ORIGINAL ARTICLE

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

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ABSTRACT

Aim Meta-community structure is a function of both local (site-specific) and regional (landscape-level) ecological factors, and the relative importance of each may be mediated by the dispersal ability of organisms. Here, we used aquatic invertebrate communities to investigate the relationship between local and regional factors in explaining distance decay relationships (DDRs) in fragmented dendritic stream networks.

Location Dryland streams distributed within a 400-km^2 section of the San Pedro River basin, south-eastern Arizona, USA.

Methods We combined fine-scale local information (flow and habitat characteristics) with regional-scale information to explain DDR patterns in community composition of aquatic invertebrate species with a wide range of dispersal abilities. We used a novel application of a landscape resistance modelling approach (originally developed for landscape genetic studies) that simultaneously assessed the importance of local and regional ecological factors as well as dispersal ability of organisms.

Results We found evidence that both local and regional factors influenced aquatic invertebrate DDRs in dryland stream networks, and the importance of each factor depended on the dispersal capacities of the organisms. Local and weak dispersers were more affected by site-specific factors, intermediate dispersers by landscape-level factors, and strong dispersers showed no discernable pattern. This resulted in a strongly hump-shaped relationship between dispersal ability and landscape-level factors, where only moderate dispersers showed evidence of DDRs. Unlike most other studies of dendritic networks, our results suggest that overland pathways, using perennial refugia as stepping-stones, might be the main dispersal route in fragmented stream networks.

Main conclusions We suggest that using a combination of landscape and local distance measures can help to unravel meta-community patterns in dendritic systems. Our findings have important conservation implications, such as the need to manage river systems for organisms that span a wide variety of dispersal abilities and local ecological requirements. Our results also highlight the need to preserve perennial refugia in fragmented networks, as they may ensure the viability of aquatic meta-communities by facilitating dispersal.

Keywords
Arizona, aquatic invertebrates, connectivity, dendritic networks, dispersal, distance decay relationship, drought, landscape resistance, meta-community.

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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 biogeographical 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, p. 236). 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 favouring 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 for at least 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 the extent to which local and regional factors structure assemblages of organisms (Bohonak & Jenkins, 2003; Cottenie & De Meester, 2004) and may be reflected in the shape of the DDR. For example, studies on aquatic invertebrate meta-communities in stream networks have reported that increasing dispersal strength results in a weakening of DDRs due to relaxation of dispersal limitation (Thompson & Townsend, 2006; Brown *et al.*, 2011). Very high dispersal rates could cause the homogenization of communities, because organisms can disperse to all available habitats and only the strongest competitors survive (Kneitel & Miller, 2003; Leibold *et al.*, 2004).

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

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

In this study, we present a novel application of a landscape resistance modelling approach, originally developed for landscape genetic studies, to understand local and regional drivers of community structure. Dryland streams were used as a model system to test how environmental stability, dispersal capacity and network topology interact to structure aquatic meta-communities in dendritic networks. These streams experience frequent droughts and floods, which lead to strong niche filtering of stream organisms (Lytle, 2002; Lytle & Poff, 2004), with perennial habitats serving as refugia for species that need water during their entire life cycle to survive (Bogan & Lytle, 2011; Phillipsen & Lytle, 2013). Therefore, the high temporal and spatial variation in environmental conditions may disrupt expected longitudinal patterns of species' replacement along the network (Bogan *et al.*, 2013). In these systems DDRs are expected to be weak or non-existent, with adjacent sites showing very different

aquatic assemblages as a result of large among-site variation in environmental conditions (e.g. one site may flow year-round, while an adjacent site may flow only during rainy seasons). We focused on aquatic invertebrates because they possess a wide range of dispersal capacities (Bilton *et al.*, 2001; Bohonak & Jenkins, 2003) and are present over a wide range of environmental conditions (Rosenberg & Resh, 1993; Merritt *et al.*, 2008), as exemplified by the great diversity of biological traits that they exhibit (Statzner *et al.*, 2004; Poff *et al.*, 2006).

The aim of our study was to use DDRs to investigate the relationship between local and regional factors in explaining aquatic meta-community structure in fragmented dendritic networks. Here we define fragmentation as the loss of surface water connectivity along the river network. During low precipitation periods (typically in late spring and summer) some dryland streams experience very low flow, with sections becoming disconnected pools separated from one another by dry stream reaches. We used fine-scale local environmental variables and landscape resistance metrics to quantify the influence of local and regional drivers on DDRs for groups of species with different dispersal capacities. The following hypotheses were tested:

H_1: DDRs should be weak for very strong and very weak dispersers (at the ends of the dispersal gradient) because meta-communities of weak dispersers show little spatial structure and meta-communities of strong dispersers are homogenized by competition. We predicted that DDR would be strongest in species with moderate dispersal strength.

H_2: Owing to high network fragmentation in dryland streams (i.e. longitudinal flow disruption during long dry seasons), no significant DDR should be found when using network distance. We predicted that network distance would have low explanatory power because of high spatial and temporal stream fragmentation, while our approach that considers landscape resistance to dispersal would provide greater explanatory power.

H_3: Owing to strong niche filtering (i.e. high environmental heterogeneity), DDRs associated with flow and environmental characteristics should be consistently stronger than DDRs associated with landscape resistance variables, regardless of the dispersal strength of the organisms. We predicted that DDRs associated with flow and environmental characteristics would be significant, regardless of species' dispersal abilities.

MATERIALS AND METHODS

Study site and field sampling

We sampled aquatic invertebrates at 28 sites across seven dryland streams distributed within a 400-km² section of the Upper San Pedro River basin, south-eastern Arizona, USA (Fig. 1; Schriever *et al.*, in press). Streams in the area generally have perennial flow in montane headwaters, intermittent

flow in upper alluvial fan reaches, ephemeral flow lower on alluvial fans, and then alternating perennial and intermittent reaches in valley rivers (Bogan *et al.*, 2013). We distributed our sample sites among perennial, intermittent and ephemeral reaches (classification follows Levick *et al.*, 2008), but used a continuous flow metric to quantify permanence (see below). Sites were sampled three times a year (March/April, August/September, and November/December) between 2009 and 2011. The number of sites and samples collected differed among streams because not all sites had flow or all microhabitats during each sampling event. The study period spanned numerous dry seasons, several periods of ephemeral flows from summer monsoon rains, and one period of intermittent flows resulting from a wet winter. The majority of the sampling occurred during the fall (Nov/Dec) and winter (Mar/Apr) seasons for a total of 144 site × sampling event combinations.

Both riffle and pool microhabitats were sampled at each site, when present. For riffle samples we disturbed 0.33 m² of stream substrate to a depth of 5 cm while capturing invertebrates immediately downstream with a D-net (500-μm mesh). Pool samples consisted of sweeping the entire pool area including water column, surface, and pool benthos with a D-net at an effort of 10 s for every 1 m² of pool habitat (following Bogan & Lytle, 2007). Abundances from replicate microhabitat samples collected from the same site during the same sampling event (e.g. three riffles in November) were summed for each taxon and divided by the number of replicates to acquire relative abundances. Samples were preserved in 95% ethanol and invertebrates were identified in the laboratory to the finest taxonomic level practical, usually to genus or species for insects (including Chironomidae) and family or order for non-insects.

During each visit, we measured water temperature, pH (Whatman pH indicators; Whatman International, Maidstone, UK) and conductivity (Milwaukee waterproof EC meter C65; Milwaukee Instruments, Rocky Mount, NC, USA), visually estimated canopy cover and benthic substrate on a percentage cover scale (0–100%; substrate categories: silt, sand, gravel, cobble and bedrock). We measured the timing and duration of streamflow through the deployment of 15 electrical resistance sensors (Jaeger & Olden, 2012), each representing the hydrological conditions at the nearest location of invertebrate sampling. The sensors logged the presence or absence of water in the stream channel at 15-min intervals from April 2010 to December 2011. From the sensor data, we calculated four hydrological metrics for each site: % flow permanence by year, mean % flow permanence by season (spring = May–June; monsoon = July–September; fall = October–November; winter = December–April), mean duration (number of days) of zero flow periods (ZFP) each year, and total number of ZFP each year. For the two flow permanence metrics and duration of ZFP, we summed 15-min time periods of both wet and dry conditions for the sampling period and for individual zero flow periods, converting the time unit to either days or years as
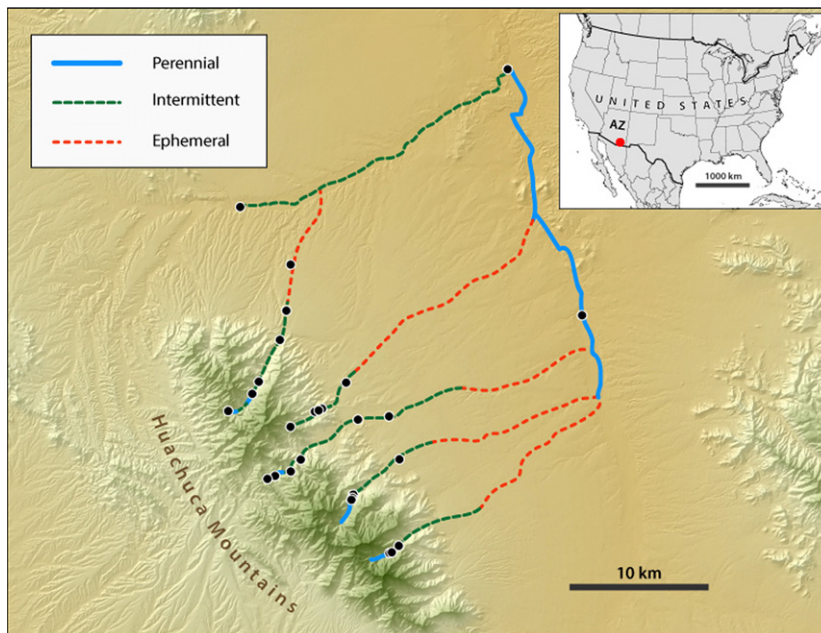
Figure 1 Map of sampling localities for stream invertebrates in south-eastern Arizona (USA). Inset map shows the location of the study area. Continuous blue line, perennial streams; short-dashed green line, intermittent streams; long-dashed red line, ephemeral streams. Black circles represent sampling localities. The map is based on a digital elevation model (DEM) at 10 m resolution.

appropriate for the final stream flow metric. We used an average of 2010 and 2011 flow data to estimate flow conditions for the November 2009 invertebrate sampling period (16 samples) that occurred prior to the deployment of sensors. Flow permanence is the percentage of time a given reach is wetted or flowing, while the duration of ZFP indicates how long (in days) a given reach is dry during each drying event. For example, a site with permanent stream flow would have a flow permanence of 100% and would receive a value of 0 for ZFP duration. While these metrics were all calculated from the flow sensor records, they were designed to characterize distinct components of the hydrological regime that may influence aquatic invertebrate occurrence and abundance.

Distance measures

We used four regional distance metrics (Table 1, Fig. 2), two of which described the physical distance between sites (geographical distance and network distance) and two of which described the resistance of the landscape to dispersal (topographic distance and perennial distance). *Geographical distance* is simply the straight-line Euclidean distance between two sites as determined from map coordinates. *Network distance* was generated via a least-cost path analysis in ArcGIS 9.3 (ESRI, Redlands, CA, USA). For this variable, only one pathway connects each pair of sites, and this pathway is restricted to the stream network. *Topographic distance* assumes that dispersal occurs along concave corridors such as streambeds, dry gullies, or low saddle points along mountain ridges. Flying and crawling insect adults are likely to follow these relatively cool and moist pathways to disperse from one wetted site to another (Bogan & Boersma, 2012; Phillipsen & Lytle, 2013). *Perennial distance* assumes that isolated perennial freshwater habitats act as stepping-stones for dispersal among communities in fragmented dendritic net-

works. For example, in arid landscapes perennial habitats are known to be critical for the survival of certain aquatic species when rivers cease to flow during droughts (Chester & Robson, 2011).

We generated the four regional distance measures from landscape data layers obtained from the Arizona State Land Department (https://land.az.gov/). Data layers used in our analyses included a digital elevation model (DEM; 10 m resolution), the stream network of the region (from the National Hydrology Dataset), and a map of perennial stream habitats. The latter was constructed using data for the San Pedro River watershed from the Nature Conservancy (http://www.azconservation.org/) combined with observations from field studies in the region (e.g. Bogan & Lytle, 2007; Bogan *et al.*, 2013). We used ArcGIS 9.3 to generate new data layers and to calculate the distance (km) between all pairs of sites. The distances related to landscape resistance (topographic and perennial distances) were generated from the GIS data layers in the form of pixelated maps (i.e. rasters). Each raster map was used as input for the program CIRCUITSCAPE (McRae, 2006). CIRCUITSCAPE calculates the resistance of the landscape to dispersal between each pair of sites (analogous to electrical resistance in a circuit diagram), allowing for multiple pathways between sites. This pairwise resistance is a summation of the resistances of individual pixels in the input map. Pixels with high input values are hypothesized to offer high resistance to movement, and vice versa. Thus, pairwise resistances from CIRCUITSCAPE model the structural connectivity of communities, based on the landscape/habitat feature represented by the input map. We used the original values of the map pixels to assign resistance values to the raster maps. Using the original pixel values is more conservative than assigning relative costs of landscape features based on expert opinion (a practice that some have questioned; Spear *et al.*, 2010). Before running the CIRCUITSCAPE analy-
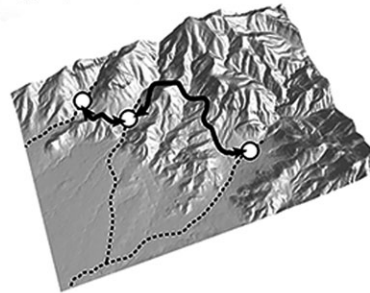
Table 1 Details of the four regional distance metrics used in this study.

| Distance metric	Explanation	Hypothesized relationship to species flow
Geographical distance	Straight-line distance between sites in two-dimensional space.	Dispersal increases when the geographical distance between a pair of sites decreases.
Topographic distance	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 distance	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.
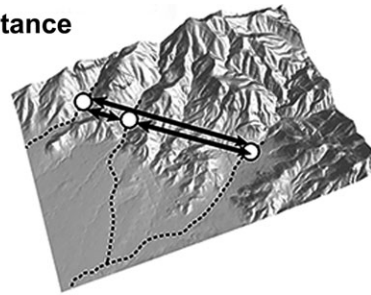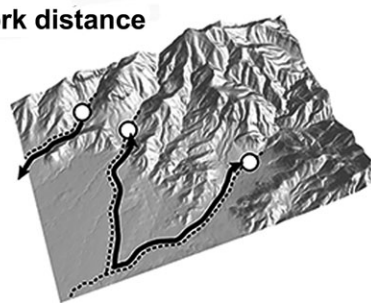
Figure 2 Hypothetical scenarios of species dispersal among sites in dryland streams based on each of the four regional distance metrics. In each scenario, the locations of three hypothetical communities are shown as white circles in a generic mountain landscape. Streams are depicted by dotted lines and thick black lines with arrowheads represent bi-directional species flow between pairs of communities. The paths of species dispersal in each scenario are determined by the hypothesized resistance to dispersal associated with the given landscape variable. In the topography scenario, for example, the underlying hypothesis is that dispersal is easiest in areas with strongly concave topography. Thus, species dispersal is expected to be highest through areas with concave topography (shown as grey polygons in the figure). See Table 1 for more detail on each of the regional distance metrics.

sis, we transformed the original values of the maps so that they were all on the same scale (1 for lowest resistance, 10,000 for highest resistance; results were qualitatively similar for different values of highest resistance). We performed a separate CIRCUITSCAPE analysis for both topographic and perennial distances, generating their two independent data sets of all pairwise resistance distances as output. See Phillipsen & Lytle (2013) for an example of CIRCUITSCAPE output in a population evolution context and how this relates to the underlying distance metrics.

In addition to the four regional distance measures, two local ecological distance measures were calculated: habitat

distance and flow regime distance. *Habitat distance* was calculated as the dissimilarity between the multivariate centroids of each pair of sites based on their environmental characteristics, including canopy cover, conductivity, pH, and % of bedrock, cobble, gravel, sand and fines. *Flow regime distance* was calculated as the dissimilarity between the multivariate centroids of each pair of sites from a composite of flow metrics: % flow permanence in year of sample, % flow permanence by season, duration of zero flow periods each year (mean) and total number of zero flow periods each year. All variables were normalized (mean = 0; SD = 1) before analysis.

Statistical analyses

Prior to analyses, we placed each of the 225 aquatic invertebrate taxa into one of four categories: weak, local, moderate and strong dispersers (see Appendix S1 in Supporting Information). Weak dispersers (17 taxa) are aquatic obligates that spend nearly all of their life cycle within the stream (e.g. *Abedus herberti*). Local dispersers (142 taxa) have flying adult stages but can only travel short distances owing to their short life cycles and/or weak flying musculature (e.g. *Hydrobaenus* sp.). Moderate dispersers (64 taxa) have flying adult stages that can travel long distances but cannot cover the entire geographical range of our study (e.g. *Enochrus aridus*). Strong dispersers (10 taxa) are powerful fliers that can travel between any of the sites in our studied geographical range (e.g. *Lethocerus medius*). These categories were derived from a trait database specific to the study region built from over 80 publications from primary literature, existing databases and expert judgment (Schriever *et al.*, in press). Abundance data were log $(x + 1)$ transformed and then used to calculate the Chao dissimilarity index among all pairs of sites (using the function 'vegdist' in the R package vegan; Oksanen *et al.*, 2013). The Chao index was the most appropriate dissimilarity index to use because each dispersal ability group had a different number of taxa; it is intended to account for the effect of unseen shared species and thus reduce sample-size bias (Chao *et al.*, 2005). Habitat distance, flow regime distance and the four landscape distances (Table 1) were used as independent explanatory variables of Chao's index for each group of species (weak, local, moderate and strong dispersers). Spearman correlation tests were performed between all pairs of the explanatory variables. For those variables showing strong correlation (i.e. Spearman's $\rho > 0.5$ and $P < 0.01$), we used partial Mantel tests (mantel function in vegan package) to compare community data to the explanatory variable of interest while controlling for the correlated variable (Legendre & Legendre, 2012). The differences in the relationship between community dissimilarity and each of the distance metrics (geographical, network, topographic, perennial, flow regime and habitat distances) across dispersal classes was tested through an analysis of covariance (ANCOVA; Legendre & Legendre, 2012) with Chao dissimilarity as the dependent variable, each driver as a covariate, and the dispersal class as the grouping factor.

We fitted linear models to each distance metric, and performed *F*-tests to assess model performance. Models were tested for linearity using the diagnostic plots for generalized linear models (see Appendix S2). We used the glm.diag.plots function in the R package boot (Davison & Hinkley, 1997; Canty & Ripley, 2014), which makes a plot of jackknife deviance residuals against linear predictor, normal scores plots of standardized deviance residuals, plot of approximate Cook statistics against leverage/(1 − leverage), and case plot of Cook statistic. After validating the models we used an information-theoretic approach to compare the contribution of different explanatory variables that best described differences in invertebrate community composition. We derived the log-likelihood for each model and calculated Akaike's information criterion (AIC; Akaike, 1973; Burnham & Anderson, 2002) to rank the models from lowest to highest AIC. We only compared single variable models and the combination of local environmental distance metrics (flow regime and habitat) and landscape distance metrics (geographical, topographic, perennial and network distances), because our aim was to compare the importance of local versus regional filters for aquatic invertebrate meta-communities across a gradient of dispersal strength. Information for the rest of the models is shown in Appendix S3. Once the models were ranked, additional information-theoretic metrics were calcu-

Table 2 Adjusted R^2 values, *F* statistic and *P*-value for each combination of aquatic invertebrate dispersal category (weak, local, moderate, and strong) and explanatory environmental variables (habitat distance and flow regime distance) and spatial variables (geographical, topographic, perennial and network distances). Bonferroni correction was used to adjust *P*-values for multiple comparisons. Significant relationships ($P < 0.05$) are shown in bold. Aquatic invertebrates were sampled in 28 sites across seven dryland streams distributed within a 400-km^2 section of the Upper San Pedro River basin, south-eastern Arizona, USA.

Explanatory variable	Weak			Local			Moderate			Strong		
	Adj R^2	F	P	Adj R^2	F	P	Adj R^2	F	P	Adj R^2	F	P
Habitat distance	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 distance	0.09	37.2	**< 0.01**	0.25	119.8	**< 0.01**	0.08	29.6	**< 0.01**	0.11	46.4	**< 0.01**
Geographical distance	0	2.4	0.120	0.03	10.5	**< 0.01**	0.07	29.1	**< 0.01**	0.09	37.7	**< 0.01**
Topographic distance	0	0	0.964	0.06	25.3	**< 0.01**	0.24	109.2	**< 0.01**	0.02	9.6	**< 0.01**
Perennial distance	0.02	8	**< 0.01**	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

Figure 3 Pairwise correlations among all local and landscape distance metrics calculated between 28 sites across seven dryland streams distributed within a 400-km² section of the Upper San Pedro River basin, south-eastern Arizona, USA. HAB, habitat distance; GEO, geographical distance; TOP, topographic distance; FLO, flow regime distance; NTW, network distance; PRN, perennial distance. Blue indicates a positive correlation, while red indicates a negative correlation. The intensity of the colour indicates the strength of the correlation. Spearman's ρ values are shown inside each box. * $0.01 < P < 0.05$; ** $0.001 < P < 0.01$; ***$P < 0.001$.

Akaike weights, the probability that the model is actually the best-fitting of the candidate models. The sum of Akaike weights across the models is 1.0. When the weight of the model with the lowest AIC is not close to 1.0, there is evidence for model selection uncertainty. We accounted for the non-independence of our data (represented by pairwise distances among sites) by using an R^2 approach for fixed effects in a linear mixed model to adjust for the inflation of sample size (Edwards *et al.*, 2008). As both the AIC and mixed model approaches yielded similar results, we only report the adjusted R^2 values for fixed effects (Table 2). The selection of AIC over adjusted R^2 values was based on the limited use of adjusted R^2 values in model building, owing to the lack of diagnostic and selection tools for linear mixed models (Edwards *et al.*, 2008). All analyses were conducted in R version 3.0.2 (R Core Team, 2013) and significance was assigned at $P < 0.05$. Bonferroni correction was used to adjust P-values for multiple comparisons.

RESULTS

The six distance metrics displayed weak pairwise correlations. Only geographical, topographic and perennial distances were strongly (Spearman's ρ > 0.5) and significantly correlated (Fig. 3). Habitat and flow regime distances significantly explained community dissimilarity, regardless of the species' dispersal abilities (Table 2). Geographical, topographic and perennial distances significantly explained community dissimilarity for all dispersal groups except for the weak dispers-
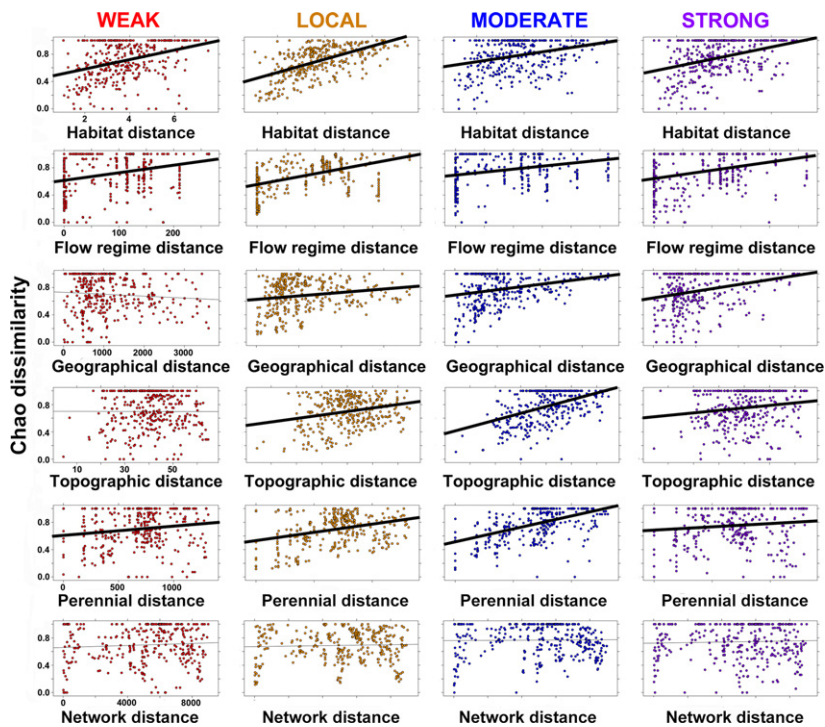
lated. The difference between the AIC of a particular model and the AIC of the estimated best-fitting model (i.e. the model with the lowest AIC) is ΔAIC. We also calculated

Figure 4 Distance decay relationships for each dispersal group of stream invertebrates sampled at 28 sites across seven dryland streams distributed within a 400-km² section of the Upper San Pedro River basin, south-eastern Arizona, USA. WEAK, weak dispersers; LOCAL, local dispersers; MODERATE, moderate dispersers; STRONG, strong dispersers.

Table 3 Results of the ANCOVA analyses with Chao dissimilarity value as the dependent variable, each distance metric as a covariate, and the aquatic invertebrate dispersal category (weak, local, moderate, and strong) as the grouping factor. Significant relationships ($P < 0.05$) are shown in bold. Aquatic invertebrates were sampled in 28 sites across seven dryland streams distributed within a 400-km^2 section of the Upper San Pedro River basin, south-eastern Arizona, USA.

Variable	*F* statistic	*P*
Habitat distance	5.11	**< 0.01**
Flow regime distance	2.69	**0.045**
Geographical distance	12.41	**< 0.01**
Topographic distance	13.44	**< 0.01**
Perennial distance	9.82	**< 0.01**
Network distance	0.23	0.873

Table 4 Partial Mantel test results among those distance metrics that showed strong correlation between each other (Fig. 3). GEO, geographical distance; TOP, topographic distance; PRN, perennial distance. *$0.01 < P < 0.05$; **$P < 0.01$; n.s., not significant. Distances were calculated for 28 sites across seven dryland streams distributed within a 400-km^2 section of the Upper San Pedro River basin, south-eastern Arizona, USA.

Comparison	Control matrix	*r*	*P*
Weak dispersers vs. GEO	TOP	−0.12	n.s.
Local dispersers vs. GEO	TOP	−0.02	n.s.
Moderate dispersers vs. GEO	TOP	−0.11	n.s.
Strong dispersers vs. GEO	TOP	0.28	**
Weak dispersers vs. TOP	GEO	0.08	n.s.
Local dispersers vs. TOP	GEO	0.2	n.s.
Moderate dispersers vs. TOP	GEO	0.43	**
Strong dispersers vs. TOP	GEO	−0.09	n.s.
Weak dispersers vs. PRN	TOP	0.19	n.s.
Local dispersers vs. PRN	TOP	0.22	n.s.
Moderate dispersers vs. PRN	TOP	0.33	**
Strong dispersers vs. PRN	TOP	0.04	n.s.
Weak dispersers vs. TOP	PRN	−0.11	n.s.
Local dispersers vs. TOP	PRN	0.09	n.s.
Moderate dispersers vs. TOP	PRN	0.26	*
Strong dispersers vs. TOP	PRN	0.11	n.s.

ers, and had a higher explanatory power for strong dispersers (Table 2). Network distance was not a significant predictor for any dispersal group. Associations between community dissimilarity and the explanatory variables varied considerably among the four dispersal groups (Fig. 4). The relationship between community dissimilarity and the six distance metrics differed across the dispersal categories for all but one metric (network distance; Table 3).

Partial Mantel tests revealed that: (1) geographical distance was significantly correlated with the composition of strong dispersing taxa after controlling for topographic distance; (2) topographic distance was significantly correlated with the composition of moderate dispersers while accounting for geographical distance; and (3) topographic and perennial distances were correlated with the composition of moderate dispersers while controlling for each other (Table 4). Of all the models, local drivers (habitat distance plus flow regime distance) demonstrated the strongest relationships (i.e. the lowest AIC for single variable models) with the composition of weak, local and strong dispersers, while regional drivers (geographical, topographic, perennial and network distances) best-explained moderate dispersers (Table 5).

DISCUSSION

We used distance decay relationships to examine the importance of local and regional drivers of aquatic invertebrate meta-community structure in dryland streams. DDRs have been used to examine the interaction of processes operating at local and regional scales for a wide range of organisms and ecosystems (Cottenie, 2005; Soininen *et al.*, 2007), including stream networks (Thompson & Townsend, 2006; Leprieur *et al.*, 2009; Brown & Swan, 2010; Warfe *et al.*, 2013). However, past studies have largely not explored the relative roles of local- and regional-scale landscape drivers within connected networks. The only published study that used DDRs to address the effect of hydrological connectivity on stream meta-communities showed, rather counter-intuitively, that the loss of connectivity enhanced DDR in a variety of organisms (Warfe *et al.*, 2013). However,

environmental conditions in that study were not independent of geographical distance; therefore dispersal limitation and niche partitioning both played a role in shaping assemblage structure. Our results suggest that fragmentation impacts DDRs by altering the viable dispersal pathways, with organisms dispersing overland instead of using the stream network. As we hypothesized, meta-community structure was determined by three main factors: niche filtering due to local among-habitat differences, dispersal ability of the species, and landscape resistance (geographical distance, topography and availability of perennial refugia).

Niche filtering due to among-habitat differences

We hypothesized that high environmental heterogeneity would generate significant environmental DDRs for all dispersal categories. Indeed, we found that the local filters of habitat and flow regime had a stronger effect on community dissimilarity than regional filters across all dispersal classes, except for moderate dispersers. At intermediate levels of dispersal, organisms might be able to survive harsh environmental conditions such as floods and droughts by escaping and finding refugia (Velasco & Millan, 1998; Lytle, 1999), but at the same time they might not be able to reach all the available habitats, preventing meta-community homogenization via mass effects (Kneitel & Miller, 2003; Leibold *et al.*, 2004). The significant influence of local filters on meta-community patterns was not surprising given the high temporal and spatial variation in environmental conditions in the study region. Highly variable seasonal and interannual precipitation patterns and various geomorphic settings (e.g. bedrock canyons, alluvial fans) interact to create a patchy stream

Table 5 ΔAIC (Akaike's information criterion) and weight for single variable models and the combinations (in italics) of habitat distance and flow regime distance (local distance metrics) and geographical, topographic, perennial and network distances (regional distance metrics). The lower the AIC, the higher the explanatory power of the model for each of the four invertebrate dispersal categories (weak, local, moderate and strong). Lowest AIC of single variables and combinations of variables for each dispersal category are marked in bold. Aquatic invertebrates were sampled in 28 sites across seven dryland streams distributed within a 400-km^2 section of the Upper San Pedro River basin, south-eastern Arizona, USA.

Variable	Weak		Local		Moderate		Strong	
	ΔAIC	Weight	ΔAIC	Weight	ΔAIC	Weight	ΔAIC	Weight
Habitat distance	**15**	< 0.001	**60**	< 0.001	98	< 0.001	**20**	< 0.001
Flow regime distance	27	< 0.001	112	< 0.001	102	< 0.001	32	< 0.001
Geographical distance	60	< 0.001	205	< 0.001	102	< 0.001	40	< 0.001
Topographic distance	63	< 0.001	191	< 0.001	35	< 0.001	67	< 0.001
Perennial distance	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

landscape. In these dryland streams, perennial reaches are adjacent to intermittent reaches, and intermittent reaches with seasonal flow in a wet year can be completely dry during the same period in a dry year (Jaeger & Olden, 2012; Bogan *et al.*, 2013). The amount of water and how it is distributed within the year (i.e. frequency and timing of droughts and floods) have important consequences for water quality and habitat variables (e.g. canopy cover, river substratum). Accordingly, these local habitat filters should be extremely strong in dryland streams. Our results validate previous studies that linked these patchy environmental conditions to disruptions in the longitudinal patterns of stream invertebrate communities in the region (Bogan *et al.*, 2013). They are also in agreement with a recent study from north-western Australia, which found that flow and channel width best explained invertebrate meta-community patterns across a range of perennial and intermittent streams (Warfe *et al.*, 2013). Moreover, the importance of niche filtering in structuring meta-communities has been demonstrated for a variety of ecosystems (Soininen *et al.*, 2007), including ponds (Urban, 2004; Chase, 2007) and streams (Thompson & Townsend, 2006; Brown & Swan, 2010). As the loss of connectivity among stream reaches results from high flow heterogeneity (leading to high environmental heterogeneity), niche filtering can be expected to be strong in fragmented stream networks.

Dispersal ability

Aquatic invertebrates are known to have very different dispersal capacities, ranging from a few metres to thousands of kilometres (Kovats *et al.*, 1996; Bilton *et al.*, 2001; McCauley, 2006). Given that meta-community structure is highly dependent on geographical scale (Brown *et al.*, 2011; Maloney & Munguia, 2011; Nekola & McGill, 2014), differences in dispersal can be expected to affect DDRs (Nekola & White, 1999). Increasing dispersal ability is expected to enhance community similarity among sites and reduce beta diversity among habitat patches (Shurin *et al.*, 2009). Recent

studies on invertebrate meta-communities in stream networks have provided evidence for this pattern, with DDR being weakened by increasing dispersal strength (Thompson & Townsend, 2006; Brown & Swan, 2010; Bonada *et al.*, 2012). However, we found a more complex unimodal pattern, with DDR peaking at intermediate dispersal strength for different measures of landscape resistance. This pattern might result from assemblages of weak dispersers showing no
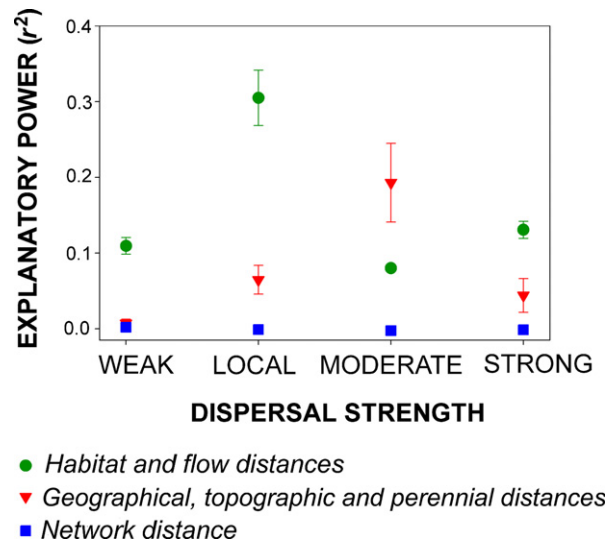

● *Habitat and flow distances*
▼ *Geographical, topographic and perennial distances*
■ *Network distance*

Figure 5 Explanatory power of three different groups of distance metrics over stream invertebrates' community dissimilarity among 28 sites across seven dryland streams distributed within a 400-km^2 section of the Upper San Pedro River basin, south-eastern Arizona, USA. Groups of distances: (a) habitat and flow distances; (b) geographical, topographic and perennial distances; and (c) network distance. Group (a) represents local environmental filters and group (b) represents regional landscape filters. The network distance is shown separately as having a very low power to predict community dissimilarity. The explanatory power is plotted against different categories of dispersal strength of stream invertebrates: weak, local, moderate and strong (see Materials and Methods for a description of each category).

spatial structure as a result of dispersal limitation, whereas assemblages of strong dispersers are more homogeneous across the landscape as a result of the absence of dispersal restrictions (Kneitel & Miller, 2003; Leibold *et al.*, 2004). Figure 5 illustrates this pattern by showing the explanatory power of local (habitat and flow distances) and landscape (geographical distance, topography and availability of perennial refugia) filters along the dispersal strength gradient.

Our results could be influenced by the lower flow connectivity and environmental stability in our dryland study system compared to more mesic stream systems. In low connectivity systems, weak dispersers are highly isolated, leading to species distributions ruled by ecological drift and niche filtering (Hu *et al.*, 2006). Therefore, in these fragmented systems, low connectivity coupled with differing environmental conditions can lead to adjacent sites having very different assemblages of weak dispersal species. Previous investigations on the flightless aquatic obligate *Abedus herberti* within our study area reported strong population genetic structure, with populations within the same stream drainage (less than 5 km apart) showing significant genetic differentiation (Finn *et al.*, 2007; Phillipsen & Lytle, 2013). This same pattern has been observed for the blackfly *Prosimulium neomacropyga* in isolated alpine headwater streams (Finn & Poff, 2011). On the other side of the spectrum, extremely strong dispersers can break down geographical barriers, occurring in all suitable habitats (Townsend *et al.*, 2003; McCauley, 2006; Thompson & Townsend, 2006; Brown & Swan, 2010; Bonada *et al.*, 2012). This would explain the decrease in the explanatory power of landscape variables over meta-community structure at the upper end of the dispersal strength gradient in the present study (Fig. 5). We suggest that regional drivers should be important predictors of meta-community structure up to a certain dispersal distance threshold, beyond which dispersal is strong enough to break the limitation imposed by geographical barriers.

Distance among sites

Network distance did not significantly affect community dissimilarity for any of the four dispersal groups, as we hypothesized. This contradicts the general rule of aquatic invertebrates using the stream network as the main 'highway' for dispersal (Petersen *et al.*, 2004). While evidence supporting the ideas of the stream channel as the primary dispersal route and restricted overland dispersal between catchments continue to accumulate in the literature (Hughes, 2007; Brown & Swan, 2010; Rouquette *et al.*, 2013), previous investigations within our study area suggest that dryland streams might be exceptions to this rule. Many aquatic invertebrate species in our study region disperse laterally from stream corridors in search of other wetted habitats (Bogan & Boersma, 2012). Additionally, Bogan *et al.* (2013) reported an interruption of the river continuum, where invertebrate communities in distant headwater and lowland perennial streams were more similar to one another than to those in

intervening intermittent reaches. Furthermore, Phillipsen & Lytle (2013) found no significant relationship between network distance and population genetic structure of *Abedus herberti*. Instead, they found that topography best explained genetic structure and suggested that overland dispersal resulted from flood-escape behaviour (Lytle, 1999; Lytle *et al.*, 2008), where individuals crawl from streams during floods and accidentally end up in adjacent drainages.

We found significant (but generally weak) DDRs for perennial habitat distance in all cases and for topographic distance in all cases except weak dispersers. This supports the hypothesis of overland dispersal (flight and crawling) being the main dispersal pathway for aquatic invertebrates in highly fragmented stream networks, such as those inhabiting dryland regions. Similarly, Campbell Grant *et al.* (2010) found evidence of high overland dispersal rates in newly metamorphosed juveniles of stream salamanders and suggested that the salamanders followed that dispersal strategy to increase population persistence across isolated headwater streams.

CONCLUSIONS

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

Our DDR approach has the potential to generate timely management insights, such as the importance of preserving perennial habitat patches in fragmented river networks. Meta-communities of weak dispersal species are highly disconnected in dryland stream networks. As most of these species depend on perennial water sources for their survival (Bogan & Lytle, 2011; Hermoso *et al.*, 2013), intensifying droughts may have effects at both meta-population and meta-community levels. Our results suggest that perennial habitat patches may facilitate dispersal of aquatic invertebrates and thereby may ensure the long-term viability of populations. Conserving perennial habitats is of vital importance in dryland streams, and it will become increasingly important in basins

experiencing flow reduction due to warmer temperatures and increased anthropogenic water use (Marshall *et al.*, 2010). Given the different responses of invertebrate meta-communities to our various geographical and environmental distance measures, we encourage future investigations to incorporate multiple regionally relevant measures of landscape resistance into their studies. Further research is needed to better understand how environmental stability affects the balance between local and regional factors structuring meta-community patterns in dendritic networks, including work at different spatial scales and degrees of fragmentation.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Aquatic invertebrate taxa list (sampled in 28 sites across seven dryland streams distributed within a 400-km^2 section of the Upper San Pedro River basin, south-eastern Arizona, USA) including their assignation into one of four dispersal categories: weak, local, moderate and strong dispersers.

Appendix S2 Diagnostic plots for generalized linear models fitted to each distance metric and aquatic invertebrates' dispersal category.

Appendix S3 Sum of residuals, likelihood ratios and AIC values for all combinations of explanatory variables (habitat, flow regime, geographical, topographic, perennial and network distances) for each dispersal group (weak, local, moderate and strong).

BIOSKETCH

Miguel Cañedo-Argüelles is an aquatic ecologist, interested in the response of aquatic ecosystems to disturbance and how aquatic organisms are connected through the landscape.

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