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Flow-ecology relationships are spatially structured and differ among flow regimes

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Abstract

1. In streams, hydrology is a predominant driver of ecological structure and function. Providing adequate flows to support aquatic life, or environmental flows, is therefore a top management priority in stream systems.

2. Flow regime classification is a widely accepted approach for establishing environmental flow guidelines. However, it is surprisingly difficult to quantify relationships between hydrology and ecology (flow-ecology relationships) while describing how these relationships vary across classified flow regimes. Developing such relationships is complicated by several sources of spatial bias, such as autocorrelation due to spatial design, flow regime classification, and other environmental or ecological sources of spatial bias.

3. We used mixed moving-average spatial stream network models to develop flow-ecology relationships across classified flow regimes and to assess spatial patterns of these relationships. We compared relationships between fish traits and life-history strategies with hydrologic metrics across flow regimes and assessed whether spatial autocorrelation influenced these relationships.

4. Trait-hydrology relationships varied between flow regimes and across all streams combined. Some relationships between traits and hydrologic metrics fit predictions based on life-history theory, while others exhibited unexpected relationships with hydrology. Spatial factors described a large proportion of variability in fish traits and different patterns of spatial autocorrelation were observed in different flow regimes.

Synthesis and Applications. Further work is needed to understand why flow-ecology relationships vary across classified flow regimes and why these relationships may not fit predictions based on life-history theories. Managers determining environmental flow standards need to be aware that different hydrologic metrics are often important drivers of fish trait diversity in different flow-regimes. Flow-ecology relationships may therefore be confounded by spatial structure inherent in flow regime classification and much existing biological data. Complex patterns of spatial bias should be considered when managing stream systems within an environmental flows framework.

Keywords: environmental flows, fish, hydrology, life-history strategies, spatial autocorrelation, streams, traits, spatial stream network models

Introduction

Maintaining natural flow dynamics in streams is recognized as a water management priority (Poff et al., 2010). Natural flow regimes are critical for sustaining freshwater ecosystems (Bunn & Arthington, 2002; Postel & Richter, 2003; Poff, 2009), but are increasingly threatened by water demands, landscape changes, and climate change (Postel & Richter, 2003; Palmer et al., 2008). Alterations of natural flow regimes can have profound effects on the biophysical attributes and ecological functioning of lotic systems (Infante, Wiley & Seelback, 2006; Poff & Zimmerman, 2010; Webb et al., 2013). Therefore, we are faced with the challenge of managing water use to meet societal demands while also maintaining natural flow regimes and the ecological integrity of streams.

Environmental flows (Brisbane Declaration, 2007) are water management guidelines derived from data-driven estimates of flow-ecology relationships in streams. This requires quantifying flow patterns and linking them to ecological responses (Arthington et al., 2006). Many hydrologic metrics have been developed to quantify ecologically important components of flow regimes including magnitude, duration, timing, rate of change, and frequency of flow events (Richter et al., 1996, Olden & Poff, 2003, Poff et al., 1997). Quantifying flow-ecology relationships and developing effective flow standards for all streams within a management area is a data- and resource-intensive task. Hydrological and biological data can only be collected from relatively few streams, and ecological responses to hydrology likely depend on the type of stream in question (*e.g.* intermittent, perennial, groundwater-influenced). Classifying streams into hydrologically similar groups (flow regimes) allows data-driven flow standards to be generalized more effectively among streams with similar flow patterns (Poff et al., 2010).

Trait-based approaches may be advantageous over species-specific analyses for identifying flow-ecology relationships across broad spatial scales (Heino, Schmera & Erös, 2013). Trait-based approaches assume species traits like reproductive strategies, maturation time, and longevity, will converge when environmental pressures (e.g. hydrology) are similar, regardless of the specific taxa involved (Southwood, 1988). Based on this theory, categorizing species by different traits allows for the study of communities across biogeographic boundaries (Schluter, 1986; Statzner, Dolédec, & Hugueny, 2004). The ability to develop flow-ecology relationships across biogeographic boundaries is important because flow classification schemes or management areas are likely to include multiple drainage basins with different species pools. For example, a recent environmental flow study found family-level macroinvertebrate community indices were best described by ecoregion and did not show a response to natural flow variability (Buchanan et al., 2013). This inability to observe variation in ecological response variables to natural flow variations hindered the development of flow classification schemes (Buchanan et al., 2013).

Traits are also advantageous because they facilitate the use of existing biological data. Existing datasets may offer the spatial coverage necessary to develop flow-ecology relationships at coarse spatial scales, but inconsistent sampling methods, taxonomic bias, and other issues often make abundance data unreliable. Trait-based approaches can more effectively utilize presence-absence data to mitigate these issues. Traits also represent long-term patterns in community structure (Poff & Allan, 1995; Poff et al., 2006; Tedesco et al., 2008), which is important because flow regime classification is based on long-term hydrologic trends (i.e. decades), not short-term hydrological events like a severe flood in a single year (Kennard et al., 2010). Trait-based approaches may also be advantageous because the mechanisms driving ecological-flow relationships can be hypothesized more directly than when assessing taxonomic relationships (Southwood, 1977; Poff ,1997; Heino et al., 2013).

Spatial autocorrelation likely influences the interpretation of flow-ecology relationships based on traits because spatial patterns are inherent in most hydrological and biological data. Spatial autocorrelation represents the degree of statistical dependency between random variables based on proximity—nearby sites tend to be similar to one another (Cressie, 1993). Stream hydrology is influenced by broad-scale factors including climate, geology, topography, and vegetation (Poff & Ward, 1989), so streams with similar hydrology are likely spatially clumped along these environmental gradients. Spatial autocorrelation can also arise from biological processes like dispersal limitation, historical biogeography, and small-scale habitat heterogeneity (Erős & Schmera, 2010). Logistical constraints and other sources of sampling bias may also lead to spatial autocorrelation via geographically clumped sites in ecological response datasets or bias in sampling locations (for example, wadeable streams near road crossings; Domisch et al. 2015).

Spatial autocorrelation can be accounted for using geostatistical models, a common approach in terrestrial studies, but streams present unique challenges for spatial models because they are organized into hierarchical networks with unidirectional flow. The degree of similarity between neighboring sites depends on the direction of flow and the stream distance between them, not just Euclidean distance. Due to the historical lack of appropriate models to represent spatial autocorrelation in streams (Ver Hoef & Peterson, 2010), the role of spatial drivers of ecological patterns within stream networks has been largely ignored.

We used a trait-based approach to quantify flow-ecology relationships in classified flow regimes and assessed the influence of spatial autocorrelation on our inferences. Our main objective was to compare relationships between stream hydrology and fish traits among flow regimes. For comparison, we also assessed these relationships for all streams combined, ignoring flow regime classifications. Several studies have documented strong relationships between fish traits and hydrology at broad spatial scales, but these studies did not account for differences among flow regimes (Poff & Allan 1995; Poff et al., 2010; Mims & Olden, 2012; Mims & Olden, 2013; McManamay, Bevelhimer, & Frimpong, 2015; McManamay & Frimpong, 2015). We contribute to this body of work by testing these relationships in specific flow regimes at a regional, management level spatial scale.

Materials and Methods

Fish Assemblage Data

We used fish assemblage data from the Arkansas GAP Analysis (MORAP, 2009), which included observations of fish species occurrences at over 7,700 sampling locations from over 3,700 stream segments across Arkansas, USA. Government agencies, academic institutions, and museums collected these data between 1927 and 2009 using a variety of sampling methods (electrofishing, seines, rotenone, visual counts, or other methods). We converted abundance data to species presence-absence to help control for differences in collection methods and sampling periods within the dataset. We felt this was appropriate because our trait-based questions focused on occurrences of fish traits within the community and not necessarily abundances of species possessing those traits. We only used data from 1980 and later to assemble the presence-absence records for each stream segment. This long temporal sampling period allowed us to balance capturing both relatively contemporary and long-term patterns of community composition at each site.

Site Selection

Because we were interested in associations between fish traits and natural flow regimes, we only included streams with minimal flow alteration. We identified those streams based on six relevant watershed characteristics: road density, urban development, pasture and cropland cover, dam density, dam storage, and density of pollution discharge sites. These metrics were the basis for the widely used Hydrologic Disturbance Index (Falcone, Carlisle, & Weber, 2010). We only kept data from sites with values less than the medians for all six metrics. To minimize sampling bias, we only included sites sampled at least three times (Figure 1). Our final set of sites included 302 least-disturbed streams (Figure 2). See Appendix S1 in Supporting Information for more details about site selection and geo-processing.

Hydrologic Data

Flow regime classifications for all sites were derived from the flow classification scheme of Leasure, Magoulick, and Longing (2016). We grouped their seven flow regimes into three broad classes: groundwater, intermittent, and runoff (Figure 1). Groundwater streams have fewer than two low flow spells per year (i.e. < 5% of mean daily flow) and never dry completely. They have less flow variability than runoff or intermittent streams. Runoff streams average more low flow spells, lower base flows, and more zero flow days per year. Intermittent streams are characterized by more variability than both runoff and groundwater streams and may dry completely for up to three months each year. All three flow regimes covered a similar range of stream sizes (i.e. catchments of about 4 to 800 km^2).

We used random forest models (Breiman, 2001) to predict 11 flow metrics (Table 1) using GIS-based watershed characteristics of our sites (Appendix S2). We built a random forest model for each flow metric using the R package *randomForest* (Liaw & Wiener, 2002). These 11 flow metrics were selected by Leasure et al. (2016) following the methods of Olden and Poff (2003) to best distinguish natural flow regimes in our study area. We reduced this set of 11 metrics to five after removing those that were highly correlated at our sites (Table 1). Flood frequency (FH7) and fall rate (RA3) were log(x+1) transformed to improve normality. See Appendix S2 for more details about our random forest modeling to predict hydrologic metrics at our sites.

Fish Traits

We used the FishTraits database (Frimpong & Angermeier, 2009) to assign trait values to all fish species in our data set (Appendix S3). For species with inadequate data in the FishTraits database (*Etheostoma artesiae, Etheostoma fragi, Etheostoma uniporum*, and *Percina fulvitaenia*), we assigned trait values first by searching the literature, and if information was not available we used traits of the closest relative (Near et al. 2011). These four species were relatively uncommon across our study sites. We chose to focus on life-history and reproductive traits (Table 2) because previous studies documented broad trends between these traits and hydrology (Olden & Kennard, 2010; Mims & Olden, 2012; McManamay et al., 2015).

Species with common ancestry likely share similar traits, so it was necessary to account for phylogenetic effects to ensure independence of traits among species (Gittleman & Luh, 1992). We used generalized linear models (Gaussian, Poisson, or binomial depending on the trait) to account for variation in traits described by phylogeny (McManamay et al., 2015). We used family number (Nelson, 2006), which describes the phylogenetic position of families relative to other families (Frimpong & Angermeier, 2009), to represent phylogenetic relationships. We used deviance residuals from these models in all proceeding analyses to represent trait values corrected for phylogeny (McManamay et al., 2015).

We assigned each species to one of the three life-history strategies described by Winemiller and Rose (1992): equilibrium, periodic, or opportunistic (Appendix S4). Because we did not have all the data necessary to assign species to life-history categories in the same manner as Winemiller and Rose (1992), we followed the methods of McManamy et al. (2015) and Mims et al. (2010) to assign life-history strategies. We compared the Euclidean distance between species and endpoints representing each life-history strategy in multivariate space (Appendix S4). Endpoints represented hypothetical extremes of each life-history strategy based on the trait characteristics in our global community trait database. Our endpoints were based on traits described by both Mims et al. (2010) and McManamay et al. (2015). Mims et al. (2010) defined the opportunistic endpoint based on the minimum fecundity, minimum juvenile investment, and minimum maturation size observed across the entire species pool, whereas McManamay et al. (2015) defined the opportunistic endpoint as the maximum value for serial spawning and season length, and minimum values for maximum length, age at maturation, longevity, fecundity, and parental care. Individual species were assigned to the same life-history strategy based on both sets of endpoints for 61% of species. For species in which assignments were not the same, we used life-history strategy classifications presented in other published works or the closest relative in our data set (same genus) to make final life history classifications.

Statistical Analysis

We used mixed moving-average spatial stream network (SSN) models to identify relationships between hydrologic metrics and fish traits while also accounting for spatial autocorrelation (Ver Hoef, Peterson & Theobald, 2006; Peterson & Ver Hoef, 2010). We completed analyses separately for each flow regime and for all sites combined to determine how flow-ecology relationships and spatial patterns differ across groundwater, intermittent, and runoff flow regimes. Spatial autocorrelation is often present in fish and hydrology data due to stream network structure, connectivity, and flow direction (Peterson & Ver Hoef, 2010). SSN uses three covariance structures to represent these different spatial patterns: "tail-up" (TU), "tail-down" (TD), and classic Euclidean distance (EUC). Tail-up covariance matrices are based on stream distances between sites and only allow spatial autocorrelation to occur between flow-connected sites (i.e. water must move from one site to the other). Tail-down covariance matrices are also based on stream distances, but they allow correlation between flow-unconnected sites as well as flow-connected sites. This covariance function may be important to fish because they can move both upstream and downstream in the network. Tail-up models include spatial weights that create an additive function downstream throughout the network. These weights split the moving average function at confluences. We used spatial weights for tail-up models based on watershed area, so upstream sites with larger watershed areas had stronger correlations with downstream sites than smaller upstream sites. As recommended by Peterson and Ver Hoef (2010), we included all three covariance structures in our models (EUC, TU, and TD).

We developed SSN models with the following fish traits as response variables (Table 2): age at maturity, length of spawning season, spawning mode (open spawners, brood hiders, open substrate guarders, indifferent spawners, and nest guarders), and life-history strategies (equilibrium, periodic, and opportunistic). All response variables (trait values) were average deviance residuals derived from phylogenetic correction models for each trait. Life-history strategies were represented at each site by the proportion of species in each group. Covariates in each model included five hydrologic metric predictors, watershed area, and average annual air temperature range. We included watershed area and air temperature because stream size and temperature are two variables known to influence fish community structure. Because we were interested in comparing trait-hydrology relationships among flow regimes, we did not use model selection procedures. All models used Gaussian link functions because response variables were normally-distributed after phylogenetic correction. We created 44 spatial models: one for each flow regime and one with data combined across all sites for each of the 11 response variables. All spatial models were implemented using the SSN (Ver Hoef et al., 2014) package in R (R Core Team, 2014). All geo-processing required to develop SSN models was completed using the STARS package (Peterson and Ver Hoef, 2014) implemented in ArcGIS (ESRI, 2016) and is described in Appendix S1.

Several different models are available for the EUC (Gaussian, exponential, spherical, Cauchy), TU (linear sill, Epanechnikov, Mariah, exponential, spherical), and TD (linear sill, spherical, exponential, Epanechnikov, Mariah) covariance structures (see Ver Hoef & Peterson, 2010; Garreta et al., 2010). We compared all combinations of the covariance structures for each response variable. We selected covariance structures for the final models based on root-mean-square-prediction error (RMSPE; Appendix S5). All final models were fit using restricted maximum likelihood (REML) for parameter estimation. Diagnostic plots of residuals were used to check heteroscedasticity and influence of outliers. Scatterplot matrices and variance inflation factors (VIF) were used to assess multicollinearity. We compared leave-one-out cross validation predictions to the observed data to calculate pseudo R^2 values and prediction intervals. Based on model diagnostics, we removed open substrate guarders and substrate indifferent spawners from analyses, and we removed watershed area from all models for the runoff flow regime.

We also fit non-spatial linear regression models containing the same response variables (phylogenetically corrected traits) and predictors (five hydrologic metrics, watershed area, and annual average temperature range) as SSN models. We compared the amount of variance explained by each model and the number of significant predictors obtained from non-spatial regression models to those obtained using SSN models.

Results

Summary of fish traits

The final assemblage dataset included 102 species from 14 families across 302 reference sites. Table 2 summarizes the range of trait values and number of species classified in each life-history category. Trait average deviance (corrected by family number) varied within and between flow regimes, but there was no apparent difference in trait values between flow regimes, although this was not statistically tested (Figure 3). Notable exceptions include the greater age at maturity and shorter spawning season in runoff streams relative to groundwater and intermittent streams.

Flow-ecology models

SSN model performance varied across traits and flow regimes, but many (11) models exhibited relatively good fit (pseudo $R^2 > 0.5$, Table 3). All SSN models described more variance than non-spatial linear regression models (Figure 4, Table 3). Non-spatial linear models produced 6 more significant relationships with covariates than SSN models (Tables 3 and 4). These relationships included both hydrologic metrics and non-hydrologic metrics, but there were more significant relationships between hydrologic metrics and fish traits in non-spatial models (Table 4). For example, across all flow regimes SSN models only produced 2 significant relationships between traits and hydrologic metrics, while non-spatial models produced 9 significant relationships between traits and hydrologic metrics. For a given trait, SSN and non-spatial models also predicted different hydrologic and non-hydrologic metrics to be significant (Table 4). In SSN models brood hiders from intermittent streams had significant relationships with MA4 and DL4, but in non-spatial models brood hiders had significant relationships with MA4 and TA1.

SSN models revealed fish traits responded to different hydrologic and non-hydrologic factors in groundwater, runoff, and intermittent streams (Table 4). No covariates were significant predictors of any traits in runoff streams. Watershed area was an important predictor for most traits in intermittent streams, and across all sites combined. Variability in daily flows (MA4) was a significant predictor of opportunistic strategists, open substrate spawners, brood hiders, and nest guarders in intermittent streams. Minimum 30-day flow (DL4) was an important predictor in groundwater and intermittent streams, but was important for different traits. Periodic strategists had a positive relationship with number of high flow events (FH7) in groundwater streams, but no relationship with hydrology in any other flow regime. Age at maturity responded to rates of declining flows (RA3) in groundwater and intermittent streams with a negative relationship in groundwater streams and a positive relationship in intermittent streams. The length of spawning season had a significant positive relationship with hydrology (constancy, TA1) across all streams combined. Equilibrium strategists had a significant negative relationship with average annual air temperature ranges in both intermittent streams and across all sites combined.

We compared the relative importance of different spatial covariance structures and covariates, including both hydrologic and non-hydrologic variables (Figure 4). Covariates described more than 20% of fish trait variance in 9 of 32 final SSN models. Covariates explained the most variance in groundwater streams relative to other flow regimes or all sites combined. Spatial autocorrelation accounted for most variation across all sites combined, with TU as an important predictor of life-history strategies across all flow regimes combined and EUC as an important predictor of open substrate spawners and brood hiders. In intermittent streams, a mixture of TU and EUC terms accounted for most of the variation, while in runoff streams, EUC was an important predictor for most traits. There was relatively low unexplained variance (nugget) for groundwater and intermittent streams, as well as across all sites combined, while there was relatively high unexplained variance in runoff streams. There was no dominant spatial covariance structure describing the variation in any trait, except age at maturity and brood hiders. Variation in age at maturity was best described by covariates in groundwater streams, and EUC in runoff and intermittent streams. Brood hiders were best described by EUC in runoff and intermittent streams, as well as across all streams combined.

Discussion

We compared relationships between fish community traits and hydrologic metrics across classified flow regimes, accounting for the role of spatial relationships in the river network. Relationships between hydrologic metrics and fish traits differed among flow regimes, emphasizing the importance of developing water management standards tailored to a flow regime. Spatial patterns described a large proportion of variance in fish traits within flow regimes, as well as across our global pool of sites, indicating spatial patterns need to be controlled for in the development of flow-ecology relationships. Fish traits, life-history strategies, and flow regimes also differed in their spatial structures, highlighting the importance of considering site layout when designing sampling strategies for flow-ecology studies and providing insight into what types of covariates need to be included.

Three hydrologic metrics consistently predicted fish traits and life-history strategies: 30-day minimum flows (DL4), daily flow variability (MA4), and fall rate (RA3). The repeated significance of these metrics suggests they may be important for developing flow standards in our study area, and maybe even more broadly. Low flow conditions, in general, were important drivers of fish traits across all sites. During drought conditions, we may expect to see streams dominated by fish that mature very quickly, such as Western Mosquitofish (*Gambusia affinis*) or Fathead Minnows (*Pimephales promelas*). Variability of daily flows (MA4) and fall rate (RA3) were especially important in intermittent streams and across all sites combined. Both metrics are related to daily variability of flows. While we know fish respond to annual hydrologic variability, such as seasonal changes in the hydrograph (Nesler, Muth, & Wasowicz, 1988; Jespen et al., 1999; Humphries & Lake, 2000), this finding suggests fish are also responding to short term hydrologic variability. Providing flows of varying magnitudes on a seasonal basis may not be enough to sustain fish communities, and environmental flow schemes that incorporate short-term flow variability may be necessary.

We observed complex and sometimes unexpected relationships between hydrology and fish traits and life-history strategies. While some of the relationships we observed fit predictions based on life-history studies, we will restrict our discussion to our unexpected results to point out potentially important new information about trait-hydrology relationships, as the expected relationships are discussed elsewhere (Olden & Kennard, 2010; Mims & Olden, 2012; Mims & Olden, 2013). For example, we observed a negative relationship between the variability of daily flows (MA4) and opportunistic strategists. Previous studies document positive relationships between opportunistic species and measures of flow variability or disturbance (Olden & Kennard, 2010; Mims & Olden, 2013). This unexpected result may be due to the temporal scale of the hydrologic metrics. Metrics used in previous studies represented annual variability, while MA4 captured daily variability averaged over the entire flow record. Although opportunistic strategists are predicted to favor environments with frequent and intense disturbances, the negative relationship with the variability of daily flows may indicate that opportunistic strategists are not well adapted to variability at all temporal scales. Also unexpectedly, we did not observe any relationships between periodic strategists and metrics capturing predictability. We did, however, observe a positive relationship with the number of flood events (FH7) in groundwater streams. Although this metric does not capture predictability or seasonality of floods, this relationship emphasizes the importance of variability to periodic strategists. Interestingly, this relationship was observed in groundwater streams, which have the most stable hydrographs of the flow regimes in the current study. Hydrologic metrics capturing extreme events may be more important for periodic strategists in relatively stable streams compared to those occupying more variable flow regimes.

Some traits and life-history strategies had opposite responses to hydrology in different flow regimes. This may have important consequences for the implementation of flow-standards in classified flow regimes. Many documented flow-ecology relationships are based on changes in community structure after flow alteration (Freeman et al., 2001; Humphries, Serafini, & King, 2002; Poff & Zimmerman, 2010; Webb et al., 2013; Rolls & Arthington, 2014), but few studies have compared flow-ecology relationships across a regional flow classification scheme (see Poff & Allan, 1995; Monk et al., 2006; Chinnayakanahalli, Hawkins, Tarboton, & Hill, 2011; Mims & Olden, 2012; McManamay et al., 2015). Like the current study, Mims and Olden (2012) observed predicted relationships between hydrologic metrics and fish life-history strategies across all sites combined. However, within classified flow regimes, Mims and Olden (2012, Appendix B) observed relationships that differed between regimes and did not fit predictions based on life-history theory. While we may expect different hydrologic metrics to have varying degrees of ecological relevance across flow regimes, opposite trait responses between flow regimes is an unexpected result. Further empirical and conceptual work is needed to understand how our perception of flow-ecology relationships may depend on the specific flow metrics used and how differences among flow regimes may be incorporated in predictive models and in the development of environmental flow standards.

Observed relationships (and lack of relationships) between traits and hydrology may have been influenced by the regional scale of our study. Similar studies exhibiting strong relationships with distributions of fish traits and life-history strategies across flow regimes were completed at national scales (Mims & Olden, 2012; McManamay et al., 2015). Not only can flow classification schemes vary depending on the spatial scale of classification (McManamay, Orth, Dolloff, & Frimpong, 2012), but trait values may also exhibit less variation at smaller spatial scales. We may expect stronger relationships between fish traits and hydrology at broad spatial scales that include larger environmental gradients and species pools. When developing flow-ecology relationships, the choice to use trait-based approaches may be dependent on the scale of the study.

Trait values assigned to each species may also affect the strength of relationships with hydrology. In the current study, each species was assigned trait values from the FishTraits database (Frimpong & Angermeier, 2009). We did not observe clear separation of any traits among flow regimes, suggesting either trait values did not capture the true variability of species traits or trait composition was similar across flow regimes. Intraspecific or regional variations in trait values were not accounted for in the national traits database. In addition, the similarity of trait distributions across flow regimes may have been due to our use of occurrence data rather than abundance data. We may have seen stronger separation between flow regimes in trait space if our data were weighted by the abundance of different species at each site. These issues are likely common in trait-based studies using existing data and highlight our need for higher resolution (reliable species abundances, regional trait variation) community data at coarse spatial scales.

Trait-flow relationships were also likely influenced by our choice of hydrologic metrics. We chose metrics that described the most variability in hydrology across the study area and were used to develop the flow classification scheme in the region. This point has very important implications for the development of flow-ecology relationships. While we can assess which metrics capture the most hydrologic variability in a region before conducting ecological studies, it can be difficult to predict *a priori* which of the many (hundreds) hydrologic metrics are ecologically significant. The hydrologic metrics used to classify flow regimes may not be the most ecologically meaningful. We also analyzed the same metrics across all flow regimes. As our data suggests, different hydrologic metrics may be important in different flow regimes. When determining flow-ecology standards, it may be important for managers to identify which components of hydrology have the strongest ecological responses for individual flow regime types.

Lastly, despite our focus on least-disturbed streams, fish communities at these sites may have been influenced by some flow alteration or other impacts that we did not consider. The hydrologic metrics used in this study represented predicted natural flow conditions and did not account for flow alteration. This was a necessary limitation because gage data are not available from most sites with existing fish survey data. While predicting flow alteration at ungauged sites is beyond the scope of this paper, the issue of identifying least-disturbed sites is not unique to the current study. For example, reservoirs and water withdrawals have altered flow regimes on one sixth of the global land area (Döll et al., 2009), while climate change will likely alter flow regimes on 90% of Earth’s land mass by 2050 (Döll and Zhang 2010). Identifying reference sites to understand “natural” flow-ecology relationships to define baseline conditions will likely continue to become more difficult. Identifying environmental flow standards using methods that are not reliant on historic or baseline conditions may be necessary to overcome these issues (discussed in Poff and Matthews, 2013).

SSN models indicated fish traits were spatially autocorrelated in the study area, and this appears to be driven by the distribution of our study sites. Groundwater streams were clumped in the Ouachita Mountains, while runoff streams were clumped in the Boston

Mountains. This clumping likely drove the importance of tail-down models for several traits in these regimes (Figure 4). Similarly, Euclidean distance was important in intermittent streams, which were widely distributed across the entire study area. In these widely distributed sites, network connectivity may be less important relative to the broad-scale environmental variation captured by Euclidean distance. The use of SSN models captured these different spatial structures and helped account for the differences in site distributions between flow regimes.

Other studies utilizing compilations of existing data likely also exhibit spatial clumping of sites, which violates assumptions of independence required for most statistical models. Failure to account for spatial autocorrelation may lead to elevated type I error rates (Legendre, 1993), having potentially large impacts on the interpretation of flow-ecology relationships. Like other studies (Isaak et al., 2014), we found SSN models explained more variance and had less significant relationships than traditional linear models (Tables 3 and 4), suggesting that failing to account for spatial autocorrelation may lead to spurious findings when developing environmental-flow standards.

In addition to controlling for spatial autocorrelation, SNN models also helped us identify potential covariates to improve future model performance. For example, length of spawning season only exhibited significant relationships with hydrology across all sites combined. The lack of relationships between hydrology and length of spawning season in any flow regime may be due to regional environmental differences like water temperature influencing spawning season. Our models support this inference because Euclidean distance, which captures broad scale environmental variability, described a large (45-94%) proportion of variance for the length of spawning season. McManamay et al. (2015) also found length of spawning season had a higher affiliation with geographic regions than hydrology, with length of spawning season varying along a latitudinal gradient, potentially related to temperature differences from north to south. Similarly, 75% of the variation in the distribution of equilibrium strategists in groundwater streams was captured by the tail-down covariance component, representing spatial autocorrelation independent of flow direction. Although the proportion of equilibrium strategists varied across the study area, there was clumping of equilibrium strategists within stream networks. The large proportion of variability captured by the tail-down covariance component may suggest that local conditions such as water chemistry, sediment, riparian characteristics, or temperature may be influencing the distribution of equilibrium strategists. Because we know processes work at multiple spatial scales to influence streams, SSN models can help us identify an appropriate scale for environmental covariates that may improve our interpretation of flow-ecology relationships.

This study provides new considerations for the development of flow-ecology relationships necessary for the implementation of environmental flow standards. First, some flow metrics may influence community structure within a study region regardless of flow regime classification. Identifying important metrics such as these may help set management priorities before or during the development of flow classification schemes. Second, relationships between traits and hydrologic metrics can be complex when compared across classified flow regimes and may not always fit predictions. Expected relationships between traits and hydrologic metrics may differ among flow regimes and when flow regimes are ignored. Third, spatial autocorrelation is important and needs to be considered in the development of flow-ecology relationships, especially considering the spatial layout of sites. Considering flow-ecology relationships within a spatial context may improve the interpretation of observed relationships, help identify important environmental covariates, and develop new flow-ecology hypotheses.

Authors' Contributions

LB, DL, and DM conceived ideas and designed methodology. DL and LB collected and analyzed the data. LB led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data Accessibility

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.2f7h7t6 (Bruckerhoff, Leasure, and Magoulick, 2018).

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Table 1. Hydrologic metrics used as predictors of fish traits in the current study.

Code	Metric Name	Definition
MA4	Variability in daily flows 2	Coefficient of variation of the logs in daily flows corresponding to the {5th, 10th, 15th,…,85th, 90th, 95th} percentiles.
TA1	Constancy	Varies inversely with amplitude of variation in mean flow. Calculated using the equation of Colwell (1974). See Henriksen et al. (2006, Appendix 5).
FH7	Flood frequency 1	Mean number of high flow events per year using an upper threshold of 7 times median flow over all years
RA3	Fall rate	Mean rate of negative changes in flow from 1 day to the next.
DL4	Annual minima of 30 day means of daily discharge	Magnitude of minimum annual 30-day flow.

Table 2. Traits derived from the FishTraits database (Frimpong & Angermeier 2009) used to determine life-history strategies and used in analyses. Median, minimum, and maximum trait values are displayed for numerical traits, while the percentage of species in each category is provided for categorical traits and life history strategies.

Trait	Description	Median	Minimum	Maximum	Percentage
Maximum total length	Maximum total length or asymptotic length in centimeters.	15	4	200	
Age at maturity	Mean, median, or modal age at maturity in years averaged across populations for females or males if female data were not available.	1.5	0.3	10	
Fecundity	Maximum reported fecundity (count).	1,500	37	20,000,000	
Longevity	Longevity in years based on life in the wild or captivity if wild not available.	4	1	45	
Serial	Serial or batch spawners.				55
Season	Sum of proportions of each month in which spawning occurs.	2.5	1	6.5	
Open Spawners	Nonguarders; spawn over open substrates.				39
Brood Hiders	Nonguarders; brood hiders.				25
Open Guarders	Guarders, open substrate for spawning.				1

Nest Guarders	Guarders, nest spawners.	34
Substrate Indifferent	Lumping of all bearers, spawning generalists.	1
Parental Care Index	Calculated following McManamay et al. (2015) based on degree of parental investment.	
Equilibrium	Life history strategy characterized by slow maturation, low fecundity and high juvenile survivorship.	32
Opportunistic	Life history strategy characterized by fast maturation, low fecundity, and low juvenile survivorship.	44
Periodic	Life history strategy characterized by slow maturation, high fecundity, low juvenile survivorship.	24

Table 3. Non-spatial linear models produced more significant relationships, but explained less variance than spatial (SSN) models. All spatial models included three spatial covariance structures (Tail-Up, Tail-Down, and Euclidean), five flow metrics, and two landscape metrics. Pseudo R^2 values calculated from the correlation coefficient between the observed values and those predicted by leave-one-out-cross-validation are provided for all spatial models, while adjusted R^2 is provided for non-spatial models. Highest R^2 values of spatial and non-spatial models are bold.

		Spatial Models		**Non-Spatial Models**	
Flow Regime	Response	Pseudo R^2	# Significant Covariates	Adjusted R^2	# Significant Covariates
Groundwater	Age at Maturity	**0.56**	2	0.18	0
	Season	**0.74**	0	0.32	0
	Equilibrium	0.06	0	**0.14**	0
	Opportunistic	**0.2**	0	0.03	1
	Periodic	**0.26**	1	0.15	0
	Open Spawners	**0.64**	0	0.34	0
	Brood Hiders	**0.58**	0	0.55	0
	Nest Guarders	0.01	0	**0.10**	0
Runoff	Age at Maturity	**0.26**	0	0.01	0
	Season	**0.56**	0	0.31	1
	Equilibrium	0.04	0	**0.09**	0
	Opportunistic	**0.21**	0	0.03	0
	Periodic	**0.64**	0	0.17	1
	Open Spawners	**0.39**	0	0.02	0
	Brood Hiders	**0.51**	0	0.05	0
	Nest Guarders	0.03	0	**0.10**	2
Intermittent	Age at Maturity	**0.46**	1	0.18	1
	Season	**0.28**	0	0.05	1
	Equilibrium	**0.45**	2	0.09	2
	Opportunistic	**0.47**	2	0.17	1
	Periodic	**0.02**	0	0.01	0
	Open Spawners	**0.51**	2	0.18	4
	Brood Hiders	**0.61**	3	0.33	3
	Nest Guarders	**0.42**	3	0.10	2
All Flow Regimes	Age at Maturity	**0.52**	0	0.24	2
	Season	**0.43**	1	0.14	1
	Equilibrium	**0.34**	1	0.05	1
	Opportunistic	**0.34**	1	0.13	3
	Periodic	**0.14**	1	0.04	1
	Open Spawners	**0.53**	1	0.18	3
	Brood Hiders	**0.60**	3	0.30	3
	Nest Guarders	**0.29**	1	0.10	2

Table 4. Model results from spatial and non-spatial models for significant covariates for each trait for each flow regime. Non-spatial model results are highlighted to aid in readability.

Flow Regime	Model Type	Response	Metric	Estimate	Std. Error	T Value	P Value
Groundwater	Spatial	Age at Maturity	DL4	0.010	0.027	3.740	0.001
			RA3	-0.162	0.070	-2.314	0.031
		Periodic	FH7	1.098	0.310	3.555	0.002
	Non- Spatial	Periodic	FH7	0.589	0.254	2.317	0.031
Runoff	Spatial	---	---	---	---	---	---
	Non- Spatial	Season	Temperature	0.006	0.002	3.184	0.004
		Periodic	DL4	0.160	0.056	2.853	0.008
		Nest Guarders	RA3	-0.023	0.010	-2.316	0.022
			Temperature	-0.001	0.001	-2.216	0.028
Intermittent	Spatial	Age at Maturity	RA3	0.083	0.030	2.738	0.007
		Equilibrium	Watershed Area	-0.037	0.015	-2.535	0.012
			Temperature	-0.006	0.002	-2.805	0.006
		Opportunistic	MA4	-0.627	0.305	-2.055	0.042
			Watershed Area	0.049	0.015	3.217	0.002
		Open Spawners	MA4	-4.189	1.626	-2.577	0.011
			Watershed Area	0.044	0.014	3.084	0.002
		Brood Hiders	MA4	-1.293	0.346	-3.735	<0.001
			DL4	-0.139	0.051	-2.729	0.007
			Watershed Area	-0.058	0.015	-3.935	<0.001
		Nest Guarders	MA4	0.576	0.246	2.339	0.021
			DL4	0.068	0.035	1.978	0.050
			RA3	0.089	0.044	2.015	0.050
		Season	TA1	0.531	0.243	2.177	0.031
	Non-Spatial	Age at Maturity	RA3	0.061	0.026	2.370	0.019
		Season	TA1	0.647	0.262	2.473	0.015
		Equilibrium	TA1	-0.661	0.329	-2.101	0.046
			Watershed Area	-0.002	0.015	-2.406	0.017
		Opportunistic	Watershed Area	0.051	0.016	3.151	0.002
		Open Spawners	MA4	0.745	0.267	2.786	0.006
			TA1	0.968	0.321	3.017	0.003
			Watershed Area	0.032	0.015	2.179	0.031
		Brood Hiders	MA4	-1.351	0.279	-4.830	<0.001
			TA1	-0.897	0.336	-2.674	0.008
			Watershed Area	-0.044	0.016	-2.784	0.006
		Nest Guarders	RA3	-0.023	0.010	-2.316	0.022
			Temperature	-0.001	<0.001	-2.216	0.028
All Flow Regimes	Spatial	Equilibrium	Temperature	-0.004	0.002	-2.174	0.031
		Opportunistic	Watershed Area	0.040	0.013	3.001	0.003
		Periodic	Watershed Area	-0.024	0.010	-2.376	0.018
		Open Spawners	Watershed Area	0.032	0.012	2.77	0.006
		Brood Hiders	MA4	-0.892	0.285	-3.129	0.002
			RA3	0.078	0.039	1.982	0.049
			Watershed Area	-0.053	0.011	-4.613	<0.001
		Nest Guarders	Watershed Area	0.024	0.009	2.703	0.007
	Non-Spatial	Age at Maturity	DL4	0.034	0.015	2.197	0.029

	Temperature	-0.002	0.001	-2.286	0.023
Season	TA1	0.643	0.202	3.386	0.001
Equilibrium	TA1	-0.575	0.257	-2.233	0.027
Opportunistic	DL4	-0.069	0.030	-2.294	0.023
Periodic	Watershed Area	-0.023	0.010	-2.362	0.019
Open Spawner	MA4	0.680	0.224	3.032	0.003
	TA1	0.714	0.251	2.842	0.005
Brood Hiders	MA4	-1.120	0.229	-5.215	<0.001
	TA1	-0.631	0.257	-2.458	0.015
	Watershed Area	-0.036	0.012	-2.928	0.004
Nest Guarders	RA3	-0.023	0.010	-2.316	0.022
	Temperature	-0.001	<0.001	-2.216	0.028

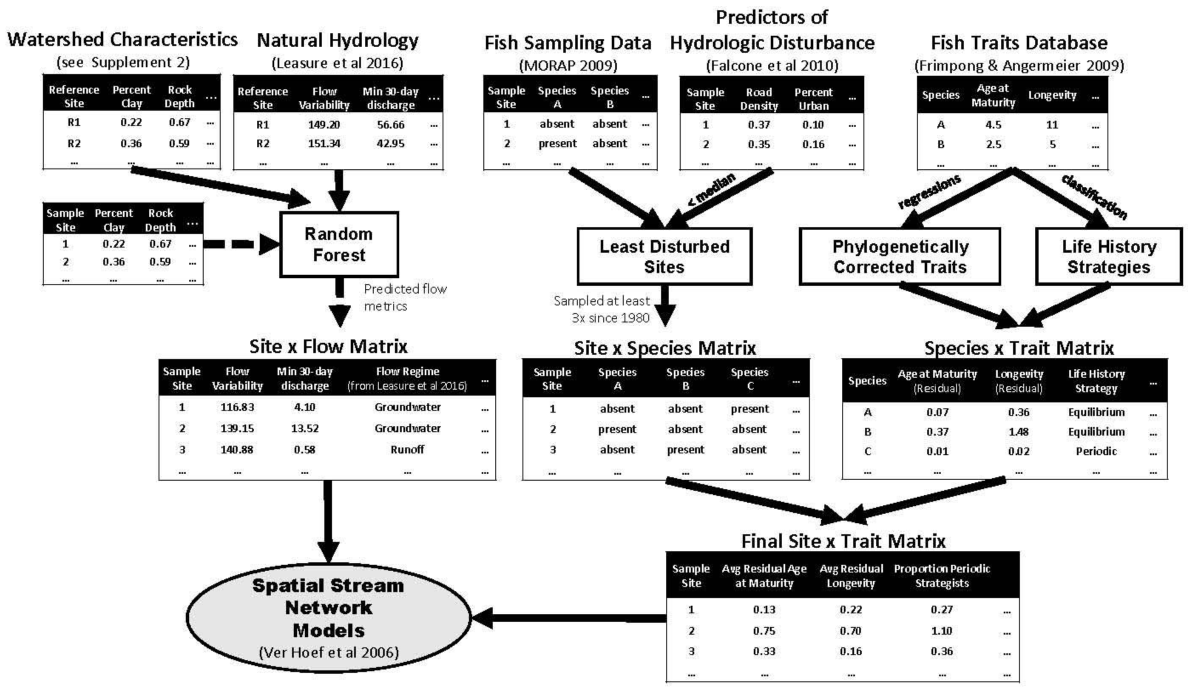
Figure Legends

Figure 1. Summary of the workflow used in analyses. The top row represents a sample of the raw data compiled for the current study, arrows represent processing between various forms of each data matrix.

Figure 2. Natural flow regime classifications of streams in the Ozark-Ouachita Interior Highlands of Arkansas, USA. Circles indicate fish community sampling locations and the flow regime classification of each site.

Figure 3. Box plots (median, interquartile distances, and outliers) of deviance residuals of the final set of fish traits (corrected for phylogeny) and proportion of life-history strategists within flow regime classes (groundwater (black), runoff (dark-grey), and intermittent (light-grey)). Note open substrate and substrate indifferent spawners were removed as they were not included in final models.

Figure 4. Proportion of variance explained for each trait in spatial (a.) and non-spatial (b.) models by covariates (hydrologic and landscape metrics), tail-up, tail-down, and Euclidean covariance structures, and the nugget (residual) effect for groundwater, runoff, intermittent, and all sites combined. In spatial models, the nugget is the amount of unexplained (residual) variance. Generalized R^2 values are shown for traits in which covariates explained more than 20% of the variance.



Reference Site	Percent Clay	Rock Depth	…
R1	0.22	0.67	…
R2	0.36	0.59	…
…	…	…	…

Reference Site	Flow Variability	Min 30-day discharge	…
R1	149.20	56.66	…
R2	151.34	42.95	…
…	…	…	…

Sample Site	Percent Clay	Rock Depth	…
1	0.22	0.67	…
2	0.36	0.59	…
…	…	…	…

Sample Site	Species A	Species B	…
1	absent	absent	…
2	present	absent	…
…	…	…	…

Sample Site	Road Density	Percent Urban	…
1	0.37	0.10	…
2	0.35	0.16	…
…	…	…	…

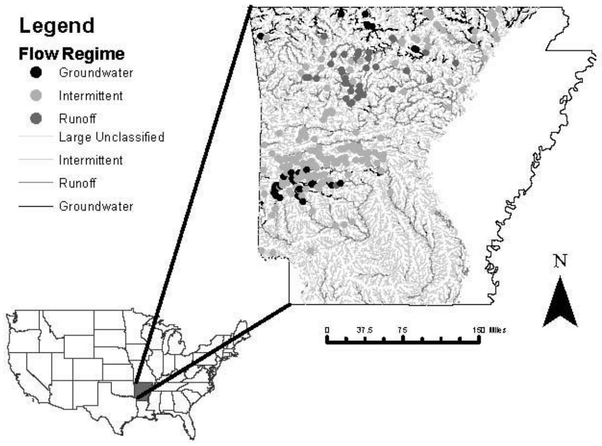
Species	Age at Maturity	Longevity	…
A	4.5	11	…
B	2.5	5	…
…	…	…	…

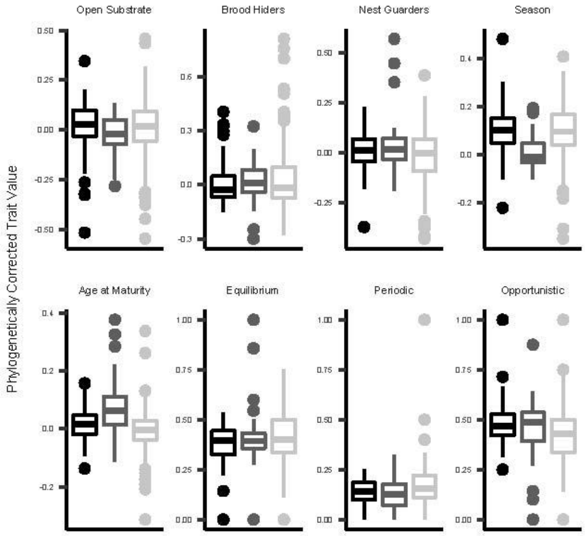
Sample Site	Flow Variability	Min 30-day discharge	Flow Regime (from Leasure et al 2016)	…
1	116.83	4.10	Groundwater	…
2	139.15	13.52	Groundwater	…
3	140.88	0.58	Runoff	…
…	…	…	…	…

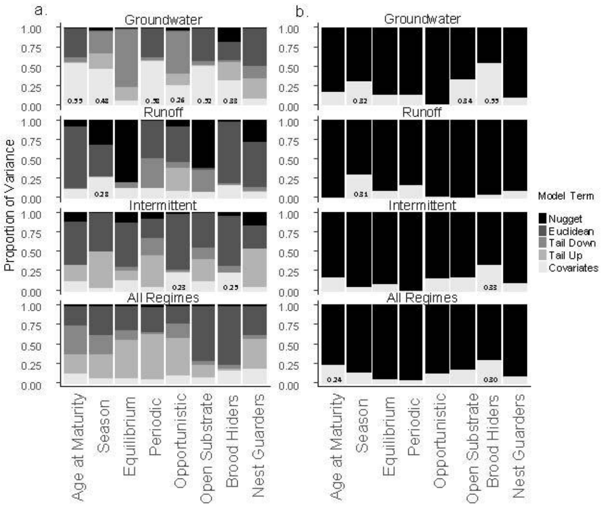
Sample Site	Species A	Species B	Species C	…
1	absent	absent	present	…
2	present	absent	absent	…
3	absent	present	absent	…
…	…	…	…	…

Species	Age at Maturity (Residual)	Longevity (Residual)	Life History Strategy	…
A	0.07	0.36	Equilibrium	…
B	0.37	1.48	Equilibrium	…
C	0.01	0.02	Periodic	…
…	…	…	…	…

Sample Site	Avg Residual Age at Maturity	Avg Residual Longevity	Proportion Periodic Strategists	
1	0.13	0.22	0.27	…
2	0.75	0.70	1.10	…
3	0.33	0.16	0.36	…
…	…	…	…	…




Phylogenetically Corrected Trait Value
Open Substrate
0.50
0.25
0.00
-0.25
-0.50
Brood Hiders
0.6
0.3
0.0
-0.3
Nest Guarders
0.50
0.25
0.00
-0.25
Season
0.4
0.2
0.0
-0.2
Age at Maturity
0.4
0.2
0.0
-0.2
Equilibrium
1.00
0.75
0.50
0.25
0.00
Periodic
1.00
0.75
0.50
0.25
0.00
Opportunistic
1.00
0.75
0.50
0.25
0.00


a.
b.
Groundwater
Runoff
Intermittent
All Regimes
Proportion of Variance
1.00
0.75
0.50
0.25
0.00
0.55
0.48
0.58
0.26
0.52
0.33
0.28
0.23
0.25
0.32
0.34
0.55
0.31
0.33
0.24
0.30
Age at Maturity
Season
Equilibrium
Periodic
Opportunistic
Open Substrate
Brood Hiders
Nest Guarders
Model Term
Nugget
Euclidean
Tail Down
Tail Up
Covariates