COMMUNITY ECOLOGY – ORIGINAL RESEARCH

Functional strategies drive community assembly of stream fishes along environmental gradients and across spatial scales

Matthew J. Troia · Keith B. Gido

Abstract Trade-offs among functional traits produce multi-trait strategies that shape species' interactions with the environment and drive the assembly of local communities from regional species pools. Stream fish communities vary along stream size gradients and among hierarchically structured habitat patches, but little is known about how the dispersion of strategies varies along environmental gradients and across spatial scales. We used null models to quantify the dispersion of reproductive life history, feeding, and locomotion strategies in communities sampled at three spatial scales in a prairie stream network in Kansas, USA. Strategies were generally underdispersed at all spatial scales, corroborating the longstanding notion of abiotic filtering in stream fish communities. We tested for variation in strategy dispersion along a gradient of stream size and between headwater streams draining different ecoregions. Reproductive life history strategies became increasingly underdispersed moving from downstream to upstream, suggesting that abiotic filtering is stronger in headwaters. This pattern was stronger among reaches compared to mesohabitats, supporting the premise that differences in hydrologic regime among reaches filter reproductive life history strategies. Feeding strategies became increasingly underdispersed moving from upstream to downstream, indicating that environmental filters associated with stream size affect the dispersion of feeding and reproductive life history in opposing ways. Weak differences in strategy dispersion were detected between ecoregions, suggesting that different abiotic filters or strategies drive community differences between ecoregions. Given the pervasiveness of multi-trait strategies in plant and animal communities, we conclude that the assessment of strategy dispersion offers a comprehensive approach for elucidating mechanisms of community assembly.

Keywords Environmental filtering · Feeding · Locomotion · Prairie streams · Reproductive life history

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Introduction

Biotic and abiotic environmental conditions influence local community composition by acting on functional traits (McGill et al. 2006) and the dispersion of these traits within a local community can provide insight into mechanisms of community assembly (Weiher and Keddy 1995). When the distribution of traits within a local community is more dispersed (i.e., variable) than that of communities assembled randomly from regional species pools, competitive exclusion is invoked as the mechanism of community assembly. In contrast, a distribution of traits that is less dispersed than randomly assembled communities is taken as evidence for abiotic environmental filtering. Traits correspond to multiple aspects of a species' ecology, such as physicochemical tolerance, resource acquisition, predator avoidance, and dispersal. Environmental filters operate on

traits associated with physicochemical tolerance whereas traits associated with the acquisition of limiting resources should be influenced by interspecific competition (Weiher and Keddy 1995). Not surprisingly, some traits may be overdispersed while others are underdispersed in the same community as a consequence of different assembly mechanisms simultaneously operating on different types of traits. For example, in rockfish communities of the eastern Pacific Ocean, gill raker morphology, an indicator of food resource use, is overdispersed due to competitive exclusion whereas eye size is associated with depth and is underdispersed due to environmental filtering along a vertical light gradient (Ingram and Shurin 2009). In stream fish communities, conceptual frameworks and empirical studies suggest that communities are assembled primarily by abiotic filtering, whereas interspecific competition plays a lesser role (Jackson et al. 2001). Studies of trait dispersion are rare for stream fish communities, but are important for elucidating the mechanisms driving the assembly of these communities.

Although the dispersion of single traits can provide insight into mechanisms of community assembly, traits may not interact individually with the environment; rather, suites of coevolved traits often convey ecological strategies that interact with environmental conditions during community assembly (Westoby et al. 2002; Statzner et al. 2004; Poff et al. 2006a). Among freshwater fish species, trade-offs in three reproductive life history traits (size at maturity, annual fecundity, and parental investment per progeny) form a trilateral continuum with three strategic endpoints: opportunistic (small size at maturity, low annual fecundity, and low investment per progeny), periodic (large size at maturity, high annual fecundity, and low investment per progeny), and equilibrium (moderate size at maturity and annual fecundity and high investment per progeny) (Winemiller and Rose 1992). Interannual and seasonal hydrologic regimes act as environmental filters and constrain the reproductive life history strategies that persist in streams with different hydrologic regimes (Poff and Allan 1995; Olden et al. 2006). Other examples of multi-trait strategies of freshwater fishes include feeding guilds [e.g., sensory, mouth, and gut morphology (Goldstein and Simon 1999)] and locomotion guilds [e.g., body morphology and fin size and positioning (Lamouroux et al. 2002)]. Given the ubiquity of multi-trait strategies in plant and animal communities (Westoby et al. 2002; Statzner et al. 2004), evaluating the dispersion of strategies might be a more realistic and comprehensive approach to characterize ecological variability among species (as opposed to individual traits) and therefore be a more informative approach to test mechanisms of community assembly.

Community assembly mechanisms also are scale dependent and the dispersion of traits or strategies

associated with environmental filtering and competitive exclusion may differ across spatial resolutions and extents (Swenson et al. 2007; Weiher et al. 2011). Spatial resolution—that is, the geographic area defined as the local community—influences the amount of environmental heterogeneity within localities and can affect community assembly in two ways. First, different environmental gradients vary innately at different spatial scales. For example, climatic variables operate as broader scale abiotic filters than do geomorphic variables which are constrained by topographic variability within homogeneous climatic regions (Poff 1997). Second, processes driving trait dispersion also vary in the spatial scale at which they operate. For example, competition for resources occurs among individuals and therefore is restricted to the spatial scale of individual home ranges, which can vary greatly among species (Skalski and Gilliam 2000). On the other hand, spatial extent—that is, the geographic area defined as the regional species pool—influences the amount of environmental heterogeneity among localities. Environmental heterogeneity among localities should increase with spatial extent and lead to niche processes (environmental filtering or competitive exclusion) driving community assembly, whereas the low environmental heterogeneity among localities apparent at narrow spatial extents should lead to neutral assembly processes (Leibold et al. 2004; Weiher et al. 2011).

Unidirectional flow of water through stream networks results in hierarchical structuring of habitat and abiotic environmental gradients varying (and potentially filtering) at multiple spatial scales (Frissell et al. 1986). Studies of species-environment and trait-environment relationships suggest that environmental factors varying among reaches within a basin are important drivers of community composition. Longitudinal position in the stream network (hereafter "stream size") is a strong environmental correlate of stream fish community composition (Horwitz 1978; Schlosser 1987; Pease et al. 2012) and multiple environmental gradients associated with such stream-size gradients are likely to filter functional strategies. First, gradual changes in resource type from headwaters to large rivers influence strategies associated with foraging behavior and trophic position (Vannote et al. 1980; Ibanez et al. 2009; Pease et al. 2012). Second, depth and current velocity increase with discharge (which increases with stream size) resulting in the filtering of locomotion strategies associated with swimming endurance, maneuverability in complex habitats, and vertical positioning in the water column (Pease et al. 2012). Within stream reaches, depth and current velocity are inversely correlated—varying between pool and riffle mesohabitats—and also filter locomotion strategies at this finer spatial resolution (Lamouroux et al. 2002). Third, community assembly mechanisms vary along

Fig. 1 **a** Big Blue River basin in Kansas, USA. *Dashed lines* represent ecoregion boundaries and *circles* represent five headwater reaches in the Flint Hills ecoregion (*black*), nine headwater reaches in the plains ecoregions (*gray*), and 26 mainstem sites distributed throughout all ecoregions (*white*). **b** A reach on the Little Blue River. *Black lines* represent stream margins, *light gray* areas are sandbars, *dark gray* areas are log complexes, and *hatched rectangles* represent 12 sampled mesohabitats. **c** Three spatial scales at which null models were developed, defining the reach as the regional pool and mesohabitats as local communities (*left*), the basin as the regional pool and mesohabitats as local communities (*center*), or the basin as the regional pool and reaches as local communities (*right*)
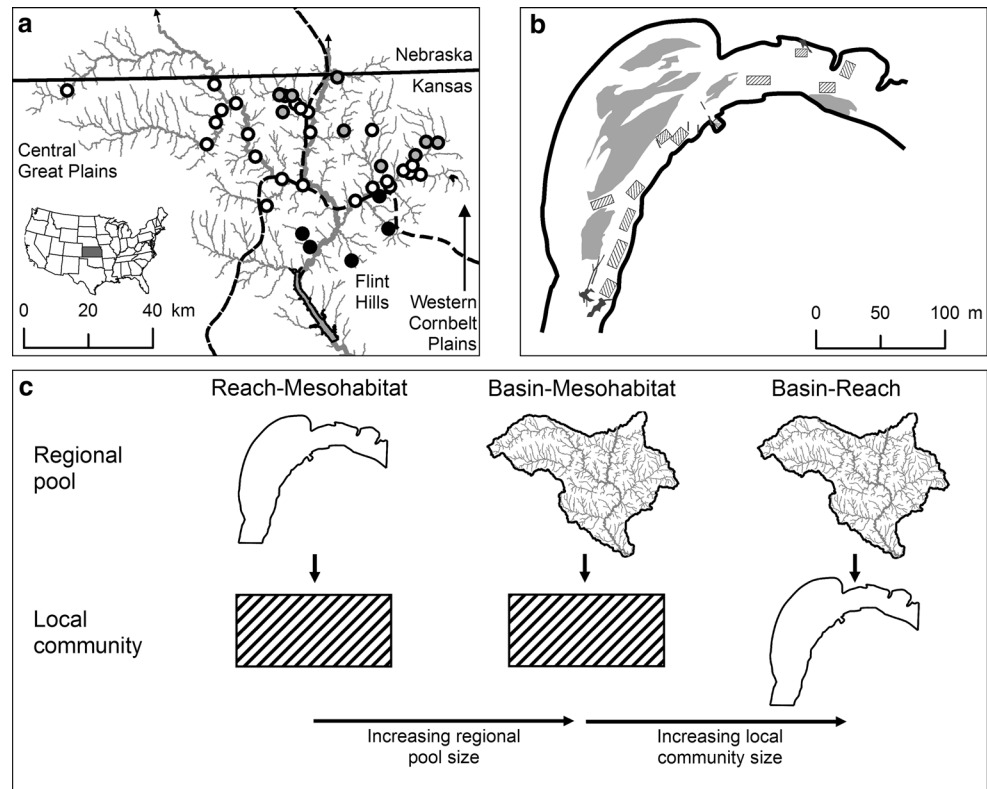
gradients of environmental disturbance (Weiher and Keddy 1995). In streams the frequency, magnitude, and timing of discharge-related disturbances can filter reproductive life history strategies (Schlosser 1987; Poff and Allan 1995; Olden et al. 2006). Such hydrologic disturbances increase from downstream to upstream (Dodds et al. 2004) as well as between ecoregions that differ in soil, geology and land cover characteristics (Poff et al. 2006b; Neff and Jackson 2012).

The goal of this study was to test mechanisms of community assembly for Great Plains stream fishes. Our first objective was to characterize tradeoffs among traits and identify strategies within each of three categories of strategies: reproductive life history, feeding, and locomotion. Our second objective was to evaluate the dispersion of strategies within each of these categories at three spatial scales: mesohabitats within reaches, mesohabitats within the basin, and reaches within the basin (Fig. 1). Our third objective was to test for variation in strategy dispersion along a stream size gradient and between headwater streams draining different ecoregions. We hypothesized that mechanisms of community assembly (inferred from strategy dispersion) would depend on the category of strategy, the spatial scales at which local communities and regional pools are defined, and the location of a local community along environmental gradients associated with stream size and ecoregional transitions (Table 1).

Materials and methods

Fish and environmental sampling

This study took place in the Big Blue River basin in north central Kansas, USA (Fig. 1a) where taxonomic composition of stream fish communities varies along gradients of stream size and between geologically distinct ecoregions (Gido et al. 2006). The southern portion of the Big Blue River basin flows through the Flint Hills Environmental Protection Agency Level III ecoregion and is characterized by high-gradient, spring-fed headwater streams. These streams have alternating pool-riffle mesohabitat sequences and drain catchments composed mostly of native tallgrass prairie. In contrast, headwater streams in the northern portion of the basin drain the Central Great Plains and Western Cornbelt Plains ecoregions. These streams have low gradients, are dominated by homogeneous run habitat with finer substrates, and drain catchments composed mostly of row crop agriculture.

Fish communities were sampled in eight to 13 mesohabitats distributed among 40 reaches (440 mesohabitats in total) from July to August 2012. Reaches were 200–400 m in length and represented a variety of mesohabitat types (Fig. 1a, b). We define a mesohabitat as a stream habitat patch with homogeneous depth, current velocity, substrate composition and in-channel cover (e.g., undercut bank,

Table 1 Hypothesized (*H*) effects of stream size, ecoregion, and spatial scale on the dispersion of ecological strategies

Strategy category	Hypothesized assembly mechanism	Environmental filter	Spatial scale	Hypothesized dispersion	Supporting references
Reproductive life history (H₁)	Environmental filtering	Hydrologic regime along stream size gradient	Basin-Reach	Underdispersion; stronger in headwaters	Winemiller and Rose (1992), Poff and Allan (1995)
Reproductive life history (H₂)	Environmental filtering	Hydrologic regime along ecoregional gradient (geology and land use)	Basin-Reach	Underdispersion; stronger in plains ecoregions	Winemiller and Rose (1992), Gido et al. (2006)
Feeding (H₁)	Limiting similarity if food resources are limiting	N/A	Reach-Mesohabitat	Overdispersion	Taylor (1996), Resetarits (1997)
Feeding (H₂)	Environmental filtering if food resource type is spatially heterogeneous	Food resource type along stream size gradient	Basin-Reach	Underdispersion	Vannote et al. (1980), Ibanez et al. (2009)
Locomotion (H₁)	Environmental filtering	Depth and current velocity gradients between pools and riffles	Reach-Mesohabitat	Underdispersion	Lamouroux et al. (2002)
Locomotion (H₂)	Environmental filtering	Depth and current velocity gradients along stream size gradient	Basin-Reach	Underdispersion	Leopold (1953), Pease et al. (2012)

log complex, bankgrass, or rootwad) (Frissell et al. 1986). Community sampling followed a modified version of the protocol used by Gorman (1988). Mesohabitats averaged 13.1 m^2 in area and were selected to represent the diversity of mesohabitat types (all combinations of in-channel cover, depth, velocity, and substrate) present within a reach. This mesohabitat sampling scheme assured accurate representation of the environmental heterogeneity present within each reach. Fish communities were sampled with a seine (5-m width, 1.5-m height, 5-mm mesh diameter). When in-channel cover was absent, seine hauls were made in the downstream direction. For mesohabitats containing in-channel cover, the seine was positioned around the perimeter of cover which was then disturbed by the samplers to drive fish into the seine. Fish >200 mm in total length were identified to species, measured for total length, and released. Fish <200 mm were euthanized with MS-222, preserved in buffered 10 % formalin, and returned to the laboratory where all specimens were identified, measured, and counted.

Functional trait data

A total of 23 functional traits associated with reproductive life history, feeding, and locomotion were compiled for the 38 species collected during fish community sampling and were used to characterize functional strategies within each of these categories (Table 2; Online Resources 1–3). Seven reproductive life history traits known to represent tradeoffs in reproductive life history strategies were compiled from published literature (Winemiller and Rose 1992; Olden et al. 2006). When more than one literature source was available, mean trait values were used. Seven morphological traits representing tradeoffs in feeding strategies were measured from five specimens taken from community samples to represent the size distribution of the individuals present in our collections. Gut length is representative of trophic position where species with longer guts feed at lower trophic levels (Pease et al. 2012). Mouth position is representative of foraging behavior and vertical habitat use with high angles indicative of a terminal mouth position characteristic of water column or surface foraging species and low angles indicative of subterminal mouth positions characteristic of benthic foraging species (Pease et al. 2012). Gape width, head length, and head depth are representative of the size of prey that a species is capable of consuming. Gill raker length is representative of food acquisition, with longer gill rakers indicative of filter feeding (Gatz 1979; Pease et al. 2012). Eye diameter represents the importance of visual versus olfactory senses in foraging, with large-eyed species relying more strongly on vision (Bonner and Wilde 2002). Nine morphological traits representing tradeoffs in locomotion strategies were

Table 2 Twenty-three functional traits used to characterize three categories of functional strategies: reproductive life history, feeding, and locomotion

Strategy category	Trait	Code	Description
Reproductive life history	Age at maturity[a]	mat.age	Minimum age at reproductive maturity
	Length at maturity[a]	mat.len	Minimum length at reproductive maturity
	Maximum length[a]	max.len	Maximum body length
	Longevity[a]	longev	Maximum life span
	Annual fecundity[a]	fecund	Mean annual fecundity
	Egg diameter[a]	egg.dia	Mean diameter of fully yolked oocyte
	Parental care[a]	parent	Nominal score (0–4) based on energetic investment in eggs or juveniles (Olden et al. 2006)
Feeding	Gut length[b]	gut.len	Ratio of gut length to body length
	Mouth position[a]	mouth.pos	Angle between a line connecting the tips of the open jaws and a line running between the center of the eye and the posterior-most vertebra
	Gape width[c]	gape	Distance between the left and right medial margins of the premaxilla
	Head length[b]	head.len	Distance from the tip of the jaw to the posterior edge of the operculum
	Head depth[b]	head.dep	Distance from dorsum to ventrum passing through the center of the eye
	Gill raker length[c]	gill.rak	Length of the longest gill raker
	Eye diameter[b]	eye.dia	Horizontal distance from anterior to posterior eye margin
Locomotion	Pelvic fin position[d]	pelv.pos	Angle between the midline and a line passing through the insertions of the pelvic and pectoral fins
	Shape factor[e]	shape.fact	Ratio of total length to maximum body depth
	Swim factor[e]	swim.fact	Ratio of minimum caudal peduncle depth to maximum caudal fin depth
	Dorsal fin height[b]	dors.ht	Maximum distance from the proximal to distal margin
	Dorsal fin length[b]	dors.len	Distance from the anterior proximal margin to the posterior proximal margin
	Anal fin height[b]	anal.ht	Maximum distance from the proximal to distal margin
	Anal fin length[b]	anal.len	Distance from the anterior proximal margin to the posterior proximal margin
	Pectoral fin length[b]	pect.len	Maximum distance from the proximal to distal margin
	Pelvic fin length[b]	pelv.len	Maximum distance from the proximal to distal margin

[a] Estimated from literature

[b] Proportion of total length measured from vouchers

[c] Interpolated to mean length measured from vouchers

[d] Measured from vouchers, independent of body size

[e] Unitless ratio measured from vouchers

also measured from voucher specimens. Pelvic fin position represents an evolutionary change in fin morphology with high angles typical of derived species (e.g., Perciformes) that use both pelvic and pectoral fins for maneuvering in structurally complex habitats, whereas low angles represent ancestral species (e.g., Cypriniformes) that use pectoral and pelvic fins for stability during sustained swimming (Moyle and Cech 2004). Shape factor represents body shape along the median plane with high values indicative of vertically compressed species capable of sustained swimming in high current velocities and low values indicative of deep-bodied species capable of greater maneuverability. Swim factor represents caudal fin morphology with small values indicative of strong swimmers (Webb 1984). Fin lengths and heights also are associated with swimming endurance and

maneuverability with longer and taller fins representative of greater maneuverability (Pease et al. 2012).

Data analysis

Three Euclidean dissimilarity matrices were developed to represent the functional similarity based on each of the three categories of strategies (reproductive life history, feeding, locomotion). Trait values were z-score transformed prior to calculation of Euclidean distance to standardize mean and variance such that each trait contributed equally to Euclidean distances between species (Cornwell et al. 2006). Principal component analysis (PCA) was used to visualize tradeoffs among traits and visualize positions of species in relation to one another in multivariate trait

space. Separate PCAs were carried out for each of the three strategy categories.

Mantel tests were used to measure the concordance between the three strategy categories to validate that each category represented a statistically independent index of ecological similarity (three Mantel tests). Mantel tests were also used to measure the concordance between phylogeny and each strategy category to test for a phylogenetic signal in each strategy category (three Mantel tests). Phylogenetic relatedness was inferred from taxonomic relationships between species following the method of Tedesco et al. (2008) because a complete molecular phylogenetic hypothesis including the 38 species in the Big Blue River basin was not available. The phylogenetic dissimilarity matrix was created by assigning values of 1.0, 0.5, 0.33, or 0.25 to pairs of species in the same genus, family, order, or class, respectively.

Strategy dispersion of local communities was evaluated using an analytic approach adopted from phylogenetic dispersion analyses (Webb et al. 2002), except we replaced species' pair-wise cophenetic distances inferred from phylogenetic trees with species' pair-wise Euclidean distances inferred from functional strategies. Strategy dispersion was quantified using two metrics: the mean nearest neighbor distance (MNND) and the mean pairwise distance (MPD). These metrics are widely used in studies quantifying phylogenetic and trait dispersion (Webb et al. 2002; Liu et al. 2013; Kembel et al. 2010). Simulation models have shown that nearest neighbor metrics (e.g., MNND) have greater power to detect overdispersion, whereas total community similarity metrics (e.g., MPD) have greater power to detect underdispersion (Kraft et al. 2007). Null models were used to test for non-random strategy dispersion in each local community (40 reaches or 440 mesohabitats). A subset of species (equal to the richness of the local community) was drawn from the regional species pool using an abundance-weighted independent swap algorithm and MNND and MPD were calculated for this null community. This process was repeated 999 times and a mean and SD of MNND and MPD of the 999 null local communities were calculated. A standardized effect size (SES) was calculated using Eq. 1 and used in subsequent analyses to test for variation in functional strategy dispersion among strategy categories, across spatial scales, between ecoregions and along a stream-size gradient.

$$\text{SES} = -1 \times \frac{\text{Obs} - \text{Mean}_{\text{random}}}{\text{Stdev}_{\text{random}}} \tag{1}$$

Positive SES values indicate local communities in which strategies are underdispersed compared to randomly assembled communities and negative SES values indicate local communities in which strategies are overdispersed compared to random communities.

Three null models were developed for each strategy category by redefining the spatial extent of the local community and regional pool (Fig. 1c). These null models included: (1) mesohabitats as local communities and reaches as the regional pools, (2) mesohabitats as local communities and the basin as the regional pool, and (3) reaches as local communities and the basin as the regional pool. Each combination of resolution and extent is hereafter referred to as a "spatial scale." Comparison of strategy dispersion between spatial scales provides the opportunity to evaluate the effect of changing the locality size while maintaining the same regional size and vice versa (Fig. 1c).

We tested for non-random strategy dispersion for each strategy category, spatial scale, and trait dispersion metric using Wilcoxon signed rank tests. Significant under- or overdispersion of functional strategies was inferred when the null hypothesis that SES is not different from zero was rejected (Ingram and Shurin 2009; Liu et al. 2013). We tested for differences in SES values from headwater reaches and mesohabitats draining the Flint Hills versus those draining the plains ecoregions using Wilcoxon rank sum tests. Headwater reaches in the Western Cornbelt Plains and Central Great Plains were grouped because previous studies indicate that environmental conditions and community composition of fishes are similar between these ecoregions (Gido et al. 2006). These two ecoregions collectively are referred to as "plains" hereafter. We restricted this test of ecoregional differences to headwater streams (link magnitude ≤27) because the catchments of larger streams are not contained entirely within a single ecoregion (Fig. 1a). Lastly, we tested for linear relationships between SES and stream size ($\log_{10}$-transformed link magnitude). Models were developed for SES values representing MNND and MPD for the three strategy categories and three spatial scales (18 models in total). Significance of all statistical tests was evaluated at $\alpha < 0.05$ and P-values were adjusted for multiple comparisons using the false discovery rate approach of Benjamini and Hochberg (1995). All analyses were performed with the R statistical language (R Development Core Team 2012) using the vegan (Oksanen et al. 2012), FD (Laliberté and Legendre 2010), picante (Kembel et al. 2010), ape (Paradis et al. 2004), and ade4 (Dray and Dufour 2007) packages.

Results

Functional strategies

Ordination of functional traits revealed tradeoffs among traits indicative of functional strategies (Fig. 2). For the reproductive life history category, the first axis explained 58.6 % of trait variation and represented a tradeoff between

Fig. 2 Principal component analysis showing tradeoffs among **a**, **c**, **e** traits representing reproductive; **a**, **b** life history; **c**, **d** feeding; and **e**, **f** locomotion strategies of **b**, **d**, **f** 38 species. See Electronic Supplementary Material for species codes and Table 2 for trait definitions and codes

longevity and early maturation, which separates periodic and equilibrium strategists (low axis 1 scores) from opportunistic strategists (high axis 1 scores). The second axis explained 22.0 % of trait variation and represented a tradeoff between parental care and fecundity, which separates periodic strategists (low axis 2 scores) from equilibrium strategists (high axis 2 scores). Periodic strategists were represented by catostomids and common carp (*Cyprinus carpio*), equilibrium strategists by ictalurid catfishes and

centrarchids, and opportunistic strategists by small-bodied cyprinids and percid darters (Fig. 2a, b).

For the feeding category, the first axis explained 32.5 % of trait variation and represented tradeoffs among gut length, mouth position, and eye diameter. This axis distinguished benthic foraging omnivores and algivores with long guts, subterminal mouths and small eyes (low axis 1 scores) from water-column foraging piscivores and invertivores with short guts, terminal mouths, and large eyes (high

Table 3 Summary of statistical tests presented in Figs. 3, 4

Metric	Spatial scale	Strategy category	Underdispersion		Ecoregion		Stream size		
			V	P	W	P	P	r^2_{adj}	Slope
MNND	Reach-Mesohabitat	Reproductive life history	94,567	<0.0001	2116.0	0.39	0.80	0.00	0.01
		Feeding	93,275	<0.0001	1843.0	0.10	*0.0071*	*0.02*	*0.11*
		Locomotion	86,382	<0.0001	2846.0	0.15	*0.0008*	*0.03*	*0.16*
	Basin-Mesohabitat	Reproductive life history	96,427	<0.0001	1808.5	0.084	*<0.0001*	*0.07*	*−0.13*
		Feeding	95,939	<0.0001	2054.5	0.30	*<0.0001*	*0.13*	*0.26*
		Locomotion	93,768	<0.0001	2296.5	0.85	0.33	0.00	0.05
	Basin-Reach	Reproductive life history	820	<0.0001	12.0	0.30	*0.0026*	*0.21*	*−0.21*
		Feeding	820	<0.0001	22.0	1.00	*0.0014*	*0.24*	*0.20*
		Locomotion	820	<0.0001	17.0	0.67	*0.0045*	*0.18*	*−0.25*
MPD	Reach-Mesohabitat	Reproductive life history	93,841	<0.0001	1917.0	*0.015*	0.51	0.00	−0.03
		Feeding	93,431	<0.0001	1488.0	*0.0036*	*0.0003*	*0.03*	*0.18*
		Locomotion	86,733	<0.0001	3059.0	*0.027*	*<0.0001*	*0.04*	*0.23*
	Basin-Mesohabitat	Reproductive life history	95953	<0.0001	2064.5	0.30	*<0.0001*	*0.12*	*−0.23*
		Feeding	95,962	<0.0001	1516.5	*0.0036*	*<0.0001*	*0.15*	*0.34*
		Locomotion	94,147	<0.0001	2450.5	0.85	*0.0158*	*0.01*	*0.13*
	Basin-Reach	Reproductive life history	820	<0.0001	11.0	0.30	*<0.0001*	*0.40*	*−0.26*
		Feeding	820	<0.0001	12.0	0.30	*0.0008*	*0.27*	*0.37*
		Locomotion	820	<0.0001	23.0	1.00	0.80	−0.02	0.03

Statistically significant *P*-values are in *italic*

MNND Mean nearest neighbor distance, *MPD* mean pairwise distance

axis 1 scores). The second axis explained 26.6 % of trait variation and represented traits associated with the use of different prey sizes, including gape width, gill raker length and head size. This axis distinguished small-bodied cyprinids and percid darters (low axis 2 scores) from large-bodied ictalurids and centrarchids (high axis 2 scores) (Fig. 2c, d).

For the locomotion category, the first axis explained 43.7 % of trait variation and represented a morphological tradeoff between two evolutionary lineages of actinopterygiian fishes (Cypriniformes and Perciformes). This axis distinguished cyprinids, catostomids, and ictalurids with low values of pelvic fin position and high shape factors (low axis 1 scores) from centrarchids and percids with high values of pelvic fin position and low shape factors (high axis 1 scores). This axis represents a tradeoff separating species with vertically compressed bodies and pelvic and pectoral fins adapted for sustained swimming from tall-bodied species with pectoral and pelvic fins adapted for maneuvering in structurally complex habitats (Fig. 2e, f).

Associations between strategy categories and phylogeny

Mantel tests indicated statistically significant relationships between all pairs of dissimilarity matrices for the three strategy categories and between strategy categories and phylogeny. Reproductive life history strategies

were moderately related to feeding strategies (*r* = 0.41, *P* = 0.0004) and locomotion strategies (*r* = 0.25, *P* = 0.015). Feeding strategies were moderately related to locomotion strategies (*r* = 0.40, *P* = 0.0004). Locomotion strategies were strongly related to phylogeny (*r* = 0.65, *P* < 0.0001). Reproductive life history and feeding strategies were moderately related to phylogeny (*r* = 0.29, *P* = 0.001 and *r* = 0.34, *P* = 0.0003, respectively).

Dispersion of functional strategies and environmental correlates

Wilcoxon signed rank tests indicated that SES values were significantly greater than zero for all three strategy categories, three spatial scales, and two dispersion metrics, which indicates that communities are consistently underdispersed (Table 3; Figs. 3, 4 white box plots).

Wilcoxon rank sum tests indicated that SES values based on MNND did not differ between plains and Flint Hills ecoregions, regardless of the strategy category, spatial resolution or extent (Table 3; Fig. 3 gray and black squares). Based on MPD, SES values for feeding strategies were significantly higher (more underdispersed) for headwater communities in the plains compared to headwater communities in the Flint Hills; however, this difference was apparent at the mesohabitat resolution but not at the reach
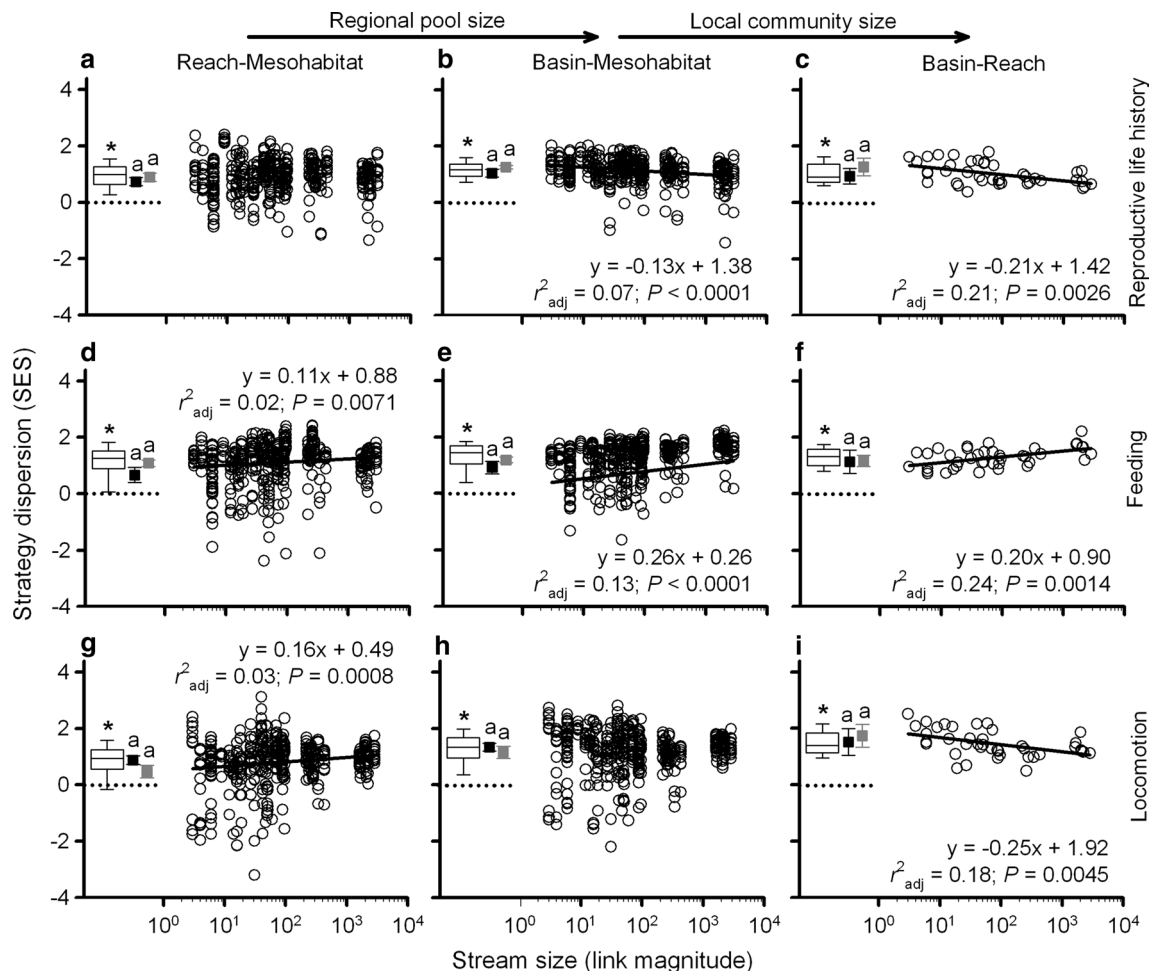
Fig. 3 Dispersion of **a–c** reproductive life history, **d–f** feeding, and **g–i** locomotion strategies at three spatial scales: **a, d, g** mesohabitat within reach ($n = 440$), **b, e, h** mesohabitat within basin ($n = 440$), **c, f, i** reach within basin ($n = 40$). Functional strategy dispersion was calculated as the standardized effect size (*SES*) of the mean nearest neighbor distance. *Boxplots* show the distribution of SES values and *asterisks* indicate statistically significant underdispersion (i.e., SES values significantly greater than zero) based on Wilcoxon signed rank tests. *Squares* show mean (±95 % confidence intervals) SES for headwater reaches/mesohabitats located in the Flint Hills (*black*) and in the Great Plains (*gray*) and *different letters* denote statistically significant differences based on Wilcoxon rank sum tests. *Scatterplots* show the relationship between stream size (link magnitude plotted on a log10 scale) and SES. *Regression lines* are presented for statistically significant relationships. See Table 3 for summary of statistical tests

resolution (Table 3; Fig. 4d, e, gray and black squares). Also based on MPD, SES values for locomotion strategies were significantly higher for headwater communities in the Flint Hills compared to the plains at the reach-mesohabitat scale.

Linear regression indicated statistically significant relationships between SES values based on MNND and stream size (link magnitude) for seven of nine models (Table 3; Fig. 3 scatterplots). Although several models for the mesohabitat resolution were statistically significant, variance explained was generally low and did not represent ecologically significant relationships. SES of reproductive life history strategies was negatively related to link magnitude at the basin-mesohabitat and the basin-reach scales, but not at the reach-mesohabitat scale (Fig. 3a–c). SES of feeding

strategies was positively related to link magnitude at all three scales (Fig. 3d–f). SES of locomotion strategies was positively related to link magnitude at the reach-mesohabitat scale, negatively related at the basin-reach scale scale, and not significantly related at the basin-mesohabitat scale (Fig. 3g–i).

Based on MPD, linear regression indicated statistically significant relationships between SES values based on MPD and stream size for seven of nine models (Table 3; Fig. 4 scatterplots). SES of reproductive life history strategies was negatively related to link magnitude at the basin-mesohabitat and basin-reach scales, but not at the reach-mesohabitat scale (Fig. 4a–c). SES of feeding strategies were positively related to link magnitude at all three scales (Fig. 4d–f). SES of locomotion strategies were positively
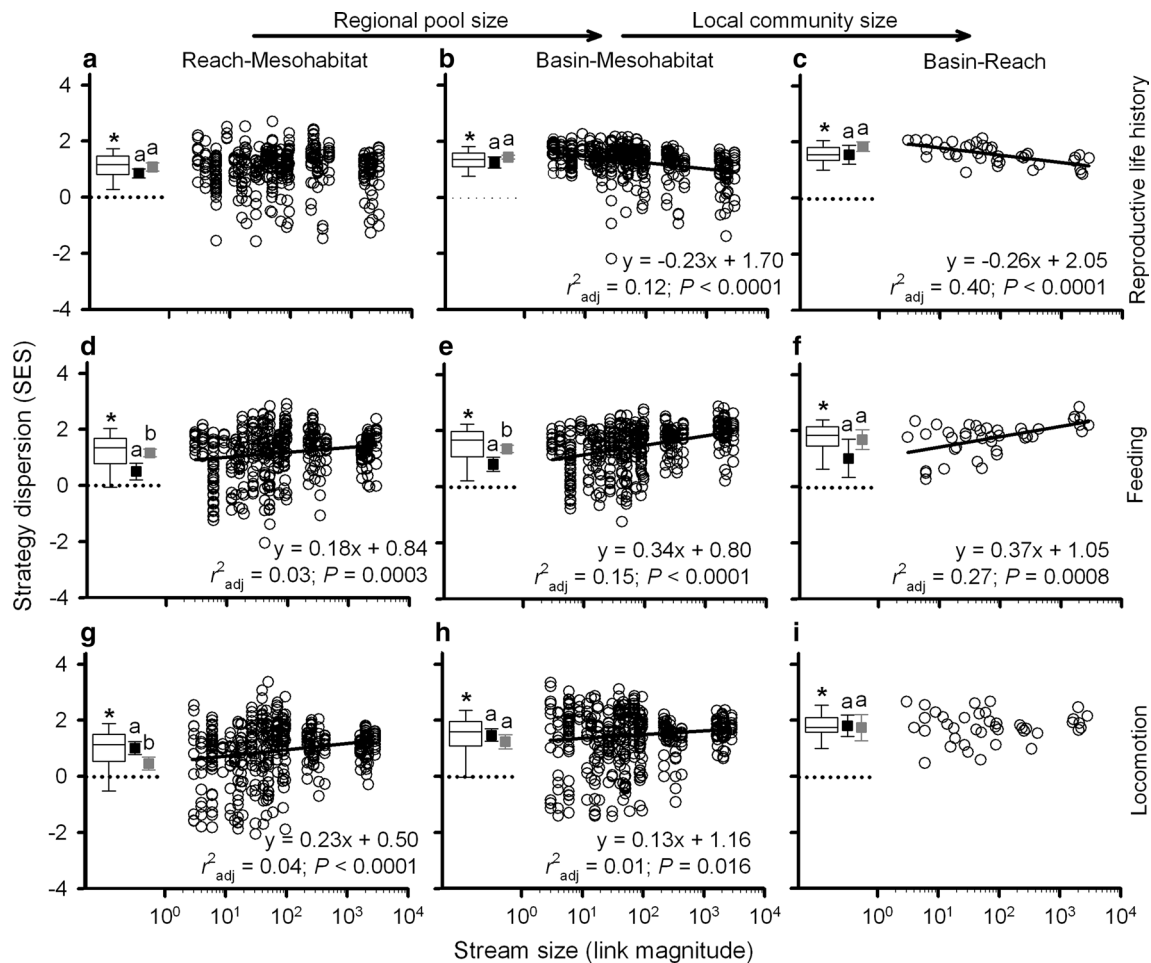
Fig. 4 As in Fig. 3, except SES are calculated from mean pairwise distance

related to link magnitude at the reach-mesohabitat and basin-mesohabitat scales, but not at the basin-reach scale (Fig. 4g, h, i).

Discussion

Community assembly in stream fishes

Most empirical evidence suggests that temperate stream fish communities are structured by abiotic environmental filtering and to a lesser extent by competitive interactions among species (Jackson et al. 2001). Our results lend support to this paradigm in that reproductive life history, feeding, and locomotion strategies were generally underdispersed within local communities of the Big Blue River basin. Nevertheless, the magnitude of strategy dispersion depended on the type of functional strategy, the spatial scale at which local communities and regional pools were defined, and location of local communities along a stream size gradient.

Identifying the appropriate spatial scale (both resolution and extent) is fundamental for understanding mechanisms of community assembly (Swenson et al. 2006; Weiher et al. 2011). Much of the past work on scale dependency of community assembly comes from tropical forest communities and is inferred from phylogenetic (as opposed to trait) dispersion (Webb et al. 2002). From these studies, increasing spatial resolution shifts the phylogenetic community structure from overdispersion to underdispersion, which implies that interspecific competition drives assembly between adjacent individuals whereas filtering of traits by topographic and edaphic gradients operates at broader spatial scales (Swenson et al. 2007). We did not observe this shift from competitive exclusion to environmental filtering in our study and three explanations are plausible. First, competitive exclusion will operate only when traits or strategies affect the acquisition of limiting resources. This condition is often satisfied in tropical forest communities where mineral nutrients limit growth of trees (Hubbell 2001), whereas food resources of fishes generally are not limiting

in prairie streams where frequent hydrological disturbances maintain fish populations below carrying capacity (Dodds et al. 2004). Moreover, small-bodied minnows (Teleostei: Cyprinidae) often occur in multispecies shoals to avoid predation and facilitate foraging (Gorman 1988). Such shoaling behavior often occurs among trophically similar species and would preclude our ability to detect overdispersion in feeding strategies. Second, the topographic and edaphic gradients that filter tropical tree species vary at much broader spatial scales than do the species interactions driving competitive exclusion (Swenson et al. 2006). By contrast, abiotic gradients in streams (mainly depth and current velocity) occur at both fine (e.g., pool versus riffle mesohabitats) and broad (e.g., headwater versus mainstem reaches) spatial resolutions (Frissell et al. 1986). These environmental gradients filtering species' traits at multiple spatial scales might explain why we observed environmental filtering at both spatial resolutions. Third, competitive exclusion is more likely to be detected when the regional pool is restricted to a narrower taxonomic group and functional redundancy is high (Swenson et al. 2006). The regional pool of our communities was composed of a phylogenetically diverse group of species representing nine families with low genus-to-species ratios (mean 1.4), which reduces the likelihood of species competitively excluding one another. Winston (1995) observed evidence of competitive exclusion in stream fish communities of the southern Great Plains; however, this study was restricted to one family (cyprinids) and carried out in a zoogeographic region with higher regional species richness and probably greater functional redundancy (mean genus-to-species ratio of 3.0).

When spatial extent is reduced, community assembly may appear increasingly neutral (i.e., traits are neither under- nor overdispersed) because a combination of low environmental heterogeneity among localities and small regional species pools precludes species sorting by environmental gradients (Leibold et al. 2004; Weiher et al. 2011). We did not observe such a decrease in underdispersion when narrowing the spatial extent from basin to reach. This is probably a consequence of equally high environmental heterogeneity among mesohabitats within a reach compared to mesohabitats within the basin, stemming from hierarchically structured habitat patches (Frissell et al. 1986).

Mechanisms of community assembly should also vary along gradients of abiotic variability or disturbance frequency (Weiher and Keddy 1995). Competitive exclusion is predicted to decrease in importance, whereas environmental filtering is expected to increase in importance with increasing environmental variability or disturbance frequency. In temperate freshwater fish communities, this is apparent in hydrologically stable natural lakes where species interactions have strong influences on species composition (e.g., Helmus et al. 2007), whereas frequent

hydrologic disturbances in streams often have overriding influences on species composition (e.g., Grossman et al. 1982). Such gradients of environmental variability also exist within individual stream networks, where hydrological regimes are more severe in headwater streams compared to river mainstems (Poff and Allan 1995; Dodds et al. 2004). We showed that reproductive life history strategies are more strongly filtered in headwater reaches compared to river mainstem reaches. Indeed, fish communities in headwater streams of the Big Blue River basin are limited mostly to opportunistic life history strategists (e.g., minnows and darters), whereas river mainstem communities are composed of a more diverse group of life history strategists including periodic (e.g., suckers) and equilibrium (e.g., catfishes and sunfishes) strategists (Gido et al. 2006). In contrast, feeding strategies are more strongly filtered in river mainstem reaches compared to headwater reaches. Although headwater communities are numerically dominated by opportunistic life history strategists, these species are trophically diverse relative to the dominant river mainstem species. For example, *Campostoma anomalum*, *Etheostoma spectabile*, and *Semotilus atromaculatus* typically make up the majority of the individuals in headwater communities (Gido et al. 2006), yet these species exhibit very different feeding strategies, representing a benthic algivore, a benthic invertivore, and a water column insectivore/piscivore, respectively (Pflieger 1997). River mainstems are numerically dominated by small-bodied omnivores such as *Cyprinella lutrensis*, *Notropis stramineus*, and juvenile *Carpoides carpio* (Pflieger 1997; Gido et al. 2006).

Although taxonomic composition of headwater communities differs between ecoregions in our study area (Gido et al. 2006), we did not observe strong differences in the dispersion of functional strategies, which is contrary to our prediction that hydrologic disturbance filters would be weaker in spring-fed headwater streams draining the Flint Hills ecoregion relative to the plains ecoregions. Perhaps hydrologic regimes are driven by the broader regional climate and were equally severe in the Flint Hills and plains ecoregions. The taxonomic differences in community composition probably stem from other environmental gradients filtering functional traits or strategies that we did not evaluate. Several species characteristic of headwater streams in the Flint Hills are cool-water adapted (*Chrosomus erythrogaster*, *Luxilus cornutus*, *Semotilus atromaculatus*) and populations in the Flint Hills are at the southern periphery of their geographic range (Pflieger 1997). As such, we suspect that warm and variable thermal regimes in streams draining the plains ecoregions operate as an environmental filter limiting the abundance of these cool-water species, whereas cool and stable thermal regimes in spring-fed headwaters of the Flint Hills would not filter thermal tolerance traits.

Trait, strategy, and phylogenetic approaches to community assembly

Elucidating mechanisms of community assembly from an observational standpoint requires knowledge of ecological variability (dispersion) among species within local communities relative to the variability contained within the regional pool. Investigators most frequently have measured such ecological variability using the dispersion of individual traits (e.g., Rabosky et al. 2007) or have inferred it from phylogenetic dispersion (e.g., Helmus et al. 2007). Fewer community assembly studies have characterized ecological variability within a local community using multi-trait strategies (e.g., Cornwell et al. 2006). Traits evolve in combinations and multiple traits often convey ecological strategies or trait syndromes (Westoby et al. 2002; Poff et al. 2006a; Sternberg and Kennard 2014). Such coevolution of traits may arise from positive or negative interactions between multiple traits, which stem from synergism or fitness trade-offs, respectively. Alternatively, traits may evolve in combination with one another not as a consequence of selection for particular trait combinations that are adaptive, but due to constraints imposed by physiology, biomechanics, or allometry (Lande and Arnold 1983). That traits evolve in combination has several implications for testing community assembly mechanisms.

When characterizing the dispersion of individual traits or multi-trait strategies, it may be difficult to ascertain whether abiotic filters or interspecific competition are acting holistically on multi-trait strategies or simply on one trait that happens to be correlated with many others (Poff et al. 2006a). Knowledge about trait-environment relationships and the life histories of community members is important when developing a priori hypotheses of how a particular community is assembled, interpreting dispersion patterns, and concluding whether filters are acting on strategies per se or on a single trait. This issue was apparent in our study where we observed underdispersion of reproductive life history strategies at the mesohabitat resolution despite previous studies demonstrating that these strategies are filtered by flow regimes operating at the reach resolution (Poff and Allan 1995). We suspect that this underdispersion is a consequence of covariation between reproductive life history strategies and body size, which was probably filtered by a depth gradient distinguishing riffle and pool mesohabitats. Large-bodied species are more susceptible to predation by terrestrial predators and occupy deep pools to avoid predation risk, whereas small-bodied species avoid predation by pool-dwelling piscivorous fishes by occupying riffles and shallow pool margins (Schlosser 1987). Thus, we hypothesize that reproductive life history strategies were filtered by hydrologic regimes at the reach resolution, whereas body size was filtered by depth at the mesohabitat resolution.

Several analytic approaches can aid in teasing apart the effects of individual traits versus multi-trait strategies including functional ecology (Wainwright 1996), intercontinental comparisons of trait-environment relationships among disparate phylogenetic groups possessing different combinations of traits (Lamouroux et al. 2002; Olden and Kennard 2010), and analyses of trait evolution (Poff et al. 2006a; Sternberg and Kennard 2014). Nevertheless, separating independent and interactive effects of strategies and functional traits remains a challenge of identifying cause-effect mechanisms that drive community assembly.

It is important to consider the phylogenetic relationships among species in the regional pool because correlations among traits are a direct consequence of their shared evolutionary history. In study systems where the investigator-defined regional pool spans areas with different biogeographic histories, phylogeny can directly and strongly affect community assembly. At narrower spatial extents where all local communities have the same biogeographic history, phylogeny is less important as a direct driver of community assembly (Leibold et al. 2010). Nevertheless, phylogenetic signal in traits or strategies can have important implications when interpreting patterns of dispersion. For example, if two strategy categories exhibit a strong phylogenetic signal and show the same pattern of dispersion in local communities, then it is difficult to determine if one, the other, or both are being operated on assembly. In our study, reproductive life history, feeding and locomotion strategy categories exhibited moderate to strong phylogenetic signals. However, it is likely that these three categories represent separate and unique functional aspects of this species pool because all three showed different dispersion patterns with regard to stream size. Given the increasing recognition of the role phylogeny plays in biodiversity patterns (Leibold et al. 2010), studies that evaluate phylogenetic and trait dispersion simultaneously are essential to disentangle the relationships between phylogenetic relationships, traits, and strategies, and community assembly (Swenson and Enquist 2009; Liu et al. 2013). In general multi-trait strategies are pervasive in plant and animal communities (Winemiller and Rose 1992; Westoby et al. 2002; Statzner et al. 2004; Poff et al. 2006a). We conclude that the assessment of strategy dispersion offers a comprehensive approach for elucidating mechanisms of community assembly.

Toward a mechanistic understanding of community organization

Observational studies that characterize the dispersion of traits or strategies in real communities are useful for identifying the relative roles of environmental filtering and limiting similarity; however, a deeper understanding of

how traits or strategies affect individual- and population-level performance is ultimately necessary to reach the goal of predicting community composition in novel environments (McGill et al. 2006; Adler et al. 2013). This next step requires the implementation of experiments to measure individual- or population-level performance, which can be an overwhelming task when considering the number of potential causal environmental gradients that can be manipulated, performance currencies that can be measured, and species represented in a regional pool (McGill et al. 2006; Troia and Gido 2014). Furthermore, condition-specific competition or predation often plays a role in community assembly (e.g., Taniguchi and Nakano 2000) and adds yet another layer of complexity to experimental tests of performance-environment relationships. We assert that observational studies of strategy dispersion help to prioritize the types of performance-environment relationships that should be experimentally evaluated. For example, a lack of strategy overdispersion in fish communities of the Big Blue River basin indicate that experimental tests should focus on measuring performance along abiotic gradients as opposed to tests of interspecific competition. Experimental measures of performance can also further refine estimates of trait values used in trait and strategy dispersion studies. Indeed the most informative functional traits take the form of direct performance measurements such as survival, growth, or fecundity (Violle et al. 2007). Performance experiments also expand knowledge of the range of trait values or performance values for a given species, what environmental factors affect such intraspecific variation, and how such intraspecific variation affects community assembly (Violle et al. 2012).

Conclusion

This study illustrates that the use of null models to characterize strategy dispersion is an effective, yet underutilized approach to test mechanisms of community assembly in stream fish communities. We show that functional strategies of stream fishes generally are underdispersed, lending support for the paradigm of abiotic filtering in stream fish communities. Whereas testing the dispersion of multi-trait functional strategies provided a broad understanding of community assembly, it remains a challenge to separate the role of a multi-trait strategy from a single influential trait. The effects of scaling on the perceived importance of environmental filtering versus competitive exclusion in our study differed from studies in other regions and taxonomic groups. These differences probably stem from a combination of taxon-specific differences in community assembly (i.e., competitive exclusion is rare in stream fish communities) and differences in environmental variability (i.e.,

abiotic gradients are hierarchically structured in stream networks). Lastly, future efforts should integrate observational studies of strategy dispersion with experiments of performance-environment relationships to build more informative trait databases and ultimately gain a mechanistic and predictive understanding of community assembly and composition.

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