Dispersal strength determines meta-community structure in a dendritic riverine network

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9

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30   **Abstract**
31   **Aim**
32   Meta-community structure is a function of both local (site-specific) and regional
33   (landscape-level) ecological factors, and the relative importance of each may be
34   mediated by the dispersal ability of organisms. Here, we used aquatic invertebrate
35   communities to investigate the relationship between local and regional factors in
36   explaining distance decay relationships (DDRs) in fragmented dendritic stream
37   networks.
38
39   **Location**
40   Dryland streams distributed within a 400 km^2 section of the San Pedro River basin,
41   southeastern Arizona, USA.
42
43   **Methods**

44 We combined fine-scale local information (flow and habitat characteristics) with
45 regional-scale information to explain DDR patterns in community composition of
46 aquatic invertebrate species with a wide range of dispersal abilities. We used a novel
47 application of a landscape resistance modeling approach (originally developed for
48 landscape genetic studies) that simultaneously assessed the importance of local and
49 regional ecological factors as well as dispersal ability of organisms.
50
51 **Results**
52 We found evidence that both local and regional factors influenced aquatic invertebrate
53 DDRs in dryland stream networks, and the importance of each factor depended on the
54 dispersal capacities of the organisms. Local and weak dispersers were more affected by
55 site-specific factors, intermediate dispersers by landscape-level factors, and strong
56 dispersers showed no discernable pattern. This resulted in a strongly hump-shaped
57 relationship between dispersal ability and landscape-level factors, where only moderate
58 dispersers showed evidence of DDRs. Unlike most other studies of dendritic networks,
59 our results suggest that overland pathways, using perennial refugia as stepping-stones,
60 might be the main dispersal route in fragmented stream networks.
61
62 **Main conclusions**
63 We suggest that using a combination of landscape and local distance measures can help
64 to unravel meta-community patterns in dendritic systems. Our findings have important
65 conservation implications, such as the need to manage river systems for organisms that
66 span a wide variety of dispersal abilities and local ecological requirements. Our results
67 also highlight the need to preserve perennial refugia in fragmented networks, since they
68 may ensure the viability of aquatic meta-communities by facilitating dispersal.
69
70 **Keywords:** aquatic invertebrates, dendritic networks, distance decay relationship,
71 drought, dispersal, connectivity, landscape resistance, meta-community.

Introduction

Studying patterns of biological diversity has been the foundation of numerous ecological pursuits over the past two centuries. Distance decay relationships (DDRs) – which describe the biogeographic phenomenon where taxonomic similarity between localities decreases or decays as the distance between them increases – have received considerable interest among ecologists (Nekola & White, 1999). Indeed, this ecological pattern is encapsulated in Tobler's first law of geography, which states that 'everything is related to everything else, but near things are more related than distant things' (Tobler, 1970). DDRs have now been studied across a wide range of organisms and environments (reviewed in Soininen *et al.* 2007), but are still relatively understudied in riverine ecosystems (Thompson & Townsend 2006, Leprieur *et al.* 2009, Brown & Swan 2010, Bonada *et al.* 2012, Warfe *et al.* 2013). This is largely because streams and rivers are organized as complex dendritic networks rather than simple linear systems (Benda *et al.*, 2004; Campbell Grant *et al.*, 2007; Erős *et al.*, 2012), thus necessitating the incorporation of network connectivity to explore the interactions among communities that are linked by dispersal (Fausch *et al.*, 2002).

The environmental phenomena that drive any particular DDR can be decomposed into local and regional factors. Local factors include site-specific attributes such as water chemistry and habitat structure that serve as filters, excluding some taxa and favoring others (Poff, 1997; Townsend *et al.*, 1997). Regional factors include landscape-level features that facilitate or impede the movement of organisms across landscapes. These features may include the dendritic structure of stream networks (Fausch *et al.*, 2002; Benda *et al.*, 2004), the spatial arrangement of suitable habitat patches across the landscape (Campbell Grant *et al.*, 2007; Erős *et al.*, 2012; Phillipsen & Lytle, 2013), and the simple Euclidean distance between sites. Therefore, a full understanding of the ecological processes underlying DDR patterns in stream networks must account at least for three main factors: environmental filters, dispersal of organisms and network topology.

Environmental harshness can influence the role of local and regional forces shaping biodiversity patterns (Brown *et al.*, 2011; Heino, 2011). For example, unstable environments (e.g. aquatic habitats that experience severe, recurrent droughts) show a high degree of niche filtering, allowing only those species adapted to the local conditions to persist (Poff, 1997; Chase, 2007). Therefore, harsh environmental conditions may cause meta-communities to be structured by local factors (Urban, 2004) and DDRs may not meet the expectation of decreasing community similarity with increasing distance.

Dispersal of aquatic-obligate riverine organisms is highly constrained by flow connectivity (Fausch *et al.*, 2002; Hughes, 2007; Schick & Lindley, 2007). In contrast, aquatic organisms that can disperse overland, such as flying forms of adult aquatic insects, can move both along drainages and across drainage divides (Bilton *et al.*, 2001; Petersen *et al.*, 2004). Therefore, variability in dispersal mode and ability will determine

116   the extent to which local and regional factors structure assemblages of organisms
117   (Bohonak & Jenkins, 2003; Cottenie & De Meester, 2004) and may be reflected in the
118   shape of the DDR. For example, studies on aquatic invertebrate meta-communities in
119   stream networks have reported that increasing dispersal strength results in a weakening
120   of DDRs due to relaxation of dispersal limitation (Thompson & Townsend, 2006;
121   Brown *et al.*, 2011). Very high dispersal rates could cause the homogenization of
122   communities, since organisms can disperse to all available habitats and only the
123   strongest competitors will survive (Kneitel & Miller, 2003; Leibold *et al.*, 2004).

125   The network topology, or spatial structure of the river network, also has important
126   implications for dispersal and resulting meta-community structure (Muneepeerakul *et*
127   *al.*, 2008; Auerbach & Poff, 2011). The use of within-network and overland dispersal
128   pathways by aquatic organisms largely depends on the connectivity between the habitat
129   branches, with the loss of connectivity constraining within-network dispersal (Fagan,
130   2002). Therefore, within-network DDR should be weaker when populations are disjunct
131   within the river network, as is the case with headwater specialist organisms.

133   Although critical for understanding the potential mechanisms shaping DDRs (Brown *et*
134   *al.*, 2011), landscape resistance to the dispersal of organisms has been largely neglected
135   in meta-community analyses (Moritz *et al.*, 2013). Landscape resistance quantifies
136   "distances" between communities that may yield more biologically informative DDRs
137   than straight-line Euclidean distance, such as those associated with barriers to dispersal
138   (e.g. high mountains or cliffs). To the present date, only Euclidean and network distance
139   (i.e. the distance between sites along the riverine dendritic network) have been applied
140   to stream networks, which fails to consider more realistic landscape variables in DDR
141   analyses (McRae *et al.*, 2008).

143   In this study, we present a novel application of a landscape resistance modeling
144   approach, originally developed for landscape genetic studies, to understand local and
145   regional drivers of community structure. Dryland streams were used as a model system
146   to test how environmental stability, dispersal capacity and network topology interact to
147   structure aquatic meta-communities in dendritic networks. These streams experience
148   frequent droughts and floods, which lead to strong niche filtering of stream organisms
149   (Lytle, 2002; Lytle & Poff, 2004), with perennial habitats serving as refugia for species
150   that need water during their entire life cycle to survive (Bogan & Lytle, 2011; Phillipsen
151   & Lytle, 2013). Therefore, the high temporal and spatial variation in environmental
152   conditions may disrupt expected longitudinal patterns of species' replacement along the
153   network (Bogan *et al.*, 2013). In these systems DDRs are expected to be weak or non-
154   existent, with adjacent sites showing very different aquatic assemblages due to large
155   among-site variation in environmental conditions (e.g. one site may flow year-round,
156   while an adjacent site may flow only during rainy seasons). We focused on aquatic
157   invertebrates because they possess a wide range of dispersal capacities (Bilton *et al.*,
158   2001; Bohonak & Jenkins, 2003) and are present over a wide range of environmental

159 conditions (Rosenberg & Resh, 1993; Merritt *et al.*, 2008), as exemplified by the great
160 diversity of biological traits that they exhibit (Statzner *et al.*, 2004; Poff *et al.*, 2006).
161
162 The aim of our study was to use DDRs to investigate the relationship between local and
163 regional factors in explaining aquatic meta-community structure in fragmented dendritic
164 networks. Here we define fragmentation as the loss of surface water connectivity along
165 the river network. During low precipitation periods (typically in late Spring and
166 Summer) some dryland streams experience very low flow, with sections becoming
167 disconnected pools separated from one another by dry stream reaches. We used fine-
168 scale local environmental variables and landscape resistance metrics to quantify the
169 influence of local and regional drivers on DDRs for groups of species with different
170 dispersal capacities. The following hypotheses were tested:
171
172 H1: DDRs should be weak for very strong and very weak dispersers (at the ends of the
173 dispersal gradient) because meta-communities of weak dispersers show little spatial
174 structure and meta-communities of strong dispersers are homogenized by competition.
175 We predicted that DDR would be strongest in species with moderate dispersal strength.
176 H2: Due to high network fragmentation in dryland streams (i.e. longitudinal flow
177 disruption during long dry seasons), no significant DDR should be found when using
178 network distance. We predicted that network distance would have low explanatory
179 power due to high spatial and temporal stream fragmentation, while our approach that
180 considers landscape resistance to dispersal would provide greater explanatory power.
181 H3: Due to strong niche filtering (i.e. high environmental heterogeneity), DDRs
182 associated with flow and environmental characteristics should be consistently stronger
183 than DDRs associated with landscape resistance variables, regardless of the dispersal
184 strength of the organisms. We predicted that DDRs associated with flow and
185 environmental characteristics would be significant, regardless of species' dispersal
186 abilities.
187
188 **Methods**
189 *Study site and field sampling*
190 We sampled aquatic invertebrates at 28 sites across seven dryland streams distributed
191 within a 400 km^2 section of the Upper San Pedro River basin, southeastern Arizona,
192 USA (Figure 1; Schriever *et al.*, in press). Streams in the area generally have perennial
193 flow in montane headwaters, intermittent flow in upper alluvial fan reaches, ephemeral
194 flow lower on alluvial fans, and then alternating perennial and intermittent reaches in
195 valley rivers (Bogan *et al.*, 2013). We distributed our sample sites among perennial,
196 intermittent and ephemeral reaches (classification follows Levick *et al.*, 2008), but used
197 a continuous flow metric to quantify permanence (see below). Sites were sampled three
198 times a year (March/April, August/September, and November/December) between 2009
199 and 2011. The number of sites and samples collected differed among streams because
200 not all sites had flow or all microhabitats during each sampling event. The study period
201 spanned numerous dry seasons, several periods of ephemeral flows from summer
202 monsoon rains, and one period of intermittent flows resulting from a wet winter. The

203   majority of the sampling occurred during the fall (Nov/Dec) and winter (Mar/Apr)
204   seasons for a total of 144 site x sampling event combinations.
205
206   Both riffle and pool microhabitats were sampled at each site, when present. For riffle
207   samples we disturbed 0.33 m^2 of stream substrate to a depth of 5 cm while capturing
208   invertebrates immediately downstream with a D-net (500-μm mesh). Pool samples
209   consisted of sweeping the entire pool area including water column, surface, and pool
210   benthos with a D-net at an effort of 10 seconds for every 1 m^2 of pool habitat (following
211   Bogan & Lytle, 2007). Abundances from replicate microhabitat samples collected from
212   the same site during the same sampling event (e.g. three riffles in November) were
213   summed for each taxon and divided by the number of replicates to acquire relative
214   abundances. Samples were preserved in 95% ethanol and invertebrates were identified
215   in the laboratory to the finest taxonomic level practical, usually to genus or species for
216   insects (including Chironomidae) and family or order for non-insects.
217
218   During each visit, we measured water temperature, pH (Whatman pH Indicators,
219   Whatman International, Maidstone, England) and conductivity (Milwaukee waterproof
220   EC meter C65; Milwaukee Instruments, Rocky Mount, NC, U.S.A.), visually estimated
221   canopy cover and benthic substrate on a percent cover scale (0 - 100%; substrate
222   categories: silt, sand, gravel, cobble and bedrock). We measured the timing and duration
223   of streamflow through the deployment of 15 electrical resistance sensors (Jaeger &
224   Olden, 2012), each representing the hydrologic conditions at the nearest location of
225   invertebrate sampling. The sensors logged the presence or absence of water in the
226   stream channel at 15 minute intervals from April 2010 to December 2011. From the
227   sensor data, we calculated four hydrologic metrics for each site: % flow permanence by
228   year, mean % flow permanence by season (spring = March-June; monsoon = July-
229   September; fall = October – November; winter = December-April), mean duration
230   (number of days) of zero flow periods (ZFP) each year, and total number of ZFP each
231   year. For the two flow permanence metrics and duration of ZFP, we summed 15-minute
232   time periods of both wet and dry conditions for the sampling period and for individual
233   zero flow periods, converting the time unit to either days or years as appropriate for the
234   final stream flow metric. We used an average of 2010 and 2011 flow data to estimate
235   flow conditions for the November 2009 invertebrate sampling period (16 samples) that
236   occurred prior to the deployment of sensors. Flow permanence is the percentage of time
237   a given reach is wetted or flowing, while the duration of ZFP indicates how long (in
238   days) a given reach is dry during each drying event. For example, a site with permanent
239   stream flow would have a flow permanence of 100% and would receive a value of 0 for
240   ZFP duration. While these metrics were all calculated from the flow sensor records,
241   they were designed to characterize distinct components of the hydrologic regime that
242   may influence aquatic invertebrate occurrence and abundance.
243
244   *Distance measures*
245   We used four regional distance metrics (Table 1, Fig. 2), two of which described to the
246   physical distance between sites (geographic and network distance) and two of which

247 described the resistance of the landscape to dispersal (topography and perennial
248 distance). *Geographic distance* is simply the straight-line Euclidian distance between
249 two sites as determined from map coordinates. *Network distance* was generated via a
250 least-cost path analysis in ArcGIS 9.3 (Environmental Systems Research Institute,
251 Redlands, CA). For this variable, only one pathway connects each pair of sites, and this
252 pathway is restricted to the stream network. *Topography distance* assumes that dispersal
253 occurs along concave corridors such as streambeds, dry gullies, or low saddle points
254 along mountain ridges. Flying and crawling insect adults are likely to follow these
255 relatively cool and moist pathways to disperse from one wetted site to another (Bogan
256 & Boersma, 2012; Phillipsen & Lytle, 2013). *Perennial distance* assumes that isolated
257 perennial freshwater habitats act as stepping-stones for dispersal among communities in
258 fragmented dendritic networks. For example, in arid landscapes perennial habitats are
259 known to be critical for the survival of certain aquatic species when rivers cease to flow
260 during droughts (Chester & Robson, 2011).
261
262 We generated the four regional distance measures from landscape data layers obtained
263 from the Arizona State Land Department (www.land.state.az.us). Data layers used in
264 our analyses included a digital elevation model (DEM; 10 m resolution), the stream
265 network of the region (from the National Hydrology Dataset), and a map of perennial
266 stream habitats. The latter was constructed using data for the San Pedro River watershed
267 from the Nature Conservancy (www.azconservation.org) combined with observations
268 from field studies in the region (e.g. Bogan & Lytle, 2007; Bogan *et al.*, 2013). We used
269 ArcGIS 9.3 to generate new data layers and to calculate the distance (km) between all
270 pairs of sites. The distances related to landscape resistance (topography and perennial
271 distances) were generated from the GIS data layers in the form of pixelated maps (i.e.
272 rasters). Each raster map was used as input for the program CIRCUITSCAPE (McRae,
273 2006). CIRCUITSCAPE calculates the resistance of the landscape to dispersal between
274 each pair of sites (analogous to electrical resistance in a circuit diagram), allowing for
275 multiple pathways between sites. This pairwise resistance is a summation of the
276 resistances of individual pixels in the input map. Pixels with high input values are
277 hypothesized to offer high resistance to movement, and vice versa. Thus, pairwise
278 resistances from CIRCUITSCAPE model the structural connectivity of communities,
279 based on the landscape/habitat feature represented by the input map. We used the
280 original values of the map pixels to assign resistance values to the raster maps. Using
281 the original pixel values is more conservative than assigning relative costs of landscape
282 features based on expert opinion (a practice that some have questioned; Spear *et al.*
283 2010). Before running the CIRCUITSCAPE analysis, we transformed the original
284 values of the maps so that they were all on the same scale (1 for lowest resistance, 10
285 000 for highest resistance; results were qualitatively similar for different values of
286 highest resistance). We performed a separate CIRCUITSCAPE analysis for both
287 topography and perennial distances, generating their two independent data sets of all
288 pairwise resistance distances as output. See Phillipsen & Lytle (2013) for an example of
289 CIRCUITSCAPE output in a population evolution context and how this relates to the
290 underlying distance metrics.

291

292   In addition to the four regional distance measures, two local ecological distance

293 measures were calculated: habitat distance and flow regime distance. *Habitat distance*

294 was calculated as the dissimilarity between the multivariate centroids of each pair of

295 sites based on their environmental characteristics, including canopy cover, conductivity,

296 pH, and % of bedrock, cobble, gravel, sand and fines. *Flow regime distance* was

297 calculated as the dissimilarity between the multivariate centroids of each pair of sites

298 from a composite of flow metrics: % flow permanence in year of sample, % flow

299 permanence by season, duration of zero flow periods each year (mean) and total number

300 of zero flow periods each year. All variables were normalized (mean = 0; SD = 1)

301 before analysis.

302

303 *Statistical analyses*

304 Prior to analyses, we placed each of the 225 aquatic invertebrate taxa into one of four

305 categories: weak, local, moderate and strong dispersers (Appendix S1). Weak dispersers

306 (17 taxa) are aquatic obligates that spend nearly all of their life cycle within the stream

307 (e.g. *Abedus herberti*). Local dispersers (142 taxa) have flying adult stages but can only

308 travel short distances due to their short life cycles and/or weak flying musculature (e.g.

309 *Hydrobaenus* sp.). Moderate dispersers (64 taxa) have flying adult stages that can travel

310 long distances but cannot cover the entire geographic range of our study (e.g. *Enochrus*

311 *aridus*). Strong dispersers (10 taxa) are powerful fliers that can travel between any of

312 the sites in our studied geographic range (e.g. *Lethocerus medius*). These categories

313 were derived from a trait database specific to the study region built from over 80

314 publications from primary literature, existing databases and expert judgment (Schriever

315 *et al.*, in press). Abundance data were log (x+1) transformed and then used to calculate

316 the Chao dissimilarity index among all pairs of sites (using the function vegdist in the

317 vegan package: Minchin *et al.*, 2013). The Chao index was the most appropriate

318 dissimilarity index to use because each dispersal ability group had a different number of

319 taxa; it is intended to account for the effect of unseen shared species and thus reduce

320 sample-size bias (Chao *et al.*, 2005). Habitat distance, flow regime distance and the four

321 landscape distances (Table 1) were used as independent explanatory variables of Chao's

322 index for each group of species (weak, local, moderate and strong dispersers). Spearman

323 correlation tests were performed between all pairs of the explanatory variables. For

324 those variables showing strong correlation (i.e. Spearman's rho > 0.5 and p-value <

325 0.01), we used partial Mantel tests (mantel function in vegan package) to compare

326 community data to the explanatory variable of interest while controlling for the

327 correlated variable (Legendre & Legendre, 2012). The differences in the relationship

328 between community dissimilarity and each of the distance metrics (geographic,

329 network, topography, perennial, flow regime, and habitat distances) across dispersal

330 classes was tested through an analysis of covariance (ANCOVA; Legendre & Legendre,

331 2012) with Chao dissimilarity as the dependent variable, each driver as a covariate, and

332 the dispersal class as the grouping factor.

333

334 We fitted linear models to each distance metric, and performed F-tests to assess model
335 performance. Models were tested for linearity using the diagnostics plots for
336 generalized linear models (Appendix S2). We used the glm.diag.plots function in R,
337 which makes a plot of jackknife deviance residuals against linear predictor, normal
338 scores plots of standardized deviance residuals, plot of approximate Cook statistics
339 against leverage/(1-leverage), and case plot of Cook statistic. After validating the
340 models we used an information-theoretic approach to compare the contribution of
341 different explanatory variables that best described differences in invertebrate
342 community composition. We derived the log-likelihood for each model and calculated
343 Akaike's information criterion (AIC; Akaike, 1973; Burnham & Anderson, 2002) to
344 rank the models from lowest to highest AIC. We only compared single variable models
345 and the combination of local environmental distance metrics (flow regime and habitat)
346 and landscape distance metrics (geographic, topography, perennial and network
347 distances), since our aim was to compare the importance of local versus regional filters
348 for aquatic invertebrate meta-communities across a gradient of dispersal strength.
349 Information for the rest of the models is shown in Appendix S3. Once the models were
350 ranked, additional information-theoretic metrics were calculated. The difference
351 between the AIC of a particular model and the AIC of the estimated best-fitting model
352 (i.e. the model with the lowest AIC) is ΔAIC. We also calculated Akaike weights, the
353 probability that the model is actually the best-fitting of the candidate models. The sum
354 of Akaike weights across the models is 1.0. When the weight of the model with the
355 lowest AIC is not close to 1.0, there is evidence for model selection uncertainty. We
356 accounted for the non-independence of our data (represented by pairwise distances
357 among sites) by using an R-squared approach for fixed effects in a linear mixed model
358 to adjust for the inflation of sample size (Edwards *et al.*, 2008). Since both the AIC and
359 mixed model approaches yielded similar results, we only report the adjusted R-squares
360 for fixed effects in the Supplementary Material. The selection of AIC over adjusted R-
361 squares was based on the limited use of adjusted R-square values in model building, due
362 to the lack of diagnostic and selection tools for linear mixed models (Edwards *et al.*,
363 2008). All analyses were conducted in R version 3.0.2 (R Core Team, 2013) and
364 significance was assigned at $P < 0.05$. Bonferroni correction was used to adjust p-values
365 for multiple comparisons.
366
367 **Results**
368 The six distance metrics displayed weak pairwise correlations. Only geographic,
369 topography and perennial distance were significantly correlated (Fig. 3). Habitat and
370 flow regime distances significantly explained community dissimilarity, regardless of the
371 species' dispersal abilities (Table 2). Geographic, topography and perennial distances
372 significantly explained community dissimilarity for all dispersal groups except for the
373 weak dispersers, and had a higher explanatory power for strong dispersers (Table 2).
374 Network distance was not a significant predictor for any dispersal group. Associations
375 between community dissimilarity and the explanatory variables varied considerably
376 among the four dispersal groups (Fig. 4). The relationship between community

377 dissimilarity and the six distance metrics differed across the dispersal categories for all
378 but one metric (network distance; Table 3).
379
380 Partial Mantel tests revealed that: (1) geographic distance was significantly correlated
381 with the composition of strong dispersing taxa after controlling for topography, (2)
382 topography was significantly correlated with the composition of moderate dispersers
383 while accounting for geographic distance and (3) topography and perennial distance
384 correlated with the composition of moderate dispersers while controlling for each other
385 (Table 4). Of all the models, local drivers (habitat distance plus flow regime distance)
386 demonstrated the strongest relationships (i.e. lowest AIC for single variable models)
387 with the composition of weak, local and strong dispersers, while regional drivers
388 (geographic, topography, perennial and network distances) best-explained moderate
389 dispersers (Table 5).
390
391 **Discussion**
392 We used distance decay relationships to examine the importance of local and regional
393 drivers of aquatic invertebrate meta-community structure in dryland streams. DDRs
394 have been used to examine the interaction of processes operating at local and regional
395 scales for a wide range of organisms and ecosystems (Cottenie, 2005; Soininen *et al.*,
396 2007), including stream networks (Thompson & Townsend, 2006; Leprieur *et al.*, 2009;
397 Brown & Swan, 2010; Warfe *et al.*, 2013). However, past studies have largely not
398 explored the relative roles of local- and regional-scale landscape drivers within
399 connected networks. The only published study that used DDRs to address the effect of
400 hydrological connectivity on stream meta-communities showed, rather
401 counterintuitively, that the loss of connectivity enhanced DDR in a variety of organisms
402 (Warfe *et al.*, 2013). However, environmental conditions in that study were not
403 independent of geographic distance; therefore dispersal limitation and niche partitioning
404 both played a role in shaping assemblage structure. Our results suggest that
405 fragmentation impacts DDRs by altering the viable dispersal pathways, with organisms
406 dispersing overland instead of using the stream network. As we hypothesized, meta-
407 community structure was determined by three main factors: niche filtering due to local
408 among-habitat differences, dispersal ability of the species and landscape resistance
409 (geographic distance, topography and availability of perennial refugia).
410
411 *Niche filtering due to among-habitat differences*
412 We hypothesized that high environmental heterogeneity would generate significant
413 environmental DDRs for all dispersal categories. Indeed, we found that the local filters
414 of habitat and flow regime had a stronger effect on community dissimilarity than
415 regional filters across all dispersal classes, except for moderate dispersers. At
416 intermediate levels of dispersal, organisms might be able to survive harsh
417 environmental conditions such as floods and droughts by escaping and finding refugia
418 (Velasco & Millan, 1998; Lytle, 1999), but at the same time they might not be able to
419 reach all the available habitats, preventing meta-community homogenization via mass
420 effects (Kneitel & Miller, 2003; Leibold *et al.*, 2004). The significant influence of local

421 filters on meta-community patterns was not surprising given the high temporal and
422 spatial variation in environmental conditions in the study region. Highly variable
423 seasonal and interannual precipitation patterns and various geomorphic settings (e.g.
424 bedrock canyons, alluvial fans) interact to create a patchy stream landscape. In these
425 dryland streams, perennial reaches are adjacent to intermittent reaches, and intermittent
426 reaches with seasonal flow in a wet year can be completely dry during the same period
427 in a dry year (Jaeger & Olden, 2012, Bogan *et al*., 2013). The amount of water and how
428 it is distributed within the year (i.e. frequency and timing of droughts and floods) have
429 important consequences for water quality and habitat variables (e.g. canopy cover, river
430 substratum). Accordingly, these local habitat filters should be extremely strong in
431 dryland streams. Our results validate previous studies that linked these patchy
432 environmental conditions to disruptions in the longitudinal patterns of stream
433 invertebrate communities in the region (Bogan *et al.*, 2013). They are also in agreement
434 with a recent study from northwestern Australia, which found that flow and channel
435 width best explained invertebrate meta-community patterns across a range of perennial
436 and intermittent streams (Warfe *et al.*, 2013). Moreover, the importance of niche
437 filtering in structuring meta-communities has been demonstrated for a variety of
438 ecosystems (Soininen *et al.*, 2007), including ponds (Urban, 2004; Chase, 2007) and
439 streams (Thompson & Townsend, 2006; Brown & Swan, 2010). Since the loss of
440 connectivity among stream reaches results from high flow heterogeneity (leading to
441 high environmental heterogeneity), niche filtering can be expected to be strong in
442 fragmented stream networks.
443
444 *Dispersal ability*
445 Aquatic invertebrates are known to have very different dispersal capacities, ranging
446 from a few meters to thousands of kilometers (Kovats *et al.*, 1996; Bilton *et al.*, 2001;
447 McCauley, 2006). Given that meta-community structure is highly dependent on
448 geographic scale (Brown *et al.*, 2011; Maloney & Munguia, 2011; Nekola & McGill,
449 2014), differences in dispersal can be expected to affect DDRs (Nekola & White 1999).
450 Increasing dispersal ability is expected to enhance community similarity among sites
451 and reduce beta diversity among habitat patches (Shurin *et al.*, 2009). Recent studies on
452 invertebrate meta-communities in stream networks have provided evidence for this
453 pattern, with DDR being weakened by increasing dispersal strength (Thompson &
454 Townsend, 2006; Brown & Swan, 2010; Bonada *et al*. 2012). However, we found a
455 more complex unimodal pattern, with DDR peaking at intermediate dispersal strength
456 for different measures of landscape resistance. This pattern might result from
457 assemblages of weak dispersers showing no spatial structure due to dispersal limitation
458 while assemblages of strong dispersers are more homogeneous across the landscape due
459 to the absence of dispersal restrictions (Kneitel & Miller, 2003; Leibold *et al.*, 2004).
460 Figure 5 illustrates this pattern by showing the explanatory power of local (habitat and
461 flow distances) and landscape (geographic distance, topography and availability of
462 perennial refugia) filters along the dispersal strength gradient.
463

464 Our results could be influenced by the lower flow connectivity and environmental
465 stability in our dryland study system when compared to more mesic stream systems. In
466 low connectivity systems, weak dispersers are highly isolated, leading to species
467 distributions ruled by ecological drift and niche filtering (Hu *et al.*, 2006). Therefore, in
468 these fragmented systems, low connectivity coupled with differing environmental
469 conditions can lead to adjacent sites having very different assemblages of weak
470 dispersal species. Previous investigations on the flightless aquatic obligate *Abedus*
471 *herberti* within our study area reported strong population genetic structure, with
472 populations within the same stream drainage (less than 5 km apart) showing significant
473 genetic differentiation (Finn *et al.*, 2007; Phillipsen & Lytle, 2013). This same pattern
474 has been observed for the blackfly *Prosimulium neomacropyga* in isolated alpine
475 headwater streams (Finn & Poff, 2011). On the other side of the spectrum, extremely
476 strong dispersers can break down geographic barriers, occurring in all suitable habitats
477 (Townsend *et al.*, 2003; McCauley, 2006; Thompson & Townsend, 2006; Brown &
478 Swan, 2010; Bonada *et al.* 2012). This would explain the decrease in the explanatory
479 power of landscape variables over meta-community structure at the upper end of the
480 dispersal strength gradient in the present study (Fig. 5). We suggest that regional drivers
481 should be important predictors of meta-community structure up to a certain dispersal
482 distance threshold, beyond which dispersal is strong enough to break the limitation
483 imposed by geographical barriers.
484
485 *Distance among sites*
486 Network distance did not significantly affect community dissimilarity for any of the
487 four dispersal groups, as we hypothesized. This contradicts the general rule of aquatic
488 invertebrates using the stream network as the main 'highway' for dispersal (Petersen *et*
489 *al.*, 2004). While evidence supporting the ideas of the stream channel as the primary
490 dispersal route and restricted overland dispersal between catchments continue to
491 accumulate in the literature (Hughes, 2007; Brown & Swan, 2010; Rouquette *et al.*,
492 2013), previous investigations within our study area suggest that dryland streams might
493 be exceptions to this rule. Many aquatic invertebrate species in our study region
494 disperse laterally from stream corridors in search of other wetted habitats (Bogan &
495 Boersma, 2012). Additionally, Bogan *et al.*, (2013) reported an interruption of the river
496 continuum, where invertebrate communities in distant headwater and lowland perennial
497 streams were more similar to one another than to those in intervening intermittent
498 reaches. Furthermore, Phillipsen & Lytle (2013) found no significant relation between
499 network distance and population genetic structure of *Abedus herberti.* Instead, they
500 found that topography best explained genetic structure and suggested that overland
501 dispersal resulted from flood-escape behavior (Lytle, 1999; Lytle *et al.*, 2008), where
502 individuals crawl from streams during floods and accidentally end up in adjacent
503 drainages.
504
505 We found significant (but generally weak) DDRs for perennial habitat distance in all
506 cases and for topography distance in all cases except weak dispersers. This supports the
507 hypothesis of overland dispersal (flight and crawling) being the main dispersal pathway

508 for aquatic invertebrates in highly fragmented stream networks, such as those inhabiting
509 dryland regions. Similarly, Campbell Grant *et al*. (2010) found evidence of high
510 overland dispersal rates in newly metamorphosed juveniles of stream salamanders and
511 suggested that the salamanders followed that dispersal strategy to increase population
512 persistence across isolated headwater streams.

Conclusion

515 Our DDR analyses suggests that in highly heterogeneous stream networks, where
516 environmental conditions vary greatly across space and time, local factors (i.e. niche
517 filtering) may swamp regional influences (i.e. landscape filters) on aquatic invertebrate
518 meta-community structure. However, this interaction between local and regional factors
519 is dependent on a species' dispersal capacity, which determines their ability to colonize
520 suitable habitats. Using a combination of landscape and local distance measures, we
521 found evidence that local and weak dispersers were affected by local-scale factors,
522 intermediate dispersers were affected by landscape-level factors, and strong dispersers
523 showed no discernable pattern. This resulted in a hump-shaped relationship between
524 dispersal ability and landscape-level factors, where only moderate dispersers showed
525 significant DDRs. Stream corridors may not be a primary dispersal pathway in these
526 networks, where frequent drought and flood disturbances generate habitat patches with
527 low connectivity. Overland pathways, using perennial refugia as stepping-stones, might
528 be the main dispersal route for aquatic invertebrates in these dryland stream networks
529 (Phillipsen & Lytle, 2013).

531 Our DDR approach has the potential to generate timely management insights, such as
532 the importance of preserving perennial habitat patches in fragmented river networks.
533 Meta-communities of weak dispersal species are highly disconnected in dryland stream
534 networks. Since most of these species depend on perennial water sources for their
535 survival (Bogan & Lytle, 2011; Hermoso *et al.*, 2013), intensifying droughts may have
536 effects at both meta-population and meta-community levels. Our results suggest that
537 perennial habitat patches may facilitate dispersal of aquatic invertebrates and thereby
538 may ensure the long-term viability of populations. Conserving perennial habitats is of
539 vital importance in dryland streams, and it will become increasingly important in basins
540 experiencing flow reduction due to warmer temperatures and increased anthropogenic
541 water use (Marshall *et al.*, 2010). Given the different responses of invertebrate meta-
542 communities to our various geographic and environmental distance measures, we
543 encourage future investigations to incorporate multiple regionally relevant measures of
544 landscape resistance into their studies. Further research is needed to better understand
545 how environmental stability affects the balance between local and regional factors
546 structuring meta-community patterns in dendritic networks, including work at different
547 spatial scales and degrees of fragmentation.

13

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761 **SUPPORTING INFORMATION**
762 Additional Supporting Information may be found in the online version of this article:
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764
765 **Appendix S1:** aquatic invertebrate taxa list (sampled in 28 sites across seven dryland streams distributed
766 within a 400 km^2 section of the Upper San Pedro River basin, southeastern Arizona, USA) including their
767 assignation into one of four dispersal categories: weak, local, moderate and strong dispersers.
768
769 **Appendix S2:** diagnostics plots for generalized linear models fitted to each distance metric and aquatic
770 invertebrates' dispersal category.
771
772 **Appendix S3:** sum of residuals, likelihood ratios and AIC values for all combinations of explanatory
773 variables (habitat, flow regime, geographic, topography, perennial and network) for each dispersal group
774 (weak, local, moderate and strong).
775
776 **BIOSKETCHES**
777 **Miguel Cañedo-Argüelles** is an aquatic ecologist, interested in the response of aquatic
778 ecosystems to disturbance and how aquatic organisms are connected through the
779 landscape.
780
781 **Author contributions (in alphabetical order)**
782 Designed research (MC, DL, IP), performed research (DL, MB, JO, KB), analyzed data
783 (MC, IP), wrote the paper (all authors).
784
785 Editor: Ladle, Richard.
786
787 **TABLES**
788 **Table 1:** Details of the four regional distance metrics used in this study.

Distance metric	Explanation	Hypothesized relationship to species flow
Geographic distance	Straight-line distance between sites in two-dimensional space.	Dispersal increases when the geographic distance between a pair of sites decreases.
Topography	Pairwise resistances between sites based on low resistance of map pixels with concave topography and high resistance of pixels with convex topography.	Dispersal is highest in areas with strongly concave topography. Dispersal is lowest across areas with strongly convex topography.

Perennial	Pairwise resistances between sites based on low resistance of map pixels in patches of perennial freshwater habitats and high resistance of pixels in the matrix between these patches.	Dispersal increases in the presence of perennial freshwater habitats.	
Network distance (stream network)	Pairwise least-cost paths between sites that strictly follow the stream/river network. Only one path exists between any pair of sites.	Dispersal occurs only within the stream/river network.	

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790
791 **Table 2:** Adjusted R-square, F statistic and p-value for each combination of aquatic invertebrate dispersal
792 category (weak, local, moderate, and strong) and explanatory environmental (habitat distance and flow
793 regime distance) and spatial (geographic, topography, perennial and network distance) variables.
794 Bonferroni correction was used to adjust p-values for multiple comparisons. Significant relationships
795 (p<0.05) are shown in bold.

Explanatory variable	Weak			Local			Moderate			Strong		
	Adj R^2	F	p-value	Adj R^2	F	p-value	Adj R^2	F	p-value	Adj R^2	F	p-value
Habitat	0.13	51.1	**<0.01**	0.36	195.1	**<0.01**	0.08	33.3	**<0.01**	0.15	61.1	**<0.01**
Flow regime	0.09	37.2	**<0.01**	0.25	119.8	**<0.01**	0.08	29.6	**<0.01**	0.11	46.4	**<0.01**
Geographic distance	0	2.4	0.120	0.03	10.5	**0.001**	0.07	29.1	**<0.01**	0.09	37.7	**<0.01**
Topography	0	0	0.964	0.06	25.3	**<0.01**	0.24	109.2	**<0.01**	0.02	9.6	**0.002**
Perennial	0.02	8	**0.005**	0.1	40.9	**<0.01**	0.27	129.3	**<0.01**	0.01	5.6	**0.019**
Network distance	0	1.7	0.195	0	0.6	0.457	0	0.1	0.788	0	0.5	0.481

796
797 **Table 3:** Results of the ANCOVA analyses with Chao dissimilarity value as the dependent variable, each
798 distance metric as a covariate, and the aquatic invertebrate dispersal category (weak, local, moderate, and
799 strong) as the grouping factor. Significant relationships (p<0.05) are shown in bold.

	F statistic	p-value
Habitat	5.11	**<0.01**
Flow regime	2.69	**0.045**
Geographic distance	12.41	**<0.01**
Topography	13.44	**<0.01**
Perennial	9.82	**<0.01**
Network distance	0.23	0.873

800
801
802 **Table 4:** Partial Mantel test results among those distance metrics that showed strong correlation (Fig. 3).
803 GEO = geographic distance; TOP = topography; PRN = perennial distance; * = 0.01< p < 0.05; ** = p <
804 0.01; ns = not significant.

Comparison	Control matrix	r	p
Weak dispersers vs GEO	TOP	-0.12	ns
Local dispersers vs GEO	TOP	-0.02	ns
Moderate dispersers vs GEO	TOP	-0.11	ns
Strong dispersers vs GEO	TOP	0.28	**

Weak dispersers vs TOP	GEO	0.08 ns
Local dispersers vs TOP	GEO	0.2 ns
Moderate dispersers vs TOP	GEO	0.43 **
Strong dispersers vs TOP	GEO	-0.09 ns
Weak dispersers vs PRN	TOP	0.19 ns
Local dispersers vs PRN	TOP	0.22 ns
Moderate dispersers vs PRN	TOP	0.33 **
Strong dispersers vs PRN	TOP	0.04 ns
Weak dispersers vs TOP	PRN	-0.11 ns
Local dispersers vs TOP	PRN	0.09 ns
Moderate dispersers vs TOP	PRN	0.26 *
Strong dispersers vs TOP	PRN	0.11 ns

805

806 **Table 5:** ΔAIC (Akaike's information criterion) and weight for single variable models and the
807 combinations (in italics) of habitat distance and flow regime distance (local distance metrics) and
808 geographic, topography, perennial and network distance (regional distance metrics). The lower the AIC,
809 the higher the explanatory power of the model for each of the four dispersal categories (weak, local,
810 moderate and strong). Lowest AIC of single variables and combinations of variables for each dispersal
811 category are marked in bold.

|	Weak		Local		Moderate		Strong	
	ΔAIC	Weight	ΔAIC	Weight	ΔAIC	Weight	ΔAIC	Weight
Habitat	**15**	<0.001	**60**	<0.001	98	<0.001	**20**	<0.001
Flow regime	27	<0.001	112	<0.001	102	<0.001	32	<0.001
Geographic distance	60	<0.001	205	<0.001	102	<0.001	40	<0.001
Topography	63	<0.001	191	<0.001	35	<0.001	67	<0.001
Perennial	55	<0.001	177	<0.001	**20**	<0.001	71	<0.001
Network distance	61	<0.001	215	<0.001	130	<0.001	76	<0.001
Local drivers	**0**	1	**0**	1	86	<0.001	**0**	1
Regional drivers	53	<0.001	179	<0.001	**0**	1	37	<0.001

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FIGURE CAPTIONS

815 **Figure 1** Map of sampling localities for stream invertebrates in southeastern Arizona (USA). Inset map
816 shows the location of the study area. Continuous blue line = perennial streams. Short-dashed green line =
817 intermittent streams. Long-dashed red line = ephemeral streams. Black circles represent sampling
818 localities. The map is based on a DEM (digital elevation model) at 10 m resolution.
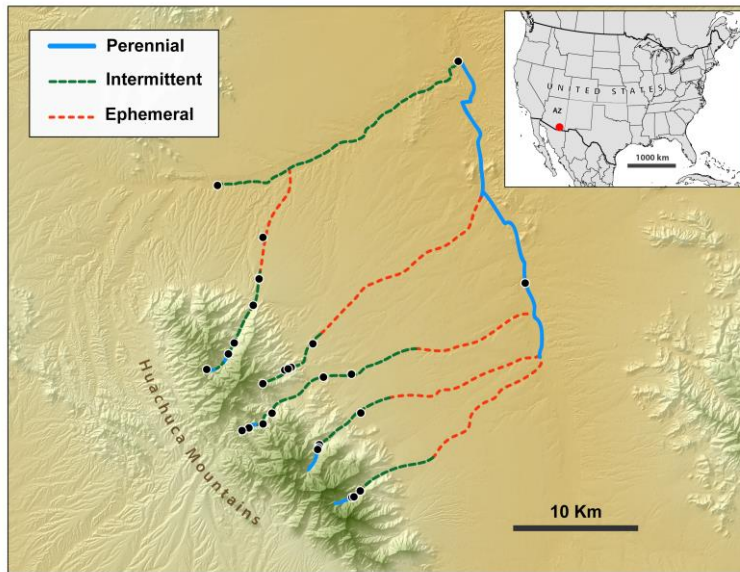
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821 **Figure 2:** Hypothetical scenarios of species dispersal among sites in dryland streams based on each of the
822 four regional distance metrics. In each scenario, the locations of three hypothetical communities are
823 shown as white circles in a generic mountain landscape. Streams are depicted by dotted lines and thick
824 black lines with arrowheads represent bi-directional species flow between pairs of communities. The
825 paths of species dispersal in each scenario are determined by the hypothesized resistance to dispersal
826 associated with the given landscape variable. In the Topography scenario, for example, the underlying
827 hypothesis is that dispersal is easiest in areas with strongly concave topography. Thus, gene flow is
828 expected to be highest through areas with concave topography (shown as grey polygons in the figure).
829 See the Table 1 for more detail on each of the regional distance metrics.


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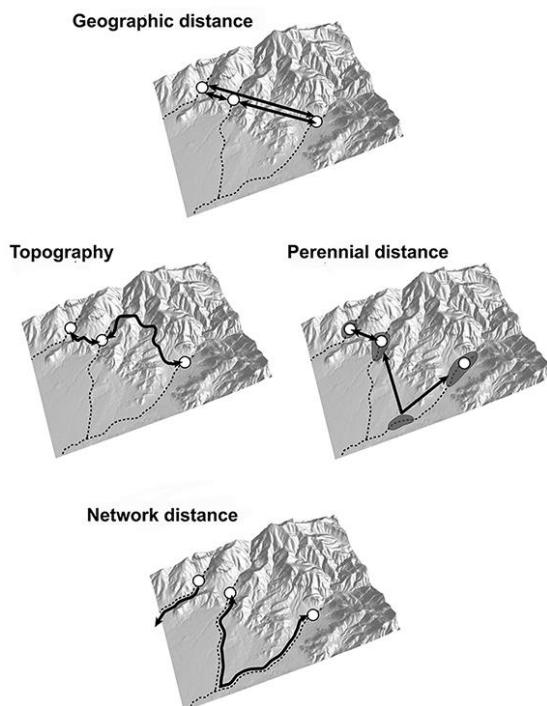
Figure 3: Pairwise correlations among all local and landscape distance metrics calculated between 28 sites across seven dryland streams distributed within a 400 km^2 section of the Upper San Pedro River basin, southeastern Arizona, USA. HAB = habitat distance; GEO = geographic distance; TOP = topography; FLO = flow regime distance; NTW = network distance; PRN = perennial distance. Blue color indicates a positive correlation, while red color indicates a negative correlation. The intensity of the color indicates the strength of the correlation. Spearman's rho are shown inside each box. * = 0.01 < p-value < 0.05; ** = 0.001 < p-value < 0.01; *** = p-value < 0.001.
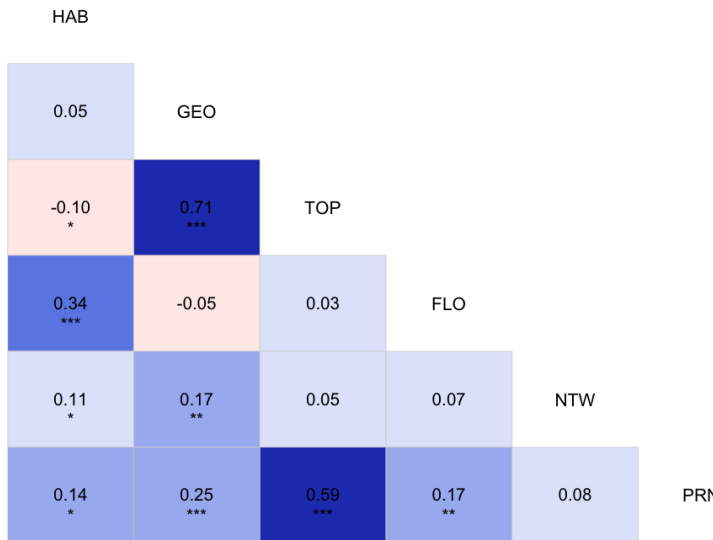
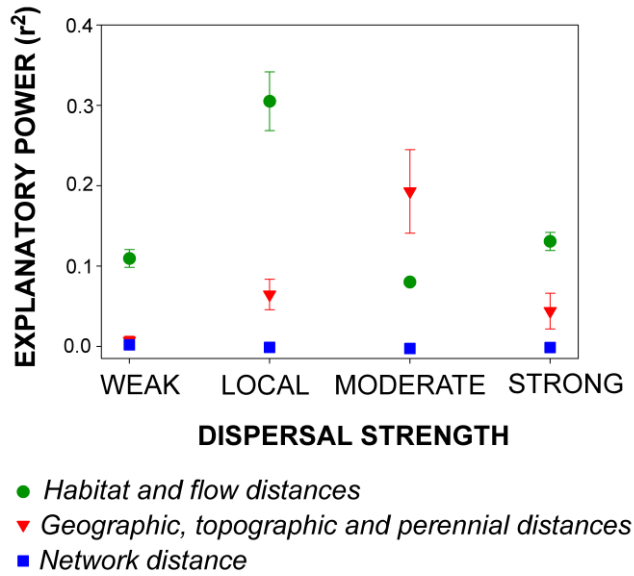**Figure 4:** Distance decay relationships for each dispersal group of stream invertebrates sampled at 28 sites across seven dryland streams distributed within a 400 km^2 section of the Upper San Pedro River basin, southeastern Arizona, USA. WEAK = weak dispersers; LOCAL = local dispersers; MODERATE = moderate dispersers; STRONG = strong dispersers.
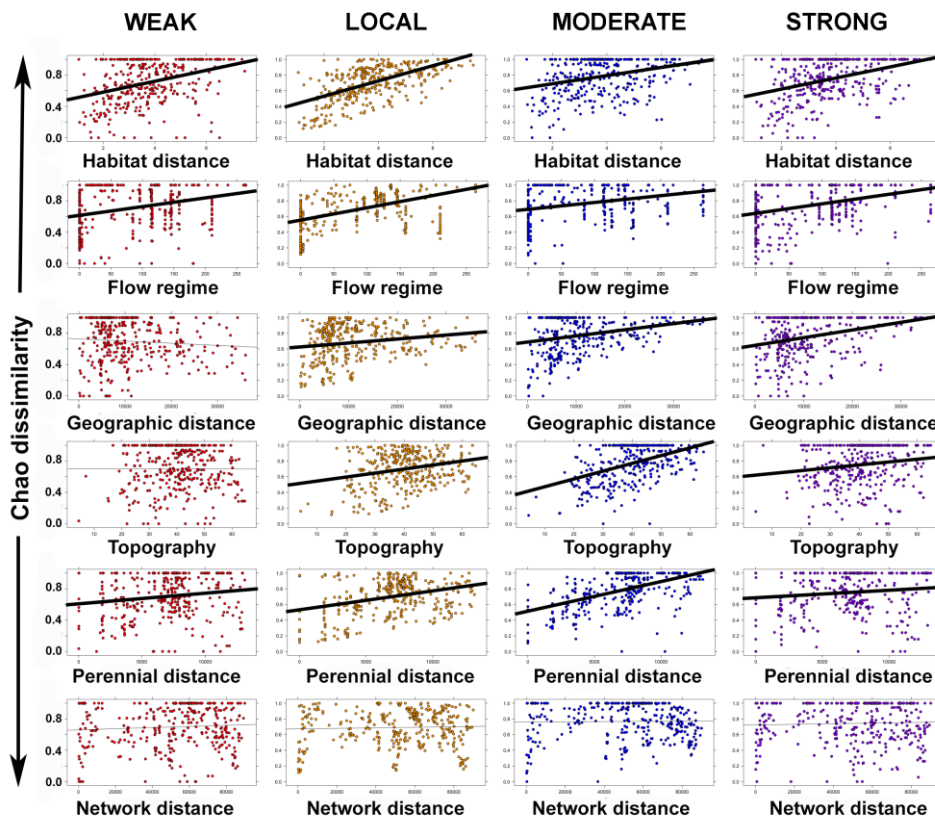
846 **Figure 5:** Explanatory power of three different groups of distance metrics over stream invertebrates'
847 community dissimilarity among 28 sites across seven dryland streams distributed within a 400 km^2
848 section of the Upper San Pedro River basin, southeastern Arizona, USA. Groups of distances: a) habitat
849 & flow distances; b) geographic, topography & perennial distances; and c) network distance. Group a
850 represents local environmental filters and group b represents regional landscape filters. The network
851 distance is shown separately as having a very low power to predict community dissimilarity. The
852 explanatory power is plotted against different categories of dispersal strength of stream invertebrates:
853 weak, local, moderate and strong (see methods section for a description of each category).

- ● Habitat and flow distances
- ▼ Geographic, topographic and perennial distances
- ■ Network distance

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