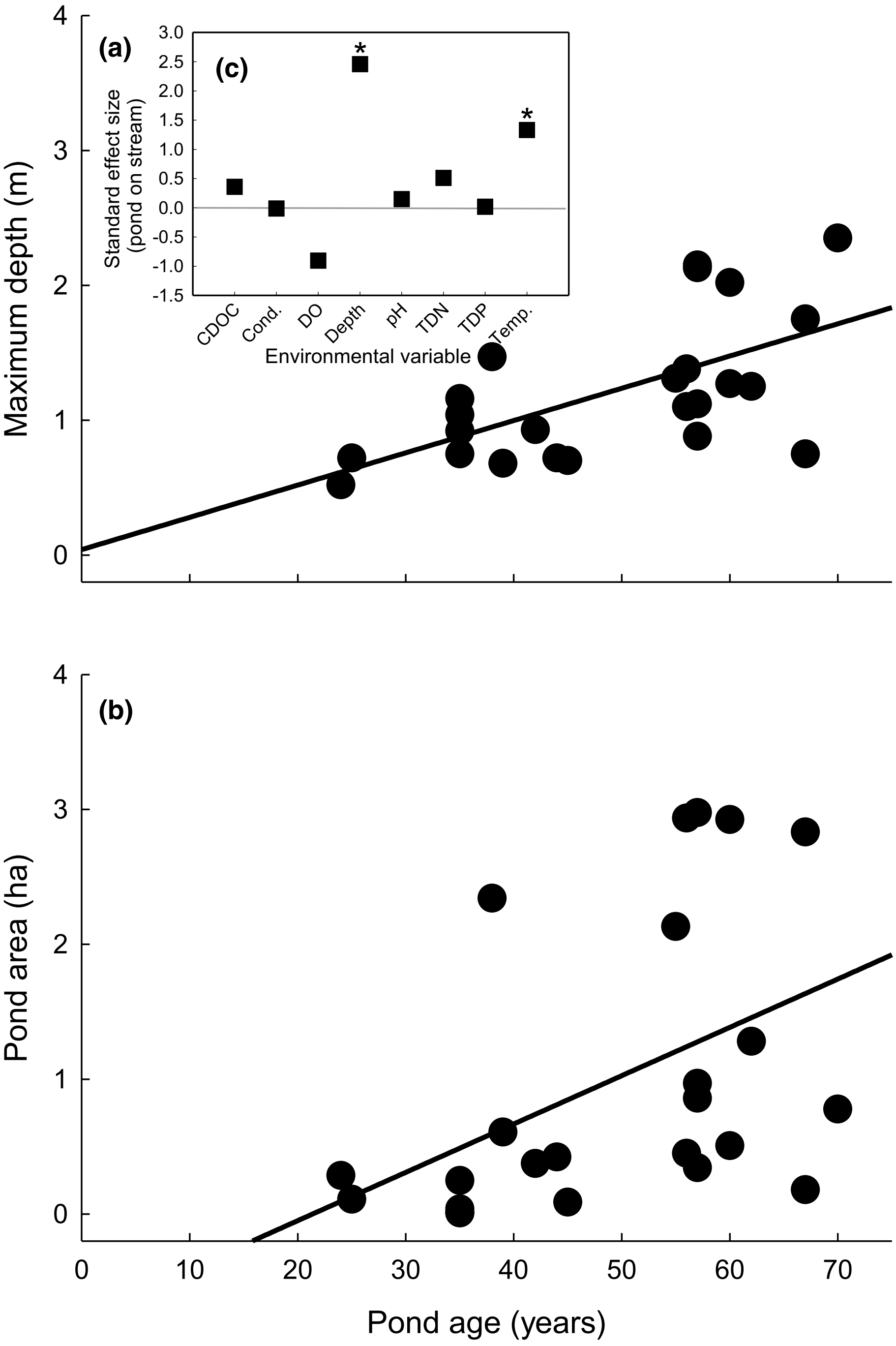

Fig. 3 **a** Maximum depth (m) and **b** pond area (ha) by pond age (years). Maximum depth represents the mean of the three sampling periods, while pond area represents a one-time measure ($n = 24$ ponds; filled circles). **c** The pond environment relative to the stream environment (pond effect) for colored dissolved organic carbon (CDOC), conductivity (Cond.), dissolved oxygen (DO), maximum depth (Depth), pH, total dissolved nitrogen (TDN), total dissolved phosphorus (TDP), and water temperature (Temp.). The standard effect size was measured as the difference between the pond mean value and the stream mean value divided by the mean of the pond and stream standard deviations. Environmental data used in the analysis represented the mean of three sampling periods for the pond-stream pairs ($n = 9$ pairs, except for water temperature where $n = 8$; filled squares). Asterisks indicate significant difference in pond and stream values in *t* tests ($P < 0.05$, Online Resource 6: Table S4)

in Metacommunity B suggested relatively greater biotic or abiotic homogenization in that group of communities and environments, respectively. Metacommunity C results demonstrated significant effects of hydrologic distance and thus the dominant influence of connectivity in structuring component local communities. The differences in the significance of correlation between habitat age and community composition among the three metacommunities can be explained by the pond age range within each region: Metacommunity A = 46 years, B = 22 years, and C = 42 years (Fig. 5a). Likewise, the significant relationship between hydrologic distance and composition in Metacommunity C reflected relatively stronger local community connectivity through greater dispersal potential via shorter distances between pond habitats as indicated by the mean hydrologic pairwise distances: Metacommunity A = 6.0 km, B = 9.6 km and C = 4.6 km (Fig. 5b).

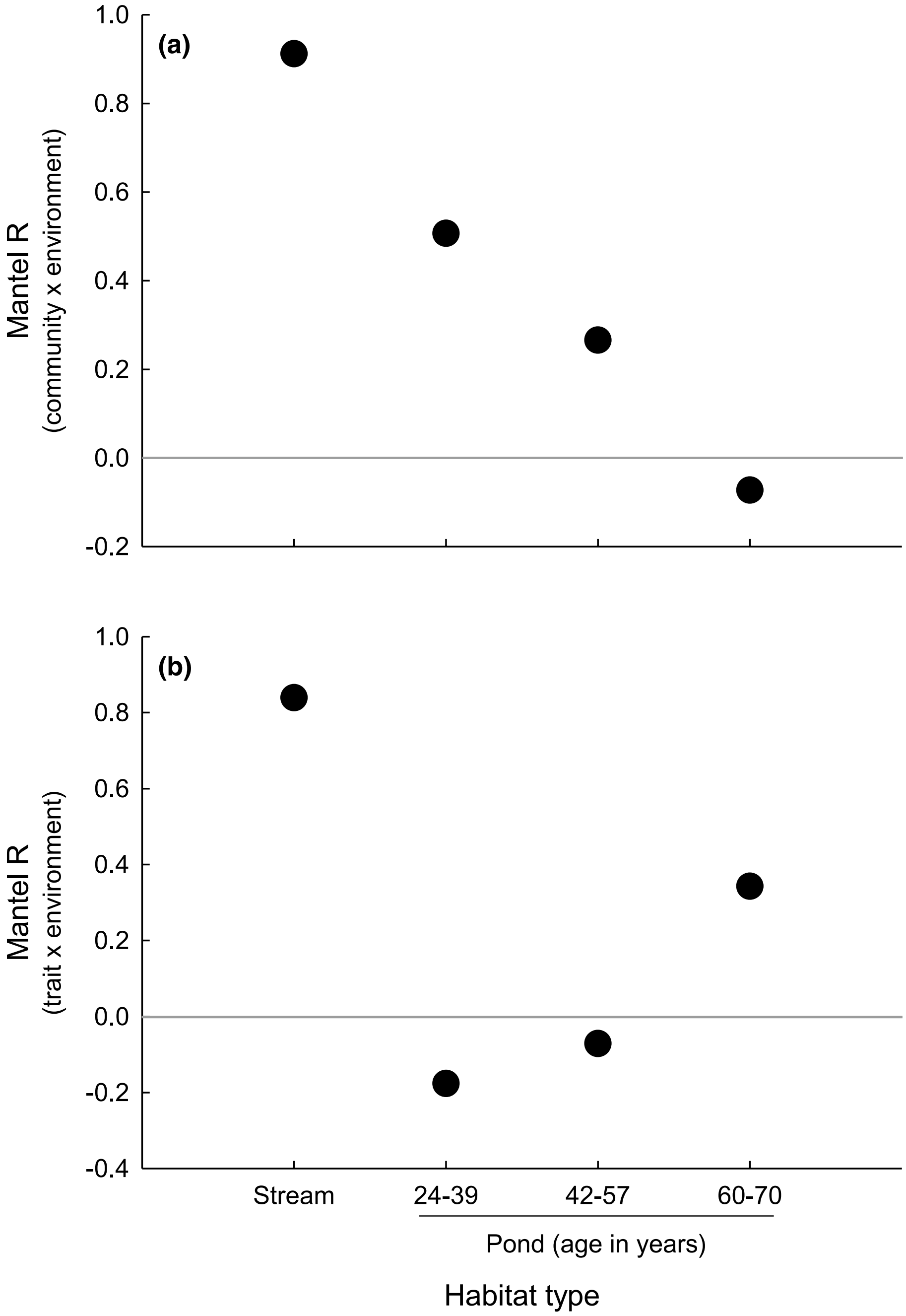

Fig. 4 The correlation between **a** community dissimilarity and **b** trait dispersion with differences in the local environment by habitat type. Habitat type includes streams ($n = 9$) and ponds aggregated by age class, including those 24–39 years of age ($n = 8$), 42–57 years of age ($n = 10$), and 60–70 years of age ($n = 6$). Values are the standardized Mantel statistic (r)

Discussion

The influence of regional and local processes in the successional metacommunity mosaics had differential and novel structuring effects on community and functional trait diversity. Counter to theoretical predictions, local environmental processes became less important in shaping communities over succession but were more important in filtering species traits. This response resulted in a lack of the hypothesized species richness relationship with succession (Mouquet et al. 2003), but did yield declines in beta diversity and trait richness while producing some species that reflected successional stages in their abundance. The trait sorting in older habitats likely was forced by the larger and deeper pond ecosystems of the late successional stages. In contrast to these effects, local processes strongly shaped the low richness and high turnover observed in the reference stream habitats. Among the three regions undergoing succession, habitat age and connectivity were more influential than local processes in structuring pond fish metacommunities. The relative contributions of these drivers were region- and scale-dependent with temporal

Table 1 Partial Mantel test correlations between fish community dissimilarity and pairwise combinations of environmental, spatial hydrologic, and temporal (pond age) distance predictors within three pond metacommunities

Metacommunity × predictor	Predictor controlled for					
	Environment		Hydrologic		Temporal	
	Correlation	*P* value	Correlation	*P* value	Correlation	*P* value
Metacommunity A						
× environment	–	–	0.05	0.43	− 0.08	0.62
× hydrologic	0.03	0.42	–	–	0.05	0.38
× temporal	0.35	**0.05**	0.35	**0.05**	–	–
Metacommunity B						
× environment	–	–	0.04	0.36	0.09	0.26
× hydrologic	0.14	0.32	–	–	0.14	0.31
× temporal	− 0.09	0.32	− 0.02	0.49	–	–
Metacommunity C						
× environment	–	–	0.08	0.34	0	0.47
× hydrologic	0.42	**0.03**	–	–	0.46	**0.03**
× temporal	− 0.19	0.21	− 0.29	0.11	–	–

Significant probability values ($P < 0.05$) in bold

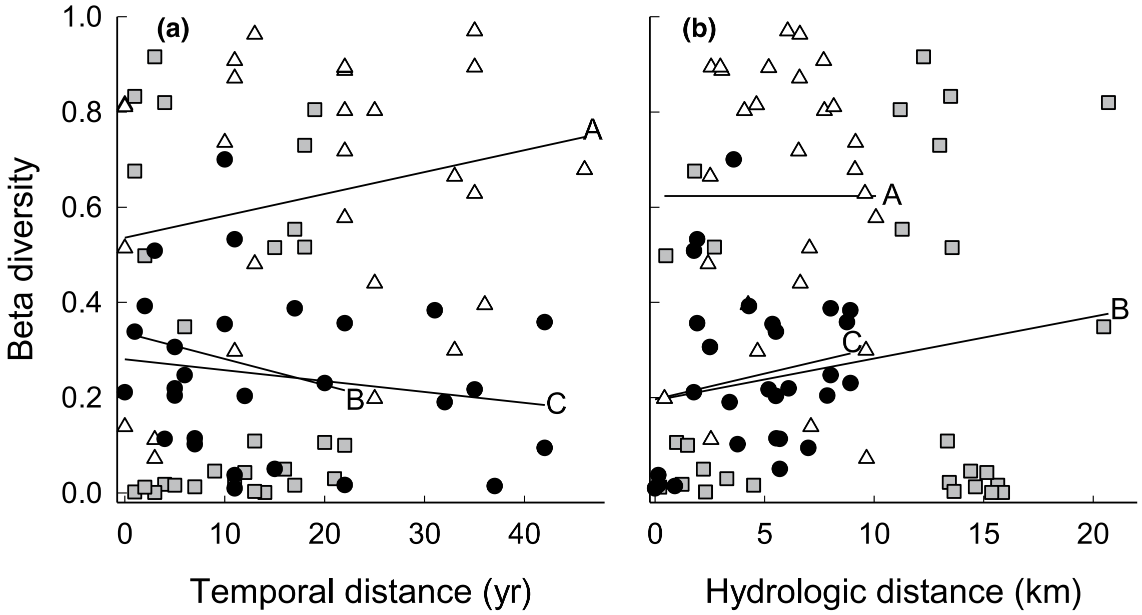

Fig. 5 Beta diversity (Raup–Crick dissimilarity) as a function of **a** temporal (age difference in years) and **b** spatial hydrologic (km) distance between pond pairs within each of the three metacommunities (A, B, C). Lines represents metacommunity-specific regressions and ranges by distance measure

effects being dominant in the metacommunity supporting the longest chronosequence and spatial effects being dominant in the more connected metacommunity. Together, the results highlight the unique contributions of local and regional processes in differentially assembling taxonomic and trait diversity over succession. They further underscore the role of both temporal and spatial scale-dependent structuring mechanisms occurring in landscapes experiencing disturbance and thus suggest the incorporation of succession into metacommunity ecology can improve understanding of drivers of diversity.

Over succession, communities exhibited lower beta diversity and a decline in trait richness driven by filtering from the local environment despite a limited response of species richness. The observed mid- and late stage patterns in community convergence and trait richness indicated stronger biotic filtering as communities approach equilibrium (Li et al. 2016). Older ponds were deeper thus generating a new niche and thermal refuge, and thereby selected for pond/lake specialists in the same family (Centrarchidae: *Lepomis* spp. and *Micropterus* spp.; Cooke and Philipp 2009) which contributed to lower species turnover and increased trait sorting through functional convergence. This increase in pond depth over succession is a consequence of the compounded effects of active beaver excavation of pond bottom sediments to seal dams and lodges and prevent water flow or intrusion (Gurnell 1998; Meentemeyer and Butler 1999). Younger ponds were shallower and thus more susceptible to drought effects and associated environmental forcing (Sferra et al. 2017). The decreasing influence of environmental processes on community composition over succession may also result from larger dams in older ponds serving as a barrier to dispersal of stream species and colonization from downstream pond populations (Schlosser 1995). The lack of species richness response to succession contrasted with the hypothesis of a unimodal diversity–age relationship based upon theoretical predictions of succession in competitive metacommunities (Mouquet et al. 2003) and with observations in zooplankton documented previously in the system (Sferra et al. 2017). The diversity–age response in zooplankton was driven by succession-driven differences in pond depth among 15 ponds, while the response of traits was not assayed. Zooplankton are not constrained to only hydrologic dispersal, have relatively short generation times, and thus may be better able to track succession-driven differences in the local environment than fish (Beisner et al. 2006). Additionally, very young ponds were not observed in this study and the earliest successional stage began 24 years post-disturbance. Any initial dispersal limitation or priority effects in these communities were likely diminished at the time of sampling from species sorting as new migrants colonized over two decades (Moyle and Light 1996; Li et al. 2016). Taken together, the unique responses of fish trait and species richness to succession highlight that traits can impart valuable information about the importance of structuring processes as compared to species richness alone.

The increase in ecosystem size after local disturbance generated new niches and expanded the volume of functional trait space available for species to occupy yielding higher species and trait richness (HilleRisLambers et al. 2012; Smith and Mather 2013). Importantly, there were observed shifts in species incidence and abundance over pond successional stages. The transition from a small-bodied indicator species (*F. olivaceus*) characterized by a short lifespan and low fecundity in young ponds, to medium- and larger-bodied indicator species (*L. gulosus* and *M. punculatus*) characterized by longer lifespans and greater fecundity in mid-aged and older ponds, are positive trends in life history traits that parallel the progression of ecosystem area and depth (Online Resource 7). These three species also highlight a shift in trophic guild over succession, transitioning from an omnivorous diet in younger ponds to an invertivore-piscivore diet in older ponds. This successional shift to a higher trophic position follows an increase in suitable zooplankton prey available in the older and deeper ponds (*Daphnia*; Sferra et al. 2017) that can support planktivory, ontogenetic diet shifts of piscivores, and ultimately piscivory of planktivores. Consequently, the temporal distribution of fishes illustrates clear patterns of correlation between ecological and life history trait composition and the local habitat conditions (Villéger et al. 2010; Giam and Olden 2016). Small-scale studies usually lack the necessary scope of limiting local conditions making it difficult to detect trait filtering effects of the environment (Jackson et al. 2001), but this limitation has been overcome in this larger-scale study encompassing multiple regions. The observed trends in trait gradients may reflect differences in assembly processes within the broader community (Hoeinghaus et al. 2007; Fitzgerald et al. 2017) and indicate an increase in trait sorting via environmental filtering later in succession.

Habitat age and connectivity were the most important factors structuring community composition within metacommunities but effects were scale-dependent. Temporal structuring dominated in the metacommunity with the longest chronosequence (Metacomm. A). This pattern likely emerged from the greatest range of assembly processes represented by the different successional stages, including any latent compositional effects of stochastic assembly in early succession to late-stage deterministic processes (Mouquet et al. 2003; Fukami 2015). Spatial structuring mechanisms operated in the metacommunity with the shortest hydrologic distance among habitats (Metacomm. C). In this region, the close proximity to source populations and higher local immigration rates may be more important regulators of community composition than succession (Mouquet and Loreau 2003; Viana and Chase 2019). Finally, the third metacommunity (Metacomm. B) supported longer hydrologic distances and half the habitat age range of the other two regions, yet had no detectable structuring processes. The similar successional states likely experienced common pressures and without apparent dispersal limitation, thus yielding little variation in community composition and the local environment. While previous studies have emphasized the importance of either habitat age (Horsák et al. 2012; Amici et al. 2013) or spatial connectivity (Beisner et al. 2006; Brown et al. 2011) in shaping community structure, the results of this study highlight the scale-dependent role of both temporal and spatial processes operating within metacommunities undergoing secondary succession.

The results reported herein emphasize that taxonomic and trait diversity can differentially impart community assembly responses to succession and that such effects often require broad habitat age ranges relative to the generation times of study organisms (Allen et al. 2011; Sferra et al. 2017).

Temporal scale-dependent diversity responses may be particularly common in studies of secondary succession which are often constrained by short time periods due to frequent local disturbance. As supporting examples, results from following invertebrate community assembly in temporary rock pools over 12–140 days showed that life history dispersal mode influenced the contrasting species richness response to hydroperiod length (Vanschoenwinkel et al. 2010). During woody plant succession of tropical dry forests, functional groupings defined by dispersal syndrome contributed to the community assembly of plants only after 15 years (López-Martínez et al. 2013). Together with this study, these works illustrate that species and trait sorting processes can exhibit stage-specific mechanisms (Loranger et al. 2016) and further convey the benefit of a functional approach to succession dynamics and community assembly (Fukami et al. 2005; Meiners et al. 2015). As these are observed patterns among complex multi-trophic ecosystems, however, the underlying drivers producing the taxonomic and functional trait responses cannot be definitively tested or identified. In addition to insights gained from simplified experiments that are often used to confront metacommunity theory, natural model systems that are undergoing succession such as ponds and forest fragments will play an important role in testing theoretical predictions situated at the interface of succession and metacommunity ecology (Logue et al. 2011). The key finding that local and regional processes differentially influence taxonomic and functional diversity over succession in natural spatial mosaics reinforces the need to integrate the role of succession into metacommunity ecology.

This study is one of the first tests of the predicted mechanisms structuring species and trait diversity in multiple successional metacommunity mosaics. Theory communicates an increased role for local processes in driving species and trait sorting over succession (Mouquet et al. 2003); yet, results from three metacommunities of fish assemblages reveal that the local environment is generally less important in structuring communities but more important in structuring traits in older ecosystems. This response highlights the unique contributions of local and regional processes in influencing taxonomic versus trait diversity over multiple successional stages. Among regions, habitat age and connectivity were more influential in governing mosaics of fish assemblages than the environment, but their relative importance was scale-dependent by metacommunity. The major finding that succession can contribute to species and trait diversity in metacommunities suggests that habitat age and successional stage should routinely be considered in studies isolating drivers of diversity, with responses contrasted across ecosystems and taxa. These results support a paradigm shift in community ecology building from a recent focus on spatial processes (Leibold et al. 2004; Logue et al. 2011) towards the integration of equally important temporal processes which, together, will be required to fully understand regulators of biological and trait diversity (Alexander et al. 2012; Chang and Turner 2019).

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Author contribution statement JGH and CTO conceived and designed the study. CTO performed the fieldwork. CTO, JGH, JLH performed and advised statistical analyses. CTO and JGH wrote the manuscript while JLH provided editorial advice.

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