

INFLUENCE OF SUCCESSION ON FISH ASSEMBLAGES  
IN POND METACOMMUNITIES

by

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## ABSTRACT

Metacommunity ecology focuses on the influence of regional and local processes structuring sets of communities, and theory predicts that the relative importance of those processes will change over time since initiation of community assembly. Determining the effects of regional and local processes on species and trait diversity over succession in metacommunities remains largely unaddressed to date, yet could confer an improved mechanistic understanding of community assembly. To test theoretical predictions of the increasing importance of local processes over succession in metacommunities, we evaluated fish species and functional trait diversity and dispersion in three pond metacommunities undergoing succession from beaver (*Castor canadensis*) disturbance. Additionally, processes influencing taxonomic and functional diversity in pond communities were contrasted with reference stream communities. The beaver modified habitats exhibited different environmental conditions by successional stage. Pond area and maximum water depth significantly increased with the number of years since pond formation. Further, ponds were deeper and warmer than streams. Species and functional richness was greater, and beta diversity was lower, in ponds than in streams. Diversity measures among pond age classes differed less than between ponds and streams, but indicated a decline in species and functional diversity and reduced community turnover later in succession. There was no influence of habitat type on functional dispersion. The analyses of the relative importance of regional and local processes over succession suggest that habitat age and dispersal were more important than local processes in structuring fish assemblages in pond metacommunities. The relative contributions were metacommunity and temporal scale-dependent as habitat age effects

were only dominant in the longest chronosequence represented in the region. Counter to predictions, local environmental processes became less important in structuring pond communities over later successional stages but did exert a stronger effect on trait sorting in older ponds. In contrast to the temporal and spatial effects operating in the successional pond metacommunity mosaics, local processes primarily structured species and trait diversity in the streams. Together, the results of this study highlight that community and, subsequently, metacommunity structure can be shaped by succession mediated shifts among regional and local structuring processes in landscapes experiencing locally heterogeneous disturbance.

## DEDICATION

I am humbly grateful to my family for their support throughout these efforts. It is a tremendous honor to be the first individual within our family to graduate college. Specifically, I am grateful to my father, David Olinger, and brother, Josh Olinger, for their unwavering support and humor.

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## LIST OF ABBREVIATIONS AND SYMBOLS

|            |   |
|------------|---|
| Adj. $R^2$ | Adjusts the $R^2$ statistic based on the number of independent variables in the model                     |
| ANOVA      | Analysis of variance  |
| C          | Centigrade  |
| CDOC       | Colored dissolved organic carbon  |
| DD         | Decimal degrees   |
| d.f.       | Degrees of freedom: number of values free to vary after certain restrictions have been placed on the data |
| DO         | Dissolved oxygen  |
| E          | Environmental (predictor category for complementary redundancy analysis variation partitioning)           |
| e.g.       | exempli gratia (roughly “for example”)  |
| $F$        | Fisher’s $F$ ratio: A ration of two variances   |
| g          | Gram  |
| GF/F       | Glass fiber filters   |
| GIS        | Geographic information system   |
| GPS        | Geographic positioning system   |
| ha         | Hectares  |
| HSD        | Honest significant difference   |
| i.e.       | id est (roughly “that is”)  |
| km         | kilometer   |

|          |   |
|----------|---|
| L        | Liter   |
| log      | Logarithmic   |
| m        | Meter   |
| mg       | Milligram   |
| mm       | Millimeter  |
| n        | Number in a trial or sample   |
| ODO      | Optical dissolved oxygen  |
| P        | Ponds (category for indicator species analysis)   |
| <i>P</i> | Probability associated with the occurrence under the null hypothesis of a value as extreme as or more extreme than the observed value |
| r        | Pearson correlation, measures a linear dependence between two variables   |
| $R^2$    | Proportion of the variation in the dependent variable explained by the independent variable for a linear regression model             |
| S        | Spatial (predictor category for complementary redundancy analysis variation partitioning)   |
| S        | Streams (category for indicator species analysis)   |
| SD       | Standard deviation  |
| SE       | Standard error  |
| SL       | Standard length   |
| spp.     | Several species   |
| T        | Temporal (predictor category for complementary redundancy analysis variation partitioning)  |
| <i>t</i> | Computed value of <i>t</i> test   |
| Temp     | Temperature   |
| TDN      | Total dissolved nitrogen  |

|     |                            |
|-----|----------------------------|
| TDP | Total dissolved phosphorus |
| USA | United States of America   |
| UV  | Ultraviolet                |
| YSI | Yellow springs instruments |
| +   | Addition                   |
| °   | Degree                     |
| =   | Equal to                   |
| >   | Greater than               |
| <   | Less than                  |
| μ   | Micro                      |
| μg  | Microgram                  |
| #   | Number                     |
| %   | Percent                    |
| +   | Plus                       |
| ±   | Plus minus                 |



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## INTRODUCTION

Sources of biological and functional trait diversity and the processes mediating them operate over both space and time (Chesson 2000, Levin 2000). To predict and explain patterns of biodiversity over multiple spatial scales, the metacommunity concept invokes both local and regional scale processes (Hubbell 2001, Leibold et al. 2004). While ecological communities are often nested within landscapes that experience disturbance events, the incorporation of succession in metacommunity research to explain patterns of species and trait diversity has remained largely absent (Sferra, Hart, and Howeth 2017). Anthropogenic and natural perturbations to a community can occur at both small and large spatial scales, returning patches or entire landscapes to an earlier stage of assembly or creating a mosaic of communities at different successional stages (Young, Chase, and Huddleston 2001, Levin and Paine 1974, Fukami 2015). Despite the frequency of secondary succession operating in contemporary landscapes, the relative importance of regional and local processes in influencing community and trait assembly along successional mosaics in metacommunities remains largely unaddressed.

The time since disturbance may mediate community assembly and functional trait diversity as the relative importance of regional and local processes changes over succession (Drake 1990, Fukami 2015, Mouquet et al. 2003). Early successional stages are characterized by rapid colonization and potentially high species turnover, influenced by both regional aspects (e.g., dispersal) and trait-based drivers (e.g., colonization-competition tradeoffs or growth rate) (Pacala and Rees 1998, Young, Chase, and Huddleston 2001, Li et al. 2016). Dispersal limitation

in heterogeneous landscapes characterized by low connectivity can shape species coexistence mechanisms and metacommunity organization (Moritz et al. 2013, Ward, Tockner, and Schiemer 1999, Bie et al. 2012). Low connectivity landscapes allow fewer species to reach the newly disturbed patches, effectively limiting species colonization potential during the first stages of succession (Cook et al. 2005). This places increased importance on priority effects influencing community assembly. Priority effects occur when competition-colonization tradeoffs drive fast local dynamics while limiting immigration rates (Yu and Wilson 2001). Conversely, late successional stages may be more structured by species sorting effects and associated competitive exclusion dynamics, 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 1993, 1996), and there is greater functional trait convergence (Fukami et al. 2005). Since dispersal is often no longer limiting late in succession, communities demonstrate colonization failures based upon strong biotic interactions, inadequate resource availability, or existing resilient assemblages (Inouye and Tilman 1995, Cadotte et al. 2006). In contrast to these successional stage-dependent patterns, high connectivity landscapes often do not experience dispersal limitation or priority effects and are characterized by homogenous communities and trait distributions (Chase and Ryberg 2004, Van der Gucht et al. 2007, 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 successional stages after disturbance.

In low and moderately connected landscapes, local environmental characteristics that can structure community and trait composition often vary throughout succession with different possible response trajectories (Odum 1966, Gleason 1927, Clements 1936, Horn 1974), Odum

(1966) suggests succession can alter biogeochemical cycling, preventing loss of, or expand the storage of, major nutrients such as calcium, nitrogen, and phosphorus in both terrestrial and aquatic ecosystems. These environmental shifts during the successional trajectory can influence multiple local processes, having the potential to structure communities and the ecological and life history trait composition of component species (Fukami et al. 2005, Mouillot et al. 2013, Tilman 2004). Subsequent changes in local dynamics may depend on the resource gradients restricting species (Keddy 1992, Moyle and Light 1996), the exclusion of weaker competitors by stronger ones (Hardin 1960, Moyle and Light 1996), and the risk of predation and availability of adequate prey refuges (Jackson, Peres-Neto, and Olden 2001, Howeth and Leibold 2010). These processes can lead to the convergence of viable local functional trait strategies in a successional stage. In contrast, the local niche space available along the environmental gradient may promote limiting similarity (Winemiller 1991, MacArthur and Levins 1967) and stabilizing mechanisms (Chesson 2000, Shea and Chesson 2002) that regulate functionally unique species and lead to the divergence of traits within an assemblage. Together, these processes may operate differentially over successional stages 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 local and regional processes in jointly structuring species and trait diversity in successional metacommunity mosaics remains untested. The successional trajectories of beaver-formed (*Castor* spp.) ponds offer a model system for testing these diversity relationships. The ponds are spatially discrete aquatic patches connected via a stream network in watershed landscapes, and vary in their time of formation and thus successional stage (Johnston and Naiman 1990a). Beavers can have large effects on the biological, chemical, and physical characteristics of aquatic ecosystems as they convert streams to ponds from dam construction

(Naiman, Johnston, and Kelley 1988, Collen and Gibson 2000, Rosell et al. 2005). The differential effects of beavers on local ecosystem properties depending on pond age is poorly understood, but recent work suggests linear environmental trajectories along successional chronosequences (Sferra et al. 2017). Habitat alterations catalyzed by beaver dams can change local hydrology from shifting stream to pond ecosystems, and can thereby increase physical habitat heterogeneity (Smith and Mather 2013) that correspondingly influences community composition (Nummi 1989, Gibson, Olden, and O'Neill 2015), trophic diversity (Anderson and Rosemond 2007), and life history traits (Bush and Wissinger 2016). Previous studies demonstrate effects on the biomass of phytoplankton (Hanson and Campbell 1963, Johnston 2017), the diversity of zooplankton (Sferra, Hart, and Howeth 2017), macroinvertebrates (Sprules 1941, Law, McLean, and Willby 2016), and macrophytes (Ray, Rebertus, and Ray 2001), and the attributes of fish assemblages (Collen and Gibson 2000). The differential response of fish community and trait composition to the unique successional stage-dependent environments of beaver ponds and regional dispersal processes remains understudied; however, where earlier work has only evaluated the response of fish community composition in streams versus ponds (Smith and Mather 2013) or to very coarse successional stages (Schlosser and Kallemeyn 2000, Snodgrass and Meffe 1998). The joint effect of beaver pond successional stage on local species and trait diversity may depend on the spatial, temporal, and environmental template maintained by successional stages in the metacommunity, but the combined and independent effects of these processes remain unaddressed in any taxonomic group to date.

Ponds located along stream corridors can shift the dominant local fish species via strong environmental filtering from the habitat transition away from streams (Rahel 1984, Tonn and Magnuson 1982, Bylak and Kukuła 2018). Stream fish communities are often structured by



water flow velocity and substrate heterogeneity (Jackson, Peres-Neto, and Olden 2001, Schlosser 1991), while beaver pond fish communities are partially determined by water temperature and dissolved oxygen (Schlosser and Kallemeyn 2000, Bylak and Kukuła 2018, Gibson, Olden, and O'Neill 2015). The presence and active maintenance of intact beaver dams can reduce the potential for fish colonization from downstream sources (Schlosser 1995), possibly limiting the ability of pond fish communities to track any changes in habitat heterogeneity associated with dam formation and yielding a mismatch between local community composition and the pond environment. The barrier imposed by dams can also selectively alter the directionality of fish migration and generate source-sink dynamics among ponds and streams (Schlosser 1995, 1982). Although no work has addressed the response of ecological and life history traits in fishes to beaver pond successional stage, previous studies evaluating effects of low-head dams on streams demonstrate influences on trophic and reproductive traits (Helms et al. 2011, Smith et al. 2017). Demonstrated disparities in the availability of spawning and rearing habitats, shifts within invertebrate communities, and fish dispersal in undisturbed versus beaver-impounded streams suggest that beaver pond age should yield differential effects on fish community composition, and trophic and reproductive trait structure.

To test predictions of the relative importance of local and regional processes on species and trait diversity over multiple successional stages in metacommunity mosaics, we quantified fish community and trait structure in replicated mosaics of beaver-formed ponds of different ages. Pond age and successional stage were determined from a previous study in the same system (Sferra, Hart, and Howeth 2017) and by using a combination of dendrochronology and historic aerial photography. Processes influencing diversity and composition in pond fish communities of different successional stages were contrasted with stream fish communities, and were predicted

to increase local species richness in pond habitats following an increase in local habitat heterogeneity after dam formation (Schlosser and Kallemeyn 2000, Smith and Mather 2013, Snodgrass and Meffe 1999). The stream conversion to a more heterogeneous pond environment can generate new niches (e.g., from macrophyte establishment) (Ray, Ray, and Rebertus 2004) and, thereby increase the potential for the maintenance of novel traits and foster higher functional trait diversity (HilleRisLambers et al. 2012). Relative to ponds in later successional stages, we predicted that the fish communities in younger ponds would be structured more by regional effects and consequently would exhibit low species and trait richness (Vanschoenwinkel, Buschke, and Brendonck 2013, Mouquet et al. 2003) and higher beta diversity among communities in the same early successional stage (Purschke et al. 2013) from dispersal limitation. During mid-successional stages, local processes were predicted to become relatively more important in structuring communities in increasingly heterogeneous pond habitats (Ray, Rebertus, and Ray 2001, Ray, Ray, and Rebertus 2004); and therefore, species richness would be higher (Sferra, Hart, and Howeth 2017, Mouquet et al. 2003), beta diversity would be lower (Fukami 2015), 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) and beta diversity (Cadotte 2007, Fukami 2015, Purschke et al. 2013) were hypothesized to decline in these more stable communities that are near equilibrium. The covariation between species and trait diversity was predicted to be strongest in the late successional stages from the greatest amount of time for species and trait sorting and compositional convergence to occur and as indicated by a parallel decline in species and trait richness (Li et al. 2016, Fukami 2015, Cadotte 2007).

## METHODS

### *Study regions and ponds*

The study sites include 24 ponds and nine upstream reference reaches distributed among three watersheds in the Oakmulgee District of the Talladega National Forest in central Alabama, USA (Figure 1). All ponds are actively maintained by the North American beaver (*Castor canadensis*) and represent stream-connected habitats that vary in time of formation (successional stage). Eight beaver ponds and three reference stream sites were located in each of three United States Geological Survey (USGS) 12-digit hydrologic unit code (HUC-12) watersheds, corresponding to three replicate study regions or metacommunities. Sites situated in the Big Sandy Creek, Elliott's Creek, and Fivemile Creek tributaries drain to the Black Warrior River (HUC-031601130103, hereafter watershed, region, or metacommunity 'A', and HUC-031601130401, 'B'), and sites on the Affonee Creek tributary drain to the Cahaba River (HUC-031502020505, 'C'). Downstream of the study system, the Black Warrior River converges with the Lower Tombigbee River, and the Cahaba River converges with the Alabama River. The confluence of the Lower Tombigbee and Alabama Rivers form the Mobile River, located approximately 72 km upstream from the Mobile Bay in the Gulf of Mexico. 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.

### *Pond age*

An estimated year of pond formation (pond age) for 16 sites was established using a combination of dendrochronological methods and historical aerial photography. The age of eight

ponds used in the study was previously determined from the application of these same methods in Sferra et al. (2017). Dendrochronological methods can be used to identify the year of local inundation through flooding effects on tree mortality and arrested annual ring development (Ray, Rebertus, and Ray 2001, Rypel, Haag, and Findlay 2009). These methods were adapted to evaluate flood-induced mortality and stress in trees standing within the study ponds. Tree species were selected for coring based on their intolerance to flood events, climatic sensitivity, and proximity to the beaver dam. Species cored included flood intolerant black tupelo (*Nyssaa sylvatica*) and loblolly pine (*Pinus taeda*). These two species experience reduced wood vessel growth or senescence during continuous flooding (Bedinger 1971, Burton 1971).

For cores taken from senesced trees, it was assumed that the year of tree death corresponded to the date of pond formation. Tree coring occurred at breast height using a 40.6-cm increment borer (Haglöf, Sweden). Cores were processed and measured using standard laboratory methods (Phipps 1985, Stokes 1996). Cores were air-dried, glued to wooden mounting blocks with cells vertically aligned, sanded using progressively finer abrasives, and then scanned at 600 dpi using a Canon CanoScan LiDE 700F scanner (Melville, New York, USA) to create a digital image of the core. Adobe Photoshop CC (Adobe Systems Incorporated, San Jose, California, USA) was used to align and edit the digital image. Annuli number and distance were measured on the images using CooRecorder v7.9 (Larsson 2003). To determine the year of tree formation, tree cores were cross-dated in CofechaXP (pjk 2012) (Grissino-Mayer 2001) against an anchored chronology created for the region using *Pinus palustris* (Bhuta 2011). The date of tree formation was accepted as statistically well supported if a Pearson correlation coefficient ( $r$ ) value  $\geq 0.4$  was obtained, following the standard acceptance threshold (Holmes 1983, Rozas 2005). The year of pond formation was estimated by adding the total number of

annuli, from pith to bark (i.e., number of years to death), to the year of tree formation. A target of three independent cores with formation dates,  $r \geq 0.4$ , was used to estimate the age of each pond.

If a pond did not support three measurable cores from dead trees with  $r \geq 0.4$ , cores were subsequently sampled from inundated living trees standing in the pond. Cores were examined for an annuli section indicating flooding stress and slow growth, as reflected by reduced interannual ring distances and staining (George and Nielsen 2003). For these cores, the year of pond formation was estimated by counting the number of annuli, from bark to the stunted growth section, and subtracting the count from bark sample date (2016).

Aerial photographs from the United States Forest Service were used to estimate the year of formation of all ponds (Johnston and Naiman 1990b, Martin et al. 2015). Aerial photography provided coverage of the study region during years 1937, 1939, 1949, 1950, 1951, 1954, 1955, 1956, 1958, 1959, 1960, 1972, 1981, 1984, 1985, 1988, 1991, and 1992. Photography and satellite imagery from Google Earth (Google Incorporated, Mountain View, California, USA) provided additional coverage for 1988 to 2016. To create a pond map layer on which to compare to historic aerial images, pond geographic coordinates were taken at the beaver dam of each pond with a handheld global positioning system (GPS; Garmin Model eTrex10, Olathe, Kansas, USA) and imported into ArcMap 10 (Environmental Systems Research Institute, Redlands, California, USA) and Google Earth. Throughout the time series, photographs were visually inspected for pond occurrence. The earliest year of pond detection was used as the estimated year of pond formation from aerial photography. The oldest date of pond formation from either dendrochronology or aerial photography analyses was selected as the best estimate of formation year and used in statistical analyses for the study.

## *Sampling*

Fish communities were sampled in the 24 ponds and nine stream reaches over three survey periods in 2016 and 2017: (survey 1) April 13 – June 4; (survey 2) June 28 – August 29; and (survey 3) October 2 – February 4. 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 (Figure 1).

Each pond fish community survey consisted of a standardized combination of seine, fyke net, and minnow trap sampling. Four seine (1.2 m x 3.0 m net, 4.76 mm mesh) hauls along the pond perimeter were conducted. One fyke net (0.6 m x 1 m, two 3.7 m wings, 6.35 mm mesh) was deployed in each pond for 12-hours from dusk to dawn. Twelve minnow traps were also set for 12-hours with a standardized combination of three aperture widths to target different fish size classes: 25.4 mm, 38.1 mm, and 50.8 mm. To capture larger individuals that may be missed utilizing the other survey methods, the ponds were additionally sampled with 1) two single-winged fyke nets connected by a 3.7 m lead and deployed for 12-hours during survey two and 2) one daytime two-hour angling survey during survey three. During the second survey, two ponds (Pond 8 and 22) could not be sampled because of drought conditions and associated low water levels (total precipitation, 2.34 cm, average air temperature, 20.67 °C). During the third survey, two ponds (Pond 1 and 8) were dry and could not be sampled because of drought conditions (total precipitation was 8.48 cm, average air temperature was 15.32 °C). Each stream fish community survey consisted of a standardized combination of four seine hauls, the 12-hour deployment of six minnow traps with a standardized set of the three apertures, and three 100 m passes of backpack electrofishing (Smith-Root LR-20; Smith-Root Incorporated, Vancouver, Washington, USA). For the electrofishing effort, seine nets served as block nets and were

secured perpendicular to stream flow at the beginning and end of the 100-m study reach. During survey two, streams upstream of ponds 1, 7, and 24 could not be sampled because of low flow rates associated with the drought conditions. Likewise, the stream upstream of pond 1 could not be sampled during survey three. All captured fish from the pond and stream sampling efforts were identified to species using regional references (Mettee, O'Neil, and Pierson 1996, Page and Burr 1997, Boschung and Mayden 2003), measured to the nearest 0.1 mm (standard length, SL), and weighed to the nearest 0.1 g (Ohaus Model PS251; Ohaus Corporation, Parsippany, New Jersey, USA) before being released where collected.

The pond and stream environments were characterized during each of the three fish community surveys. At the deepest location within each pond, conductivity, pH (YSI Model 63; Yellow Springs Instruments, Yellow Springs, Ohio, 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 linear distance between the point of maximum water depth to the beaver dam and to the stream inflow was measured with a GPS. The area of aquatic vegetation cover of each pond, including macrophytes and semi-aquatic vegetation, was also measured with a GPS 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, Hart, and Howeth 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, Isenhart, and Mitchell 1992). In streams, at the 50 m (halfway) location, conductivity, pH, dissolved oxygen, and water for nutrient analyses 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 hours. Pond and stream sites that were unable to be sampled for fish communities for a given survey because of drought conditions were also not surveyed for the environment.

### *Species traits*

From the literature, nine traits were identified that relate to ecology, life history, and phylogeny of fishes (Helms et al. 2011, Hitt and Roberts 2012, Howeth et al. 2016, Pool and Olden 2012) and that were accessible via a publicly available online database (FishTraits) (Frimpong and Angermeier 2009) and literature (Nelson, Grande, and Wilson 2016) (Table 1). 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 (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, guardians and substratum choosers, guardians 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) (Grafen 1989).

### *Statistical analyses*

To test the response of environmental variables to pond age, linear regression models were used. Each of nine environmental 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. Additionally, to determine if the location of maximum pond depth was closer to the dam or to the stream inflow, a two-sample t-test was used to compare the distances to the beaver dam and to the stream inflow point. To measure the pond environment relative to the stream environment, 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 for that variable (Osenberg, Sarnelle, and Cooper 1997). To test for differences in environmental variables between ponds and streams, two-sample t-tests were used. For the standard effect size and t-tests, the eight environmental variables that were measured in both habitat types and that represented the mean survey values were used for the stream-pond pairs ( $n = 9$  pairs, except for water temperature where  $n = 8$  pairs due to the delayed installation of a temperature data logger in pond and stream 10; Table 3, Table 5): CDOC, conductivity, dissolved oxygen, maximum depth, pH, TDN, TDP, and water temperature. Normality tests (Shapiro-Wilk), linear modelling, and two-sample t-tests were performed in the R statistical environment (version 3.4.2; R Foundation for Statistical Computing, Vienna, Austria).

For further statistical evaluation of the effects of the successional gradient, study sites were binned into four habitat type categories: (i) streams ( $n = 9$ ), (ii) age class one (24 – 39

years;  $n = 8$ ), (iii) age class two (40 – 57 years;  $n = 10$ ), and (iv) age class three (60 – 70 years; ponds,  $n = 6$ ).

The difference between stream and pond environments were hypothesized to differ by pond age class. The absolute value of the difference of CDOC, conductivity, dissolved oxygen, maximum depth, pH, TDN, TDP, and water temperature between paired streams and ponds by pond age class was contrasted with a one-way analysis of variance (ANOVA). Normality tests (Shapiro-Wilk), equal variance tests (Bartlett), ANOVAs, and post-hoc tests were performed in the R statistical environment.

Effects of habitat type on local fish richness, beta diversity, functional trait richness, and functional trait dispersion was tested. Cumulative local fish species richness was calculated from the three surveys. Beta diversity was measured with the incidence-based Raup-Crick index on average local abundance (Raup and Crick 1979, Chase et al. 2011). Raup-Crick dissimilarity determined if differences in beta diversity were different than would be expected by chance (Chase et al. 2011). The values range from just above 0 (identical local communities) to just below 1 (local communities share no species). The dissimilarity index was calculated with the “raupcrick” function, using the community ecology package “vegan” in R (Oksanen, Blanchet, Friendly, Kindt, Legendre, McGlin, et al. 2017). Functional trait richness was obtained using the convex hull volume calculation, and represents the multidimensional trait space occupied by each community (Cornwell, Schwilk, and Ackerly 2006, Villéger, Mason, and Mouillot 2008). The higher the hull volume the higher the functional trait richness is for a community. This index of functional trait space requires a greater number of species than the number of traits tested. For two of the stream sites in the data set, functional richness could not be calculated because observed species richness was less than the number of traits. Functional trait dispersion is

analogous to beta diversity and 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). The dispersion value increases as species differ more in their traits, but it is not dependent on the number of species in the community. Functional richness and functional dispersion were calculated from the nine traits in the data set and calculated for all stream and pond communities from average abundance data using 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 by a one-way ANOVA. Normality tests (Shapiro-Wilk), equal variance tests (Bartlett), ANOVAs, and Tukey’s HSD post-hoc tests were performed in the R statistical environment.

Fish community biomass was assessed among habitat types. Species-specific length-mass regressions (Neumann, Guy, and Willis 2012) were generated with the length and weight data acquired from the fish sampling, except for the regression for *Lepisosteus oculatus* which was obtained from the literature (only one individual captured at one study site) (Bister et al. 2000). The regressions were used to estimate the mass of individual fish that were not weighed in the field due to scale malfunctioning (n = 369 fish, survey 1 = 8.4% of total fish captured during the survey, survey 2 = 10.8%, survey 3 = 11.2%). Local fish biomass was calculated by summing individual fish biomass during each survey, and then calculating the mean biomass by site across surveys. A one-way ANOVA was used to determine differences in log-transformed mean fish biomass by habitat type. Normality tests (Shapiro-Wilk), equal variance tests (Bartlett), ANOVAs, and Tukey’s HSD post-hoc tests were performed in the R statistical environment.

In order to test for differences in community composition, the abundance-based Bray-Curtis index (Bray and Curtis 1957) was contrasted between habitat type and pond successional

stage extremes using a permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001). For the PERMANOVA analyses, (i) pond-stream pairs were binned into two community types representing the two main habitat types, streams and ponds (n = 9 habitat pairs), and (ii) pond sites were binned into two classes representing the pond age extremes and that standardized sample size, the youngest (24 – 38; n = 7) and oldest (57 – 70; n = 7) ponds in the data set. To evaluate the relationship between individual species and habitat type indicator species tests were performed (Dufrene and Legendre 1997). The response of individual taxa to stream versus pond habitat for all 33 study sites, and pond age class for the 24 study ponds, were analyzed separately. An indicator species analysis evaluates the response of each species to habitat type and pond age categories based on relative abundance and relative 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 species categorization. PERMANOVA and indicator species analyses were conducted using 9,999 permutations in PC-ORD (version 6.08, MjM software, Gleneden Beach, Oregon, USA) (McCune and Mefford 2011).

To determine the relative contribution of local processes in structuring fish community composition and functional trait dispersion throughout succession, Mantel tests were used to calculate correlations between community and trait composition and the environment (Mantel 1967, Douglas and Endler 1982). Two community dissimilarity matrices were tested for each of the four habitat type categories: (i) Bray-Curtis matrices, calculated from mean species abundance at each site, and (ii) functional trait dispersion matrices, calculated as the Euclidean distances between the trait dispersion site values. The environmental distance matrices were generated from the pairwise difference of principal component (PCA) axis 1 site scores, a

method which preserves variation in the data set (Borcard, Legendre, and Drapeau 1992). For the stream PCAs, seven centered and standardized environmental 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 centered and standardized environmental variables were used: conductivity, dissolved oxygen, maximum water 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. PCA and Mantel tests used 9,999 matrix permutations and were performed in PC-ORD.

To determine the amount of variation in fish community structure contributed by the local environment, versus pond age or spatial processes related to species dispersal among the eight ponds within each metacommunity, partial Mantel tests were performed (Smouse, Long, and Sokal 1986, Legendre and Legendre 1998). Community dissimilarity matrices were based upon Bray-Curtis distances calculated from mean species abundance at each site. Environmental distance matrices were generated from the pairwise difference of principal component (PCA) axis 1 site scores. For the PCA, eight centered and standardized environmental variables were used and represented site mean values: conductivity, dissolved oxygen, maximum water depth, pH, pond area, TDN, TDP, and vegetation cover. The resulting PCA axis I explained between 40% and 43% of the environmental variance within each metacommunity. Temporal distance matrices were based on the pairwise difference in year of pond formation. Euclidean distance matrices representing overland spatial distances among ponds were calculated as the linear distance between pond pairs using the “distGeo” function in the “geosphere” package of R (Hijmans et al. 2017). Hydrologic distance matrices, as a measure of stream network connectivity and species dispersal, were calculated as the shortest pathway distances between

ponds along streams using the Network Analyst/OD Cost Matrix Tool in ArcGIS 10. For each metacommunity, partial Mantel correlations were produced between the community matrix and all pairwise combinations of environmental, temporal, Euclidean and hydrologic distances, with each analysis controlling for a different predictor matrix. PCA and partial Mantel tests, using 9,999 matrix permutations, were performed in PC-ORD.

A complementary Redundancy Analysis (RDA) variation partitioning method (Borcard and Legendre 2002) evaluated the relative contribution of environmental, temporal, and spatial processes in structuring the 24 pond fish communities located in all three watersheds combined. The employed variance partitioning utilized two predictor matrices to explain differences in community composition (the third matrix), with unique pairwise combinations of environmental, temporal and/or spatial (Euclidean or hydrologic) predictors. The total percentage of variation explained by RDA was partitioned into unique and common contributors of the environmental, temporal and/or spatial predictors. Mean species abundance data by site was Hellinger-transformed prior to analysis to provide unbiased estimates of variation partitioning based on RDA (Peres-Neto et al. 2006). The subset of environmental variables used in the variation partitioning were identified by forward selection procedures (Blanchet, Legendre, and Borcard 2008). Centered and standardized environmental variables representing site means, including: conductivity, dissolved oxygen, maximum water depth, pH, pond area, TDN, TDP, and vegetation cover were first tested for collinearity using a variance inflation factor analysis. Variables that were significantly collinear (CDOC) were removed prior to forward selection. The temporal predictor was based on pond age in years. To generate the spatial predictors, distance-based Moran's eigenvector maps (db-MEM), which detect informative spatial distance thresholds by calculating eigenvectors that maximize Moran's index of autocorrelation, were

calculated separately from Euclidean and hydrologic distances (Dray, Legendre, and Peres-Neto 2006). Forward selection was used to identify the subset of MEM vectors to include in analyses. Significance of fractions of variation explained by the predictors was tested by 999 permutations. Statistical methods associated with the variation partitioning procedures were conducted using the “varpart,” “rda,” “decostand,” “vif.cca,” “ordiR2step,” and “dbmem” functions in the “adespatial” and “vegan” packages in R (Dray et al. 2016, Oksanen, Blanchet, Friendly, Kindt, Legendre, McGlinn, et al. 2017).

## RESULTS

### *Pond and stream environment*

Ponds ranged from 24 to 70 years of age and varied in their environmental conditions (Table 2, Table 3, Figure 1). Pond area and maximum water depth significantly increased with the number of years since pond formation (Table 4, Figure 2). The location of maximum water depth in ponds was closer to the beaver dam (mean = 3.97 m, SD = 2.42) than the stream inflow (mean = 98.08 m, SD = 87.03; two-sample t-test,  $t_{46} = -5.30$ ,  $P < 0.001$ ). Ponds were deeper and warmer than streams (Table 5, Table 6, Figure 3). Further tests showed that the maximum depth of ponds relative to the depth of their paired streams was significantly influenced by pond age, where the oldest ponds were significantly deeper than the streams relative to the younger pond age classes (Table 7, Figure 4).

### *Species and trait diversity*

There was an effect of habitat type on local fish species richness (one-way ANOVA,  $F_{3, 29} = 6.81$ ,  $P = 0.001$ , Figure 5a). 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,  $F_{3, 119} = 17.00$ ,  $P < 0.001$ , Figure 5b). 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  $P = 0.498$ ). Additionally, there was 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 significantly influenced functional trait richness (one-way ANOVA,  $F_{3, 27} = 5.34$ ,  $P = 0.005$ , Figure 5c). Functional richness was greatest in pond age class one, which supported significantly higher functional richness than streams but not the other two pond age classes (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  $P = 0.408$ ). However, the effect of habitat type did not significantly influence functional trait dispersion (one-way ANOVA,  $F_{3, 29} = 1.50$ ,  $P = 0.236$ , Figure 5d).

There was a strong effect of habitat type on local fish biomass (one-way ANOVA,  $F_{3, 29} = 65.84$ ,  $P < 0.001$ ). Fish biomass was significantly lower in streams than in any of the three pond age classes, while 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  $P < 0.0001$ , streams vs. pond age class 3  $P < 0.001$ , pond age class 1 vs. pond age class 2  $P = 0.952$ , pond age class 1 vs. pond age class 3  $P = 0.737$ , and pond age class 2 vs. pond age class 3  $P = 0.935$ ). Stream fish biomass (mean = 33.55 g, SD = 24.24) was only 2.2% of the fish biomass for pond age class one (mean = 1552.81 g, SD = 1212.60), 2.8% of age class two (mean = 1198.99 g, SD = 687.47), and 3.4% of the third age class (mean = 998.76 g, SD = 632.11).

There was a significant difference in community composition between streams and ponds (PERMANOVA,  $F_{1, 17} = 4.70$ ,  $P < 0.001$ ). Seven species were significant indicators of either pond or stream habitat (Table 8, Figure 6). Yellow Bullhead (*Ameiurus natalis*), Creek Chubsucker (*Erimyzon oblongus*), Warmouth Sunfish (*Lepomis gulosus*), Bluegill Sunfish (*L. macrochirus*), and Dollar Sunfish (*L. marginatus*) were significantly associated with ponds, while Gulf Darter (*Etheostoma swaini*) and Creek Chub (*Semotilus atromaculatus*) were associated with streams. While community composition did not differ between the youngest and oldest ponds (PERMANOVA,  $F_{1, 12} = 1.09$ ,  $P = 0.352$ ) three species were significant indicators of pond age class (Table 9, Figure 7). Blackspotted Topminnow (*Fundulus olivaceus*) was an indicator of age class one ponds. Warmouth Sunfish (*L. gulosus*) was an indicator of age class two ponds. Spotted Bass (*Micropterus punctulatus*) was an indicator of age class three ponds.

#### *Metacommunity structure*

The Mantel tests evaluating the correlation between community composition, and functional trait dispersion, with the environment showed a stronger association between these variables in streams than in any of the three pond age classes (Figure 8a). There was a negative relationship between community composition and the environment as a function of pond age. This result indicates that regional processes, such as dispersal, may be relatively more important in structuring fish communities in older ponds. While the correlation between functional trait dispersion and the environment in ponds never exceeded that of streams, it did increase with each pond age class (Figure 8b). This pattern suggests that trait sorting becomes increasingly important in later successional stages.

The partial Mantel tests determined the relative influence of the local environment, overland or watercourse distances, or pond age differences on metacommunity structure (Table

10). The results highlight differential influences of pond age on community structure by metacommunity. Mantel correlations for Metacommunity A indicate that pond age most strongly structures fish community composition in the region. In contrast, the lack of any significant temporal, spatial, or environmental predictors in metacommunity B suggests relatively greater biotic or abiotic homogenization in that group of communities and environments, respectively. Metacommunity C results demonstrate significant effects of both overland and hydrologic spatial predictors, suggesting the dominant influence of dispersal in structuring component local communities. The differences in the strength and significance of correlation between habitat age and community composition between the three metacommunities could be in part explained by the differences in pond age ranges within each watershed (youngest pond to oldest pond; A = 46 years, B = 22 years, and C = 42 years).

The complementary RDA variation partitioning analyses evaluated the independent and combined influence of environmental, spatial (overland and watercourse), and temporal predictors in explaining community structure in all 24 pond communities studied (Table 11). The forward selection analysis identified conductivity as the environmental predictor which explained the most variation in community composition (39%,  $P = 0.012$ ). No other environmental variables explained significant proportions of variation (all variables,  $P > 0.05$ ), and were therefore excluded from the environmental predictor matrix for the variation partitioning. The model including overland distance and the environment explained the most variation in fish community structure, where 11% of the variation was due to pure spatial effects and 5% of the variation was due to pure environment effects. There was no significant influence of hydrologic or temporal predictors in any of the models tested.

## DISCUSSION

The results highlight that the relative influence of habitat age, the local environment, and regional processes relating to species dispersal had two important and novel effects on community and functional trait diversity in successional metacommunity mosaics. First, habitat age and dispersal were more important than local processes in structuring fish communities and functional diversity in pond metacommunities. The relative contributions were metacommunity and temporal scale-dependent, however, with ponds age effects being dominant in the longest chronosequence represented in the region. Second, counter to predictions local environmental processes became less important in structuring pond fish communities over later successional stages but did exert a stronger effect on trait sorting in older ponds. Trait sorting in older pond habitats may have been driven by the larger and deeper ponds selecting for particular ecological and life history trait strategies. In contrast to these temporal and spatial effects operating in the successional pond metacommunity mosaics, local processes primarily structured species and trait diversity in the reference stream habitats. Together the differential importance of temporal, spatial, and local processes operating by habitat type and successional stage are reflected in contrasting diversity and compositional responses. The results underscore the importance of acknowledging the influence of local and regional processes over succession in structuring taxonomic and functional diversity in metacommunities experiencing locally heterogeneous disturbance regimes.

Habitat age and regional processes were the most important factors structuring community composition within metacommunities, but the detectable contribution of habitat age

depended upon having a large successional sequence represented in a metacommunity. Temporal structuring mechanisms dominated in the metacommunity with the longest successional sequence (Metacommunity A). This pattern likely emerged from the greatest range of structuring mechanisms represented by different successional stages, including any latent compositional effects of stochastic assembly in the earlier successional stages to the late-stage dominance of biotic filtering (Weiher and Keddy 1995, Fukami 2015, Mouquet et al. 2003). A second metacommunity (Metacommunity C) in a different river basin that encompasses nearly the same successional age range as the previous region (spans only four years less) exhibited strong spatial structuring. This pattern is perhaps, in part, a consequence of the shortest watercourse network of the three studied regions (mean hydrologic pairwise distances; A = 6.0 km, B = 9.6 km, C = 4.6 km). These fish assemblages may not be in equilibrium with the local physical environment but rather may reflect the regional equilibrium, suggesting that the proximity to source populations, immigration rates, and extinction processes are more important. Highly connected landscapes can support taxa occurring in less suitable habitats because of continuous propagule supply, thus leading to purely spatial effects. These results illustrate how high connectivity and mass effects can preclude successional replacement of community composition. Finally, the third metacommunity (Metacommunity B) supported approximately half the habitat age range of the other two regional chronosequences and exhibited no detectable factors influencing community structure. The similar successional states likely shared the same structuring mechanisms and yielded little variation in community composition and the local environment to partition. Collectively, the finding of significant spatial scale-dependent processes influencing metacommunity structure parallel those that indicate regional processes are more important in structuring fish communities in lakes and wetlands (Beisner et al. 2006, Baber et al. 2002), and

are contrary to the observed environmental processes dominating in stream communities. While other studies have found the importance of habitat age in influencing local community composition (Ray, Ray, and Rebertus 2004, Nemergut et al. 2015, Alexander et al. 2012), for the first time, the results of this study highlight the key temporal scale-dependent role of the regional successional chronosequence range in influencing metacommunity structure.

Local environmental conditions influenced community assembly processes in ponds, but with only a small increase in structuring effects later in succession apparent from greater trait sorting. Among all ponds located in three regions, the environment explained less than half as much variation as spatial processes in community composition. Of the environmental variables tested, conductivity most influenced fish community composition. Conductivity has been reported to be an important variable in structuring fish assemblages at local spatial scales across broad regions, for example: (i) native fishes clustered in lower conductivity areas in a California stream network (Marchetti and Moyle 2001), (ii) proportionally higher conductivity decreased abundance and dominance of four lake species in Argentina (Rosso and Quirós 2010), and (iii) conductivity range influenced the restructuring of functional groups in littoral assemblages in Australia (Halliday et al. 2018). These findings suggest local conditions can influence fish species community composition at biogeographic scales. However, at the local spatial scale, adequate dispersal is necessary for species to track heterogeneity in local conditions (Leibold et al. 2004) and limited dispersal will preclude species sorting (Heino and Peckarsky 2014). In early successional stages, the small scale disturbance of the initial stream modifications may not pose any dispersal barrier for fish; however, in older ponds reduced dam barrier permeability can cause significant differential immigration rates for fishes in beaver pond landscapes (Schlosser 1995). These systems become more spatially isolated by the large dam barrier in the late

successional stages limiting dispersal and possibly producing the observed mismatch between community composition and local environment in late successional stages. The differences in dam permeability and strength of biotic filtering produced contrasting species and trait sorting relationships in the late successional stage.

The beaver ponds supported higher species and trait richness and lower beta diversity than the streams. These results parallel the predicted effects on local fish assemblages from beaver modified streams (Schlosser and Kallemeyn 2000, Smith and Mather 2013, Snodgrass and Meffe 1999), and are likely directly and indirectly influenced by the observed increase in pond area and maximum depth over succession. Beaver modified landscapes tend to have a greater standing crop of plankton and regional water volume (Hanson and Campbell 1963), enhanced aquatic vegetation growth (Correll, Jordan, and Weller 2000), and a relative increase in habitat heterogeneity at the watershed level (Smith and Mather 2013), all of which are influenced by habitat size. The richness of ichthyofauna often increases as habitat complexity increases, with depth, velocity, and cover regularly being the most important variables governing this relationship (Bunn and Arthington 2002). Increases in local habitat heterogeneity related to increased depth and area of beaver ponds facilitated local niche specialization and expanded the volume of the functional space occupied by the community. The changes in local biotic conditions over succession influenced the relative importance of niche-based deterministic processes during community assembly and increased trait sorting. The pond habitats provided stable environmental conditions, including a warm thermal refuge, for fishes compared to the headwater stream habitats, which may have contributed to the observed lower species turnover. Further, the comparatively low stream habitat functional richness findings are consistent with the general theoretical expectation that environmentally variable lotic ecosystems contain more

trophic or habitat generalists and more tolerant species than do stable systems (Poff and Ward 1989). Patterns in stream fish assemblage structure and functional composition can be predominately influenced by environmental factors, specifically microhabitat type and stability (Hoeinghaus, Winemiller, and Birnbaum 2007). Lastly, the findings reported here correspond to contemporary (Smith et al. 2017) and regional (Helms et al. 2011) studies reporting altered flow regimes impact fish community composition on a functional level. Fishes may have benefited from a reduction in the intermittently harsh flow regimes of the low order streams in these three regions.

Among the pond age classes, fish communities exhibited no distinct pattern in species richness despite experiencing decreases in beta diversity and functional trait richness. Species richness for each successional stage and the early successional stage functional trait richness contrasted with our predictions based on the limited theoretical (Mouquet et al. 2003) and empirical work (Purschke et al. 2013, Vanschoenwinkel, Buschke, and Brendonck 2013, Sferra, Hart, and Howeth 2017) available in metacommunities undergoing succession. Much of the previous work accounts for initial colonization events or tracks communities immediately following disturbance. In the three regional chronosequences represented in this study, the earliest successional stage begins 24 years post-disturbance and any initial dispersal limitation or priority effects are likely diminished. Importantly, mid- and late stage patterns in community dissimilarity and trait convergence indicate stronger biotic filtering processes as the communities near equilibrium (Li et al. 2016). These contrasting responses of species and trait richness highlight that a distance-based functional diversity approach can impart differential and valuable information about the importance of structuring processes as compared to species richness. Temporal community assembly relationships are not constrained to taxonomic diversity



(Purschke et al. 2013) or initial successional stages, and often require broad habitat age ranges to develop (Sferra, Hart, and Howeth 2017, Allen, VanDyke, and Cáceres 2011). For example, in two studies of invertebrate metacommunities, species richness remained low for the first three years in newly formed ponds via dispersal limitation and, possibly, the priority effects of early colonizers (Louette, De Meester, and Declerck 2008); however, dispersal limitation exclusively affected active dispersers in the late-successional stage of temporary rock pools (Vanschoenwinkel, Buschke, and Brendonck 2013). Additionally, functional groupings significantly contributed to the forest community assembly of woody plant species only after 15 years (López-Martínez et al. 2013). In combination with observations of differential structuring relationships in this study, these works illustrate that species and trait sorting processes can exhibit stage-specific mechanisms (Loranger et al. 2016) and further emphasizes the benefit of a functional approach to succession dynamics and community assembly (Meiners et al. 2015, Fukami 2015).

There was a significant difference in community composition between streams and ponds, and there were some shifts in species incidence and abundance between pond age classes. The stream-pond habitat relationship is similar to findings suggesting the quality of spawning or rearing habitat in beaver modified landscapes are taxa-specific (Schlosser 1995, 1998). For example, the species associated with streams (*Etheostoma swaini*, *S. atromaculatus*) are pit-ridge and nest spawners that require fast-flowing areas of clear streams or small rivers with rocky and sandy substrate (Moshenko and Gee 1973, Ruple, McMichael, and Baker 1984). The viability of these nests is often limited by flow, substrate, and temperature which would be negatively influenced by the pond effect on environmental variables (Moshenko and Gee 1973, Ruple, McMichael, and Baker 1984). In contrast, the indicator species of ponds (*A. natalis*, *Erimyzon*

*oblongus*, *Lepomis* spp.) are less fastidious in their spawning and rearing habitat criteria (Selego, Merovich, and Anderson 2014, Cooke et al. 2008, Carlander 1997). While community composition differed between streams and ponds, the relationship was weaker between the youngest and oldest ponds even though three species were significant indicators of pond age class. Shifts in the relative incidence and abundance of species suggest a functional trait response to age-dependent environmental relationships (e.g., maximum water depth and pond area). The successional transition from a small-bodied indicator species (*F. olivaceus*) in younger ponds that is characterized by a relatively short lifespan and low fecundity, toward medium- and larger-bodied indicator species (*L. gulosus* and *M. punctulatus*) of mid-aged and older ponds that are characterized by longer lifespans and greater fecundity, are positive trends in life history traits that parallel the progression of area and depth in pond habitats. Additionally, these three pond age indicator species highlight a shift in trophic guild over succession, transitioning from an omnivorous diet in young ponds to an invertivore-piscivore diet in older ponds. This successional transition to a higher trophic position follows an increase in suitable zooplankton prey available in the older and deeper ponds (*Daphnia*) (Sferra, Hart, and Howeth 2017) and that can support planktivory, ontogenetic diet shifts of piscivores, and ultimately piscivory of planktivores. Consequently, the distribution of these fishes illustrates clear patterns of correlation between ecological and life history trait composition and the local habitat conditions (Frimpong and Angermeier 2009, Giam and Olden 2016, Villéger et al. 2010). Small-scale studies usually lack the necessary scope of limiting local conditions in aquatic ecosystems, making it difficult to detect trait filtering effects of environmental variables (Jackson, Peres-Neto, and Olden 2001), but these limitations have been overcome in this larger-scale study encompassing habitats in multiple regions. These observed trends in functional trait clustering may reflect differences in

assembly processes within the broader community (Fitzgerald et al. 2017, Hoeninghaus, Winemiller, and Birnbaum 2007), and indicate an increase in trait sorting via environmental filtering later in succession.

## CONCLUSIONS

In this study, we assessed the influence of secondary succession in structuring the community and functional trait composition of fish assemblages in beaver pond metacommunities. The results of the study highlight the greater influence of succession and dispersal processes on community structure and turnover. Habitat age effects reduced both beta diversity and functional trait richness by acting as a trait-based selective filter increasing the strength of deterministic processes later in succession. However, the observed effects of succession on community composition diminished in highly connected landscapes and those with a restricted habitat age range. Thus, community structure and, subsequently, metacommunity composition can be shaped by succession mediated shifts in regional and local structuring processes, but the strength of the relationship can be weakened by greater landscape connectivity and mass effects. Finally, this work contributes to the understanding of ecosystem engineers in metacommunities. To our knowledge, this is the first study to address the trait-based effects of beaver-driven succession on fishes at local and metacommunity scales.

The aspects influencing species coexistence and metacommunity composition are multifaceted (Amarasekare 2003, Logue et al. 2011, Moritz et al. 2013). A firm understanding of when and why shifts in regional and local structuring processes occur is essential if we wish to improve contemporary understanding of the impacts of biodiversity loss, climate change, and invasive species on community assembly and disassembly. Integrating succession and trait-based approaches in different taxonomic groups and metacommunities should improve direct comparison across study systems and advance the understanding of mechanisms underlying the

relationship between functional traits and species coexistence (Liu et al. 2013, Brown and Swan 2010, Bie et al. 2012).

**Table 1.** Species traits used to characterize species dissimilarity. For each variable, the type and parameters are indicated.

| Variable                | Fish Traits Field Code <sup>8</sup>  | Parameters  |
|-------------------------|--|---|
| Body size               | MAXTL  | continuous: maximum total length (cm)   |
| Fecundity               | FECUNDITY  | continuous: maximum reported fecundity (count)  |
| Longevity               | LONGEVITY  | continuous: maximum lifespan (years)  |
| Macrohabitat preference | 1. PREFLEN;<br>2. PREFLOT  | categorical: 1. lentic; 2. lotic  |
| Phylogeny               | FAMILYNUMBER   | continuous: family rank <sup>†</sup>  |
| Reproductive guild      | 1. A_1_1 - A_1_6;<br>2. A_2_3A - A_2_4C;<br>3. B_1_3A - B_1_4;<br>4. B_2_2 - B_2_7C;<br>5. C1_3_4_C2_4   | categorical: 1. nonguarders and open substratum spawners; 2. nonguarders and brood hiders; 3. guarders and substratum choosers; 4. guarders and nest spawners; 5. substrate indifferent |
| Spawning frequency      | SERIAL   | categorical: 1. batch; 2. serial  |
| Temperature tolerance   | MINTEMP; MAXTEMP   | continuous: sum of the maximum temperature and the absolute value of minimum temperature  |
| Trophic guild           | 1. ALGPHYTO; DETRITUS;<br>MACVASCU<br>2. INLVFSH<br>3. FSHCRB; INLVFSH<br>4. ALGPHYTO; DETRITUS;<br>FSHCRB; INLVFSH;<br>MACVASCU<br>5. NONFEED | categorical: 1. herbivore-detrivore; 2. invertivore; 3. invertivore-piscivore; 4. omnivore; 5. adults do not eat  |

<sup>8</sup> From Frimpong and Angermeier (2009)

<sup>†</sup> From Nelson et al. (2016)

**Table 2.** Estimated date of pond formation from dendrochronology analysis and United States Forest Service aerial photos of ponds located in the Talladega National Forest, Oakmulgee District, Alabama. The estimated date of pond formation used in statistical analyses (analysis year column) was derived from the earliest estimated date originating from dendrochronology (Pearson  $r \geq 0.40$ ) or aerial photography. Ponds without cores lacked suitable trees for dendrochronology analysis.

| Pond | Site                | Core # | Core Type | r    | Core Year | Aerial Photo Year | Analysis Year     | Pond Age (years) |
|------|---------------------|--------|-----------|------|-----------|-------------------|-------------------|------------------|
| 1    | Miles' Pond         | -      | -         | -    | -         | -                 | 1992 <sup>‡</sup> | 24.00            |
| 2    | Damselfly Pond      | 1      | Live      | 0.51 | 2006      | -                 | -                 | -                |
|      | Damselfly Pond      | 2      | Live      | 0.43 | 2004      | -                 | -                 | -                |
|      | Damselfly Pond      | 3      | Senesced  | 0.41 | 1991      | -                 | -                 | -                |
|      | Damselfly Pond      | -      | -         | -    | -         | 2006              | -                 | -                |
|      | Damselfly Pond      | -      | -         | -    | -         | -                 | 1991              | 25.00            |
| 3    | 717 Pond 2          | -      | -         | -    | -         | 1981              | -                 | -                |
|      | 717 Pond 2          | -      | -         | -    | -         | -                 | 1981              | 35.00            |
| 4    | Briar Nose Pond     | 1      | Live      | 0.54 | 2006      | -                 | -                 | -                |
|      | Briar Nose Pond     | 2      | Live      | 0.71 | 1986      | -                 | -                 | -                |
|      | Briar Nose Pond     | 3      | Live      | 0.42 | 1998      | -                 | -                 | -                |
|      | Briar Nose Pond     | -      | -         | -    | -         | 1981              | -                 | -                |
|      | Briar Nose Pond     | -      | -         | -    | -         | -                 | 1981              | 35.00            |
| 5    | Duncan's Pond       | -      | -         | -    | -         | 1981              | -                 | -                |
|      | Duncan's Pond       | -      | -         | -    | -         | -                 | 1981              | 35.00            |
| 6    | Upstream of 8 Pond  | -      | -         | -    | -         | 1981              | -                 | -                |
|      | Upstream of 8 Pond  | -      | -         | -    | -         | -                 | 1981              | 35.00            |
| 7    | Pond 5              | -      | -         | -    | -         | -                 | 1978 <sup>‡</sup> | 38.00            |
| 8    | 717 Pond 1          | 1      | Senesced  | 0.43 | 1979      | -                 | -                 | -                |
|      | 717 Pond 1          | 2      | Senesced  | 0.45 | 1992      | -                 | -                 | -                |
|      | 717 Pond 1          | 3      | Live      | 0.45 | 1977      | -                 | -                 | -                |
|      | 717 Pond 1          | -      | -         | -    | -         | 1981              | -                 | -                |
|      | 717 Pond 1          | -      | -         | -    | -         | -                 | 1977              | 39.00            |
| 9    | Pond 7              | -      | -         | -    | -         | -                 | 1976 <sup>‡</sup> | 40.00            |
| 10   | Upstream of 7 Pond  | 1      | Senesced  | 0.41 | 1974      | -                 | -                 | -                |
|      | Upstream of 7 Pond  | 2      | Senesced  | 0.53 | 1985      | -                 | -                 | -                |
|      | Upstream of 7 Pond  | 3      | Live      | 0.47 | 2003      | -                 | -                 | -                |
|      | Upstream of 7 Pond  | -      | -         | -    | -         | 1981              | -                 | -                |
|      | Upstream of 7 Pond  | -      | -         | -    | -         | -                 | 1974              | 42.00            |
| 11   | Rosy Wolfsnail Pond | 1      | Live      | 0.42 | 1992      | -                 | -                 | -                |
|      | Rosy Wolfsnail Pond | 2      | Live      | 0.43 | 1971      | -                 | -                 | -                |
|      | Rosy Wolfsnail Pond | 3      | Live      | 0.41 | 1993      | -                 | -                 | -                |

|    |                     |   |          |      |      |      |                   |       |
|----|---------------------|---|----------|------|------|------|-------------------|-------|
|    | Rosy Wolfsnail Pond | - | -        | -    | -    | 2016 | -                 | -     |
|    | Rosy Wolfsnail Pond | - | -        | -    | -    | -    | 1971              | 45.00 |
| 12 | Pig Herd Pond       | 1 | Senesced | 0.4  | 1961 | -    | -                 | -     |
|    | Pig Herd Pond       | 2 | Senesced | 0.46 | 1969 | -    | -                 | -     |
|    | Pig Herd Pond       | 3 | Senesced | 0.41 | 1967 | -    | -                 | -     |
|    | Pig Herd Pond       | - | -        | -    | -    | 1972 | -                 | -     |
|    | Pig Herd Pond       | - | -        | -    | -    | -    | 1961              | 55.00 |
| 13 | Buffer Pond         | 1 | Live     | 0.4  | 1960 | -    | -                 | -     |
|    | Buffer Pond         | 2 | Senesced | 0.41 | 1966 | -    | -                 | -     |
|    | Buffer Pond         | 3 | Live     | 0.46 | 2003 | -    | -                 | -     |
|    | Buffer Pond         | - | -        | -    | -    | 1981 | -                 | -     |
|    | Buffer Pond         | - | -        | -    | -    | -    | 1960              | 56.00 |
| 14 | Tick Pond           | 1 | Live     | 0.41 | 1979 | -    | -                 | -     |
|    | Tick Pond           | 2 | Live     | 0.43 | 1960 | -    | -                 | -     |
|    | Tick Pond           | 3 | Live     | 0.41 | 1972 | -    | -                 | -     |
|    | Tick Pond           | - | -        | -    | -    | 2006 | -                 | -     |
|    | Tick Pond           | - | -        | -    | -    | -    | 1960              | 56.00 |
| 15 | Apocalypse Pond     | 1 | Live     | 0.42 | 1986 | -    | -                 | -     |
|    | Apocalypse Pond     | 2 | Live     | 0.44 | 1991 | -    | -                 | -     |
|    | Apocalypse Pond     | 3 | Live     | 0.41 | 1973 | -    | -                 | -     |
|    | Apocalypse Pond     | - | -        | -    | -    | 1959 | -                 | -     |
|    | Apocalypse Pond     | - | -        | -    | -    | -    | 1959              | 57.00 |
| 16 | Cindy's Pond        | - | -        | -    | -    | -    | 1959 <sup>‡</sup> | 57.00 |
| 17 | Heron Pond          | - | -        | -    | -    | -    | 1959 <sup>‡</sup> | 57.00 |
| 18 | Pork Pond           | - | -        | -    | -    | 1959 | -                 | -     |
|    | Pork Pond           | - | -        | -    | -    | -    | 1959              | 57.00 |
| 19 | Pond 6              | - | -        | -    | -    | -    | 1956 <sup>‡</sup> | 60.00 |
| 20 | Pond 8              | - | -        | -    | -    | -    | 1956 <sup>‡</sup> | 60.00 |
| 21 | Dragonfly Pond      | 1 | Senesced | 0.49 | 1982 | -    | -                 | -     |
|    | Dragonfly Pond      | 2 | Live     | 0.42 | 1977 | -    | -                 | -     |
|    | Dragonfly Pond      | 3 | Senesced | 0.4  | 1954 | -    | -                 | -     |
|    | Dragonfly Pond      | - | -        | -    | -    | 1988 | -                 | -     |
|    | Dragonfly Pond      | - | -        | -    | -    | -    | 1954              | 62.00 |
| 22 | Sister Pond         | 1 | Live     | 0.5  | 1960 | -    | -                 | -     |
|    | Sister Pond         | 2 | Senesced | 0.43 | 1995 | -    | -                 | -     |
|    | Sister Pond         | 3 | Live     | 0.44 | 1972 | -    | -                 | -     |
|    | Sister Pond         | - | -        | -    | -    | 1949 | -                 | -     |
|    | Sister Pond         | - | -        | -    | -    | -    | 1949              | 67.00 |
| 23 | Wigeon Pond         | - | -        | -    | -    | 1949 | -                 | -     |
|    | Wigeon Pond         | - | -        | -    | -    | -    | 1949              | 67.00 |
| 24 | Little Canyon Pond  | - | -        | -    | -    | -    | 1946 <sup>‡</sup> | 70.00 |

<sup>‡</sup> From Sferra et al. (2017)



**Table 3.** Watershed, estimated year of pond formation (year), pond age, geographic location of pond (decimal degrees), and ten environmental variables for the 24 study ponds. Pond area was measured once in spring 2016, unless otherwise indicated. All other environmental variables were averaged across three sampling periods from April 13, 2016 to January 11, 2017, unless otherwise indicated.

| Pond | Watershed | Year | Age (years) | Latitude (DD) | Longitude (DD) | Area (ha)           | Cond. ( $\mu\text{S}$ ) | Max. Depth (m)    | pH                | Vegetation Cover (%) | DO (mg/L)         | CDOC ( $\text{m}^{-1}$ ) | TDN ( $\mu\text{g/L}$ ) | TDP ( $\mu\text{g/L}$ ) | Water Temp. ( $^{\circ}\text{C}$ ) <sup>†, 8</sup> |
|------|-----------|------|-------------|---------------|----------------|---------------------|-------------------------|-------------------|-------------------|----------------------|-------------------|--------------------------|-------------------------|-------------------------|--|
| 1    | A         | 1992 | 24          | 32.9904       | -87.4206       | 0.2856 <sup>‡</sup> | 32.07                   | 0.52              | 5.88              | 0.90                 | 2.50              | 13.28                    | 473.50                  | 28.45                   | 17.19  |
| 2    | C         | 1991 | 25          | 33.0019       | -87.3146       | 0.1093              | 18.43                   | 0.72              | 5.94              | 0.00                 | 6.26              | 1.93                     | 124.88                  | 9.38                    | -  |
| 3    | B         | 1981 | 35          | 32.8774       | -87.4296       | 0.2483              | 29.00                   | 1.04              | 5.67              | 0.02                 | 6.89              | 2.67                     | 128.11                  | 10.70                   | -  |
| 4    | A         | 1981 | 35          | 32.9522       | -87.3703       | 0.0366              | 14.27                   | 1.16              | 4.94              | 0.47                 | 5.76              | 1.07                     | 50.25                   | 7.64                    | -  |
| 5    | A         | 1981 | 35          | 32.9728       | -87.3719       | 0.0092              | 29.57                   | 0.92              | 5.81              | 0.01                 | 6.93              | 1.45                     | 127.91                  | 8.29                    | -  |
| 6    | A         | 1981 | 35          | 32.9636       | -87.4175       | 0.0069              | 25.97                   | 0.75              | 6.32              | 0.00                 | 7.88              | 1.33                     | 96.02                   | 8.49                    | 15.95  |
| 7    | B         | 1978 | 38          | 32.9068       | -87.3918       | 2.3412 <sup>‡</sup> | 28.57                   | 1.47              | 5.65              | 0.94                 | 4.10              | 2.25                     | 97.32                   | 9.24                    | 17.37  |
| 8    | B         | 1977 | 39          | 32.8840       | -87.4206       | 0.6074              | 29.10 <sup>†</sup>      | 0.68 <sup>†</sup> | 5.65 <sup>†</sup> | 0.76 <sup>†</sup>    | 6.87 <sup>†</sup> | 2.69 <sup>†</sup>        | 148.92 <sup>†</sup>     | 10.61 <sup>†</sup>      | -  |
| 9    | B         | 1976 | 40          | 32.8995       | -87.4788       | 0.4221 <sup>‡</sup> | 24.50                   | 0.72              | 5.65              | 0.82                 | 8.23              | 2.51                     | 60.20                   | 10.75                   | -  |
| 10   | B         | 1974 | 42          | 32.9008       | -87.4776       | 0.3744              | 23.47                   | 0.93              | 6.53              | 0.01                 | 6.50              | 2.59                     | 34.02                   | 10.33                   | -  |
| 11   | C         | 1971 | 45          | 32.9470       | -87.3289       | 0.0876              | 21.77                   | 0.70              | 5.63              | 0.90                 | 5.78              | 1.55                     | 59.05                   | 8.68                    | 16.95  |
| 12   | B         | 1961 | 55          | 32.8692       | -87.4318       | 2.1306              | 23.50                   | 1.31              | 5.69              | 0.02                 | 3.57              | 2.22                     | 200.50                  | 10.88                   | 16.23  |
| 13   | B         | 1960 | 56          | 32.8657       | -87.4125       | 2.9353              | 22.07                   | 1.38              | 5.35              | 0.21                 | 4.45              | 1.96                     | 120.44                  | 11.15                   | -  |
| 14   | C         | 1960 | 56          | 32.9465       | -87.3282       | 0.4501              | 23.07                   | 1.10              | 5.65              | 0.65                 | 4.81              | 1.53                     | 78.68                   | 11.51                   | -  |
| 15   | C         | 1959 | 57          | 32.9748       | -87.3213       | 0.8580              | 16.47                   | 1.12              | 6.58              | 0.02                 | 5.02              | 2.08                     | 230.13                  | 8.90                    | 15.80  |
| 16   | A         | 1959 | 57          | 32.9423       | -87.3612       | 0.9682 <sup>‡</sup> | 15.33                   | 2.15              | 5.49              | 0.53                 | 6.65              | 2.46                     | 151.31                  | 8.16                    | -  |
| 17   | A         | 1959 | 57          | 32.9771       | -87.4063       | 0.3434 <sup>‡</sup> | 21.30                   | 0.88              | 5.65              | 0.00                 | 7.57              | 3.97                     | 257.07                  | 10.54                   | -  |
| 18   | B         | 1959 | 57          | 32.8664       | -87.4309       | 2.9761              | 22.80                   | 2.13              | 5.60              | 0.96                 | 4.24              | 2.24                     | 56.76                   | 10.72                   | -  |
| 19   | C         | 1956 | 60          | 32.9708       | -87.3279       | 2.9241 <sup>‡</sup> | 19.57                   | 2.02              | 5.57              | 0.62                 | 4.10              | 1.93                     | 77.91                   | 7.81                    | 19.04  |
| 20   | A         | 1956 | 60          | 32.9637       | -87.4135       | 0.5068 <sup>‡</sup> | 24.30                   | 1.27              | 6.06              | 0.53                 | 4.82              | 1.42                     | 80.58                   | 10.02                   | -  |
| 21   | C         | 1954 | 62          | 32.9954       | -87.3183       | 1.2803              | 24.90                   | 1.25              | 5.59              | 0.00                 | 5.95              | 1.38                     | 104.58                  | 9.89                    | -  |
| 22   | C         | 1949 | 67          | 32.9478       | -87.3275       | 0.1798              | 18.10 <sup>†</sup>      | 0.75 <sup>†</sup> | 5.68 <sup>†</sup> | 0.05 <sup>†</sup>    | 5.87 <sup>†</sup> | 2.24 <sup>†</sup>        | 165.28 <sup>†</sup>     | 10.76 <sup>†</sup>      | -  |
| 23   | C         | 1949 | 67          | 32.9524       | -87.3105       | 2.8318              | 22.70                   | 1.75              | 5.52              | 0.58                 | 6.01              | 1.81                     | 147.88                  | 8.80                    | -  |
| 24   | A         | 1946 | 70          | 32.9353       | -87.3818       | 0.7778 <sup>‡</sup> | 39.50                   | 2.35              | 5.91              | 0.65                 | 3.63              | 2.39                     | 142.82                  | 11.05                   | 17.12  |

<sup>‡</sup> From Sferra et al. (2017)

<sup>†</sup> Survey 2 values not included in analyses

<sup>8</sup> Data available only for ponds paired with streams

**Table 4.** Linear regression correlation ( $R^2$ ) between pond age and nine pond environmental variables for the 24 study ponds. Area was measured once in spring 2016 ( $n = 16$ ) and taken from Sferra et al. (2017) for the remaining ponds ( $n = 8$ ). Color dissolved organic carbon, conductivity, dissolved oxygen, maximum depth, pH, total dissolved nitrogen, total dissolved phosphorus, and vegetation cover were averaged for all ponds, except ponds 1, 8, and 22, across three sampling periods. Ponds 8 and 22 were dry during the second sampling period. Ponds 1 and 8 were dry during the third sampling period. Significant probability values ( $P < 0.05$ ) in bold.

| Variable                                      | $R^2$ | $P$ -value        |
|---|-------|-------------------|
| Area <sup>†</sup>                             | 0.317 | <b>0.004</b>      |
| Colored dissolved organic carbon <sup>†</sup> | 0.058 | 0.256             |
| Conductivity                                  | 0.016 | 0.560             |
| Dissolved oxygen                              | 0.049 | 0.297             |
| Maximum depth <sup>†</sup>                    | 0.417 | <b>&lt; 0.001</b> |
| pH <sup>†</sup>                               | 0.007 | 0.692             |
| Total dissolved nitrogen <sup>†</sup>         | 0.001 | 0.885             |
| Total dissolved phosphorus <sup>†</sup>       | 0.052 | 0.285             |
| Vegetation cover <sup>†</sup>                 | 0.009 | 0.661             |

<sup>†</sup> Environmental variable violated the Shapiro-Wilk normality test, log-transformed

**Table 5.** Watershed, downstream pond number (Table 3), geographic location of stream (decimal degrees), and eight environmental variables for the nine study streams. All variables were averaged across three sampling periods from April 14, 2016 to January 11, 2017, unless otherwise indicated.

| Downstream Pond | Watershed | Latitude (DD) | Longitude (DD) | Max. Width<br>(m) | Max. Depth<br>(m) | Cond.<br>( $\mu$ S) | pH                | DO<br>(mg/L)      | CDOC<br>( $m^{-1}$ ) | TDN<br>( $\mu$ g/L) | TDP<br>( $\mu$ g/L) | Water<br>Temp. ( $^{\circ}$ C) <sup>†, 8</sup> |
|-----------------|-----------|---------------|----------------|-------------------|-------------------|---------------------|-------------------|-------------------|----------------------|---------------------|---------------------|--|
| 1               | A         | 32.9899       | -87.4191       | 1.08 <sup>†</sup> | 0.20 <sup>†</sup> | 48.05 <sup>†</sup>  | 5.63 <sup>†</sup> | 3.06 <sup>†</sup> | 6.68 <sup>†</sup>    | 243.53 <sup>†</sup> | 28.88 <sup>†</sup>  | 16.47  |
| 6               | A         | 32.9634       | -87.4181       | 4.18              | 0.25              | 25.03               | 6.34              | 7.69              | 1.29                 | 95.45               | 7.65                | 15.20  |
| 7               | B         | 32.9085       | -87.3889       | 1.29 <sup>†</sup> | 0.23 <sup>†</sup> | 25.55 <sup>†</sup>  | 5.72 <sup>†</sup> | 5.85 <sup>†</sup> | 1.96 <sup>†</sup>    | 28.67 <sup>†</sup>  | 10.59 <sup>†</sup>  | 15.93  |
| 10              | B         | 32.9024       | -87.4759       | 3.37              | 0.48              | 19.80               | 6.08              | 5.08              | 2.64                 | 47.86               | 10.48               | -  |
| 11              | C         | 32.9470       | -87.3317       | 2.20              | 0.28              | 17.97               | 5.86              | 8.21              | 1.33                 | 92.59               | 7.78                | 15.94  |
| 12              | B         | 32.8725       | -87.4309       | 4.35              | 0.44              | 22.57               | 6.10              | 5.56              | 2.03                 | 167.62              | 13.61               | 15.99  |
| 15              | C         | 32.9758       | -87.3216       | 4.47              | 0.44              | 14.97               | 6.02              | 8.08              | 1.88                 | 113.46              | 7.28                | 16.09  |
| 19              | C         | 32.9749       | -87.3362       | 3.53              | 0.45              | 30.23               | 5.84              | 6.86              | 1.79                 | 115.20              | 9.02                | 15.94  |
| 24              | A         | 32.9242       | -87.3892       | 1.50 <sup>†</sup> | 0.15 <sup>†</sup> | 27.65 <sup>†</sup>  | 5.75 <sup>†</sup> | 6.27 <sup>†</sup> | 1.16 <sup>†</sup>    | 37.79 <sup>†</sup>  | 7.47 <sup>†</sup>   | 16.47  |

<sup>†</sup> Survey 2 values not included in analyses

<sup>8</sup> Data unavailable for upstream reach of Pond 10

**Table 6.** The difference in environmental variable values between pond and stream pairs (n = 9), as measured by t-tests. Color dissolved organic carbon, conductivity, dissolved oxygen, maximum depth, pH, total dissolved nitrogen, total dissolved phosphorus, and water temperature mean values from three sampling periods were compared between ponds and streams. Significant probability values ( $P < 0.05$ ) in bold.

| Variable                       | d.f.  | <i>t</i> | <i>P</i> -value |
|--------------------------------|-------|----------|-----------------|
| Color dissolved organic carbon | 16    | 0.714    | 0.486           |
| Conductivity                   | 16    | -0.027   | 0.979           |
| Dissolved oxygen               | 16    | -1.919   | 0.073           |
| Maximum depth <sup>†</sup>     | 8.674 | 4.356    | <b>0.002</b>    |
| pH                             | 16    | 0.306    | 0.763           |
| Temperature <sup>8</sup>       | 14    | 2.433    | <b>0.029</b>    |
| Total dissolved nitrogen       | 16    | 1.034    | 0.317           |
| Total dissolved phosphorus     | 16    | 0.038    | 0.970           |

<sup>†</sup> Environmental variable violated the homogeneity of variance assumption, degrees of freedom adjusted using the Welch-Satterthwaite method

<sup>8</sup> Data unavailable for upstream reach of Pond 6, n = 8 ponds and streams in analysis

**Table 7.** The difference in pond and stream environmental variables by pond age class as evaluated by a one-way analysis of variance. Age class one includes ponds 24 - 39 years of age ( $n = 3$ ), class two includes ponds 40 - 57 years of age ( $n = 4$ ), and class three includes ponds 60 - 70 years of age ( $n = 2$ ). Color dissolved organic carbon (CDOC), conductivity, dissolved oxygen (DO), maximum depth, pH, total dissolved nitrogen (TDN), total dissolved phosphorus (TDP), and water temperature mean values from three sampling periods (unless otherwise indicated) were compared between ponds and streams. Significant probability values ( $P < 0.05$ ) in bold.

| Variable                 | d.f. | <i>F</i> | <i>P</i> -value | Contrasts        |
|--------------------------|------|----------|-----------------|------------------|
| CDOC                     | 2, 8 | 0.88     | 0.463           |                  |
| Conductivity             | 2, 8 | 0.46     | 0.651           |                  |
| DO                       | 2, 8 | 1.02     | 0.416           |                  |
| Max. depth               | 2, 8 | 8.96     | <b>0.016</b>    | (1,3↑*), (2,3↑*) |
| pH                       | 2, 8 | 0.11     | 0.901           |                  |
| Temperature <sup>†</sup> | 2, 7 | 1.74     | 0.266           |                  |
| TDN                      | 2, 8 | 0.60     | 0.578           |                  |
| TDP                      | 2, 8 | 0.37     | 0.707           |                  |

<sup>†</sup> Data unavailable for upstream reach of Pond 10

Post-hoc pairwise comparisons (Tukey's HSD) are reported for significant main effects

Abbreviations for post-hoc contrasts: 1 = age class one, 2 = age class two, 3 = age class three

Contrasts significance levels: \*,  $P < 0.05$ ; ↑, greater diversity value

**Table 8.** Indicator species analysis of fish taxon association by habitat type, ponds (P; n = 24) or streams (S; n = 9). The observed indicator value (IV) and the indicator value of randomized groups (IVR) are reported, with 100 being a perfect indicator score. Significant probability values ( $P < 0.05$ ) in bold.

| Taxon                             | Class | IV   | IVR  | P-value        |
|-----------------------------------|-------|------|------|----------------|
| <i>Ameiurus melas</i>             | P     | 8.3  | 9.1  | 0.801          |
| <i>Ameiurus natalis</i>           | P     | 82.4 | 46.7 | < <b>0.001</b> |
| <i>Aphredoderus sayanus</i>       | P     | 48.4 | 41.9 | 0.159          |
| <i>Centrarchus macropterus</i>    | P     | 20.8 | 15.5 | 0.268          |
| <i>Elassoma zonatum</i>           | S     | 31.2 | 27.5 | 0.240          |
| <i>Erimyzon oblongus</i>          | P     | 73.3 | 44.4 | < <b>0.001</b> |
| <i>Erimyzon sucetta</i>           | P     | 11.4 | 15.2 | 0.725          |
| <i>Erimyzon tenuis</i>            | P     | 16.7 | 13.3 | 0.439          |
| <i>Esox americanus americanus</i> | P     | 8.3  | 9.0  | 0.795          |
| <i>Esox niger</i>                 | P     | 46.0 | 37.7 | 0.146          |
| <i>Etheostoma swaini</i>          | S     | 52.2 | 17.1 | <b>0.002</b>   |
| <i>Fundulus notti</i>             | P     | 29.2 | 18.8 | 0.149          |
| <i>Fundulus olivaceus</i>         | P     | 11.1 | 17.1 | 0.893          |
| <i>Lampetra aepyptera</i>         | S     | 11.1 | 6.0  | 0.267          |
| <i>Lepisosteus oculatus</i>       | P     | 4.2  | 6.1  | 1.000          |
| <i>Lepomis gulosus</i>            | P     | 80.6 | 47.8 | < <b>0.001</b> |
| <i>Lepomis macrochirus</i>        | P     | 50.0 | 27.5 | <b>0.025</b>   |
| <i>Lepomis marginatus</i>         | P     | 78.4 | 45.8 | < <b>0.001</b> |
| <i>Lepomis miniatus</i>           | P     | 29.1 | 22.6 | 0.217          |
| <i>Luxilus chrysocephalus</i>     | P     | 8.3  | 9.2  | 0.797          |
| <i>Lythrurus bellus</i>           | S     | 14.6 | 15.2 | 0.411          |
| <i>Micropterus punctulatus</i>    | P     | 14.0 | 17.2 | 0.681          |
| <i>Micropterus salmoides</i>      | P     | 41.7 | 24.2 | 0.052          |
| <i>Minytrema melanops</i>         | P     | 4.2  | 6.1  | 1.000          |
| <i>Notemigonus crysoleucas</i>    | P     | 37.2 | 25.9 | 0.111          |
| <i>Notropis texanus</i>           | S     | 12.3 | 15.2 | 0.727          |
| <i>Noturus leptacanthus</i>       | S     | 18.8 | 11.0 | 0.117          |
| <i>Semotilus atromaculatus</i>    | S     | 44.4 | 12.9 | <b>0.003</b>   |
| <i>Semotilus thoreauianus</i>     | S     | 22.2 | 9.1  | 0.065          |

**Table 9.** Indicator species analysis of fish taxon association by pond age class. Age class 1 includes ponds 24 - 39 years of age (n = 8), class 2 includes ponds 40 - 57 years of age (n = 10), and class 3 includes ponds 60 - 70 years of age (n = 6). The observed indicator value (IV) and the indicator value of randomized groups (IVR) are reported, with 100 being a perfect indicator score. Significant probability values ( $P < 0.05$ ) in bold.

| Taxon                             | Class | IV   | IVR  | P-value      |
|-----------------------------------|-------|------|------|--------------|
| <i>Ameiurus melas</i>             | 2     | 8.0  | 15.0 | 0.894        |
| <i>Ameiurus natalis</i>           | 1     | 52.6 | 46.3 | 0.204        |
| <i>Aphredoderus sayanus</i>       | 1     | 39.5 | 47.4 | 0.714        |
| <i>Centrarchus macropterus</i>    | 1     | 11.9 | 26.9 | 0.951        |
| <i>Elassoma zonatum</i>           | 3     | 15.6 | 25.6 | 0.898        |
| <i>Erimyzon oblongus</i>          | 3     | 40.0 | 46.7 | 0.759        |
| <i>Erimyzon sucetta</i>           | 1     | 33.3 | 21.3 | 0.111        |
| <i>Erimyzon tenuis</i>            | 3     | 14.0 | 20.9 | 0.793        |
| <i>Esox americanus americanus</i> | 1     | 25.0 | 13.5 | 0.158        |
| <i>Esox niger</i>                 | 1     | 33.1 | 36.1 | 0.568        |
| <i>Etheostoma swaini</i>          | 3     | 16.7 | 12.5 | 0.251        |
| <i>Fundulus notti</i>             | 2     | 44.0 | 24.7 | 0.051        |
| <i>Fundulus olivaceus</i>         | 1     | 48.6 | 21.4 | <b>0.024</b> |
| <i>Lepisosteus oculatus</i>       | 2     | 10.0 | 12.5 | 1.000        |
| <i>Lepomis gulosus</i>            | 2     | 51.1 | 40.4 | <b>0.023</b> |
| <i>Lepomis macrochirus</i>        | 3     | 25.4 | 36.4 | 0.799        |
| <i>Lepomis marginatus</i>         | 1     | 43.2 | 45.6 | 0.549        |
| <i>Lepomis miniatus</i>           | 1     | 18.0 | 27.1 | 0.786        |
| <i>Luxilus chrysocephalus</i>     | 1     | 9.6  | 14.0 | 0.664        |
| <i>Lythrurus bellus</i>           | 1     | 4.5  | 15.9 | 1.000        |
| <i>Micropterus punctulatus</i>    | 3     | 46.8 | 21.6 | <b>0.049</b> |
| <i>Micropterus salmoides</i>      | 3     | 21.7 | 30.7 | 0.744        |
| <i>Minytrema melanops</i>         | 1     | 12.5 | 12.5 | 0.583        |
| <i>Notemigonus crysoleucas</i>    | 1     | 28.4 | 32.4 | 0.581        |
| <i>Notropis texanus</i>           | 1     | 23.9 | 17.3 | 0.231        |
| <i>Noturus leptacanthus</i>       | 1     | 12.5 | 12.5 | 0.583        |

**Table 10.** Partial Mantel test correlations between fish community composition (Bray-Curtis) and orthogonal pairwise combinations of environmental, Euclidean, hydrologic, and temporal predictors within three metacommunities. Significant probability values ( $P < 0.05$ ) in bold.

| Metacommunity<br>x predictor | predictor controlled for |                 |             |                 |             |                 |             |                 |
|------------------------------|--------------------------|-----------------|-------------|-----------------|-------------|-----------------|-------------|-----------------|
|                              | Environment              |                 | Euclidean   |                 | Hydrologic  |                 | Temporal    |                 |
|                              | Correlation              | <i>P</i> -value | Correlation | <i>P</i> -value | Correlation | <i>P</i> -value | Correlation | <i>P</i> -value |
| Metacommunity A              |                          |                 |             |                 |             |                 |             |                 |
| x environment                | -                        | -               | 0.03        | 0.45            | 0.05        | 0.43            | -0.08       | 0.62            |
| x Euclidean                  | 0.09                     | 0.31            | -           | -               | -           | -               | 0.09        | 0.32            |
| x hydrologic                 | 0.03                     | 0.42            | -           | -               | -           | -               | 0.05        | 0.38            |
| x temporal                   | 0.35                     | <b>0.05</b>     | 0.34        | <b>0.05</b>     | 0.35        | <b>0.05</b>     | -           | -               |
| Metacommunity B              |                          |                 |             |                 |             |                 |             |                 |
| x environment                | -                        | -               | 0.03        | 0.38            | 0.04        | 0.36            | 0.09        | 0.26            |
| x Euclidean                  | 0.12                     | 0.34            | -           | -               | -           | -               | 0.12        | 0.32            |
| x hydrologic                 | 0.14                     | 0.32            | -           | -               | -           | -               | 0.14        | 0.31            |
| x temporal                   | -0.09                    | 0.32            | -0.04       | 0.43            | -0.02       | 0.49            | -           | -               |
| Metacommunity C              |                          |                 |             |                 |             |                 |             |                 |
| x environment                | -                        | -               | 0.12        | 0.26            | 0.08        | 0.34            | 0           | 0.47            |
| x Euclidean                  | 0.48                     | <b>0.02</b>     | -           | -               | -           | -               | 0.55        | <b>0.01</b>     |
| x hydrologic                 | 0.42                     | <b>0.03</b>     | -           | -               | -           | -               | 0.46        | <b>0.03</b>     |
| x temporal                   | -0.19                    | 0.21            | -0.38       | <b>0.04</b>     | -0.29       | 0.11            | -           | -               |



**Table 11.** Results of the variation partitioning of fish community composition (abundance Hellinger-transformed) using environmental [E], spatial [S], and temporal [T] predictors of fish metacommunity structure in 24 study ponds. Spatial predictors represent the overland distances between ponds (Euclidean) and the watercourse distances between ponds via the stream network (hydrologic). The temporal predictor reflects pond age in years. Significant probability values ( $P < 0.05$ ) in bold.

| Predictors           | With environmental predictors |                   |         | With temporal predictors |             |
|----------------------|-------------------------------|-------------------|---------|--------------------------|-------------|
|                      | Adj. $R^2$                    | $P$               |         | Adj. $R^2$               | $P$         |
| Spatial (Euclidean)  |                               |                   |         |                          |             |
| [E   S]              | 0.05                          | <b>0.02</b>       | [T   S] | 0                        | 0.62        |
| [S   E]              | 0.11                          | <b>&lt; 0.001</b> | [S   T] | 0.10                     | <b>0.01</b> |
| [E + S]              | 0                             |                   | [T + S] | 0                        |             |
| Residual variation   | 0.84                          |                   |         | 0.90                     |             |
| Spatial (hydrologic) |                               |                   |         |                          |             |
| [E   S]              | 0.04                          | <b>0.04</b>       | [T   S] | 0                        | 0.76        |
| [S   E]              | 0.01                          | 0.31              | [S   T] | 0                        | 0.47        |
| [E + S]              | 0                             |                   | [T + S] | 0                        |             |
| Residual variation   | 0.95                          |                   |         | 1                        |             |
| Temporal             |                               |                   |         |                          |             |
| [E   T]              | 0.04                          | <b>0.05</b>       |         |                          |             |
| [T   E]              | 0                             | 0.77              |         |                          |             |
| [E + T]              | 0                             |                   |         |                          |             |
| Residual variation   | 0.96                          |                   |         |                          |             |

[E | S] and [E | T] is the variation explained by environmental predictors only.

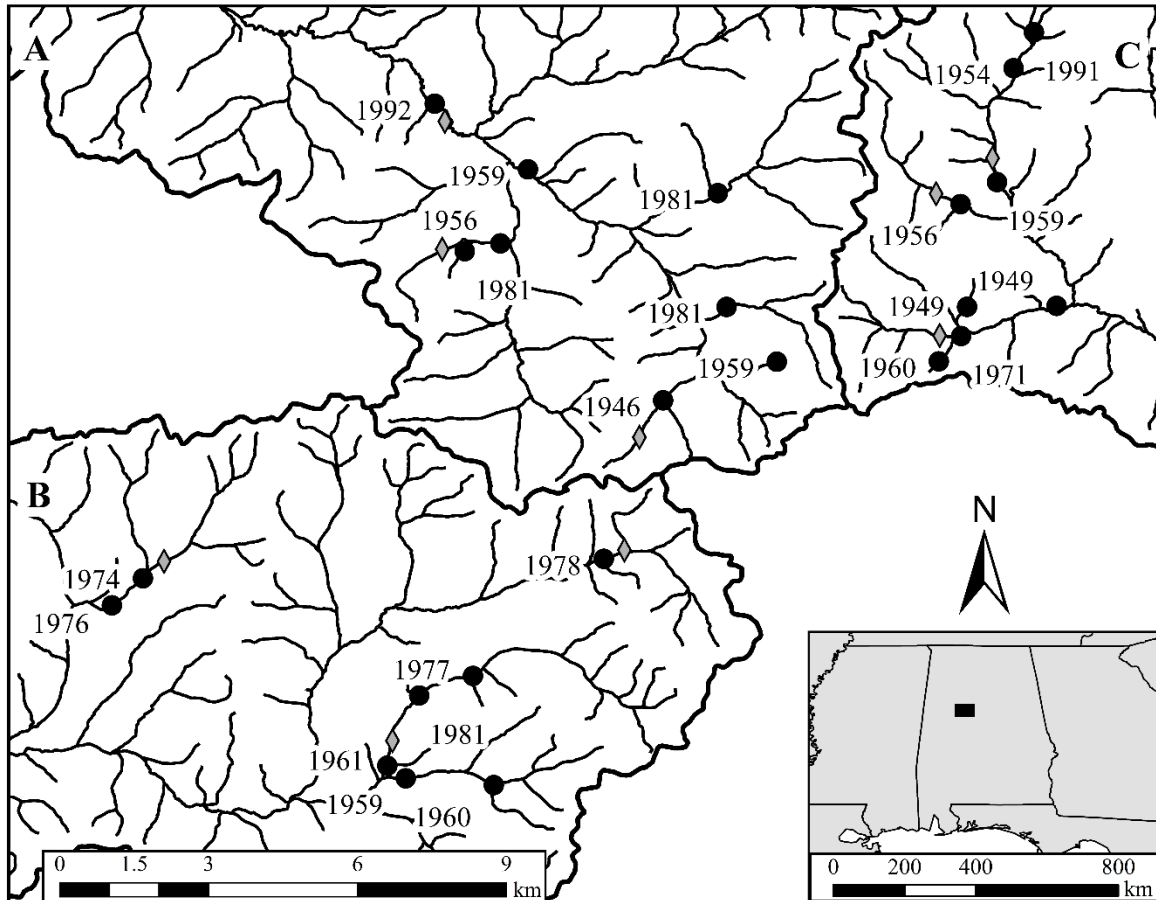
[S | E] and [S | T] is the variation explained by spatial predictors (Euclidean or hydrologic) only.

[T | E] and [T | S] is the variation explained by temporal predictors only.

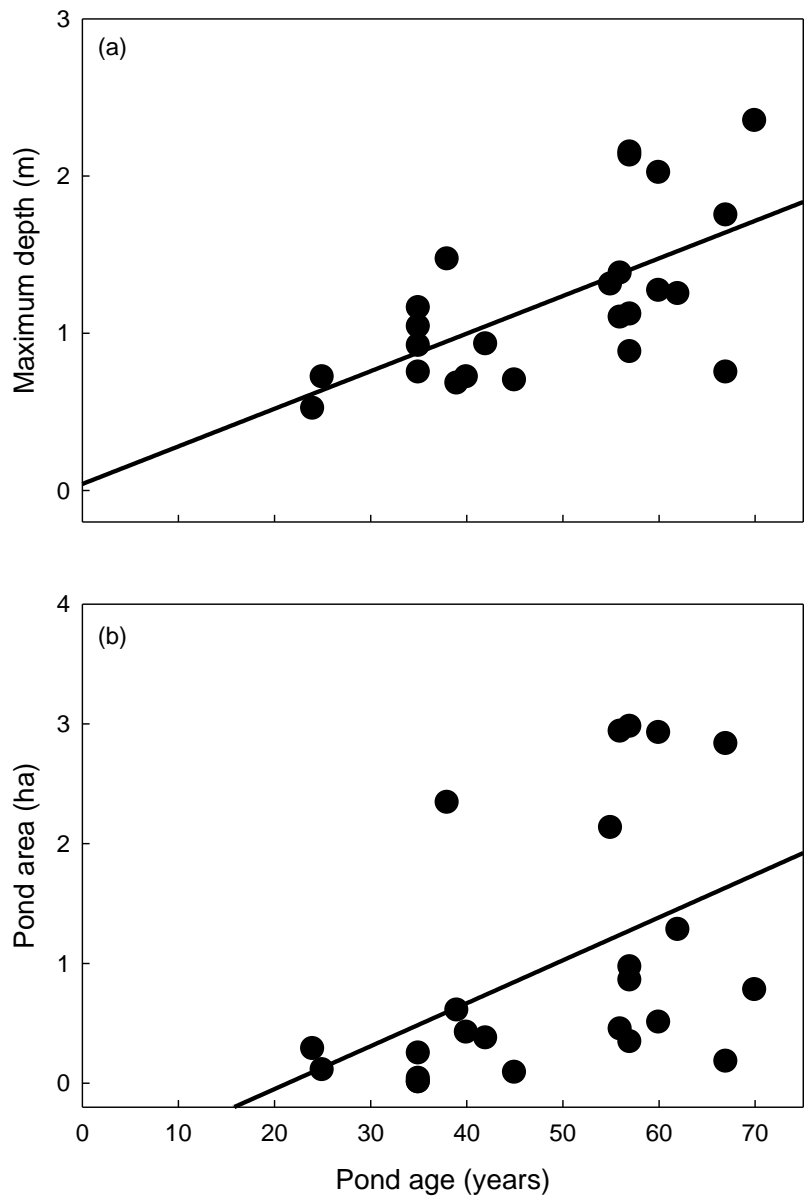
[E + S] is the variation explained by the spatially-structured environment.

[E + T] is the variation explained by the temporally-structured environment.

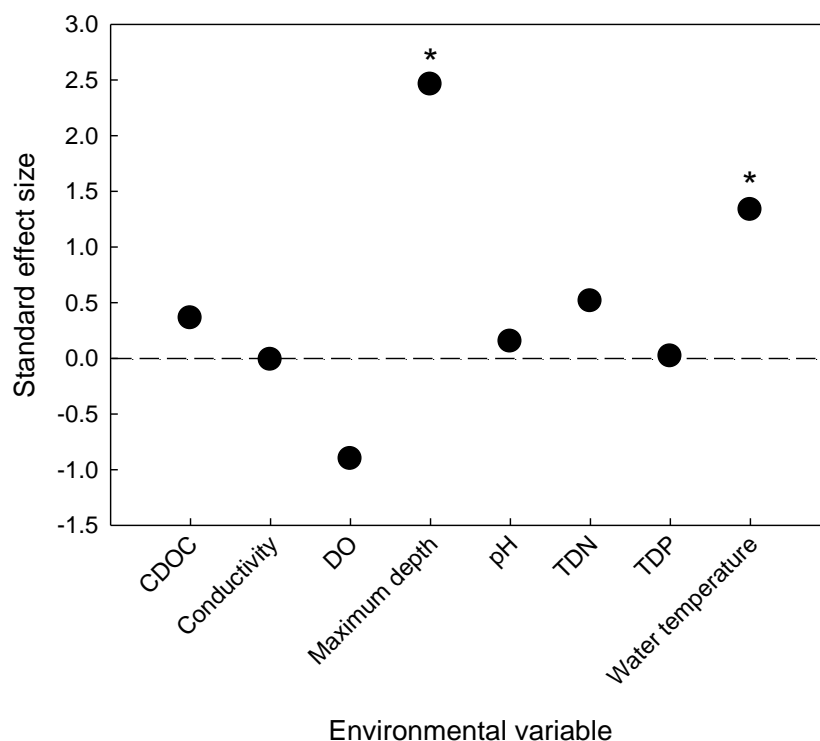
[T + S] is the variation explained by the temporal structure in space.



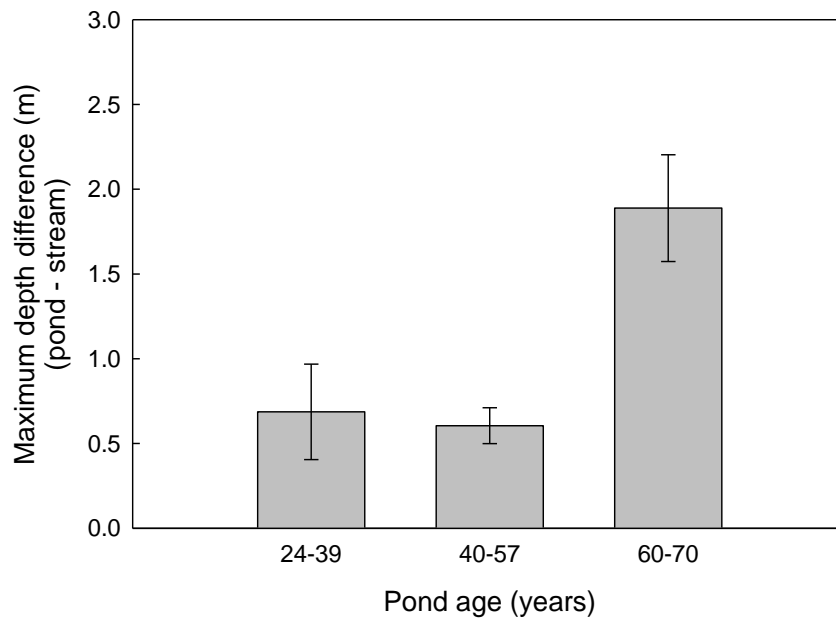
**Figure 1.** Watercourse location of the 24 ponds (black circles) and 9 streams (gray diamonds) studied in the Talladega National Forest, central Alabama (inset map), USA. Ponds are labeled with the estimated year of pond formation. A, B, C and bold black lines delineate the three study watersheds and metacommunities.



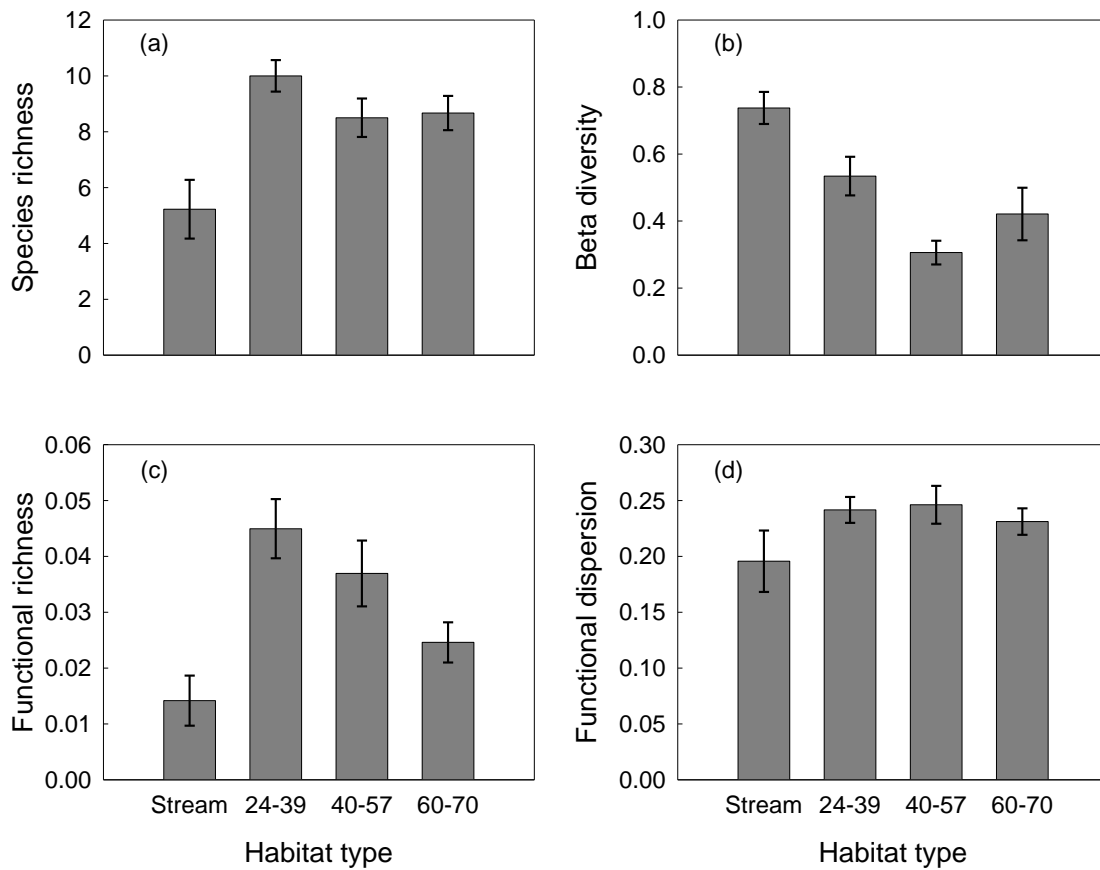
**Figure 2.** (a) Maximum depth (m) and (b) pond area (ha) by pond age (years). Maximum depth represents the mean of the three sampling periods, while pond area represents a one-time measure (n = 24 ponds).



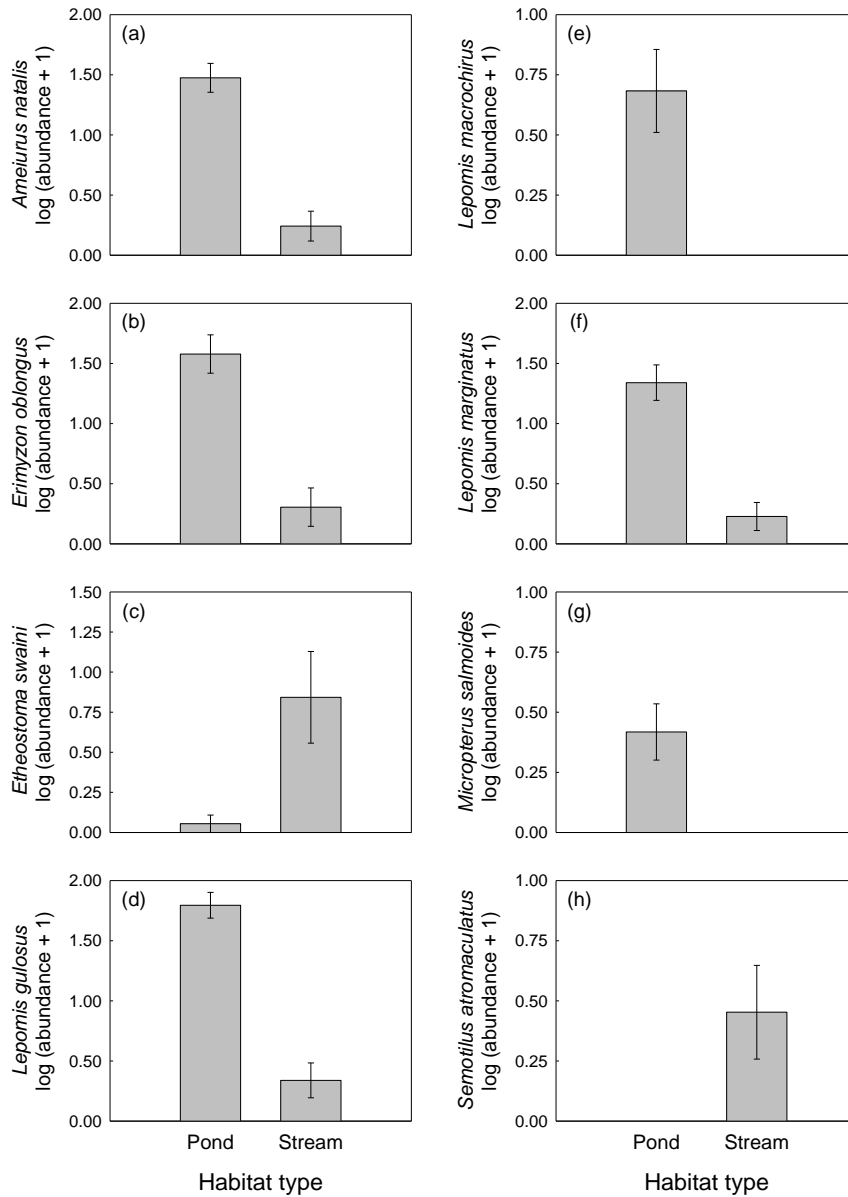
**Figure 3.** The pond environment relative to the stream environment (pond effect) for colored dissolved organic carbon (CDOC), conductivity, dissolved oxygen (DO), maximum depth, pH, total dissolved nitrogen (TDN), total dissolved phosphorus (TDP), and water temperature. The standard effect size was 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  $n = 8$ ). Asterisks indicate significant difference in pond and stream value in t-tests ( $P < 0.05$ , Table 6).



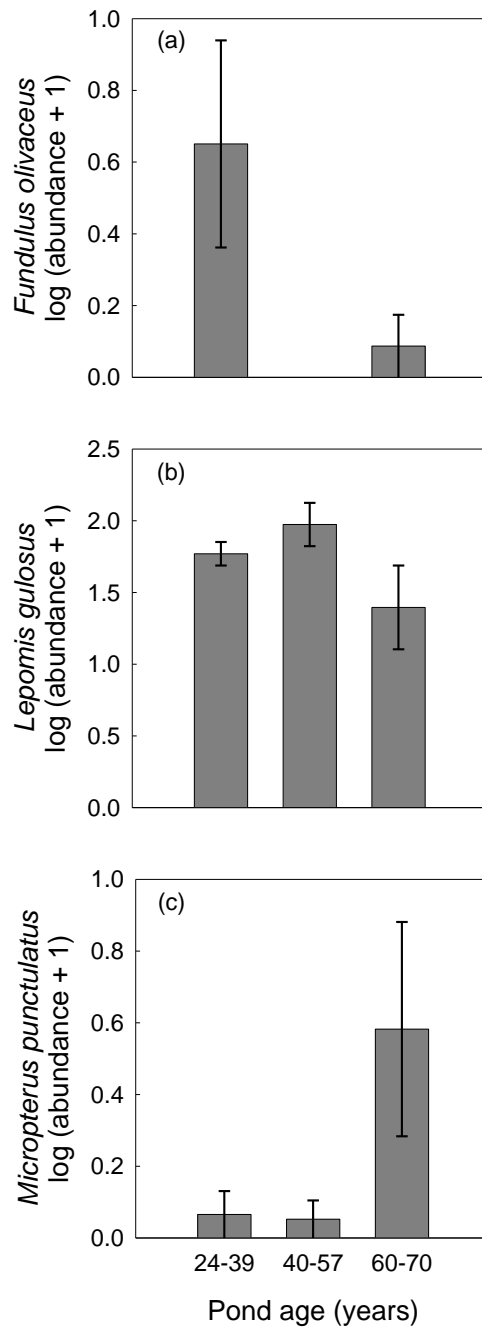
**Figure 4.** The maximum depth difference for the pond and stream pairs by pond age class. Age class one includes ponds 24 – 39 years of age ( $n = 3$ ), class two includes ponds 40 – 57 years of age ( $n = 4$ ), and class three includes ponds 60 – 70 years of age ( $n = 2$ ). Data represent the mean of three sampling periods  $\pm 1$  SE (Table 7).



**Figure 5.** (a) Species richness, (b) beta diversity, (c) functional trait richness, and (d) functional 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 ( $n = 8$ ), 40 – 57 years of age ( $n = 10$ ), and 60 – 70 years of age ( $n = 6$ ). Values are mean  $\pm$  1 SE. Beta diversity is the Raup-Crick dissimilarity for ponds within the same habitat type.

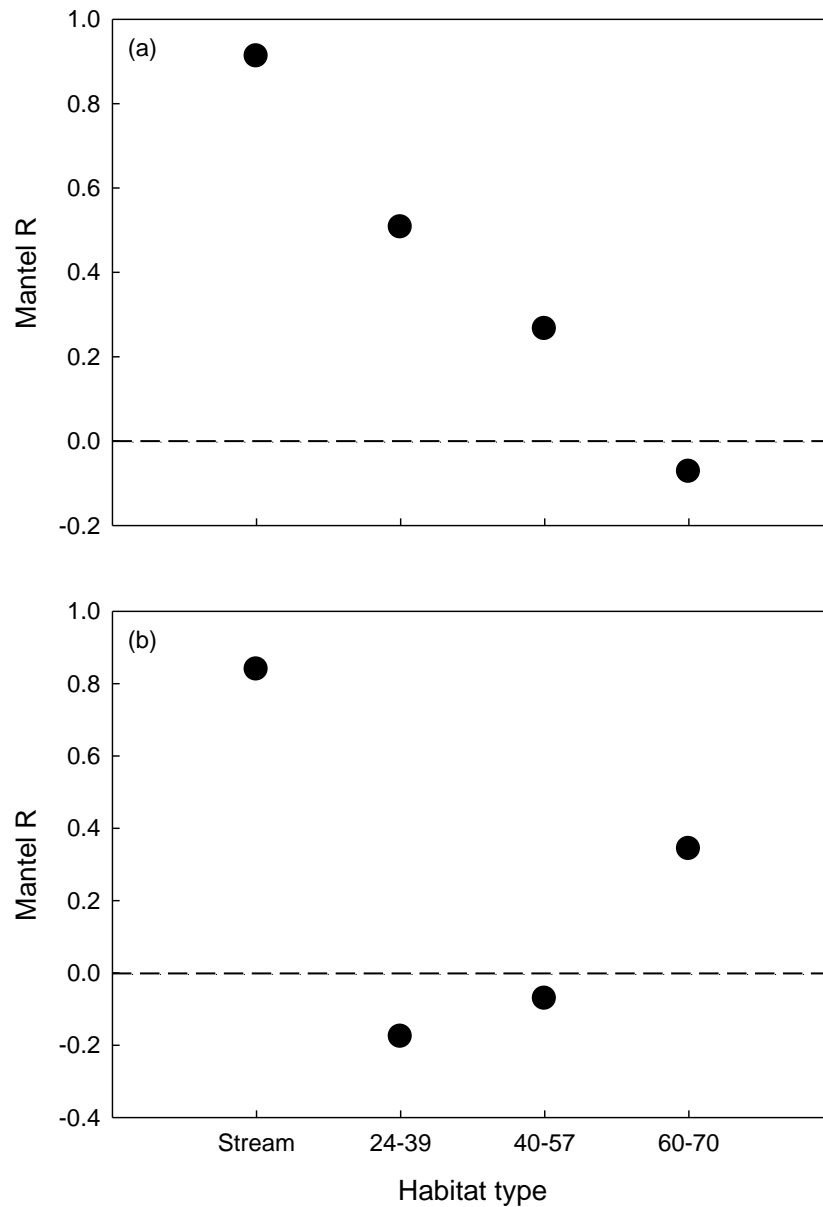


**Figure 6.** Densities of indicator species by habitat type, pond or stream. *Ameiurus natalis*, *Erimyzon oblongus*, *Etheostoma swaini*, *Lepomis gulosus*, *Lepomis macrochirus*, *Lepomis marginatus*, *Micropterus salmoides*, *Semotilus atromaculatus* density in pond (n = 24) and stream (n = 9) habitat types (mean log (abundance + 1) ± SE) over three sampling periods. *M. salmoides* was a marginally significant indicator of pond habitats (Table 8).



**Figure 7.** Densities of indicator species by pond age class. *Fundulus olivaceus*, *Lepomis punctulatus*, and *Micropterus punctulatus* density (mean log (abundance + 1)  $\pm$  SE) over three sampling periods in age class 1 (24 - 39 years, n = 8), class 2 (40 - 57 years, n = 10), and class 3 (60 - 70 years, n = 6) ponds.





**Figure 8.** The correlation between (a) community composition (Bray-Curtis distance) and (b) functional trait dispersion with 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 ( $n = 8$ ), 40 – 57 years of age ( $n = 10$ ), and 60 – 70 years of age ( $n = 6$ ). Values are the standardized Mantel statistic ( $r$ ).

## REFERENCES

- Alexander, Helen M., Bryan L. Foster, Ford Ballantyne, Cathy D. Collins, Janis Antonovics, and Robert D. Holt. "Metapopulations and Metacommunities: Combining Spatial and Temporal Perspectives in Plant Ecology." *Journal of Ecology* 100, no. 1 (2012): 88-103.
- Allen, Michael R., Jessica N. VanDyke, and Carla E. Cáceres. "Metacommunity Assembly and Sorting in Newly Formed Lake Communities." *Ecology* 92, no. 2 (2011): 269-275.
- Amarasekare, Priyanga. "Competitive Coexistence in Spatially Structured Environments: A Synthesis." *Ecology Letters* 6, no. 12 (2003): 1109-1122.
- Anderson, Christopher B., and Amy D. Rosemond. "Ecosystem Engineering by Invasive Exotic Beavers Reduces In-Stream Diversity and Enhances Ecosystem Function in Cape Horn, Chile." *Oecologia* 154, no. 1 (2007): 141-153.
- Anderson, Marti J. "A New Method for Non-Parametric Multivariate Analysis of Variance." *Austral Ecology* 26, no. 1 (2001): 32-46.
- Baber, Matthew J., Daniel L. Childers, Kimberly J. Babbitt, and David H. Anderson. "Controls on Fish Distribution and Abundance in Temporary Wetlands." *Canadian Journal of Fisheries and Aquatic Sciences* 59, no. 9 (2002): 1441-1450.
- Bedinger, M. S. "Forest Species as Indicators of Flooding in the Lower White River Valley, Arkansas, U.S. Geological Survey." *Survey Professional Paper*, (1971): 248-253.
- Beisner, Beatrix E., Pedro R. Peres-Neto, Eva S. Lindström, Allain Barnett, and Maria Lorena Longhi. "The Role of Environmental and Spatial Processes in Structuring Lake Communities from Bacteria to Fish." *Ecology* 87, no. 12 (2006): 2985-2991.
- Bhuta, Arvind Aniel Rombawa. "Variation in the Structure, Composition, and Dynamics of a Foundation Tree Species at Multiple Scales and Gradients." Ph.D. dissertation, Virginia Tech, (2011).
- Bie, T., L. Meester, Luc Brendonck, Koenraad Martens, Boudewijn Goddeeris, D. Ercken, H. Hampel et al. "Body Size and Dispersal Mode as Key Traits Determining Metacommunity Structure of Aquatic Organisms." *Ecology Letters* 15, no. 7 (2012): 740-747.

- Bister, Timothy J., David W. Willis, Michael L. Brown, Stephen M. Jordan, Robert M. Neumann, Michael C. Quist, and Christopher S. Guy. "Proposed Standard Weight (Ws) Equations and Standard Length Categories for 18 Warmwater Nongame and Riverine Fish Species." *North American Journal of Fisheries Management* 20, no. 2 (2000): 570-574.
- Blanchet, F. Guillaume, Pierre Legendre, and Daniel Borcard. "Forward Selection of Explanatory Variables." *Ecology* 89, no. 9 (2008): 2623-2632.
- Borcard, Daniel, and Pierre Legendre. "All-Scale Spatial Analysis of Ecological Data by Means of Principal Coordinates of Neighbour Matrices." *Ecological Modelling* 153, no. 1-2 (2002): 51-68.
- Borcard, Daniel, Pierre Legendre, and Pierre Drapeau. "Partialling Out the Spatial Component of Ecological Variation." *Ecology* 73, no. 3 (1992): 1045-1055.
- Boschung, Herbert T., and Richard L. Mayden. *Fishes of Alabama*. Smithsonian Books, 2004.
- Bray, J. Roger, and John T. Curtis. "An Ordination of the Upland Forest Communities of Southern Wisconsin." *Ecological Monographs* 27, no. 4 (1957): 325-349.
- Brown, B. L., and C. M. Swan. "Dendritic Network Structure Constrains Metacommunity Properties in Riverine Ecosystems." *Journal of Animal Ecology* 79, no. 3 (2010): 571-580.
- Bunn, Stuart E., and Angela H. Arthington. "Basic Principles and Ecological Consequences of Altered Flow Regimes for Aquatic Biodiversity." *Environmental Management* 30, no. 4 (2002): 492-507.
- Burton, James Donald. "Prolonged Flooding Inhibits Growth of Loblolly Pine Seedlings." U.S. Department of Agriculture. *Research Note*, (1971): 1-4.
- Bush, Bryana M., and Scott A. Wissinger. "Invertebrates in Beaver-Created Wetlands and Ponds." In *Invertebrates in Freshwater Wetlands*, pp. 411-449. Springer, Cham, 2016.
- Bylak, Aneta, and Krzysztof Kukuła. "Living with an Engineer: Fish Metacommunities in Dynamic Patchy Environments." *Marine and Freshwater Research* 69, no. 5 (2018): 883-893.
- Cadotte, Marc William. "Competition-Colonization Trade-Offs and Disturbance Effects at Multiple Scales." *Ecology* 88, no. 4 (2007): 823-829.
- Cadotte, Marc William, Donny V. Mai, Samuel Jantz, Michael D. Collins, Monica Keele, and James A. Drake. "On Testing the Competition-Colonization Trade-Off in a Multispecies Assemblage." *The American Naturalist* 168, no. 5 (2006): 704-709.

- Carlander, Kenneth Dixon. *Handbook of Freshwater Fishery Biology: Volume 3*. Iowa State University Press, 1997.
- Chase, Jonathan M., Nathan J. B. Kraft, Kevin G. Smith, Mark Vellend, and Brian D. Inouye. "Using Null Models to Disentangle Variation in Community Dissimilarity from Variation in  $\alpha$ -Diversity." *Ecosphere* 2, no. 2 (2011): 1-11.
- Chase, Jonathan M., and Wade A. Ryberg. "Connectivity, Scale-Dependence, and the Productivity-Diversity Relationship." *Ecology Letters* 7, no. 8 (2004): 676-683.
- Chesson, Peter. "Mechanisms of Maintenance of Species Diversity." *Annual Review of Ecology and Systematics* 31, no. 1 (2000): 343-366.
- Clements, Frederic E. "Nature and Structure of the Climax." *Journal of Ecology* 24, no. 1 (1936): 252-284.
- Collen, P., and R. J. Gibson. "The General Ecology of Beavers (*Castor* spp.), as Related to Their Influence on Stream Ecosystems and Riparian Habitats, and the Subsequent Effects on Fish – A Review." *Reviews in Fish Biology and Fisheries* 10, no. 4 (2000): 439-461.
- Cook, William M., Jin Yao, Bryan L. Foster, Robert D. Holt, and L. Brian Patrick. "Secondary Succession in an Experimentally Fragmented Landscape: Community Patterns Across Space and Time." *Ecology* 86, no. 5 (2005): 1267-1279.
- Cooke, S. J., P. J. Weatherhead, D. H. Wahl, and D. P. Philipp. "Parental Care in Response to Natural Variation in Nest Predation Pressure in Six Sunfish (Centrarchidae: Teleostei) Species." *Ecology of Freshwater Fish* 17, no. 4 (2008): 628-638.
- Cornwell, William K., Dylan W. Schwilk, and David D. Ackerly. "A Trait-Based Test for Habitat Filtering: Convex Hull Volume." *Ecology* 87, no. 6 (2006): 1465-1471.
- Correll, David L., Thomas E. Jordan, and Donald E. Weller. "Beaver Pond Biogeochemical Effects in the Maryland Coastal Plain." *Biogeochemistry* 49, no. 3 (2000): 217-239.
- Crumpton, William G., Thomas M. Isenhart, and Paul D. Mitchell. "Nitrate and Organic N Analyses with Second-Derivative Spectroscopy." *Limnology and Oceanography* 37, no. 4 (1992): 907-913.
- Cuthbert, Iain D., and Paul Del Giorgio. "Toward a Standard Method of Measuring Color in Freshwater." *Limnology and Oceanography* 37, no. 6 (1992): 1319-1326.
- Douglas, Michael Edward, and John A. Endler. "Quantitative Matrix Comparisons in Ecological and Evolutionary Investigations." *Journal of Theoretical Biology* 99, no. 4 (1982): 777-795.

- Drake, James A. "The Mechanics of Community Assembly and Succession." *Journal of Theoretical Biology* 147, no. 2 (1990): 213-233.
- Dray, S., G. Blanchet, D. Borcard, G. Guenard, T. Jombart, P. Legendre, and H. H. Wagner. "Adespatial: Multivariate Multiscale Spatial Analysis." *Lyon: R Package Version 0.0-4* (2016).
- Dray, Stéphane, Pierre Legendre, and Pedro R. Peres-Neto. "Spatial Modelling: A Comprehensive Framework for Principal Coordinate Analysis of Neighbour Matrices (PCNM)." *Ecological Modelling* 196, no. 3-4 (2006): 483-493.
- Dufrêne, Marc, and Pierre Legendre. "Species Assemblages and Indicator Species: The Need for a Flexible Asymmetrical Approach." *Ecological Monographs* 67, no. 3 (1997): 345-366.
- Fitzgerald, Daniel B., Kirk O. Winemiller, Mark H. Sabaj Pérez, and Leandro M. Sousa. "Using Trophic Structure to Reveal Patterns of Trait-Based Community Assembly Across Niche Dimensions." *Functional Ecology* 31, no. 5 (2017): 1135-1144.
- Frimpong, Emmanuel A., and Paul L. Angermeier. "Fish Traits: A Database of Ecological and Life-History Traits of Freshwater Fishes of the United States." *Fisheries* 34, no. 10 (2009): 487-495.
- Fukami, Tadashi. "Historical Contingency in Community Assembly: Integrating Niches, Species Pools, and Priority Effects." *Annual Review of Ecology, Evolution, and Systematics* 46 (2015).
- Fukami, Tadashi, T. Martijn Bezemer, Simon R. Mortimer, and Wim H. Putten. "Species Divergence and Trait Convergence in Experimental Plant Community Assembly." *Ecology Letters* 8, no. 12 (2005): 1283-1290.
- George, Scott St, and Erik Nielsen. "Palaeoflood Records for the Red River, Manitoba, Canada, Derived from Anatomical Tree-Ring Signatures." *The Holocene* 13, no. 4 (2003): 547-555.
- Giam, Xingli, and Julian D. Olden. "Environment and Predation Govern Fish Community Assembly in Temperate Streams." *Global Ecology and Biogeography* 25, no. 10 (2016): 1194-1205.
- Gibson, Polly P., Julian D. Olden, and Matthew W. O'Neill. "Beaver Dams Shift Desert Fish Assemblages Toward Dominance by Non-Native Species (Verde River, Arizona, USA)." *Ecology of Freshwater Fish* 24, no. 3 (2015): 355-372.
- Gleason, Henry Allan. "Further Views on the Succession-Concept." *Ecology* 8, no. 3 (1927): 299-326.

- Grafen, Alan. "The Phylogenetic Regression." *Philosophical Transactions of the Royal Society London: Series Biological* 326, no. 1233 (1989): 119-157.
- Grissino-Mayer, Henri D. "Evaluating Crossdating Accuracy: A Manual and Tutorial for the Computer Program COFECHA." *Tree-Ring Research* (2001).
- Halliday, Bryce T., S. D. Wedderburn, Jan L. Barton, and Rebecca E. Lester. "Restructuring of Littoral Fish Assemblages After Drought Differs in Two Lakes at the Terminus of a Heavily Regulated River." *River Research and Applications* 34, no. 4 (2018): 338-347.
- Hanson, Willis D., and Robert S. Campbell. "The Effects of Pool Size and Beaver Activity on Distribution and Abundance of Warm-Water Fishes in a North Missouri Stream." *American Midland Naturalist* (1963): 136-149.
- Hardin, Garrett. "The Competitive Exclusion Principle." *Science* 131, no. 3409 (1960): 1292-1297.
- Heino, Jani, and Barbara L. Peckarsky. "Integrating Behavioral, Population and Large-Scale Approaches for Understanding Stream Insect Communities." *Current Opinion in Insect Science* 2 (2014): 7-13.
- Helms, Brian S., David C. Werneke, Michael M. Gangloff, Emily E. Hartfield, and Jack W. Feminella. "The Influence of Low-Head Dams on Fish Assemblages in Streams Across Alabama." *Journal of the North American Benthological Society* 30, no. 4 (2011): 1095-1106.
- Hijmans, Robert J., Ed Williams, Chris Vennes, and Maintainer Robert J. Hijmans. "Package 'Geosphere'." (2017).
- HilleRisLambers, J., P. B. Adler, W. S. Harpole, J. M. Levine, and M. M. Mayfield. "Rethinking Community Assembly Through the Lens of Coexistence Theory." *Annual Review of Ecology, Evolution, and Systematics* 43 (2012).
- Hitt, Nathaniel P., and James H. Roberts. "Hierarchical Spatial Structure of Stream Fish Colonization and Extinction." *Oikos* 121, no. 1 (2012): 127-137.
- Hoeinghaus, David J., Kirk O. Winemiller, and Jenny S. Birnbaum. "Local and Regional Determinants of Stream Fish Assemblage Structure: Inferences Based on Taxonomic vs. Functional Groups." *Journal of Biogeography* 34, no. 2 (2007): 324-338.
- Holmes, Richard L. "Computer-Assisted Quality Control in Tree-Ring Dating and Measurement." *Tree-Ring Bulletin* (1983).
- Horn, Henry S. "The Ecology of Secondary Succession." *Annual Review of Ecology and Systematics* 5, no. 1 (1974): 25-37.

- Howeth, Jennifer G., Crysta A. Gantz, Paul L. Angermeier, Emmanuel A. Frimpong, Michael H. Hoff, Reuben P. Keller, Nicholas E. Mandrak et al. "Predicting Invasiveness of Species in Trade: Climate Match, Trophic Guild and Fecundity Influence Establishment and Impact of Non-Native Freshwater Fishes." *Diversity and Distributions* 22, no. 2 (2016): 148-160.
- Howeth, Jennifer G., and Mathew A. Leibold. "Prey Dispersal Rate Affects Prey Species Composition and Trait Diversity in Response to Multiple Predators in Metacommunities." *Journal of Animal Ecology* 79, no. 5 (2010): 1000-1011.
- Hubbell, Stephen P. "The Unified Neutral Theory of Biodiversity and Biogeography." Princeton University Press, 2001.
- Inouye, Richard S., and David Tilman. "Convergence and Divergence of Old-Field Vegetation After 11 yr of Nitrogen Addition." *Ecology* 76, no. 6 (1995): 1872-1887.
- Jackson, Donald A., Pedro R. Peres-Neto, and Julian D. Olden. "What Controls Who is Where in Freshwater Fish Communities the Roles of Biotic, Abiotic, and Spatial Factors." *Canadian Journal of Fisheries and Aquatic Sciences* 58, no. 1 (2001): 157-170.
- Johnston, Carol A. "Beaver Ponds and the Carbon Cycle." In *Beavers: Boreal Ecosystem Engineers*, pp. 201-221. Springer, Cham, 2017.
- Johnston, Carol A., and Robert J. Naiman. "Aquatic Patch Creation in Relation to Beaver Population Trends." *Ecology* 71, no. 4 (1990a): 1617-1621.
- Johnston, Carol A., and Robert J. Naiman. "The Use of a Geographic Information System to Analyze Long-Term Landscape Alteration by Beaver." *Landscape Ecology* 4, no. 1 (1990b): 5-19.
- Keddy, Paul A. "Assembly and Response Rules: Two Goals for Predictive Community Ecology." *Journal of Vegetation Science* 3, no. 2 (1992): 157-164.
- Laliberté, Etienne, and Pierre Legendre. "A Distance-Based Framework for Measuring Functional Diversity from Multiple Traits." *Ecology* 91, no. 1 (2010): 299-305.
- Larsson, L. A. "CooRecorder: Image Co-Ordinate Recording Program." *Cybis Elektronik & Data AB, Saltsjöbaden, Sweden* (2003).
- Law, Alan, Fiona McLean, and Nigel J. Willby. "Habitat Engineering by Beaver Benefits Aquatic Biodiversity and Ecosystem Processes in Agricultural Streams." *Freshwater Biology* 61, no. 4 (2016): 486-499.
- Law, Richard, and R. Daniel Morton. "Alternative Permanent States of Ecological Communities." *Ecology* 74, no. 5 (1993): 1347-1361.

- Law, Richard, and R. Daniel Morton. "Permanence and the Assembly of Ecological Communities." *Ecology* 77, no. 3 (1996): 762-775.
- Legendre, Pierre, and Louis Legendre. "Numerical Ecology: Second English Edition." *Developments in Environmental Modelling* 20 (1998).
- Leibold, Mathew A., Marcel Holyoak, Nicolas Mouquet, Priyanga Amarasekare, Jonathan M. Chase, Martha F. Hoopes, Robert D. Holt et al. "The Metacommunity Concept: A Framework for Multi-Scale Community Ecology." *Ecology Letters* 7, no. 7 (2004): 601-613.
- Levin, Simon A. "Multiple Scales and the Maintenance of Biodiversity." *Ecosystems* 3, no. 6 (2000): 498-506.
- Levin, Simon A., and Robert T. Paine. "Disturbance, Patch Formation, and Community Structure." *Proceedings of the National Academy of Sciences* 71, no. 7 (1974): 2744-2747.
- Li, Shao-peng, Marc W. Cadotte, Scott J. Meiners, Zhichao Pu, Tadashi Fukami, and Lin Jiang. "Convergence and Divergence in a Long-Term Old-Field Succession: The Importance of Spatial Scale and Species Abundance." *Ecology Letters* 19, no. 9 (2016): 1101-1109.
- Liu, Jing, Janne Soininen, Bo-Ping Han, and Steven A. J. Declerck. "Effects of Connectivity, Dispersal Directionality and Functional Traits on the Metacommunity Structure of River Benthic Diatoms." *Journal of Biogeography* 40, no. 12 (2013): 2238-2248.
- Logue, Jürg B., Nicolas Mouquet, Hannes Peter, Helmut Hillebrand, and Metacommunity Working Group. "Empirical Approaches to Metacommunities: A Review and Comparison with Theory." *Trends in Ecology & Evolution* 26, no. 9 (2011): 482-491.
- López-Martínez, Jorge Omar, Lucía Sanaphre-Villanueva, Juan Manuel Dupuy, José Luis Hernández-Stefanoni, Jorge Arturo Meave, and José Alberto Gallardo-Cruz. "β-Diversity of Functional Groups of Woody Plants in a Tropical Dry Forest in Yucatan." *PLoS One* 8, no. 9 (2013): e73660.
- Loranger, Jessy, Benjamin Blonder, Éric Garnier, Bill Shipley, Denis Vile, and Cyrille Violle. "Occupancy and Overlap in Trait Space Along a Successional Gradient in Mediterranean Old Fields." *American Journal of Botany* 103, no. 6 (2016): 1050-1060.
- Louette, Gerald, Luc De Meester, and Steven Declerck. "Assembly of Zooplankton Communities in Newly Created Ponds." *Freshwater Biology* 53, no. 11 (2008): 2309-2320.
- MacArthur, Robert, and Richard Levins. "The Limiting Similarity, Convergence, and Divergence of Coexisting Species." *The American Naturalist* 101, no. 921 (1967): 377-385.



- Mantel, Nathan. "The Detection of Disease Clustering and a Generalized Regression Approach." *Cancer Research* 27, no. 2 Part 1 (1967): 209-220.
- Marchetti, Michael P., and Peter B. Moyle. "Effects of Flow Regime on Fish Assemblages in a Regulated California Stream." *Ecological Applications* 11, no. 2 (2001): 530-539.
- Martin, Sherry L., Briana L. Jasinski, Anthony D. Kendall, Travis A. Dahl, and David W. Hyndman. "Quantifying Beaver Dam Dynamics and Sediment Retention Using Aerial Imagery, Habitat Characteristics, and Economic Drivers." *Landscape Ecology* 30, no. 6 (2015): 1129-1144.
- McCune, B., and M. J. Mefford. "PC-ORD v. 6.255 Beta." *MjM Software. Gleneden Beach, Lincoln* (2011).
- Meiners, Scott J., Marc W. Cadotte, Jason D. Fridley, Steward T. A. Pickett, and Lawrence R. Walker. "Is Successional Research Nearing its Climax? New Approaches for Understanding Dynamic Communities." *Functional Ecology* 29, no. 2 (2015): 154-164.
- Mettee, Maurice F., Patrick E. O'Neil, and J. Malcolm Pierson. *Fishes of Alabama and the Mobile Basin*. Vol. 15. Birmingham, Alabama: Oxmoor House, 1996.
- Moritz, C., C. N. Meynard, V. Devictor, K. Guizien, C. Labrune, J. M. Guarini, and N. Mouquet. "Disentangling the Role of Connectivity, Environmental Filtering, and Spatial Structure on Metacommunity Dynamics." *Oikos* 122, no. 10 (2013): 1401-1410.
- Moshenko, Robert W., and John H. Gee. "Diet, Time and Place of Spawning, and Environments Occupied by Creek Chub (*Semotilus atromaculatus*) in the Mink River, Manitoba." *Journal of the Fisheries Board of Canada* 30, no. 3 (1973): 357-362.
- Mouillot, David, Nicholas A. J. Graham, Sébastien Villéger, Norman W. H. Mason, and David R. Bellwood. "A Functional Approach Reveals Community Responses to Disturbances." *Trends in Ecology & Evolution* 28, no. 3 (2013): 167-177.
- Mouquet, N., P. Munguia, J. M. Kneitel, and T. E. Miller. "Community Assembly Time and the Relationship Between Local and Regional Species Richness." *Oikos* 103, no. 3 (2003): 618-626.
- Moyle, Peter B., and Theo Light. "Biological Invasions of Fresh Water: Empirical Rules and Assembly Theory." *Biological Conservation* 78, no. 1-2 (1996): 149-161.
- Naiman, Robert J., Carol A. Johnston, and James C. Kelley. "Alteration of North American Streams by Beaver." *BioScience* 38, no. 11 (1988): 753-762.
- Nelson, Joseph S., Terry C. Grande, and Mark V. H. Wilson. *Fishes of the World*. John Wiley & Sons, 2016.

- Nemergut, Diana R., Joseph E. Knelman, Scott Ferrenberg, Teresa Bilinski, Brett Melbourne, Lin Jiang, Cyrille Violle et al. "Decreases in Average Bacterial Community rRNA Operon Copy Number During Succession." *The ISME Journal* 10, no. 5 (2015): 1147-1156.
- Neumann, Robert M., Christopher S. Guy, and David W. Willis. "Length, Weight, and Associated Indices." In *Fisheries Techniques, 3rd edition*, pp. 637-676. American Fisheries Society, Bethesda, Maryland, 2012.
- Nummi, Petri. "Simulated Effects of the Beaver on Vegetation, Invertebrates and Ducks." In *Annales Zoologici Fennici*, pp. 43-52. Finnish Zoological Publishing Board, formed by the Finnish Academy of Sciences, Societas Scientiarum Fennica, Societas pro Fauna et Flora Fennica and Societas Biologica Fennica Vanamo, 1989.
- Odum, Eugene P. "The Strategy of Ecosystem Development." *Science* 164 (1966): 262-270.
- Oksanen, Jari, F. Guillaume Blanchet, Michael Friendly, Roeland Kindt, Pierre Legendre, Dan McGlinn, Peter R. Minchin, R. B. O'Hara, Gavin L. Simpson, and Peter Solymos. 2017. "Package 'Vegan'."
- Osenberg, Craig W., Orlando Sarnelle, and Scott D. Cooper. "Effect Size in Ecological Experiments: The Application of Biological Models in Meta-Analysis." *The American Naturalist* 150, no. 6 (1997): 798-812.
- Pacala, Stephen W., and Mark Rees. "Models Suggesting Field Experiments to Test Two Hypotheses Explaining Successional Diversity." *The American Naturalist* 152, no. 5 (1998): 729-737.
- Page, Lawrence M., and Brooks M. Burr. *A Field Guide to Freshwater Fishes: North America North of Mexico*. Houghton Mifflin Harcourt, 1997.
- Peres-Neto, Pedro R., Pierre Legendre, Stéphane Dray, and Daniel Borcard. "Variation Partitioning of Species Data Matrices: Estimation and Comparison of Fractions." *Ecology* 87, no. 10 (2006): 2614-2625.
- Phipps, Richard L. *Collecting, Preparing, Crossdating, and Measuring Tree Increment Cores*. U.S. Department of the Interior, Geological Survey, 1985.
- Poff, N. Leroy, and James V. Ward. "Implications of Streamflow Variability and Predictability for Lotic Community Structure: A Regional Analysis of Streamflow Patterns." *Canadian Journal of Fisheries and Aquatic Sciences* 46, no. 10 (1989): 1805-1818.
- Pool, Thomas K., and Julian D. Olden. "Taxonomic and Functional Homogenization of an Endemic Desert Fish Fauna." *Diversity and Distributions* 18, no. 4 (2012): 366-376.

- Prepas, E. E., and F. H. Rigler. "Improvements in Quantifying the Phosphorus Concentration in Lake Water." *Canadian Journal of Fisheries and Aquatic Sciences* 39, no. 6 (1982): 822-829.
- Purschke, Oliver, Barbara C. Schmid, Martin T. Sykes, Peter Poschlod, Stefan G. Michalski, Walter Durka, Ingolf Kühn, Marten Winter, and Honor C. Prentice. "Contrasting Changes in Taxonomic, Phylogenetic and Functional Diversity During a Long-Term Succession: Insights into Assembly Processes." *Journal of Ecology* 101, no. 4 (2013): 857-866.
- Rahel, Frank J. "Factors Structuring Fish Assemblages Along a Bog Lake Successional Gradient." *Ecology* 65, no. 4 (1984): 1276-1289.
- Raup, David M., and Rex E. Crick. "Measurement of Faunal Similarity in Paleontology." *Journal of Paleontology* (1979): 1213-1227.
- Ray, A. M., A. J. Rebertus, and H. L. Ray. "Macrophyte Succession in Minnesota Beaver Ponds." *Canadian Journal of Botany* 79, no. 4 (2001): 487-499.
- Ray, Heather L., Andrew M. Ray, and Alan J. Rebertus. "Rapid Establishment of Fish in Isolated Peatland Beaver Ponds." *Wetlands* 24, no. 2 (2004): 399-405.
- Rosell, Frank, Orsolya Bozser, Peter Collen, and Howard Parker. "Ecological Impact of Beavers *Castor fiber* and *Castor canadensis* and their Ability to Modify Ecosystems." *Mammal Review* 35, no. 3-4 (2005): 248-276.
- Rosso, Juan José, and Rolando Quirós. "Patterns in Fish Species Composition and Assemblage Structure in the Upper Salado River Lakes, Pampa Plain, Argentina." *Neotropical Ichthyology* 8, no. 1 (2010): 135-144.
- Rozas, Vicente. "Dendrochronology of Pedunculate Oak (*Quercus robur* L.) in an Old-Growth Pollarded Woodland in Northern Spain: Tree-Ring Growth Responses to Climate." *Annals of Forest Science* 62, no. 3 (2005): 209-218.
- Ruple, David L., Robert H. McMichael, and John A. Baker. "Life History of the Gulf Darter, *Etheostoma swaini* (Pisces: Percidae)." In *Environmental Biology of Darters*, pp. 45-54. Springer, Dordrecht, 1984.
- Rypel, Andrew L., Wendell R. Haag, and Robert H. Findlay. "Pervasive Hydrologic Effects on Freshwater Mussels and Riparian Trees in Southeastern Floodplain Ecosystems." *Wetlands* 29, no. 2 (2009): 497-504.
- Schlosser, Isaac J. "Fish Community Structure and Function Along Two Habitat Gradients in a Headwater Stream." *Ecological Monographs* 52, no. 4 (1982): 395-414.

- Schlosser, Isaac J. "Stream Fish Ecology: A Landscape Perspective." *BioScience* 41, no. 10 (1991): 704-712.
- Schlosser, Isaac J. "Dispersal, Boundary Processes, and Trophic-Level Interactions in Streams Adjacent to Beaver Ponds." *Ecology* 76, no. 3 (1995): 908-925.
- Schlosser, Isaac J. "Fish Recruitment, Dispersal, and Trophic Interactions in a Heterogeneous Lotic Environment." *Oecologia* 113, no. 2 (1998): 260-268.
- Schlosser, Isaac J., and Larry W. Kallemeyn. "Spatial Variation in Fish Assemblages Across a Beaver-Influenced Successional Landscape." *Ecology* 81, no. 5 (2000): 1371-1382.
- Selego, Stephen M., George T. Merovich, and James T. Anderson. "Conflicting Natural and Anthropogenic Threats Reduce Nest Success in Centrarchid Fishes." *Hydrobiologia* 732, no. 1 (2014): 161-171.
- Sferra, Christopher O., Justin L. Hart, and Jennifer G. Howeth. "Habitat Age Influences Metacommunity Assembly and Species Richness in Successional Pond Ecosystems." *Ecosphere* 8, no. 6 (2017): e01871.
- Shea, Katriona, and Peter Chesson. "Community Ecology Theory as a Framework for Biological Invasions." *Trends in Ecology & Evolution* 17, no. 4 (2002): 170-176.
- Smith, Joseph M., and Martha E. Mather. "Beaver Dams Maintain Fish Biodiversity by Increasing Habitat Heterogeneity Throughout a Low-Gradient Stream Network." *Freshwater Biology* 58, no. 7 (2013): 1523-1538.
- Smith, S. C. F., S. J. Meiners, R. P. Hastings, T. Thomas, and R. E. Colombo. "Low-Head Dam Impacts on Habitat and the Functional Composition of Fish Communities." *River Research and Applications* 33, no. 5 (2017): 680-689.
- Smouse, Peter E., Jeffrey C. Long, and Robert R. Sokal. "Multiple Regression and Correlation Extensions of the Mantel Test of Matrix Correspondence." *Systematic Zoology* 35, no. 4 (1986): 627-632.
- Snodgrass, Joel W., and Gary K. Meffe. "Influence of Beavers on Stream Fish Assemblages: Effects of Pond Age and Watershed Position." *Ecology* 79, no. 3 (1998): 928-942.
- Snodgrass, Joel W., and Gary K. Meffe. "Habitat Use and Temporal Dynamics of Blackwater Stream Fishes in and Adjacent to Beaver Ponds." *Copeia* (1999): 628-639.
- Sprules, William M. "The Effect of a Beaver Dam on the Insect Fauna of a Trout Stream." *Transactions of the American Fisheries Society* 70, no. 1 (1941): 236-248.
- Stokes, Marvin A. *An Introduction to Tree-Ring Dating*. University of Arizona Press, 1996.

- Tilman, David. "Niche Tradeoffs, Neutrality, and Community Structure: A Stochastic Theory of Resource Competition, Invasion, and Community Assembly." *Proceedings of the National Academy of Sciences of the United States of America* 101, no. 30 (2004): 10854-10861.
- Tonn, William M., and John J. Magnuson. "Patterns in the Species Composition and Richness of Fish Assemblages in Northern Wisconsin Lakes." *Ecology* 63, no. 4 (1982): 1149-1166.
- Van der Gucht, Katleen, Karl Cottenie, Koenraad Muylaert, Nele Vloemans, Sylvie Cousin, Steven Declerck, Erik Jeppesen et al. "The Power of Species Sorting: Local Factors Drive Bacterial Community Composition Over a Wide Range of Spatial Scales." *Proceedings of the National Academy of Sciences* 104, no. 51 (2007): 20404-20409.
- Vanschoenwinkel, Bram, Falko Buschke, and Luc Brendonck. "Disturbance Regime Alters the Impact of Dispersal on Alpha and Beta Diversity in a Natural Metacommunity." *Ecology* 94, no. 11 (2013): 2547-2557.
- Villéger, Sébastien, Norman W. H. Mason, and David Mouillot. "New Multidimensional Functional Diversity Indices for a Multifaceted Framework in Functional Ecology." *Ecology* 89, no. 8 (2008): 2290-2301.
- Villéger, Sébastien, Julia Ramos Miranda, Domingo Flores Hernández, and David Mouillot. "Contrasting Changes in Taxonomic vs. Functional Diversity of Tropical Fish Communities After Habitat Degradation." *Ecological Applications* 20, no. 6 (2010): 1512-1522.
- Ward, J. V., Klement Tockner, and Fritz Schiemer. "Biodiversity of Floodplain River Ecosystems: Ecotones and Connectivity." *Regulated Rivers: Research & Management* 15, no. 1 (1999): 125-139.
- Weiherr, Evan, and Paul A. Keddy. "Assembly Rules, Null Models, and Trait Dispersion: New Questions from Old Patterns." *Oikos* (1995): 159-164.
- Winemiller, Kirk O. "Ecomorphological Diversification in Lowland Freshwater Fish Assemblages from Five Biotic Regions." *Ecological Monographs* 61, no. 4 (1991): 343-365.
- Young, Truman P., Jonathan M. Chase, and Russell T. Huddleston. "Community Succession and Assembly Comparing, Contrasting and Combining Paradigms in the Context of Ecological Restoration." *Ecological Restoration* 19, no. 1 (2001): 5-18.
- Yu, Douglas W., and Howard B. Wilson. "The Competition-Colonization Trade-Off is Dead; Long Live the Competition-Colonization Trade-Off." *The American Naturalist* 158, no. 1 (2001): 49-63.