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A fresh approach reveals how dispersal shapes metacommunity structure in a human-altered landscape

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Running title: Dispersal and metacommunity structure

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Summary

1. To understand species losses from disturbed landscapes, it is important to distinguish the effects of degraded environmental conditions from those caused by barriers to dispersal between habitat patches. To assess the relative importance of these effects, we developed a new approach using permutation and association tests applied to rank abundance data, using the invertebrate fauna of two rivers in two seasons.

2. Our study streams were Hughes Creek and Seven Creeks, in south-eastern Australia, which have both been degraded by agriculture in downstream sections. We collected benthic invertebrates and also dispersing individuals (drift, terrestrial adults) during two seasons in 2007–2008. Study sites spanned strong environmental gradients as well as the main dispersal route (up- and down-channel). Environmental data were analysed to set up permutation tests on rank abundances. Survey and disperser data were contrasted using contingency table analyses.

3. The results suggest dispersal plays a strong role in community structure. Environmental effects were evident and strongest upstream, but evidence of environmental effects was weak over much of the gradient. Many species had different distributions in different data sets or dispersers that were abundant at locations distant from centres of benthic distribution.

4. Our results differ from many studies, but few have been able to evaluate dispersal effects directly. Our method provides a practical approach for evaluating the role dispersal plays in driving species abundance patterns across landscapes, thus bridging a gap between theory and practice.

5. *Synthesis and applications.* Managers typically use indices of ecosystem health that assume environmental conditions largely determine species diversity and abundance. Dispersal between habitat patches is known to be important, but there are no reliable methods to assess the role dispersal may play. We provide an approach that allows both dispersal and environmental effects on species distributions to be evaluated from survey data. This may open the way for dispersal information to be incorporated into management actions. Additionally, the approach should allow improved siting of restoration projects that depend greatly on successful dispersal of individuals for successful outcomes.

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Key-words: combinatorics, dispersal, disturbance, environmental gradients, land clearance, restoration, south-eastern Australia, species diversity, stream invertebrates, variation partitioning

Introduction

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As human impacts on the environment continue to grow, rates of species extinction are expected to climb, but we understand little about the direct causes of species losses when human impacts increase gradually (Scheffers *et al.* 2012). Losses could be due to a gradual degradation of environmental conditions (e.g. increased edge effects as habitat patches shrink in size, etc.) or because dispersal of individuals is slowly cut off as patches become increasingly isolated in a matrix of disturbed environment (Fahrig 2007). It is imperative to distinguish between these two causes but managers typically have little information about dispersal of species across landscapes. Most indices of ecosystem “health” are derived from variables measuring environmental condition, which are used as a surrogate for biological diversity (e.g. Kwok, Eldridge & Oliver 2011; Rodgers *et al.* 2012; Dobbie & Cllifford 2015). The strength of the relations between environmental condition and species abundances can be tested using basic survey data (sites X species abundances X environmental variables: e.g. Kwok, Eldridge & Oliver 2011) but there are few ways for highlighting the role that dispersal may be playing from such basic survey data.

One under-used framework for addressing these two prospective causal explanations for species losses is that of metacommunity dynamics (Montoya, Rogers & Memmott 2012). The metacommunity approach recognises that communities occur in patches of suitable habitat distributed across landscapes. Environmental conditions vary between places and have a strong impact on local species composition, but dispersal of individuals between communities is a key aspect. Species that are good dispersers can theoretically remain extant regionally even if they are periodically excluded from some communities or are disadvantaged in some localities but sustained by high rates of immigration from patches elsewhere. Thus, a metacommunity framework applied in the context of landscapes disturbed by human activities can help with identifying management actions (Bengtsson 2010).

Most metacommunity research has also used basic survey data (i.e. sites X species abundances X environmental variables) to separate environmental from dispersal effects on natural communities. A common method is variation partitioning, in which the collective effect of environmental variables on species abundances is separated from “pure” spatial variation – i.e. variation that is related to geographic location and independent of environmental conditions. Pure spatial variation is interpreted to reflect the effects of dispersal constraints on abundances (Cottenie 2005), and hence the approach contrasts the relative roles of dispersal and environmental gradients in structuring communities. However, variation partitioning is effective mostly when environmental and pure spatial variation are

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largely uncorrelated (Legendre & Legendre 2012). In many ecosystems (e.g. rivers, coastal marine habitats, corridor vegetation across landscapes) dispersal routes can be strongly directional. If environmental conditions change along such dispersal routes, then environmental and pure spatial variation will be correlated, in which case using variation partitioning to separate environmental and dispersal effects is problematic (see also Gilbert & Bennett 2010). Another approach uses presence/absence data to test for patterns of distribution that are consistent with different community models (e.g. Leibold & Mikkelson 2002; Presley, Higgins & Willig 2010) but these do not specifically test for the effects of dispersal.

Here, we present a different analytical approach, and we illustrate it using invertebrate species inhabiting rivers that are partly degraded by human impacts, which may have caused losses of species in downstream areas. Many riverine invertebrates use stream currents to disperse downstream ("the drift") and, while some species are fully aquatic, many are insects that have a terrestrial, winged adult, meaning that dispersal can also take place during this life-cycle stage. Although they may move between catchments, adult insects commonly use river corridors for dispersal (Lancaster & Downes 2013). Thus environmental gradients along channels and the effects of any dispersal constraints are likely to be correlated.

We collected benthic invertebrates as well as dispersing individuals (drifters and winged terrestrial adults) from multiple sites in two rivers and at two times and evaluated a set of predictions (Table 1, Fig. 1), as explained further below. Unlike most studies relying on survey data, our alternative approach suggests that dispersal played a prominent role in determining the distributions of species, even though environmental gradients were strong.

Materials and methods

APPROACH FOR TESTING HYPOTHESES

The first logical element of our approach uses survey data and focuses upon those locations where a species is relatively abundant. Such locations signal the environment is suitable for that species, whereas locations where a species is relatively uncommon provide ambiguous information (uncommonness could be caused by either environmental unsuitability or dispersal constraints; note that we do not consider naturally rare species that are uncommon everywhere). If species distributions are largely determined by environmental conditions, then we expect the highest abundances to occur in locations having similar environments. Using this logic, if we order sites by their relative environmental similarity, we can use this order to arrange the rank abundances of species. We expect high ranks to cluster together when the environment determines distributions. The alternative hypothesis is that species have relatively wide tolerances for environmental conditions and so

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distributions are largely determined by successful dispersal (i.e. dispersal where species are able to establish). Because dispersal can vary greatly in space and time, high abundances will sometimes occur in well-separated locations having dissimilar environmental conditions. Thus when dispersal plays a strong role, sites ordered by relative environmental similarity should sometimes have highly ranked species abundances that are well-separated ("split") or at least not clustered.

Formulae from combinatorics can provide tests to detect whether such clusters (or splits) of high ranks occur more or less often than expected by chance. Here, we consider only linear arrays of abundances because this information is relevant to the data we have collected, but the logic explained below can be extended to consider grid-based survey data (i.e. data collected across landscapes).

Combinatorics provide the formulae for calculating the probability that certain numbers occur together (a "cluster") by chance (Allenby & Slomson 2011). If we have a linear array of *n* items and *c* of these items must occur adjacent to each other but can be in any order, the number of permutations fulfilling this requirement is:

$$(n-(c-1))!\,c! \qquad \text{(Equation 1)}$$

The total number of possible permutations is *n*! Thus, the probability of gaining a cluster of size *c* by chance is:

$$P_c = \frac{(n-(c-1))!\,c!}{n!} \qquad \text{(Equation 2)}$$

(see Appendix S1 in Supporting Information for full explanation).

Because species abundances at *n* sites can be converted to ranks, Equation 2 permits us to calculate the probability that the highest ranks occur in a cluster of size *c* by chance. The value of *c* is determined by analysing environmental data, using tests designed *a priori* to identify the cluster size that captures significant differences in environmental conditions (explained further below). If there are *N* species in a data set, then NP_c is the expected number of species that are clustered by chance. The difference between expected and observed numbers of clusters can be tested using chi-square (Sokal & Rohlf 1995). If we have *M* multiple, independent data sets, we can also test whether individual species are consistently clustered, as expected if they have strong responses to environmental conditions. The probability that clustering occurs in multiple independent data sets by chance is ${P_c}^M$. The latter allows us to calculate the expected number of species that will cluster repeatedly in independent data sets by chance, which we can compare to observed numbers using chi-square.

Equation 2 can also be used to calculate the probability that a cluster of size *c* contains one or more numbers but not others (Appendix S1), which means we can also calculate the probability that the highest ranks are not within a cluster, i.e. are "split" (dispersal is frequent, environmental effects are

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weak). The ability to calculate an expected probability of splits allows further tests. We expect the frequency of splits to be significantly lower than expected by chance if environmental effects predominate and significantly greater if dispersal is common.

This approach differs from many other methods (e.g. direct gradient analyses) in which relations between species abundances and environmental variables are tested first. The effects of dispersal are discerned secondarily from outcomes that have already largely been shaped by environment-abundance relations; this therefore seems likely to privilege the environmental explanations. The benefit of our approach is that environmental data are used to set up separate predictions for each hypothesis (i.e. predominantly environment effects, predominantly dispersal effects). Each set of predictions is then evaluated independently and with potentially equal statistical power. Although variation partitioning evaluates environmental and dispersal effects simultaneously, results are difficult to interpret if environmental and spatial variation overlap greatly, i.e. are autocorrelated (Legendre & Legendre 2012). For illustration, we analysed our data with variation partitioning (see Appendix S2) to demonstrate that, as expected, spatial and environmental variation were highly overlapped. Moreover, spatially-structured environmental variation was higher than either spatial or environmental variation, and this precludes a confident assessment of environmental and dispersal effects on community data (Legendre & Legendre 2012). Note that there are more complex methods of analysis than we used, such as Moran’s eigenvector maps (MEM) (or asymmetric eigenvector maps – although the latter can produce similar results to MEM: Legendre & Legendre 2012). However, MEM have been found also to produce unreliable estimates of variation (Gilbert & Bennett 2010).

A second logical element of our approach makes use of individuals sampled at each site in the act of dispersing. The ability to sample dispersers may be infeasible for some species but is possible for many, especially those that disperse advectively (i.e. by wind or water currents), where nets or traps can be specifically deployed to capture them. Most studies demonstrate that many dispersers do not travel far from centres of high abundance (Lowe & McPeek 2014). Indeed, if environmental conditions determine species abundances, we expect dispersers to be most abundant at the same sites as settled individuals, because dispersal away from suitable environments would be maladaptive. Thus the classifications above (clustered, split, etc.) can be applied to the rank abundances of dispersing individuals. Classifications of dispersers can be compared to those of surveyed individuals of the same species using contingency table analysis (G or chi-square: Sokal & Rohlf 1995). If environmental conditions are key, we expect dispersers and surveyed species to be similarly and consistently clustered, i.e. classifications should be strongly associated. Alternatively, if dispersal is frequent, then we expect mismatches, and dispersing species may show different classifications in different data sets.

In a third logical element, outcomes for tests are compiled for each species. Those taxa for which distributions are largely determined by environmental conditions are expected to be consistently

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clustered and to have disperser distributions that consistently match those of surveyed species. Those taxa where dispersal strongly affects distributions should not be clustered, have inconsistent distributions in different data sets and mismatches between surveyed and disperser distributions.

We used the above reasoning to produce a set of specific hypotheses (Table 1, Fig. 1) to test for samples collected from our two rivers, as described below. The dispersal of stream organisms in a downstream direction using stream currents (the drift) and the fact that both larval and adult stages can disperse allowed us to erect some predictions that were specific for flowing water environments. The practical steps followed during numerical analyses are outlined in Table 2 and discussed below.

STUDY SITES AND ENVIRONMENTAL MEASURES

We used two rivers, Hughes Creek and Seven Creeks, located within an agricultural region of south-eastern Australia (Downes *et al.* 2011). Both creeks arise on Strathbogie Range but flow in different directions (their closest headwaters are ~ 7-8 km apart, a distance that is traversable by adult insects: unpublished data, Lancaster & Downes 2013) and both have sandy beds. Sand in the creek beds is sourced from erosion caused by natural events (e.g. bushfires) and by widespread clearance of catchment vegetation. Deposition of sand causes an unstable bed and a loss of habitat structure as wood, bark and leaves (the primary source of hard substrate and food in the systems: Lancaster & Downes 2014b) are smothered. Riparian vegetation (mostly *Eucalyptus camaldulensis*) is continuous along both banks but is sparse in downstream locations due to stock access, reducing contributions of detritus to the stream channel and further exacerbating declines of in-stream resources of food and living space (Reid *et al.* 2008).

The environmental gradient along each creek was characterised using eight, randomly chosen 40 m long sites (Appendix S3) from sections of each creek that were topographically accessible. These sites span strong environmental gradients (see Results). We deliberately sampled streams with two sites located in upstream areas, two located in downstream areas and four sites in-between, with an expectation that the latter would reflect conditions that were intermediate between these starkly different environments. Densities of detritus in the channel (leaves, bark, twigs) were measured at each site (Appendix S3) on each stream during summer, and in spring in Hughes Creek. Additionally, in summer, the total surface areas of wood and bark at each site were measured. Google Earth photographs were used to estimate riparian width and tree cover (Appendix S3). We took spot measures of water quality (pH, conductivity, dissolved oxygen, turbidity using a Multi 340i WTW 82362; MultiLine, Weilheim, Germany), and measured channel widths and water depths on summer dates. Regular measures of water and air temperatures were collected from 2008 to 2009 using data loggers (TruTrack Loggers, Model WT-HR). Discharge data were obtained from government sources; discharges were similar between the two study years (Appendix S3). Collectively these variables span

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the range of major environmental variation that affects the distribution and abundance of stream invertebrates (Hynes 1970).

INVERTEBRATE SAMPLING AND IDENTIFICATION

Benthic invertebrates at all sites on both creeks were sampled in summer in 2007, and Hughes Creek sites were sampled again in spring of 2007. The benthic data comprise mostly larval stages and form the survey data on species distributions. The sampling protocols have been described elsewhere (Downes *et al*. 2011) (Appendix S3). Prospective dispersers (drifting invertebrates, terrestrial adult insects) were sampled at pairs of locations on each creek near the ends of environmental gradients only (species that occurred solely in the middle of the gradient proved uncommon - see Results). Drifters were collected using drift nets and were composited into a single sample for each site and time. At the same times and dates, adults were captured using light traps and sticky traps (Appendix S3) and also compiled into a single, composited sample for each site and time. Drift numbers were corrected by the proportion of the cross-sectional area of sites that was intercepted by nets, which estimates total numbers of drifters moving hourly through sites (as per Downes & Lancaster 2010). Adult samples were counted in entirety, whereas drift and benthic samples were sub-sampled (Appendix S3). Drift and adults were sampled a year after benthic sampling. Given the environmental gradients associated with longitudinal channel profiles and discharge hydrographs do not vary greatly between years, sampling dispersers a year after benthic samples is unlikely to be problematic.

DATA PREPARATION AND STATISTICAL ANALYSES

Environmental variation along channels (Table 2, Step 2)

Environmental variables collected at each site along Hughes Ck and Seven Cks were log-transformed where necessary, normalised and converted to a dissimilarity matrix using Euclidean distances (using the statistical program PRIMER: Anderson, Gorley & Clarke 2008). We then used PRIMER to carry out non-metric, multi-dimensional scaling (NMDS) to display differences among sites with respect to position along each channel. Stress scores were used to assess the number of axes needed to display the data adequately (Anderson, Gorley & Clarke 2008). As expected, sites that were adjacent within creeks were environmentally similar and hence adjacent also within the NMDS plot (see Results).

We chose a cluster size by grouping environmentally similar sites (i.e. that were adjacent within the NMDS plot) and testing whether groups differed significantly. Thus, we first put adjacent sites into pairs (i.e. site 1 and 2 formed the first pair, site 3 and 4 the second pair, etc.), and analysed the differences between creeks and the four pairs (i.e. groups) with a factorial PERMANOVA (Anderson, Gorley & Clarke 2008) with both factors fixed. *A priori* contrasts compared adjacent pairs (i.e. 1 *vs* 2, 2 *vs* 3, 3 *vs* 4). The analysis and contrasts were repeated by creating three pairs of sites beginning

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from site 2 and ending at site 7, for a total of five contrasts using pairs of sites. We then repeated this procedure using two trios of sites (i.e. groups of three), beginning with site 1 (i.e. sites 1, 2 and 3 *vs* 4, 5 and 6), then from site 2, and then from site 3, producing three contrasts. We did not use cluster sizes of four or higher given the total number of sites was only eight and given our sampling design. The proportion of significant contrasts was used to decide choice of cluster size (i.e. either two or three). Cluster size is not a "definitive" measure of environmental variation to which all species are expected to respond. Rather, it is a group size over which environments change significantly and that should therefore be associated with changes in the abundances of environmentally responsive species. Different types of data may require a different approach to identifying cluster sizes (Table 2), and choice of cluster size can affect hypothesis tests. We discuss these issues more broadly in Appendix S4, however the most important point is that decision about cluster size must be made independently of the abundance data.

Evaluating predictions in Table 1

Benthic abundances, drift abundances and adult abundances of each species were converted into ranks across sites in each data set. The analyses for predictions 1-4 used species as replicates and, for some tests, all species in all data sets were combined. Thus the same species could potentially appear multiple times, and we address below whether this occurred and affected the results.

Following Step 3 (Table 2) and using a cluster size of three (see Results), species in the benthic data were classified as clustered, split, neither (distributions did not fit either of these extremes) or uncommon (occurred at only one site). Taxa were classified as "split" if the two highest abundances were split between the four most upstream sites and four most downstream sites *and* were not adjacent. This definition of split represents an extreme difference in the location of high abundances, and presents a strong test for this pattern. To test prediction 1, the numbers of taxa in each of the three datasets that were classified as clustered or split were compared to the numbers expected by chance using a chi-square test (Sokal & Rohlf 1995).

To test prediction 2, taxa classified as clustered were divided into the location where the highest abundances occurred (upstream: wholly present in the four most upstream sites; downstream: wholly present in the four most downstream sites; middle: clusters that straddled the transition zone between these two types of environments by occurring within the four middle sites – see Appendix S1). We used Fisher's exact test (Sokal & Rohlf 1995) to examine whether the frequency of cluster locations varied between the three data sets and chi-square to test whether they differed from the frequencies expected by chance (0.33 for each: Appendix S1). We also used chi-square to test whether species were clustered in multiple data sets more often than expected by chance. Finally, we identified species occurring only within a cluster and not at any other locations ("restricted") *vs* those where individuals occurred also at other locations along channels. We tested whether the frequency of restricted clusters differed between locations using Fisher's exact test.

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Following Step 4 (Table 2), to test for concordance between benthic and drift distributions (prediction 3) and between benthic and adult distributions (prediction 4), we re-used the above classifications, producing the following classes: Restricted upstream, highest upstream (but occurred downstream), restricted downstream, highest downstream (but occurred upstream), split. Clustered species (other than those in the middle, which were excluded) were spread between the first four classes depending on whether they were restricted or not. Species that were neither split nor clustered were mostly able to be classified into one of the first four classes. These five classes were also applied to the drift and adult data to produce analogous classifications, allowing us to examine whether benthic and drift rank abundances were concordant at gradient ends, as follows.

We first determined which benthic species were found in the drift (at comparable seasons in the same creek) and analysed the resulting 2x5 contingency table to test whether drifting species were equally common in each of the five benthic classifications. For species that drifted, we tested for congruence between their benthic and drift classifications (prediction 3), and, for those where adults were sampled, we tested for congruence between larval and adult distributions (prediction 4). For some of these contingency tables, expected numbers of species in some cells were low (<5), which violates an assumption underpinning confidence in probabilities associated with chi-square tests. However, in most such tables, the effect on probabilities of chi-square tests is minor and thus of concern only when probabilities are very near the significance boundary (i.e. P = 0.05) (Bradley *et al.* 1979).

In the final step, we compiled results by species to identify those fulfilling each of the predictions in Table 1 for environmental effects or dispersal effects (prediction 5).

Results

ENVIRONMENTAL VARIATION

NMDS achieved a stress score of 0.08, which is an adequate representation of the environmental data in two dimensions (Clarke & Warwick 2001). NMDS plots showed that both creeks had strong environmental gradients from up- to downstream (Fig. 2). Although the creeks differed from each other (PERMANOVA: Pseudo-F = 6.33, P<0.01), the interaction between creek and group was non-significant in all analyses (P > 0.05), showing that the environmental gradient was similar between the creeks. The environmental gradients reflect changes in detrital food resources, provision of hard surfaces from wood and bark, channel morphology, and in water quantities and qualities. Detrital density declined dramatically downstream in accordance with an increasingly narrower and sparser riparian zone (Appendix S3). Additionally, wide channels and shallow water depths meant both

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creeks often registered water temperatures at downstream locations of up to 36 °C during summer, which are extreme temperatures for most aquatic insects (Lancaster & Downes 2013).

Contrasts between adjacent pairs of sites were significant (i.e. $P < 0.05$) in only two of five tests, whereas all three tests between trios of sites were significantly different. Thus, we chose a cluster size of three.

PREDICTIONS 1 AND 2: CLUSTERING OF TAXA ALONG CHANNELS

Numbers of clustered taxa were significantly higher than expected in each data set (Table 3a). Split taxa (e.g. Fig. 3e *vs* 3f) were significantly more common than expected in Hughes Ck in summer, and were not different from expected in the other two data sets.

Of those species that were clustered, the proportions of up, middle and downstream species did not vary between the three data sets. Overall there were many more upstream and many fewer middle and downstream species than expected (Table 3b). A few species were clustered in two or more data sets, and at a frequency significantly greater than expected by chance (Hughes Ck summer and Seven Cks summer: $\chi^2 = 35.6$, $P<0.001$; Hughes summer and Hughes spring: χ^2 105.1, $P<0.001$). Nevertheless, 70% of the observations in Table 3b were of different species. Species richness was far higher in upstream locations, and over 50% of species clustered upstream were restricted to that zone (e.g. Fig. 3a vs Fig. 3b), whereas all middle and downstream species occurred upstream as well as in other locations (e.g. Fig. 3c, d), a statistically significant difference (Table 3c). Thus, the incidence of clustering was strongest upstream and became infrequent in a downstream direction.

PREDICTIONS 3 AND 4: BENTHIC CLASSIFICATIONS *VS* DRIFT AND ADULT CLASSIFICATIONS

Most species were found in the drift, but those absent from the drift were disproportionately likely to be restricted upstream (Table 4), with a few having split distributions and virtually none in other categories. The 14 occurrences of non-drifters that were restricted upstream were produced across 12 taxa - i.e. only two taxa showed the same pattern twice, whereas all other species showed different patterns in different datasets.

Benthic and drift classifications were significantly associated overall (Table 5a), but only two of the categories (restricted upstream, highest downstream) delivered this outcome. Of the 20 cases of concordance for restricted upstream taxa (Table 5a), 19 were unique species, and only one species produced two of these observations; all other species had different outcomes in different data sets. Overall, drift classifications were not strictly concordant with benthic classifications in about one third of cases (Table 5a).

Comparisons between juvenile and adult classifications showed a similar picture to the drift data (Table 5b). Classifications were significantly associated but taxa restricted upstream contributed mostly to this pattern. Approximately one third of cases had adult distributions that were incongruent

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with corresponding benthic juvenile distributions. Caution is required however because the sample size is small and the probability value of the chi-square is relatively close to 0.05.

PREDICTION 5: CONSISTENCY OF SPECIES' PATTERNS

Four of 43 species had distributions that were consistent with a strong effect of local environment: they were clustered, showed consistent patterns between at least two data sets, and had concordance between benthos and drift and between larvae and adults (Appendix S5). A further six species' abundances were also strongly related to environmental conditions albeit with some information missing. Alternatively, three species' abundances were consistent with strong effects of dispersal. The remaining taxa had a mix of outcomes suggesting both environmental and dispersal effects played significant roles.

Discussion

Separating the effects that environmental conditions and dispersal play in allowing species to remain extant in altered landscapes is critically important. We developed a new approach that uses several lines of evidence to test hypotheses about environmental and dispersal effects. In contrast to most other comparable research (Logue *et al.* 2011), our method highlighted the role that dispersal played in setting distributions, as well as environmental conditions, which we discuss first. We then consider how our method may open the way for dispersal effects to be incorporated into management decision-making.

Environmental effects were signalled by significant numbers of clustered rank abundances, and some species occurred only within clusters. There were more species clustered in two or more data sets than expected, and several of these species had consistently concordant benthic and disperser distributions. The results suggest these species are strongly affected by environmental conditions. Interestingly, these species were restricted almost entirely to upstream locations (found also by Brown & Swan 2010). It has been hypothesized such patterns are due to relatively few drifters at upstream locations and because adults fly across catchment boundaries to other upstream locations, not downstream (Brown & Swan 2010). In our data, species were much more likely to be absent from the drift if they were present upstream, which is consistent with this model. However, relatively few species were strict, upstream specialists. Many species that were clustered upstream in one data set occurred at other locations in another data set. Thus the prevalence of environmental effects at upstream sites appeared to be a feature of those locations rather than a result of the identity of the species that were present.

In contrast, dispersal clearly had pervasive effects along the whole environmental gradient. Split distributions were not fewer than expected by chance in two data sets and more frequent than

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expected in one. Clusters were very uncommon at middle and downstream locations rather than being equally prevalent along the entire gradient. This pattern occurred because species that tolerated harsh, downstream conditions also inhabited upstream locations and therefore had wide distributions. Thus, environmental conditions at middle and downstream sites resulted in few clusters in those locations; this pattern is expected also if there is frequent drift along channels (Prediction 2 in Table 2, also found by Brown & Swan 2010). Moreover, many taxa had inconsistent distributions and lacked consistent concordance between benthic and disperser distributions. These results highlight the influence dispersal has on the distributions of many species in these rivers. Our findings are unusual, but most comparable studies have relied on indirect estimates (using variance partitioning) and dispersal effects may have been underestimated (Gilbert & Bennett 2010).

The variable outcomes for many species suggest that a trait-based approach – in which we seek species characteristics associated with either a strong environmental or dispersal effect – is unlikely to result in useful predictions. Species traits have been used to provide a second line of evidence about dispersal effects (e.g. Brown & Swan 2010), but such traits are rarely independently tested (Verberk, van Noordwijk & Hildrew 2013) and are often applied at coarse taxonomic levels (e.g. genera, families or orders). For example, larvae of the mayfly *Baetis* are invariably classified as “good dispersers” but larvae do not drift away from natal sites in some studies (e.g. Lancaster & Downes 2014a). In contrast to these indirect methods, disperser data permit direct tests. While the linear nature of rivers makes capturing dispersers relatively straightforward, there are many other ecosystems in which dispersal is also highly directional (terrestrial systems affected by prevailing winds Gillespie *et al.* 2012; e.g. coastal ecosystems affected by currents Moritz *et al.* 2013) and methods are available to sample them. Having dispersal data means that species absences caused by dispersal constraints can be distinguished from an incapacity of dispersers to colonise new locations following arrival. In the latter situation, we expect to capture high numbers of dispersers in locations where the species is uncommon; in the former we do not expect to capture many dispersing individuals where a species is uncommon. These two hypotheses reflect different community models and have different implications for managing biological diversity but are rarely evaluated (Logue *et al.* 2011).

Species interactions also determine distribution and abundance, but effects of interactions cannot be identified using only survey data. Thus, in variation partitioning, patterns caused by interactions may contribute spuriously to environmental or pure spatial variation depending upon whether or not effects of interactions are correlated with particular environmental or spatial variables. Likewise, in our method, species’ distributions determined by interactions may have contributed spuriously to detecting patterns associated with environmental or dispersal effects. All methods using survey data have to assume that species distributions are largely independent of each other, even though it is well-known that species interactions can play strong roles in affecting abundances.

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This short-coming notwithstanding, our approach provides a practical way of assessing dispersal effects that may deliver benefits for management. Managers usually rely on indicators of ecosystem health that are based almost entirely on measures of environmental condition. Our approach would allow dispersal effects to be considered given that they can be derived from the same kind of data that are typically used to assess the worth of ecosystem-level indices (basic survey data that help verify whether species abundances correlate with environmental variables used to quantify ecosystem health e.g. Kwok, Eldridge & Oliver 2011). A benefit of our method is that it is simpler to apply than many multivariate analyses that rely on advanced statistical expertise to test hypotheses. Apart from the analysis of environmental data to determine cluster size, the approach relies on setting up logical predictions that are evaluated through the use of simple chi-square tests. If it is possible to gather multiple, independent data sets and also to catch dispersing individuals, then the complete set of logic described here can be applied, producing multiple lines of evidence about dispersal effects. Such information could lead to alternative measures of ecosystem condition that capture the role that dispersal plays and could be valuable in assessing whether some species or populations might be particularly vulnerable to extirpation if dispersal routes are cut off.

Finally, dispersal of individuals from intact areas is a key aspect of successful restoration or rehabilitation programs (Palmer, Ambrose & Poff 1997). Many restoration projects on rivers have failed to deliver increases in diversity, and lack of dispersal to restored sites is a key potential explanation (Palmer, Hondula & Koch 2014). The capacity to consider background amounts of dispersal means restoration projects could be designed to take advantage of prospective dispersal routes and realistic restoration targets identified. The results reported here, for example, are encouraging for considering restoration works to improve species diversities of these and comparable streams. Both rivers have relatively harsh environments in downstream locations, but upstream intact areas with cool, detritus-rich conditions may contain reservoirs of species that routinely disperse into downstream locales. Our results suggest that species from upstream locations would reach and colonise repairs in downstream locations if suitable resources and conditions are achieved, thus providing the impetus for such restoration efforts.

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Data accessibility

All relevant data used in this manuscript are publicly available at Dryad Digital Repository: doi: 10.5061/dryad.rt201 (Downes et al. 2016).

References

Allenby, R.B.J.T. & Slomson, A. (2011) *How To Count: An Introduction to Combinatorics,* 2nd edn. Chapman & Hall/CRC, Boca Raton, USA.

Anderson, M.J., Gorley, R.N. & Clarke, K.R. (2008) *PERMANOVA+ for PRIMER: guide to software and statistical methods*. PRIMER-e, Plymouth, UK.

Bengtsson, J. (2010) Applied (meta)community ecology: diversity and ecosystem services at the intersection of local and regional processes. *Community ecology: processes, models, and applications* (eds H.A. Verhoef & P.J. Morin), pp. 115-131. Oxford University Press, New York.

Bradley, D.R., Bradley, T.D., McGrath, S.G. & Cutcomb, S.D. (1979) Type-I error rate of the chi-square test of independence in R x C tables that have small expected frequencies. *Psychological Bulletin,* **86,** 1290-1297.

Brown, B.L. & Swan, C.M. (2010) Dendritic network structure constrains metacommunity properties in riverine ecosystems. *Journal of Animal Ecology,* **79,** 571-580.

Clarke, K.R. & Warwick, R.M. (2001) *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*. Plymouth Marine Laboratory, Plymouth.

Cottenie, K. (2005) Integrating environmental and spatial processes in ecological community dynamics. *Ecology Letters,* **8,** 1175-1182.

Dobbie, M.J. & Cllifford, D. (2015) Quantifying uncertainty in environmental indices: an application to an estuarine health index. *Marine and Freshwater Research,* **66,** 95-105.

Downes, B.J. & Lancaster, J. (2010) Does dispersal control population densities in advection-dominated systems? A fresh look at critical assumptions and a direct test. *Journal of Animal Ecology*, **79,** 235–248.

Downes, B.J., Lancaster, J., Glaister, A & Bovill, W.D. (2016) Data from: A fresh approach reveals how dispersal shapes metacommunity structure in a human-altered landscape. Dryad Digital Repository: doi: 10.5061/dryad.rt201

Downes, B.J., Lancaster, J., Hale, R., Glaister, A. & Bovill, W.D. (2011) Plastic and unpredictable responses of stream invertebrates to leaf pack patches across sandy-bottomed streams. *Marine and Freshwater Research,* **62,** 394-403.

Fahrig, L. (2007) Non-optimal animal movement in human-altered landscapes. *Functional Ecology,* **21,** 1003-1015.

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Gilbert, B. & Bennett, J.R. (2010) Partitioning variation in ecological communities: do the numbers add up? *Journal of Applied Ecology,* **47,** 1071-1082.

Gillespie, R.G., Baldwin, B.G., Waters, J.M., Fraser, C.I., Nikula, R. & Roderick, G.K. (2012) Long-distance dispersal: a framework for hypothesis testing. *Trends in Ecology and Evolution,* **27,** 47-56.

Hynes, H.B.N. (1970) *The Ecology of Running Waters*. Liverpool University Press, Liverpool, UK.

Kwok, A.B.C., Eldridge, D.J. & Oliver, I. (2011) Do landscape health indices reflect arthropod biodiversity status in the eucalypt woodlands of eastern Australia? *Austral Ecology,* **36,** 800-813.

Lancaster, J. & Downes, B.J. (2013) *Aquatic Entomology*. Oxford University Press, Oxford, UK.

Lancaster, J. & Downes, B.J. (2014a) Maternal behaviours may explain riffle-scale variations in some stream insect populations. *Freshwater Biology,* **59,** 502-513.

Lancaster, J. & Downes, B.J. (2014b) Population densities and density–area relationships in a community with advective dispersal and variable mosaics of resource patches. *Oecologia,* **176,** 985-996.

Legendre, P. & Legendre, L. (2012) *Numerical ecology,* 3rd English Edition edn. Elsevier, Amsterdam.

Leibold, M.A. & Mikkelson, G.M. (2002) Coherence, species turnover, and boundary clumping: elements of meta-community structure. *Oikos,* **97,** 237-250.

Logue, J.B., Mouquet, N., Peter, H., Hillebrand, H. & The Metacommunity Working Group (2011) Empirical approaches to metacommunities: a review and comparison with theory. *Trends in Ecology and Evolution,* **26,** 482-491.

Lowe, W.H. & McPeek, M.A. (2014) Is dispersal neutral? *Trends in Ecology and Evolution,* **29,** 444-450.

Montoya, D., Rogers, L. & Memmott, J. (2012) Emerging perspectives in the restoration of biodiversity-based ecosystem services. *Trends in Ecology & Evolution,* **27,** 666-672.

Moritz, C., Meynard, C.N., Devictor, V., Guizien, K., Labrune, C., Guarini, J.-M. & Mouquet, N. (2013) Disentangling the role of connectivity, environmental filtering, and spatial structure on metacommunity dynamics. *Oikos,* **122,** 1401-1410.

Palmer, M.A., Ambrose, R.F. & Poff, N.L. (1997) Ecological theory and community restoration ecology. *Restoration Ecology,* **5,** 291-300.

Palmer, M.A., Hondula, K.L. & Koch, B.J. (2014) Ecological restoration of streams and rivers: Shifting strategies and shifting goals. *Annual Review of Ecology, Evolution and Systematics,* **45,** 247-269.

Presley, S.J., Higgins, C.L. & Willig, M.R. (2010) A comprehensive framework for the evaluation of metacommunity structure. *Oikos,* **119,** 908-917.

Author Manuscript

This article is protected by copyright. All rights reserved

Reid, D.J., Lake, P.S., Quinn, G.P. & Reich, P. (2008) Association of reduced riparian vegetation cover in agricultural landscapes with coarse detritus dynamics in lowland streams. *Marine and Freshwater Research*, **59,** 998-1014.

Rodgers, K.S., Kido, M.H., Jokiel, P.L., Edmonds, T. & Brown, E.K. (2012) Use of integrated landscape indicators to evaluate the health of linked watersheds and coral reef environments in the Hawaiian Islands. *Environmental Management*, **50,** 21-30.

Scheffers, B.R., Joppa, L.N., Pimm, S.L. & Laurence, W.F. (2012) What we know and don't know about Earth's missing biodiversity. *Trends in Ecology and Evolution*, **27,** 501-510.

Sokal, R.R. & Rohlf, F.J. (1995) *Biometry: the principles and practice of statistics in biological research*. W.H. Freeman, New York.

Verberk, W.C.E.P., van Noordwijk, C.G.E. & Hildrew, A.G. (2013) Delivering on a promise: integrating species traits to transform descriptive community ecology into a predictive science. *Freshwater Science*, **32,** 531-547.

Supporting information

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

Appendix S1 Calculating the proportion of taxa expected to clustered or split by chance

Appendix S2 Outcome of variation partitioning

Appendix S3 Site locations, measurement of wood, detritus and riparian tree cover, discharge, and sampling details for drift and adults

Appendix S4 Considerations for deciding on cluster size using environmental data

Appendix S5 Distribution patterns of individual species

Table 1. Predictions associated with each of two general views of metacommunities for stream species, the first of which reflects overarching effects of local, environmental conditions within channels (Fig. 1a), which change in relatively predictable ways from up- to downstream, and the second of which reflects primarily the effects of dispersal, both in the drift (Fig. 1b) or by adults (Fig. 1c), which disperse in search of conditions suitable for mate location and egg-laying. Material in italics provides explanation of predictions where necessary.

Type of patterns	Local environmental effects	Dispersal effects
	Local environmental conditions predominately determine benthic abundances; dispersal has few persistent effects	Dispersal effects dominate; local environmental conditions explain comparatively little of species' distributions

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1. Incidence of clustering	Most species cluster, i.e. attain highest abundances at sites with similar environments. *In streams, these are likely to be sites that are adjacent to each other*	Most species show patchy distributions unrelated to environmental gradients and/or highest abundances occur at locations that are environmentally dissimilar. *In streams, such sites will be well separated along channels.*
2. Spread of clustering	Clustering is apparent along all parts of the channel (up-, mid- and downstream locations). *The effects of local environmental conditions should be present along the whole gradient*.	If drift dispersal is frequent or often long distance, then clustering, if present at all, becomes less frequent in a downstream direction. *Frequency of clustering weakens due to the successful arrival of increasing numbers of species drifting from various upstream locations.*
3. Benthic and drift concordance	Most drifting species are consistently and predominantly found in the zone in which they occur benthically. *Drifting out of the zone the species inhabits would be maladaptive*.	Drift abundances are often not concordant with benthic abundances. *Drifters may frequently be in search of new resources, for example*.
4. Adult and juvenile concordance	Adult and juvenile distributions consistently show concordance. *We expect most adults to be trapped near where their larvae do best.*	Adults and juvenile distributions may often be non-concordant. *Adult females may lay eggs in places driven by dispersal and choices of oviposition habitat, so larval distribution is not related to local, in-channel environmental conditions.*
5. Consistency across data sets	Most species have consistent patterns in both benthic and dispersers distributions with respect to environmental gradients when examined across different rivers	Most species' distributions have little consistency with respect to environmental gradients in different rivers or at different times

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and times.

Table 2. A summary of practical steps to analyse data, following the logical approach outlined in the text

Step 1. Develop predictions for species abundance data that relate directly to hypotheses, e.g. under environmental and dispersal explanations (i.e. create Table 1)
(a) Make predictions for surveyed abundances of species (e.g. Table 1, predictions 1 & 2) and for dispersers (e.g. prediction 3)
(b) Consider whether further predictions arise due to nature of the ecosystem or species' biology (e.g. dispersal effects in prediction 3, prediction 4)
(c) If available, make predictions for multiple data sets (e.g. prediction 5)
Step 2. Using the environmental data, decide cluster size, c.[1]
(a) Use NMDS to display differences among sites[2]
(b) Order sites by their environmental similarity[3]
(c) Group sites that are most similar environmentally[4]
(d) Use PERMANOVA with planned contrasts to assess the degree of differences among groups; repeat using different numbers of sites[5]
(e) Identify the group size that delivers the greatest degree of statistical significance among groups and designate as cluster size, *c*
Step 3. Statistically test predictions about abundance of surveyed species
(a) Decide on an appropriate definition of a split distribution
(b) Convert abundances of each species to ranks across sites
(c) Order each species' ranks according to the order of site similarity (2b, above)
(d) Classify species into those that are clustered, split, or neither (using *a priori* definitions, above)
(e) Using combinatorics, calculate the number of species expected to occur in clusters and splits by chance
(f) Using chi-square tests, compare expected and observed numbers of species in each category
Step 4. When dispersal data are available
(a) Create classes of distribution derived from clusters and splits (e.g. using location of clusters along environmental gradient, whether species are restricted to clusters or not), which will be applied to both survey data and dispersal data[6]
(b) Using ranked data (3b above), classify species in surveyed abundance data according to distribution classes (4a, above)
(c) Repeat steps 3b and 3c for dispersal data to ranks across sites, and then classify species into distribution classes (4a above)

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(d) Create a 2-way table having each distributional class for survey abundance data crossed with each distributional class for dispersal data; sum the number of species falling into each cell of the table

(e) Using contingency table analysis, test for association between classifications of abundance and dispersal data

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[1] Any legitimate, analytical approach can be used as long as decisions about cluster size are made independently of species abundance data. Note that our method is designed for community data where dispersal between sites is feasible; it is not designed to address questions about biogeographical patterns or geographic range (i.e. very large spatial scales).

[2] With large data sets, cluster analysis can help assess similarity because it provides a visual display of the major divisions among sites in their degree of similarity.

[3] We consider the simple situation where sites can be ordered along a single dimension; other data sets may be more complex and require patterns (and combinatoric formulae) that consider clusters or other patterns in two or more dimensions.

[4] Group sizes (and therefore prospective cluster size) are likely to be related to sampling design relative to environmental gradients.

[5] Ecosystems with diffuse or conflicting gradients may not deliver a definitive decision about a single cluster size. See material in Appendix S4.

[6] As in this paper, multiple classes of distributions derived from clusters and splits (e.g. locations along gradients where clusters occurred) are likely needed to capture distributions along environmental gradients.

Table 3. (a) Numbers of taxa classified as clustered, split, neither, or uncommon in each of the three data sets, with expected values for clustered and split classes given in brackets. Also given are the values for chi-square tests (χ^2) of whether the numbers of clustered (Clust χ^2) or split (Split χ^2) species differ from those expected by chance (see Appendix S1). ***, probability $P < 0.001$; **, $P<0.01$; *, $P < 0.05$; ns, $P > 0.05$. (b) For clustered species only, the observed numbers of upstream (U), middle (M) and downstream (D) species in each dataset with a chi-square test of whether numbers differ

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between datasets. Given this is non-significant, numbers were summed and compared to the numbers expected by chance (as determined by expected proportions 0.33, 0.33, 0.33, respectively, Appendix S2) using a chi-square test. Symbols as for (a). (c) For clustered species only, numbers of taxa restricted to a zone (upstream or middle + downstream) *vs* the numbers found outside of zones and a Fisher exact test of the differences in proportions. Symbols as for (a).

(a)

Data set	Clustered	Split	Neither	Uncommon	Total	Clust. χ^2	Split χ^2
Hughes Ck Summer	14 (5.25)	10 (4.39)	14	3	41	14.58***	7.16**
Seven Cks Summer	10 (4.04)	4 (3.75)	15	6	35	8.81**	0.02ns
Hughes Ck Spring	14 (4.47)	6 (3.75)	10	5	35	20.32***	1.351ns

(b)

	U	M	D	Fisher's exact
Hughes Creek Summer	11	1	2	P=0.80ns
Seven Creeks Summer	8	1	1	
Hughes Creek Spring	13	0	1	
				χ^2
Observed	32	2	4	44.42***
Expected	12.7	12.7	12.7	

(c)

	U	M+D	Fisher's exact test

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Restricted	18	0	P=0.021*
Not restricted	14	6	

Table 4. The numbers of species (across all three data sets) in different benthic classifications *vs* presence/absence in the drift at commensurate times/locations. Because only two taxa were restricted downstream, they were combined with taxa having their highest abundance downstream for this analysis. A test of independence showed there was a significant association ($\chi^2 = 10.3$, $p < 0.025$). The standardized residuals were all < 2.0, indicating that all cells contributed to the result, but the highest (1.88) was for non-drifting taxa that were restricted upstream, whereas all other cells contained negative residuals.

Benthic classification	Drift presence		
	Present	Absent	TOTAL
Restricted upstream	24	14	38
Highest upstream	16	1	17
Restricted or highest downstream	11	1	12
Split	26	8	34
TOTAL	77	24	101

Table 5. (a) For species found at least once in the drift, benthic classification *vs* drift classification and (b) juvenile *vs* adult classification across the three data sets. Benthic taxa that were restricted downstream were added to those found in highest abundances downstream because of low sample size (n=1 only; this species had a split classification in the drift). There is a significant association between benthic and drift classification ($\chi^2 = 33.4$, $p = 0.001$) and between benthic (i.e. juvenile) and adult classification ($\chi^2 = 22.1$, $p = 0.035$). Numbers in italics indicate cells where the standardized deviates were > 2, indicating a significant contribution to the test outcome. Numbers in bold indicate cells where classifications were not in strict concordance.

(a) Benthic classification *vs* drift classification

Benthic	Drift classification					
	Restricted upstream	Highest upstream	Split	Highest downstream	Restricted downstream	TOTAL

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Restricted upstream	*20*	**1**	**1**	**1**	**1**	24
Highest upstream	**7**	3	**4**	**1**	**1**	16
Split	**8**	5	5	5	**3**	26
Restricted to or highest downstream	***0***	**1**	**2**	*5*	3	11
TOTAL	35	10	12	12	8	77

(b) Juvenile (benthic) classification *vs* adult classification

Benthic	Adult classification					
	Restricted upstream	Highest upstream	Split	Highest downstream	Restricted downstream	TOTAL
Restricted upstream	*4*	**1**	0	0	0	5
Highest upstream	**4**	5	0	0	0	9
Split	0	2	4	1	**1**	8
Restricted to or highest downstream	0	**1**	**2**	1	1	5
TOTAL	8	9	6	2	2	27

Figure captions

Fig. 1 Diagrams illustrating some ways in which environmental gradients and dispersal could drive community structure, in this case along rivers where upstream, middle and downstream locations have differing environmental conditions reflecting gradients in important environmental variables. The stars, circles and squares, both filled and open, indicate different species. The presence of species and their approximate abundances in the stream benthos (symbols within squares), in the drift and as adults (whether terrestrial or aquatic) are indicated by the number and type of symbols organised under the appropriate headings. Arrow direction and length signify dispersal direction and distances. **A**. Community structure in the benthos reflects strict effects of environmental gradients and dispersal plays no significant roles in driving species abundances. Each location or zone (upstream, middle, downstream) comprises mostly species that are restricted to that zone. Species that drift remain within the appropriate zone, and adults, particularly those in the terrestrial environment, disperse only into or within the appropriate zone. **B.** One way in which drift dispersal could affect benthic distributions. Juveniles hatch from eggs laid into particular zones in the benthos and hence species are initially

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clustered but some individuals drift and settle downstream. Numbers of drifting species increase cumulatively in a downstream direction, and hence clustering is weakened in a downstream direction. **C**. Ways in which abundances of adults can be mismatched with juvenile distributions: (i) Adults are abundant at sites with low numbers of juveniles compared to other sites (open circles and squares) because adult and juvenile requirements are not correlated across locations. (ii) Adults are in high abundance where juveniles are absent either because eggs have yet to hatch or adults fail to reproduce successfully (filled squares and stars). There are no arrows because adults may potentially disperse from anywhere.

Fig. 2 NMDS plot of eight sites each in Hughes Creek and Seven Creeks based on a resemblance matrix created from environmental variables. The two-dimensional stress value indicates the NMDS plots are a good fit to the data. Numbers above points are site numbers with 1 the most upstream and 8 the most downstream.

Fig. 3 Representative examples of types of benthic distribution patterns, taken from the Hughes Creek samples from summer. (a) *Notalina fulva*: restricted to upstream sites, (b) *Triplectides ciuskus*: most abundant upstream but found downstream, (c) *Ecnomus continentalis:* most abundant at middle sites, (d) *Cheumatopsyche* sp. AV2: most abundant downstream but found upstream, (e) *Austrogomphus* sp.: a split distribution. (f) An example of a species with inconsistent patterns **-** *Austrogomphus* sp. in Seven Creeks in summer, where it was restricted to upstream sites, as compared to Hughes Creek in summer where it had a split distribution (e).

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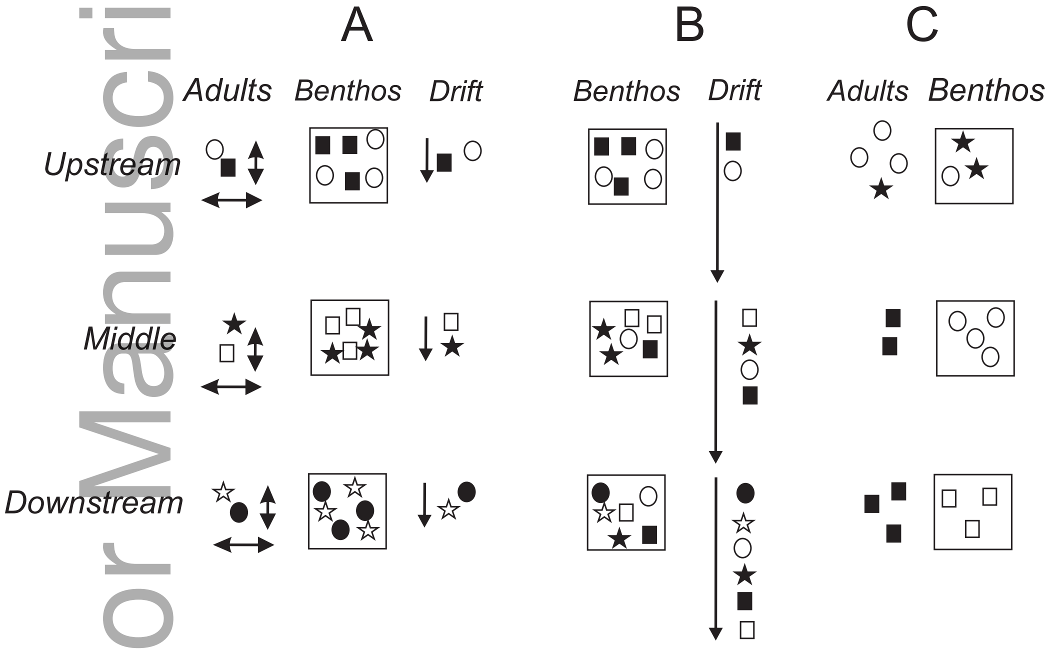

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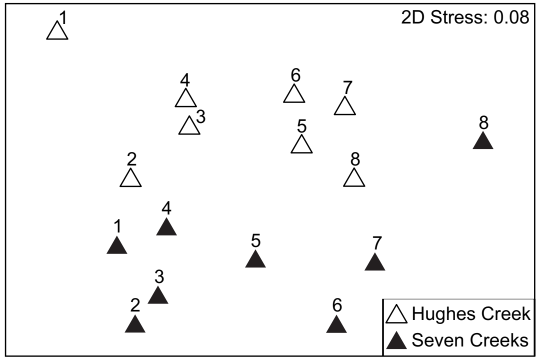

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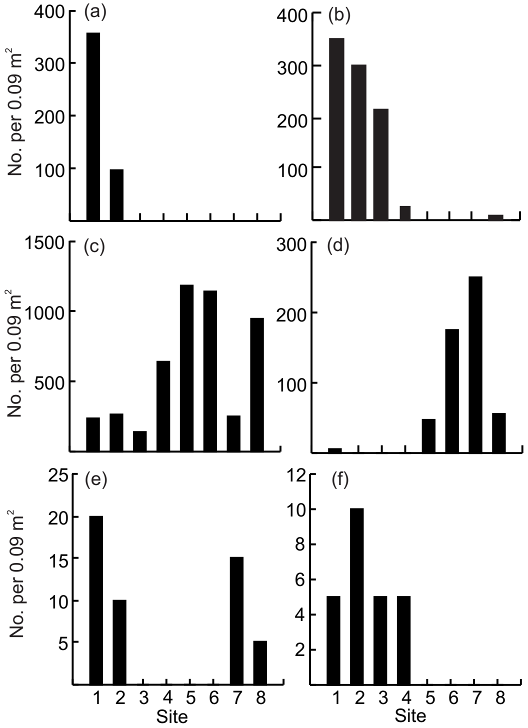

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