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Convergent diversity and trait composition in temporary streams and ponds

Tiffany A. Schriever,[1,†] and David A. Lytle

Department of Integrative Biology, Oregon State University, Corvallis, Oregon 97331 USA

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Abstract. Hydrology is the main environmental filter in aquatic ecosystems and may result in shared tolerances and functional traits among species in disparate ecosystems. We analyzed the associations between taxonomic and functional facets of diversity within aquatic ecosystems (ponds vs. streams) across a hydroperiod gradient (1–365 d) to untangle the hydrologic drivers of aquatic invertebrate diversity. We used invertebrate assemblage data from seven arid-land streams in southeastern Arizona, United States collected over 2 yr and nine temperate woodland ponds in Ontario, Canada collected over 2 yr. Our results showed that although invertebrate assemblages from streams and ponds differ taxonomically, hydroperiod had similar influence on invertebrate trait structure regardless of biogeographic and habitat differences. Streams and ponds independently showed strong positive relationships between functional richness and taxonomic richness; however, the relationship showed a shallower slope in ponds, indicating higher functional redundancy. Intermittent ponds and streams tended to have lower functional and taxonomic richness than their perennial counterparts, but harbored greater beta diversity. Our results suggest that even though ponds and streams are fundamentally different habitats with distinct faunas and unique ecological processes, hydrology produces convergent patterns in both trait composition and diversity patterns.

Key words: beta diversity; desert; functional traits; hydrology; invertebrates; resilience; resistance; vernal pools.

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[1] Present address: Department of Biological Sciences, Western Michigan University, Kalamazoo, Michigan 49008 USA.

† **E-mail:** tiffany.schriever@wmich.edu

Introduction

Environmental filtering is the process by which a subset of the regional species pool can persist in a local habitat because these species have particular traits or phenotypes suited to local environmental conditions (Southwood 1988, Poff 1997). Filtering works on the principle that species differ in their environmental requirements and tolerances. Communities that have different compositions of species are likely to have different trait diversity. Functional diversity is defined as the range of species and traits that influence ecosystem functioning (Tilman 2001). Taxonomic richness and functional richness may respond differently to environmental gradients depending on the composition of the community (e.g., dominance of generalists or functionally redundant species; Villéger et al. 2012). Additionally, beta diversity—both 'turnover' and 'variation' beta (Anderson et al. 2011)—may be a more informative measure of the effects of environmental variation than taxonomic richness alone. Variation beta diversity is defined as variation in species composition among sampling locations and turnover beta diversity measures change in community structure along a particular gradient. Thus, characterizing and comparing the

relationship between taxonomic and functional richness across multiple aquatic ecosystems and environmental gradients provides insights into community organization and ecosystem function.

Hydroperiod or flow duration describes the length of the aquatic phase over the course of a year, and is a central organizing component of freshwater ecosystems. Hydrology has been a long-standing focus of both running (lotic)- and still (lentic)-water research because of its powerful role in shaping the ecology and evolution of species (Wissinger 1999, Brooks 2000, Lytle and Poff 2004, Williams 2006) as well as ecosystem processes (Sparks 1995, Poff et al. 1997). Variation in pond hydroperiod (Wiggins et al. 1980, Semlitsch et al. 1996, Skelly 1996, Wellborn et al. 1996, Urban 2004) and stream flow duration (Poff and Ward 1989, Poff et al. 1997, Lamouroux et al. 2002, Vieira et al. 2004, Hoeinghaus et al. 2007) influences invertebrate and vertebrate species richness and composition, predator distribution, and reproductive success. Historical and current hydrologic regimes play a central role in regulating ecological processes at the species, trait, community, and ecosystem levels (Resh et al. 1988, Poff et al. 1997, Church 2008, Konar et al. 2013).

Researchers studying either ponds or streams have independently identified hydrology as a primary driver of ecological communities in freshwater ecosystems. Yet studies that make comparisons across the lotic–lentic divide are exceptionally rare (Williams et al. 2003, Wurtsbaugh et al. 2015). Because ponds and streams have fundamentally different key ecosystem properties (i.e., branching pattern, flow, sedimentation, disturbance, water chemistry) one might expect ecological patterns and processes to differ. However, if a particular environmental gradient is driving processes equally in both ecosystems, we might expect ecological congruence between ponds and streams. For instance, it is possible that similar patterns (i.e., species richness, community composition, functional traits, and ecosystem properties) result from a common hydrologic filter that operates similarly in both ponds and streams. If this is the case, we predict that because of evolved life history strategies due to a common environmental gradient (Southwood 1977), that a subset of traits will be shared among the different organisms that inhabit ponds and streams.

We took a functional trait perspective to compare invertebrate assemblages from woodland ponds in SE Ontario, Canada to arid-land streams in SE Arizona, United States that experience similar hydroperiod gradients. In this study, we hypothesized that habitats with similar hydrologic conditions, regardless of ecosystem type, should share species traits. We hypothesized that functional richness should be positively related to taxonomic richness in both ponds and streams and that ponds and streams should show similar richness patterns along a hydrologic gradient. We predicted higher taxonomic richness and functional richness in perennial ponds and streams vs. their intermittent counterparts. Additionally, we predicted that beta diversity (turnover) should decline along a gradient of long to short hydroperiod and that variation beta diversity should be higher in intermittent stream reaches and ponds because disturbance and isolation can promote higher beta diversity.

Methods

Survey of aquatic invertebrate communities

We compared invertebrate assemblages collected along a hydroperiod gradient from temperate ponds (Ontario, Canada) and dryland streams (Arizona, United States). The seasons of sampling are different between ponds and streams, but they represent the main active aquatic seasons in each habitat. Each month from April to September in 2008 and 2009, we collected aquatic invertebrates by dip-net (500 μm mesh) from fishless ponds that spanned a natural gradient from intermittent freshwater woodland ponds to perennial freshwater marshes at the Queen's University Biological Station (QUBS), Ontario, Canada (Schriever and Williams 2013). Samples were collected at several locations throughout each pond. Seven ponds were used in 2008 with two other ponds added to the study in 2009 (n = 9 ponds, total 80 collections). Pond invertebrate samples were sorted into major insect groups in the field, placed in plastic jars, and held on ice until deposited in a freezer. In the laboratory, we identified pond invertebrates to genus level

(some family and species level identifications) with a dissecting microscope.

We collected aquatic invertebrates from 23 sites distributed across seven arid-land streams in the Huachuca Mountains within the Upper San Pedro River Basin of southeastern Arizona, United States (Bogan et al. 2013, Schriever et al. 2015). All streams are fishless except for the San Pedro River; however, no fish were collected in our sampling effort. We distributed our sample sites among perennial, intermittent and ephemeral reaches (classification follows Levick et al. 2008). Sites were sampled multiple times in 2010 and 2011. Most sampling occurred during the fall and winter seasons because these seasons represent a time when streams generally have flow (November and December; March and April, respectively, total 120 collections). Riffle samples consisted of scrubbing rocks and agitating stream bed substrates in a 1 m^2 area, and dislodged macroinvertebrates were collected in a downstream dip-net. A pool sample consisted of a time × area standardized collection of the entire pool area using a dip-net at 10 s for every 1 m^2 area of pool. Stream invertebrate samples were preserved in 95% ethanol and identified in the laboratory to genus or species for insects (including Chironomidae) and family or order for noninsects.

Measuring hydroperiod

The hydroperiod of each pond was measured as the duration of the aquatic phase or days from ice-off until each pond dried, as recorded in 2008 and 2009. Each pond was visited biweekly to check depth and presence of water. In the Arizona streams, we measured flow regime through the deployment of 15 wet/dry electrical resistance (ER) sensors (Jaeger and Olden 2012) to quantify duration of stream flow near stream invertebrate sampling locations. The sensors logged relative conductivity at 15-min intervals from 15 April 2010 to 31 December 2011 as a proxy for the presence of surface water. From these conductivity data, we calculated the hydroperiod for each year of sample for each sampling site using the nearest sensor by summing 15-min time periods of both wet and dry conditions for the sampling period, converting the time units to days. Ponds and stream sites were grouped using ER data into two hydrologic categories, intermittent or perennial.

Trait data and analysis

We used a trait matrix developed by Schriever et al. (2015) for the AZ stream invertebrates and developed another for the pond invertebrates by using publications of primary literature, databases, and expert knowledge to define trait states. We selected seven traits (30 states) that are associated with biological responses to drought in arid-land streams and that describe functional composition of invertebrate communities: respiration, voltinism, primary locomotion and habit, diapause, dispersal capability, body size, and functional feeding group (Boersma et al. 2014, Schriever et al. 2015). We found sufficient trait information for 88 freshwater macroinvertebrate taxa (out of 94 identified taxa) collected from study ponds and 211 taxa from study streams (out of 225 identified) (Supplement 1 and Appendix S1 in Schriever et al. 2015). Only taxa with sufficient trait data were used to calculate functional richness for each pond and stream community. Functional richness (FRic) measures the volume of functional space occupied by a community in a multivariate trait space (Cornwell et al. 2006, Villéger et al. 2008). FRic was calculated using the R-based FD package (R Core Team 2013) and the function dbFD (Laliberté and Legendre 2010, Laliberté and Shipley 2011). Traits were given equal weights, and standardized to mean 0 and unit variance. Taxonomic richness was calculated as the number of unique taxa identified at each site.

Statistical analysis

We performed a redundancy analysis (RDA) to test for the influence of ecosystem and hydroperiod factors on trait structure. RDA is a direct gradient ordination method that tests if trait composition is related to sampling site and any constraining environmental variables. The constraining variables were ecosystem (pond or stream) and hydroperiod (continuous variable; number of days) and the response variables were the 30 trait states. We multiplied the species × traits matrix (88 pond taxa and 211 stream taxa × 30 possible trait states) by the species incidence × sites matrix

(88 taxa × 16 pond sites; 211 taxa × 23 stream sites) to arrive at a traits × sites matrix (30 traits × 39 sites), which we used, untransformed, as input in RDA along with the constraining variables. This approach allowed us to show how pond and stream sites are characterized by particular environmental variables and whether particular traits can be attributed to a specific measured predictor variable (Gotelli and Ellison 2004). We conducted permutation tests on the RDA models to test the significance of constraining variables based on 1000 randomizations. Additionally, we performed a multivariate nonparametric ANOVA of dissimilarities (PERMANOVA, Adonis function) test on the traits × site matrix. Adonis can be used to test for similar means (centroids) of groups. A permutation test is used to determine if the data are consistent with the null hypothesis of no difference of centroids.

Taxonomic richness and FRic were estimated using the accumulation of taxa across sampling events. We combined replicate stream microhabitat invertebrate samples into one sample per year from each hydrologic category for a total of 23 stream samples. We tested the relationship between FRic and taxonomic richness with linear regression. Taxonomic richness was log-transformed to meet the assumption of linearity. Separate linear regression models were run to assess the relationships between responses of FRic and taxonomic richness to hydroperiod within ponds and streams. We tested the effect of ecosystem type on the dependent variables of FRic and taxonomic richness while controlling for the effect of hydroperiod and taxonomic richness by ANCOVA. The slope of the relationship between functional and taxonomic richness determines the degree of functional redundancy in communities, which may differ between habitats. We used the interaction term from ANCOVA to analyze differences in the slopes and intercepts between streams and ponds from regressions of FRic vs. taxonomic richness and FRic and taxonomic richness vs. hydroperiod. If the interaction term was significant, we concluded streams and ponds had different slopes for the relationship tested.

We conducted the following analytical steps on both stream and pond data sets independently and on the combined data set. First, we calculated trait dissimilarity (quantitative Bray–Curtis) and taxonomic dissimilarity (binary data, Sørensen dissimilarity) between all pairwise combinations of assemblages using R Package software (Vegan, function: vegdist). Second, we calculated distance to centroid ('variation' beta diversity) and tested for homogeneity of multivariate dispersion (betadisper function) between groups (pond vs. stream and intermittent vs. perennial). This method produces an independent dissimilarity value for each sample, distance to group centroid, and has been proposed as an index of beta diversity to express variation in community structure among groups (Anderson 2006, Anderson et al. 2006). Third, we tested for differences in mean trait distances using PERMANOVA (adonis function) on the distance matrices ran with 999 permutations. The adonis function can use both factors (in our case pond vs. stream or intermittent vs. perennial) and continuous (hydroperiod) explanatory variables and handles several variables together. Adonis tests for differences in means (centroids) of groups while betadisper tests for differences in dispersion (variation beta diversity). Fourth, we examined turnover beta diversity in both the taxonomic and functional diversity components along a hydroperiod gradient using the distance matrices for invertebrate assemblages and functional traits. We plotted the pairwise dissimilarity distances against the hydroperiod gradient and performed linear regression on the relationship.

Results

Hydroperiod ranged from 65 to 365 d for ponds and 1 to 365 d for streams. Invertebrate assemblages from streams and ponds shared 14 orders, 34 families, and six genera in common (Appendix S2). Thus, at the level of genus, ponds and streams in aggregate had only 3.8% of taxa in common.

Trait composition

The two RDA axes significantly explained 54.1% of the total variation of the pond and stream invertebrate functional trait structure (permutation test $P = 0.001$). The RDA showed 50.3% of the variance was expressed on axis 1 and identified a gradient that contrasted

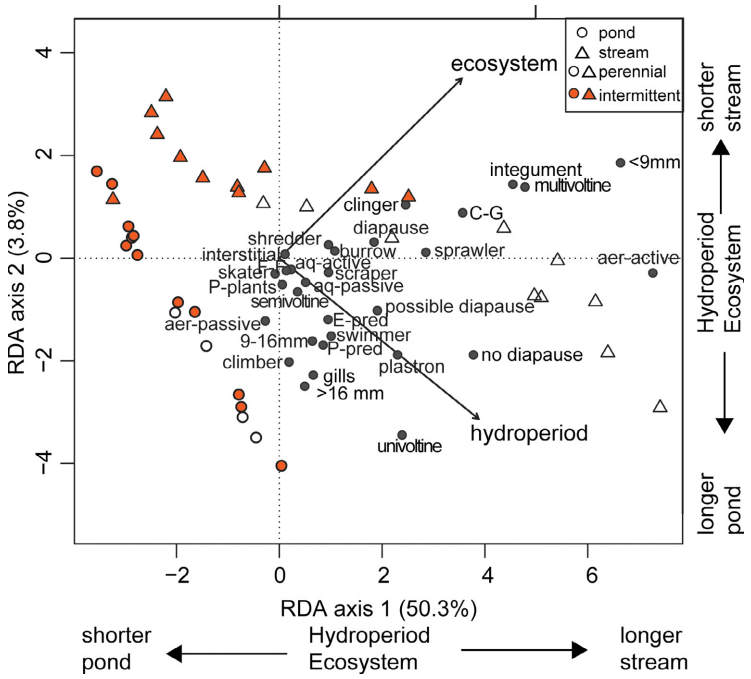

Fig. 1. Intermittent hydrology produces convergent trait structure in pond (circles) and stream (triangles) invertebrate communities. Bi-plot of the first two axes of the redundancy analysis (RDA) illustrating the relationship between predictor variables ($n = 2$, arrows), sites ($n = 37$, symbols), and traits ($n = 30$, gray dots) from invertebrate samples. Sites are coded by hydrologic category based on whether a site experienced a drying period (intermittent, orange-filled triangles and circles) or not (perennial, open triangles and circles).

perennial ponds and streams occurring in the right side of the ordination from the intermittent ponds and streams that occupied the top left side of ordination (Fig. 1, Appendix S1). Even though the species pools of ponds and streams were notably different, most intermittent sites from both ponds (58%) and streams (82%) converged in the upper left quadrate of the ordination thus, demonstrating trait similarities regardless of ecosystem type. Several traits were tied exclusively to longer hydroperiods, including the use of gills for respiration, lack of diapause ability, and univoltine reproduction. Ponds with longer hydroperiod were more likely to have larger sized taxa (>16 mm) than streams and streams with longer hydroperiod were more associated with aerial active dispersal mode. The environmental gradients of hydroperiod and ecosystem showed similar strength of correlation, but in opposite directions (−0.628 and 0.702, respectively) on axis 2. RDA axis 2 (3.8% of variance) further separated ponds and streams and reinforced the pattern of convergence among short hydroperiod sites. The higher trait redundancy in ponds may have contributed to less spread among sites in ordination space. The adonis test confirmed the patterns seen in the RDA in that the trait means (centroids) differed significantly between ponds and streams ($R^2 = 0.14$, $P = 0.01$) and among hydrologic categories ($R^2 = 0.32$, $P = 0.01$). There was also a significant interaction ($R^2 = 0.057$, $P = 0.02$). The centroid (mean) location for intermittent ponds and intermittent streams overlapped on axis 1 (Welch Two Sample t-test: $t = -1.8199$, df = 16.826, $P = 0.087$), but were significantly separated on axis 2 ($t = -4.2499$, df = 14.353, $P = 0.0008$).

Functional–taxonomic richness relationship

We found support for the hypothesis that FRic should be positively related to taxonomic richness. Streams and ponds independently showed strong positive relationships between FRic and taxonomic richness (linear regression: ponds: $R^2 = 0.825$, $F_{1,14} = 71.8$, $P < 0.0001$;

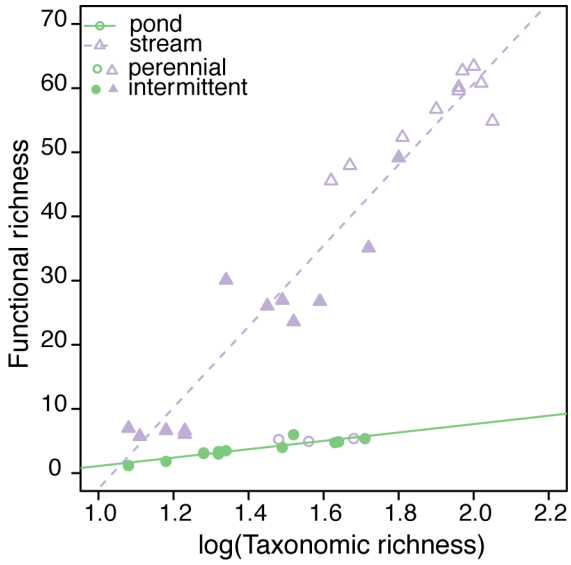

Fig. 2. Relationships between functional richness and invertebrate taxonomic richness are steeper in streams (n = 23, FRic = 63.54 × −66.13) vs. ponds (n = 16, FRic = 6.53 × −5.43). Pond functional richness values were multiplied by 10 for better graphical presentation.

streams: R^2 = 0.927, $F_{1,20}$ = 265.5, P < 0.0001). However, there was a significant difference between the slopes of FRic from ponds and streams for any incremental amount of taxonomic richness, in that streams consistently had higher FRic (ANCOVA: P = 0.002; Fig. 2). Slopes of the relationships indicate higher redundancy in ponds (nonlogged slope = 0.093 vs. stream = 0.580).

Hydroperiod-richness relationships

We found that invertebrate taxonomic richness was positively related to hydroperiod (lm: R^2 = 0.38, $F_{1,35}$ = 23.15, P < 0.0001) and that the slopes of the regression lines for ponds and streams between hydroperiod and taxonomic richness were not significantly different (ANCOVA: P = 0.14; ponds n = 16: slope = 0.06; streams n = 21: slope = 0.14), indicating that ponds and streams of the same hydroperiod had similar taxonomic richness and moderate levels of taxonomic redundancy (Fig. 3a). By contrast, ponds and streams showed different positive relationships between FRic and hydroperiod (ANCOVA: $F_{1,33}$ = 6.10, P = 0.019; Fig. 3b). In both ponds and streams, a lengthening of

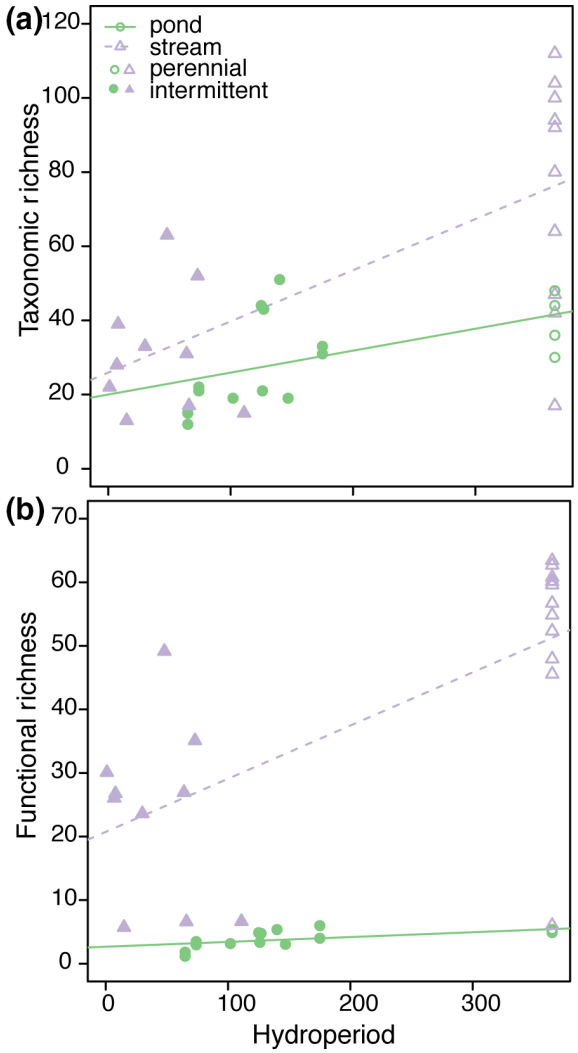

Fig. 3. Relationship between invertebrate (a) taxonomic richness and (b) functional richness across hydroperiod gradient. Taxonomic richness slopes do not differ between ponds and streams. FRic is higher in streams and the slope (0.084) differs statistically from slope of the pond FRic–hydroperiod relationship (0.008). Pond FRic values were multiplied by 10 for better graphical presentation.

hydroperiod reflected an increase in occupied niche space (FRic; ponds R^2 = 0.37, $F_{1,14}$ = 9.823, P = 0.007; streams R^2 = 0.43, $F_{1,19}$ = 15.95, P = 0.0008), but ponds had lower FRic than streams at any given hydroperiod (ponds: FRic = 0.008 × hydroperiod + 2.66; streams: FRic = 0.08 × hydroperiod + 20.72; Fig. 3b). Therefore, we found support for our hypothesis

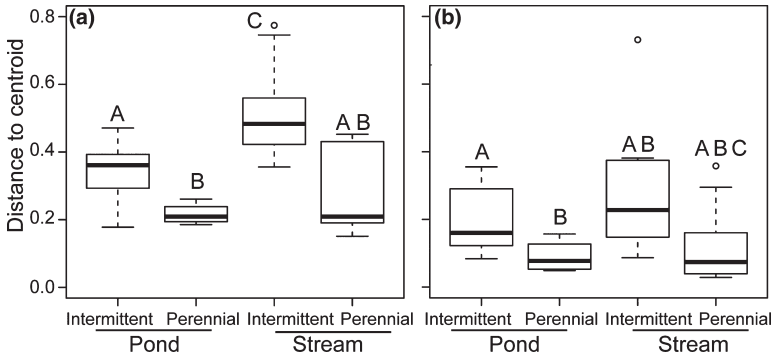

Fig. 4. Box and whiskers plot showing the variation in the distribution of distance to centroid (variation beta diversity) of pairwise comparisons among ponds and streams within each hydrologic category. (a) Invertebrate assemblages and (b) invertebrate functional traits from stream (n = 23) and pond (n = 16) sites. The letters above the groups indicate pairwise comparisons: groups with the same letter are not significantly different and groups with different letters indicate significant differences in dispersion. Variation beta describes variation in community structure among sample sites from either intermittent or perennial hydrologies. Higher values correspond to greater beta diversity (dispersion).

that ponds and streams would show similar taxonomic richness patterns across a hydroperiod gradient, but we could not accept our hypothesis that ponds and streams would show similar functional richness patterns across a hydroperiod gradient.

Beta diversity

Variation beta diversity (distance to centroid) of invertebrate assemblages varied significantly between ponds and streams (homogeneity of multivariate dispersions: P = 0.004) and was overall significantly higher in intermittent sites compared to perennial sites (0.56 and 0.44, respectively, F = 6.167, P = 0.018; Fig. 4a). The pairwise comparisons indicated that perennial ponds and streams did not differ in variation beta diversity (permuted P = 0.34). However, intermittent sites differed in variation beta diversity from their perennial counterparts (streams: P = 0.001; ponds: P = 0.015). Mean taxonomic dissimilarities showed significant differences between ponds and streams (PERMANOVA: R^2 = 0.40, P = 0.001) and between intermittent and perennial habitats (R^2 = 0.09, P = 0.015).

Trait variation beta diversity was significantly higher in streams compared to ponds (homogeneity of multivariate dispersions: 0.30 vs. 0.20, F = 5.196, P = 0.015). However, intermittent habitats were not significantly different from perennial habitats (0.27 vs. 0.20, F = 3.244, P = 0.07; Fig. 4b). Intermittent ponds and intermittent streams were similar in terms of high

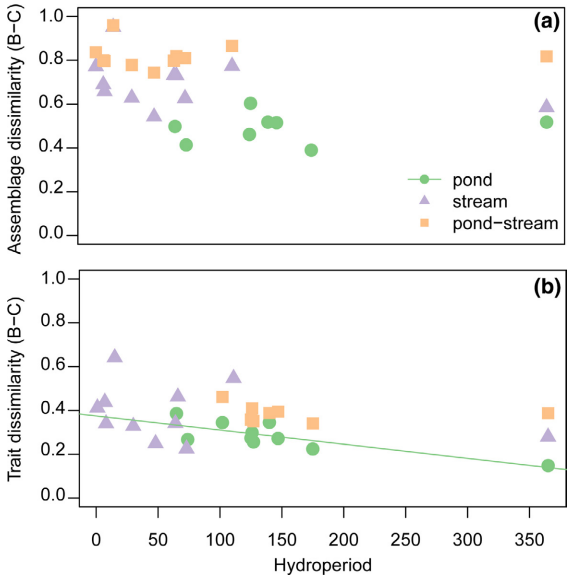

Fig. 5. Relationship between dissimilarity (turnover beta diversity) of (a) invertebrate assemblages and (b) functional traits from pond and stream sites along hydroperiod gradient. Each point is the mean pairwise comparison within pond sites, within stream sites, and the between pond-stream sites comparison. Both y-axes express dissimilarity, thus one means the two sites do not share any taxa or traits.

trait variation beta diversity (permuted $P = 0.19$). Intermittent sites had significantly higher trait variation beta diversity compared to their perennial habitat counterparts (ponds: 0.20 vs. 0.09, $P = 0.05$; streams: 0.27 vs. 0.12, $P = 0.03$). Mean trait dissimilarities were also significantly different between ponds and streams (PERMANOVA: $R^2 = 0.14$, $P = 0.002$) and between hydrologic categories $R^2 = 0.29$, $P = 0.001$).

Invertebrate assemblages exhibited relatively little turnover beta diversity (dissimilarity) across the hydroperiod gradient from intermittent to perennial habitats (linear model: $F_{1,28} = 0.091$, $P = 0.06$). There was no relationship within streams ($R^2 = 0.025$, $F_{1,9} = 1.267$, $P = 0.29$, CV = 0.15) or ponds ($R^2 = -0.14$, $F_{1,6} = -0.14$, $P = 0.74$, CV = 0.13) across a continuous hydroperiod gradient (Fig. 5a). Functional trait turnover beta diversity was variable along the hydroperiod gradient and showed a declining pattern compared to invertebrate assemblage turnover ($R^2 = 0.11$, $F_{1,27} = 4.579$, $P = 0.04$; Fig. 5b). Pond sites showed a decline in beta diversity along the hydroperiod gradient, suggesting perennial ponds were more similar to one another than intermittent ponds were to one another ($R^2 = 0.60$, $F_{1,8} = 14.42$, $P = 0.005$). There was no trend in stream sites ($R^2 = -0.027$, $F_{1,9} = 0.7414$, $P = 0.411$). Overall, ponds had lower trait dissimilarity (mean 0.28) than streams (mean 0.43) indicating pond trait compositions were more similar and had less trait turnover between ponds. It has been suggested to use Chao similarity to make among-site comparisons because in a simulation study turnover beta diversity patterns may be influenced by differences in habitat capacity among sites (Dong et al. 2015); however, our results were similar regardless of the similarity index employed.

Discussion

Hydrology is one of the primary environmental filters shaping aquatic communities. Fundamental differences in pond vs. stream habitats (or scientists' study preference for one ecosystem over another) have perhaps deterred cross-ecosystem comparisons. However, cross-ecosystem comparisons may indicate ecological patterns and processes in common. We took a functional trait perspective which allowed the comparison of aquatic invertebrate species compositions from two ecosystems and found that similar hydrologic processes led to similarity in trait composition and beta diversity. Our findings also show that temperate ponds and dryland streams show distinct patterns in their accumulation of functional richness across taxonomic richness and hydroperiod gradients. These results highlight the importance of deterministic processes such as trait filtering, in that short hydroperiods impose similar functional constraints on pond and stream organisms.

We tested whether the relationship between FRic and taxonomic richness was consistent in both ponds and streams. Indeed, each habitat alone showed a positive linear relationship, but differences in their slopes were evident. These differences reveal information about how communities might respond to ecological perturbations. For instance, a positive linear relationship (slope = 1) indicates that species additions to a community result in new ecological functions (low redundancy), as found in rocky reef fish assemblages (Micheli and Halpern 2005). A shallower positive slope (<1) indicates redundancy because some species share functional traits, which has been observed in bird assemblages (Petchey et al. 2007). We found significant positive relationships between FRic and taxonomic richness indicating moderate levels of redundancy (multiple species perform similar functions) in stream and pond invertebrate communities. However, the occupied niche space of ponds was smaller and filled with functionally redundant species compared to stream sites. Possible reasons for why ponds may have higher redundancy than streams include differences in resource availability, differences in the number of functional groups, and the taxonomic resolution of organisms.

Responses of taxonomic richness and FRic to hydroperiod also exhibited positive relationships. Both habitats similarly accumulated taxonomic richness with increasing hydroperiod, but that did not translate the same way in terms of FRic. Ponds accumulated new species more rapidly than accumulating new functions along the hydroperiod gradient from short to long, as shown by minimal change in FRic along gradient, thus exhibiting trait redundancy. Functional

redundancy results from strong environmental filtering (Weiher and Keddy 1995) thus limiting trait diversity. More functionally diverse communities are thought to offer greater resilience and aid in ecosystem recovery in response to environmental change because of greater ecological redundancy (Hooper et al. 2005). From our data, it seems that ponds, especially those with longer hydroperiods may have a better capacity to cope with or resist environmental variation (because higher average FRic) than invertebrate communities in shorter hydroperiod ponds and possibly, as a whole, stream invertebrate communities. Other aspects of the hydrologic regime, such as number of drying events, may be important in influencing this pattern.

Biogeographical history can only partly explain differences in species presence across space. There is tremendous variation in size, habitat permanence, environmental conditions, physicochemical properties, and climate between the streams and ponds we compared. These extreme environmental conditions are expected to harbor organisms with diverse adaptations to regional and local conditions and contain different species assemblages. Owing to these environmental differences, species from ponds and streams may respond differently to environmental variation. It is not uncommon to independently study either streams or ponds across different biogeographic scales. For example, studies have found hydrologic parameters to strongly structure fish assemblage traits and life history patterns in streams from different continents (Lamouroux et al. 2002, Olden and Kennard 2010). However, it is rare to see studies that cross-ecosystem types.

A functional trait perspective allowed us to compare communities that differed almost entirely in their regional species pools. We found support for the hypothesis that habitats with similar hydrologic conditions should share species traits. We found that despite differences in ecosystem type (flowing water vs. still water) and species pool, invertebrate assemblages from intermittent ponds and streams show similarity in trait structure along the hydroperiod gradient (Fig. 1; Appendix S1: Fig. S1). Therefore, functional traits in intermittent streams and ponds are similarly influenced by hydroperiod. This pattern was likely influenced by the presence of taxa that are resistant to desiccation or resilient to dynamic hydrologic environments. In our analysis we found traits that are known to be associated with resistance to drought, such as small body size, clinger habit (Townsend and Hildrew 1994, Townsend et al. 1997), and diapause capability (Bonada et al. 2007, Mellado Diaz et al. 2008) and traits that confer resilience to hydrologic variation, such as strong dispersal ability (Townsend and Hildrew 1994, Townsend et al. 1997, Vieira et al. 2004, Bogan et al. 2015) and multivoltinism (Townsend and Hildrew 1994) were highly correlated with intermittent stream habitats. Traits more common in longer hydroperiod habitats were aerial passive dispersal, large body size, lack of diapause capability, and univoltine life cycle. Our results are generally congruent with those of Cañedo-Argüelles et al. (2015), which found that dispersal ability of organisms strongly influenced community structure of aquatic invertebrates. Logez et al. (2013) similarly found fish assemblage functional structure across Europe to be mostly related to stream physicochemical factors and less so by geographical location. Our study provides evidence that a traits-based approach combined with other diversity metrics can effectively convey the underlying responses to environmental variation and ecological processes across ecosystems.

The two concepts of beta diversity (i.e., variation among sampling units and turnover in community structure along an environmental gradient) connects biodiversity at the local scale and regional species pool (Whittaker 1972). We saw parallel variation beta diversity patterns in taxonomic assemblages and functional traits indicating higher beta diversity in intermittent ponds and streams. High beta diversity indicates high variation among communities, and we speculate that in our case it stems from high habitat heterogeneity among intermittent sites. Turnover beta diversity is predicted to decline along a gradient of low to high disturbance (i.e., pond permanence, Chase 2003). Here, we predicted turnover to decline along a gradient from long (perennial) to short hydroperiod because habitat permanence acts as a disturbance to those nonresistant taxa. Although dissimilarity was variable, we did not see a decline in turnover beta diversity in invertebrate assemblages across the hydroperiod gradient. It would be interesting to

see if the pattern holds after adding sites from the hydroperiod range of 176–364. The modest turnover in functional traits among ponds along the hydroperiod gradient reflects the redundancy described in the richness relationship within ponds. Additionally, FRic was less variable in ponds (33%) and streams (56%) than taxonomic richness (41% vs. 67%, respectively) across the hydroperiod gradient, indicating ecosystem functions are maintained and the relationship is due to turnover of functionally redundant species across the gradient (Villéger et al. 2012, Trigal et al. 2014). Bogan et al. (2013) found that, despite the spatial proximity of headwater perennial stream sites to intermittent stream sites, their invertebrate assemblage composition (turnover beta diversity) was considerably different. We speculate that the hydrologic difference between headwater and nearby intermittent sites was contributing to turnover beta diversity in their study because we also observed similar differences between intermittent (average dissimilarity = 0.72) and perennial streams (0.48). Therefore, even though stream reaches may be connected at certain times of the year, the fact that sections experience drying is a stronger determinant of assemblage and trait structure than spatial proximity.

Congruence of beta diversity and richness hotspots are important for conservation planning (McKnight et al. 2007). We saw higher beta diversity, but lower FRic and taxonomic richness in intermittent habitats. This mismatch occurs because traits shift in importance and presence along the hydroperiod gradient. Fewer species may be present in an intermittent habitat, but those species have evolved unique biological traits that enable them to resist dry periods that perennial species do not possess (Lytle and Poff 2004). Additionally, the branching network shape of lotic systems vs. the more isolated nature of ponds may influence dispersal pathways and hence beta diversity.

Understanding how trait composition varies among different geographic areas, organismal groups, and across environmental gradients is of pressing concern in streams (Heino et al. 2013) and may help us identify underlying ecological patterns. Our study addresses this need for research by comparing disparate pond and stream habitats across an environmental gradient, and we have shown that general relationships exist among hydrology, taxonomic diversity, and functional richness regardless of aquatic ecosystem. Aquatic ecosystems may be more susceptible to losses in biodiversity than their terrestrial counterparts (Dudgeon et al. 2006). Therefore, patterns in trait similarity and beta diversity across a hydrologic gradient can be used to inform conservation decisions in a changing climate.

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