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Itinerant, nomad or invader? A field experiment sheds light on the characteristics of successful dispersers and colonists

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SUMMARY

1. Many hypotheses in ecology depend upon identifying species that can disperse across landscapes and colonise new habitat patches. Species differ in dispersal ability, yet some good dispersers reach new locations but fail to colonise them (“itinerants”). Additionally, successful colonists may comprise species that routinely disperse and maintain connectivity among locations (“nomads”) as well as species that can also take advantage of new situations (“invaders”). In a previously reported landscape-scale, field experiment that boosted detrital resources in Hughes Ck (south-eastern Australia), species diversity increased at manipulation sites due to successful dispersal and colonisation. The species composition at manipulation sites gradually converged on that seen at upstream sites, implying the latter locations supplied dispersers. Here we ask (i) did dispersers arise from within the same creek, and were drift and adult flight both implicated? (ii) were successful colonists (“responders”) clearly better dispersers (e.g. nomads or invaders) than those that did not colonise manipulation sites (“non-responders”)? (iii) did traits commonly assumed to denote successful dispersal provide a reliable guide to species that were actually successful colonists?

2. Simultaneous with benthic samples, we collected animals in the drift immediately upstream of control and manipulation sites, and trapped winged adults along the banks. We used PERMANOVA to contrast (i) the assemblages of species in the drift with those in the benthos and (ii) the assemblages of adults, at different sites and times. For 54 common taxa (26 responders; 28 non-responders), we used linear regression to test whether benthic densities were significantly related to drift numbers and, if so, whether the relationship was the same at manipulation and control sites (“nomads”) or delivered higher densities at manipulation sites (“invaders”). We compiled information on dispersal traits (presence in drift, voltinism, flight-capable adults) to assess whether dispersal traits predicted species that successfully colonised manipulation sites.

3. Drift assemblages were more similar to benthic assemblages at manipulation sites than to those at control sites. Adult assemblages did not differ between manipulation sites and controls, but adult

assemblages at downstream sites converged on those seen upstream. Many dispersers arose from within Hughes Creek, with ~ 60% of common taxa arriving via the drift. Among the common taxa, 4% were poor dispersers (rarely in the drift) and 33% were itinerants (drift and benthos were unrelated), with these categories equally represented among responders and non-responders. In the remaining taxa, benthic densities were related to drift numbers. Most responders were invaders, whereas most non-responders were nomads. Responders and non-responders did not differ in traits that are commonly assumed to reflect a high potential for dispersal and colonisation.

4. Responders were not demonstrably better dispersers than non-responders but instead were able to colonise manipulation sites. Contrary to common assumptions, these differences in colonisation ability were not captured by dispersal traits. Colonisation ability has rarely been separated from dispersal ability in stream studies, and yet research in other ecosystems demonstrates that differences in capacity to invade local communities are central to understanding community structure across landscapes.

Introduction

Species differ in their ability to disperse across landscapes to colonise new locations. These differences in dispersal ability can increase population numbers and cause range shifts (Lowe & McPeek, 2014), allow competing species to coexist (Chesson, 2000) and explain variation in species diversity and community structure across patchy landscapes (Logue *et al.*, 2011). Knowledge about dispersal distances and frequencies is therefore vital but both are difficult to measure. Most information about dispersal comes either from species large enough to be tagged and followed individually (e.g. many vertebrates) or from sessile organisms with mobile juveniles (e.g. plants; sessile marine invertebrates) where the appearance of new adults in habitat patches are outcomes of successful dispersal (Hixon, Pacala & Sandin, 2002). In contrast, dispersal is much more difficult to study in communities comprising small, mobile species, such as the invertebrate fauna of streams. While most invertebrates can walk along the stream bed, most such movements are probably related to acquisition of food or refuge. It is unlikely that walking routinely enables individuals to disperse between sites separated by multiple kilometres (Erman, 1986; Freilich, 1991). Alternatively, many stream invertebrates have the potential to use the drift to disperse downstream, but for most species it is unknown how often individuals drift or how far they go (Lancaster, 2008). Additionally, many stream invertebrates are insects that have terrestrial, winged adults, and dispersal can occur during this stage as well. Nevertheless, it is unclear how far most species fly, how frequently, and in what directions (Lancaster & Downes, 2013). Consequently, the extent to which stream communities and populations are affected by frequent dispersal or not is unknown.

To overcome these knowledge gaps, researchers have turned to indirect methods to quantify the effects of dispersal on populations and communities, and yet there are significant limitations associated with such methods. For example, variation partitioning is used to estimate the proportion of spatial variation in densities across landscapes that is unrelated to environmental variables. This “pure” spatial variation is often used as a measure of the role that dispersal constraints play in setting spatial distribution patterns (Logue *et al.*, 2011). Nevertheless, “pure” spatial variation may be caused by factors other than dispersal constraints (Legendre & Legendre, 2012), and variation partitioning provides unreliable estimates of dispersal when used with typical ecological data (Gilbert & Bennett, 2010; Smith & Lundholm, 2010). An alternative, indirect approach is to estimate the influence of dispersal using morphological and behavioural traits that, theoretically, capture the capacity of species to disperse. Coarse-level traits include characteristics such as whether the species swims or crawls, its frequency of occurrence in the drift, whether adults are considered “weak” or “strong” flyers, whether dispersal is “active” or “passive”, and so forth (Usseglio-Polatera *et al.*, 2000; Dolédec *et al.*, 2006; Poff *et al.*, 2006). Dispersal traits have been embraced for hypothesis-testing (e.g. Göthe *et al.*, 2017), but they are based typically on assumptions and collections of observations and “expert knowledge” (Dolédec *et al.*, 2006; Poff *et al.*, 2006) rather than data demonstrating that traits successfully predict either dispersal distances or frequencies.

A further problem with indirect methods is that they cannot distinguish between different dispersal outcomes. While poor dispersers are taxa that move rarely (e.g. fully aquatic invertebrates that rarely enter the drift), good dispersers that commonly move (e.g. are abundant in the drift) may be: (i) unsuccessful dispersers, which reach new locations but fail to colonise them (e.g. because of environmental constraints or inability to compete successfully for resources – termed “itinerants”) or (ii) successful dispersers that reach locations and also colonise them successfully (e.g. juveniles settle into the benthos; adults lay eggs and effect recruitment). These distinctions are important. By definition, itinerants may disperse but are absent as residents from some locations (e.g. Svensson, 1974; Waringer, 1991; Sode & Wiberg-Larsen, 1993; McCauley, 2006; Lancaster & Downes, 2017a), but so are poor dispersers that did not reach these locations at all. Indirect methods to quantify dispersal cannot distinguish between these two different outcomes, and thus all absences are assumed to be due to dispersal constraints. This assumption means that, for indirect methods to be useful, most absences must be caused by poor dispersal ability, not a failure to colonise sites. The frequency of unsuccessful dispersal has received insufficient attention in most empirical studies (Logue *et al.*, 2011; Lowe & McPeek, 2014) and yet evidence suggests it could be common (references above). Furthermore, successful dispersers might also comprise two groups: routinely successful dispersers (“nomads”), which simply maintain existing connectivity and population densities, and extra-successful dispersers (“invaders”), which can exploit novel situations (e.g. new habitat patches or locations with sudden increases in resources) and increase population densities in new locations. Our use here of “invader” does not reference alien or exotic species but reflects use of this term in the coexistence literature, where invaders are species that have a capacity to “invade” local communities when at low densities (Chesson, 2000). Dispersal classifications are likely to be context-dependent, i.e. a particular species may be a successful disperser in one situation and unsuccessful in another.

In this paper we report tests of how different modes of dispersal – drift and adult flight – enabled successful colonisation during a landscape-scale, field experiment, which was designed to test whether species diversity would increase at locations where resources had been boosted (Lancaster & Downes, 2017b). The experiment was carried out along a stream (Hughes Creek) that has filled with sand due to land clearance. The sand buries most terrestrial plant detritus in the stream and consequently there is little detritus present on the bed, and yet detritus is the major source of hard surfaces and energy for the food web (Reid *et al.*, 2008). Downstream, sand-affected locations have about half the species richness of upstream locations, which are less affected by sand and have higher densities of in-stream detritus (Downes *et al.*, 2017). Our experiment boosted the densities of detritus, resulting in increases in species diversities at manipulation sites that were unequivocally caused by dispersal (Lancaster & Downes, 2017b), with some taxa appearing to be invaders, as defined above. Over 12 months, the species composition of manipulation sites gradually converged on those of the more species-diverse, upstream locations. This pattern led us to hypothesize that most colonists were sourced from within the creek itself (rather than from adults flying from elsewhere) with upstream locations providing a source pool of colonists.

During the experiment, we simultaneously sampled dispersing individuals (drifters, winged adults) and benthic communities. These data allow us to ask three questions. First, were the compositions of drift and adult samples consistent with the hypothesis that many prospective colonists arose from within the community of Hughes Creek, particularly from upstream locations? Second, were successful colonists clearly better dispersers (e.g. nomads or invaders) than those that did not colonise resource-rich, manipulation sites? Third, did traits commonly assumed to denote successful dispersal provide a reliable guide to species that were actually successful colonists?

Predictions about dispersal

Our predictions are based on a simple piece of logic. If dispersers arose from within Hughes Creek, then we expected the diversity and abundances of drifters and winged adults to be associated with changes over time at manipulation sites, at both the whole-community level and at the species level for common taxa.

At the community level, we predicted that, if drift dispersal is responsible for experimental responses, then the species composition of drift assemblages should be more similar to benthic assemblages at manipulation sites than to those at controls. This same expectation applies to winged adults, but we were unable to apply the same tests partly because some taxa do not have a terrestrial stage or are difficult to sample and partly because some larvae cannot be identified to species, which prevents species-level matching between adult and benthic assemblages. We also cannot be certain whether adults arose from Hughes Creek or dispersed from another creek. However, if winged adults congregated at manipulation sites and increased benthic densities of larvae (through oviposition), then we predicted that adult assemblages should differ between manipulation sites and controls. Additionally, if many adults fly away from species-rich locations upstream, then we expect that adult assemblages at downstream locations should converge on those of upstream locations.

At the species level, we examined 54 common taxa that were analysed in Lancaster & Downes (2017b), of which 26 responded to experimental increases in detritus and 28 did not. Here, we test whether "responder" taxa dispersed primarily via the drift or by adult flight, and whether they qualify as invaders. Similarly, for the "non-responder" group we test whether they were poor dispersers or good dispersers that failed to exploit the resource-rich manipulation sites (i.e. were itinerants). To examine the role of drift as a dispersal route, we tested whether benthic densities were positively related to numbers in the drift sampled at commensurate times (employing similar logic and approaches to Downes & Lancaster, 2010). Drift numbers can be considered a predictor of (rather than just correlated with) benthic densities because drift was sampled upstream of each site (explained further below). If successful dispersal is frequently via the drift, then we expected a positive relation between benthic densities and drift numbers, whereas if drift is infrequent (poor dispersers) or drifters are unsuccessful (itinerants), then these two variables should be unrelated (Fig. 1). Drifters may be unsuccessful if environmental conditions are unsuitable or if densities of residents are sufficiently high that drifters are unable to “invade” sites.

Alternatively, if drift numbers and benthic densities are positively related, the *slope* of that line estimates the rate at which numbers in the drift contribute to benthic densities. Thus a slope of 0.2 means an average 20% of drifters contribute to benthic densities, and significantly steeper slopes mean this percentage is consistently greater. The *y-intercept* suggests the degree to which benthic densities arise solely via the drift. Thus, if the line intersects the origin, this implies that all individuals in the benthos arose from the drift and that densities do not build up over time (if drift = 0, then benthic densities = 0). In contrast, if the *y*-intercept is significantly > 0, then benthic densities may build up over time from the drift but also potentially via other dispersal routes (e.g. recruitment via egg-laying by adults).

We can use this reasoning to identify species that are nomads because these taxa will have slopes and *y*-intercepts that are the same for both manipulation and control sites – i.e. they are species that dispersed and colonised sites routinely from the drift but did not respond when resources were increased. Invaders may show either of two outcomes: (1) a steeper slope at manipulation sites than control sites, which shows a higher rate of colonisation from the drift when detrital densities are increased (Fig. 1) or (2) lines that have the same slope but with a greater *y*-intercept for manipulation sites compared to controls (Fig. 1). In this second outcome, drift may be responsible for the build-up in densities at manipulation sites but recruitment following oviposition by adults may also contribute.

When drift is the main source of colonists, manipulation sites could theoretically build up densities so high that these sites then contribute to the drift, which could therefore gradually shift the distribution of species in a downstream direction. We did observe such zonal changes during the experiment (Lancaster & Downes, 2017b). For example, some upstream specialists (species that are restricted to or with highest densities in upstream locations) gradually colonised locations further and further downstream. If drift caused such changes, then zonal shifts in densities should be explained entirely or mainly by adding drift as a covariate to re-analyses of benthic densities.

For commonly trapped species of adults, we tested whether manipulation sites attained higher numbers than control sites, following the logic above. We also tested whether adult numbers were correlated with benthic densities of larvae. Although the direction of cause-and-effect is unclear (high larval densities can deliver high local emergence of adults or high local densities of adults can deliver high densities of larvae following oviposition), the existence of such associations would suggest a potential route for successful dispersal.

To examine the efficacy of traits in predicting which species would respond to the experimental manipulation over 12 months, we tested whether the frequencies of certain characteristics differed between responding and non-responding taxa. First, we examined the frequencies of taxa with some traits that are commonly assumed to be associated with successful dispersal (i.e., good dispersal and colonisation) in stream invertebrates and that could be assigned with confidence to the taxa in this system: voltinism, presence in the drift, flight-capable adults. Second, we examined frequencies of taxa categorised as different kinds of disperser using empirical data from this study (poor, itinerant, nomad or invader).

Methods

Study site and experimental design

Hughes Creek is in central Victoria, south-eastern Australia, and has been described extensively in previous research (Downes *et al.*, 2011; Downes *et al.*, 2017; Lancaster & Downes, 2017b). In brief, the creek arises on the Black Range and drains the granitic Strathbogie batholith, which produces coarse sandy sediment when eroded. Upper parts of the channel originally comprised chain of ponds with percolines (underground networks of water seepage zones and soil pipes: Erskine, 2016), but land clearance (coupled with bushfires and floods) created incision gullying and increased erosion rates; this produced an extensive sand slug in Hughes Creek, which did not exist prior to the 1920s (Erskine, 2016). The sand has buried the original stream bed, and the active channel is now much wider and the water shallower. Most terrestrially sourced plant detritus is either swept away during floods or buried under sand. Sandy locations thus have sparsely treed riparian zones, low densities of detritus, a bed of shifting sand and shallow, warm water. Temperature loggers showed that water temperatures at downstream locations were often > 29 °C and reached up to 36 °C on hot days, e.g.

where air temperature exceeded 40 °C (Downes *et al.*, 2017). Downstream locations have approximately half the number of invertebrate species found in cooler, more intact upstream areas (Downes *et al.*, 2017). Movement of animals in these sandy zones is predominantly through swimming and the drift, with few individuals walking across the sand (Lancaster & Downes, unpublished observations).

The experiment, described in detail in Lancaster & Downes (2017b) was carried out over a 22 km length of Hughes Creek, with two control and two manipulation sites in each of three zones (upstream, middle and downstream) that reflected the changing environment of the stream. Upstream locations were above the sand slug, downstream sections were fully swamped with sand, and middle sites reflected a transition zone with gradually increasing amounts of sand across the bed. Sites were 40 m channel lengths and were on average 1.6 km apart (range of 0.6 to 3.7 km). We boosted the density of plant detritus (leaves, bark, wood) at manipulation sites using pairs of stakes hammered into the stream bed, which trapped and held detritus floating downstream (density of pairs ranged from 0.13 to 0.19 per m^2 depending on local channel morphology). Control sites received no stakes. Detritus and benthic densities were sampled pre-manipulation, 1, 4, 9 and 12 months following the start of the experiment in January 2013. Our sampling methods have been described in detail in previous studies (Downes & Lancaster, 2010; Downes *et al.*, 2017). In brief, on each sampling occasion we collected 10–15, randomly placed benthic samples per site using a Surber sampler (0.09 m^2, 250 µm mesh). Sites are replicates in our statistical analyses so samples were composited, and then subsampled to provide a single estimate of detritus and invertebrate densities per site (further details in Lancaster & Downes 2017b).

The stakes increased the density of detritus greatly (up to 42x at downstream manipulation sites compared to control sites). This was matched by 1.3x, 1.9x and 1.6x increases in species richness at manipulation sites compared to controls in upstream, middle and downstream zones, respectively. The species composition of communities in middle and downstream manipulation sites gradually became more similar to upstream sites, in strong contrast to controls, which showed only inter-annual variation and changes reflecting seasonality (Lancaster & Downes, 2017b).

Drift and adult sampling protocols

Drift nets (20 x 30 cm opening, 150 µm mesh size) were installed in a row across the creek and located 2 – 3 m upstream of the upstream boundary of each site. We used between three and five nets, with more nets deployed for wider streams. Nets were installed at variable heights in the water column to ensure it was representatively sampled but nets were at least 3–4 cm above the stream bed. We measured the cross-sectional area of the stream in front of nets (depths were measured every 50 cm). We collected drifting insects for two hours beginning at the end of civilian twilight on the same dates benthic samples were collected post-manipulation (above). Samples from all nets at a site were composited into a single sample and preserved.

For two hours after twilight, we sampled adults using light traps, which comprised a black tub inside which an ultraviolet light (6W, 12V triphosphor fluorescent lamp, 225 mm long) was laid over a tray containing ethanol. Placing lights inside tubs ensured that light did not spill sideways, and only adults flying above traps were attracted (Collier & Smith, 1998). Three light traps were used at each site, with one each placed at the upstream and downstream ends and one in the approximate middle. All adult insects trapped at each site were combined into a single sample.

In the laboratory, drifting invertebrates were identified to the lowest taxonomic level possible (usually species, sometimes genus) and total numbers of individuals in each composited sample were counted. We calculated the proportion of the cross-sectional area of the stream that was intercepted by nets, and used this proportion to estimate the total numbers of each taxon that drifted into each site. We did not standardize drift numbers for differing discharges flowing through nets. Although this standardization is common, our question requires estimates of the total numbers of drifters, not drift numbers per unit volume of water – i.e. drift densities – which are not germane (Downes & Lancaster, 2010; Lancaster, Downes & Arnold, 2011). Moreover, drift numbers and discharge can be unrelated, resulting in very poor estimates of densities (Downes & Lancaster, 2010; Downes, 2010).

For adult samples, we identified and counted all species, genera or families known to live in streams, with the exception of Diptera. The majority of non-dipteran, aquatic taxa were Trichoptera, Coleoptera and Hemiptera, because light traps typically do not attract other taxa effectively (e.g. Ephemeroptera or Plecoptera). Only males could be identified to species for some caddisfly taxa, and so counts of males were used for tests for these species.

Statistical analysis

Multivariate analyses

Drift and adult data were 4th root transformed and similarity matrices for each data set created using the Bray-Curtis coefficient (Anderson, Gorley & Clarke, 2008). We first tested whether drift assemblages that arrived at control sites differed from those that arrived at manipulation sites. Although manipulation and control sites were intermingled along the creek, control sites downstream of one or more manipulation sites might receive differing numbers or identities of animals. We tested for this possibility by using a 3-factor, repeated measures PERMANOVA (Anderson *et al.*, 2008). The model contained the crossed factors of Zone (upstream, middle, downstream), Treatment (manipulation, control) and Date (a repeated measure). Then, we compared drift and benthic assemblages using a 4-factor, repeated measures PERMANOVA (same terms with the addition of Sample type). Assemblages of adults were compared between manipulation and control sites, zones and times using a 3-factor, crossed design in PERMANOVA. We illustrated significant differences in PERMANOVA models using non-metric multidimensional scaling (NMDS) (Anderson *et al.*, 2008).

Univariate analyses

For each of the 54 common taxa examined by Lancaster and Downes (2017b), we tested whether benthic densities were related to drift numbers across the 12 sites sampled on the four post-manipulation occasions (N = 48 pairs) using ANCOVA applied to log-transformed data. The model contained the fixed factor of treatment (control vs manipulation sites), the covariate of drift numbers and an interaction between treatment and drift numbers (which tests whether the slope of the line varied between treatments). For species where the slopes of lines were the same, the Treatment term tests whether the *y*-intercepts were statistically different following adjustment for the covariate.

To test whether drift explained changes to zonal distributions, we re-analysed the benthic data of responders using a 2-factor factorial ANCOVA, with Treatment crossed with Zone, with drift numbers as a covariate.

For common adult taxa, we tested whether abundances were higher at manipulation sites than controls using a 3-way ANOVA, and whether larval densities and adult numbers were associated using the Pearson correlation coefficient.

Finally, we categorised each of the common 54 taxa into one of four groups as illustrated in Figure 1: (1) rarely occurred in the drift (poor dispersers); (2) no relation between drift and benthic densities for both control and manipulation sites (itinerants); (3) a significant relation between drift and benthos with similar slopes and *y*-intercepts for manipulation and control sites (nomads); (4) significant relations between drift and benthos with slopes or *y*-intercepts that varied between treatments (invaders). We tested whether the frequency of taxa in each class varied between responding and non-responding taxa, using Fisher's exact test. We also compared the frequencies of taxa with traits commonly assumed to reflect successful dispersal between responding and non-responding taxa, specifically voltinism, presence in the drift and terrestrial winged adults. Thus, invertebrates that are good drifters, have flight capable adults and short generation times (multivoltine) are often assumed to have a high potential for successful dispersal and colonisation over the time scale of this experiment (12 months).

All statistical tests were two-tailed and used $\alpha = 0.05$.

Results

Multivariate analyses of assemblages

Drift did not vary systematically between manipulation and control sites on any date or in any zone (all terms involving Treatment with P > 0.05; analysis not shown for brevity) and thus manipulation and control sites were exposed to similar drift assemblages. This finding is consistent with previously published tests that showed that spatial autocorrelation between sites did not affect hypothesis tests on benthic densities (Supplementary Appendix 5 of Lancaster & Downes, 2017b). When drift and benthos were compared, unsurprisingly drift assemblages differed from benthic assemblages, however the degree of difference varied with both time and treatment (Table 1a, Sa × Trt × Time term). Benthic communities at control sites were dissimilar to drift samples on every date (pair-wise tests, all with $P < 0.05$). Benthic communities at manipulation sites were also dissimilar to drift assemblages, but less so, and after four months drift and benthic communities were statistically the same (Fig. 2). On NMDS plots for nine and 12 months following the start of the experiment, benthic assemblages at manipulation sites occupied a position between benthic assemblages at controls and all drift assemblages (Fig. 2).

Large numbers of adults were trapped only during the summer months, hence analysis was restricted to data from 1 and 12 months (February 2013 and January 2014). Additionally, unseasonal cold weather on one day in February 2013 resulted in very few adults trapped at the middle sites being sampled on that day. Consequently, we used data only from up- and downstream sites. Multivariate analysis of these data showed that manipulation and control sites did not differ in species composition (Table 1b, Treatment effect). Upstream and downstream assemblages differed from each other but this difference changed over time (Table 1b, Zone × Time term). Twelve months after the experiment was started, the assemblage of adults at downstream sites more closely resembled those found at upstream sites than they did at the start (Fig. 3).

Relations between drift and benthos

Benthic densities were significantly related to drift numbers for 34 taxa (successful dispersers), with the remaining 20 taxa showing no relationship between these variables (Table 2, Table S1 – for brevity, outcomes of these 54 statistical tests are not reported). Model R^2 values for successful dispersers varied (responders: 47 – 73%; non-responders: 43 - 79%), but were typically much higher than for unsuccessful dispersers (responders: 29 – 53%; non-responders: 8 – 47%). For two taxa, drift numbers were too small to permit analysis, suggesting these taxa drifted infrequently (i.e. poor dispersers). The remaining 18 taxa were unsuccessful dispersers – i.e. itinerants.

Of the 34 taxa defined as successful dispersers, 13 were nomads and 16 were invaders (Table 2, Fig. 4). In 4 of 13 nomads (one responder and 3 non-responders: Table S1), the *y*-intercept was greater than zero, whereas the line passed through the origin for all others. For most invaders, lines for most manipulation sites lay above those of controls (i.e. different *y*-intercepts) but slopes of the lines did not differ between treatments. Slopes differed between treatments for only three taxa, two responders (both stoneflies) and one non-responder (snails) (Table S1). Five taxa could not be classified: one with indefinite findings due to too many zero values, two where detritus appeared to deter density increases, and two with complicated responses. The latter (both classes of Diptera) showed drift-benthos relations at controls but no such relations for manipulation sites.

Did drift rates explain zonal changes?

In 11 responders, benthic densities were related to drift numbers with similar slopes of lines at manipulation sites and controls (Table S1), which permitted re-analyses of their benthic data with the inclusion of drift numbers as covariates. These analyses altered the outcomes of tests on zonal differences for three species (Table S2). The upstream specialist *Austrosimulium furiosum* (a blackfly) colonised manipulation sites in middle and downstream zones during the experiment (Lancaster & Downes, 2017b). This zonal change became non-significant with the inclusion of drift numbers as a covariate, suggesting drift played a major role in the appearance of this species downstream. Likewise, *Cheumatopsyche* sp. AV2 (a downstream specialist) showed benthic increases at manipulation sites downstream (Lancaster & Downes, 2017b), but the inclusion of drift numbers in the analysis removed zonal differences. In the third taxon (*Ecnomus continentalis*) the inclusion of drift as a covariate created a zonal difference, with downstream locations having significantly lower benthic densities than middle or upstream sites once benthic densities had been adjusted for drift rates.

Analyses of adults

Virtually all the common taxa were insects with winged adults. The two non-winged taxa (snails, limpets) were equally represented in the responder and non-responder groups. Taxa with terrestrially based, winged adults occurred in similar proportions in responder and non-responder groups (92% and 82%, respectively, a non-significant difference). Of the 54 common taxa, 27 were non-dipteran insects and 14 were caught in light traps. These 14 taxa showed no differences in numbers trapped at control and manipulation sites, a pattern that was also true for all other species of adults we caught (99 of 105 separately identified taxa). In three of the 14 taxa, numbers of trapped adults correlated with larval, benthic densities. Two of these were the caddisflies *Cheumatopsyche* AV2 ($r = 0.80$, $P < 0.001$) and *Ecnomus continentalis* ($r = 0.59$, $P = 0.02$), which were both responders. In each case, the highest numbers of adults and benthic larval densities were collected at downstream sites, for both taxa. The third taxon was *Laccobius* spp. ($r = 0.75$, $P = 0.001$), a genus of beetles that did not respond to the manipulation.

Traits for successful colonisation

Responding and non-responding taxa did not differ in traits that are commonly assumed to reflect a high potential for dispersal and colonisation (Table 3). Statistical tests were non-significant for each trait tested individually, or combined, i.e. the frequency of taxa having all three of the best traits (multivoltine, common in the drift drifters and adult flight). Using the drift dispersal types defined empirically, the frequency of poor, unsuccessful and successful disperses did not differ between responders and non-responders (Table 2). The responders classified as poor or unsuccessful drifter dispersers all had flight-capable adults. Considering only the successful drift dispersers, most responders were invaders. Most non-responders were nomads, but four were invaders (Table 2).

Discussion

This paper provides rare, direct evidence of which taxa are successful dispersers and colonisers in a community of stream invertebrates, and their modes of dispersal (drift vs adult flight). Direct, empirical evidence of dispersal is difficult to collect and we used a novel, field-based approach that can differentiate between different kinds of dispersers. During a field experiment that successfully increased benthic species diversities at resource-rich manipulation sites along Hughes Creek (Lancaster & Downes, 2017b), we simultaneously collected independent data on dispersers. In conjunction with benthic data from the experiment, these new data on dispersers indicate that successful colonists mainly arose from individuals present in the same creek, dispersal constraints did not preclude colonisation by almost any taxon, and traits commonly assumed to reflect the potential for successful dispersal were not reliable in predicting which species responded to the experiment. Successful colonists were, however, more likely to be invaders capable of exploiting novel situations.

Many successful colonists arose from individuals present in Hughes Creek, and predominantly from upstream areas, in this relatively short term (12 months) and large-scale experiment (22 km stream length). Dispersal via the drift appeared to play a strong role in colonisation of manipulation sites. Drift assemblages were associated with changes in the benthos at manipulation sites, including one month where these two types of assemblages were not statistically different. At the species level, drift was associated with benthic densities in ~ 60% of common responders, including taxa where drifters rarely colonised control sites (e.g. stoneflies). Drift also explained shifts in distributions of taxa that gradually appeared at downstream locations. These outcomes suggest that manipulation sites acted as “stepping stones” that allowed species to move gradually further and further downstream. For species that were predominantly upstream specialists, manipulation sites allowed these taxa to shift their distributions by up to 20 km downstream. Overall, this apparently strong role of drift dispersal would explain why the faunal composition of middle and downstream sites converged on that of upstream sites (Lancaster & Downes, 2017b).

Benthic changes caused by dispersal during the adult stage are more difficult to pinpoint because we cannot determine the origin of trapped adults (from Hughes Creek or another stream), but two findings suggest adult movement played a role in the experiment. The similarity in adult numbers between control and manipulation sites plus the convergence of downstream adult assemblages on those upstream after 12 months both suggest adults disperse along the channel. Nonetheless, it is difficult to separate the effects on benthic densities of adult movement (followed by recruitment) from those caused by dispersal of individuals in the drift. For example, larval densities of both the hydropsychid *Cheumatopsyche* sp. AV2 and the ecnomid *Ecnomus continentalis* were correlated with adult numbers during summer, particularly at downstream sites. Both of these caddisflies lay their eggs on bark and wood (Macqueen & Downes, 2015) and this provides a simple mechanism for how larval densities could have been increased by oviposition in detritus-rich locations. Nevertheless, benthic densities of both species were also strongly related to drift numbers, which explained increases at downstream sites in both cases. It is thus difficult to separate effects of adult and larval dispersal but for these taxa it is likely that both played a role.

There were no obvious differences in dispersal *ability*, when measured using drift, between species that responded to the experiment compared to those that did not. Non-responders and responders were just as likely to be good drifters, and an equivalent proportion of their taxa were successful dispersers (i.e. drift numbers associated with benthic densities). Thus, non-responders were not poor dispersers that failed to reach manipulation sites. Rather, the difference between responders and non-responders lay in the outcomes for successful dispersers. Thus, responders were all invaders, except for two nomads (the caddisflies *Cheumatopsyche* sp. AV2 and *Triplectides ciuskus*), and, for these two taxa, adult flight may be more important than drift (as considered above). Alternatively, most non-responders were nomads but interestingly four were invaders. This latter outcome suggests that drift contributed to their benthic densities at manipulation sites, but that the colonisation success of drifters was not sufficiently high across all sites and times to increase densities across the board. These taxa may be good examples of species that may become responders under different circumstances. Nevertheless, the overall predominance of successful dispersers show that many taxa clearly maintain connectivity and benthic densities along the stream length via the drift. Non-responders and responders were also just as likely to have a terrestrial winged adult, and their adults were present at all sites. Most of the poor or unsuccessful drifters in the responder group also had winged adults, and adult dispersal may therefore have been involved in their response. Overall, dispersal ability *per se* thus did not differ between those taxa that responded and those that did not.

This poses a question: why did half of the common taxa not respond to the experiment? One possible explanation is that these taxa did not require detrital resources, but this seems unlikely for at least two reasons. First, packs of plant detritus offered a broad array of resources, such as food (e.g. biofilm, leaves, organic particles), places to attach (e.g. for filter-feeders), and refuge from flow or predators. Second, many non-responders were taxonomically related to species that did respond and/or had similar resource requirements. For example, the caddisfly *Ecnomus continentalis* responded whereas *E. cygnitis* did not, despite both having similar habitat and resource requirements (both taxa spin nets to capture prey). Other comparable responder/non-responder pairs include the filter-feeding blackflies *Austrosimulium furiosum* vs *Simulium ornatipes*; the grazer/scraper mayflies *Offadens* sp. vs *Tasmanocoenis tillyardi* and the chironomid grazer/scrapers *Thienemanniella* sp. vs *Corynoneura* sp. (Lancaster & Downes, 2017b). A similar pattern of species that dispersed successfully but failed to colonise sites (i.e. itinerancy) was also seen among some adult caddisflies in a separate study. Adults of three species of *Ecnomus* and seven other species of caddisflies from four different families were routinely trapped along Hughes Creek over three years, but their larvae were very scarce and more often absent (Lancaster & Downes, 2017a).

Unsuccessful colonisation may be due to environmental constraints. For example, water temperatures at downstream locations exceed 29 °C when the air temperature reaches ~34 °C, which is a relatively common occurrence during summers (Downes *et al.*, 2017). Water temperatures of 30 °C are extreme for most insects (Lancaster & Downes, 2013) and can be associated with low oxygen concentrations in Hughes Creek as well (Lancaster, Downes & Glaister, 2009). Such conditions could present significant barriers to colonisation by some species. However, most non-responders had wide distributions (i.e. were in downstream locations: Table S1), which suggests that environmental conditions did not by themselves constrain colonisation. A remaining possibility is that non-responders were unable to compete for resources with responders or were more vulnerable to predation (by fish, platypus or invertebrate predators), but we have no data that can bear on this speculation.

Traits commonly assumed to reflect good dispersal ability and colonisation success could not reliably predict which species would colonise manipulation sites. Dispersal traits are based on assumptions about dispersal ability based on body morphology, observations of behaviour or swimming ability (often made in laboratories), frequency in the drift, perceived flight capacity of adults, and so forth (references above). These traits can only measure the influence of movement if most good dispersers are also successful dispersers. If instead colonisation ability more often dictates successful dispersal, as seen here, then dispersal traits will provide little guidance. Moreover, it is rare for empirical studies to acknowledge that colonisation ability is important and that unsuccessful dispersers may become successful if conditions within locations change (e.g. physical environment becomes more suitable, resources increase, etc.). In these situations, dispersal traits will underestimate the role that dispersal can play in community dynamics. Of course, dispersal ability may play a stronger role over spatial scales larger than we have examined here, but dispersal over large spatial scales may reflect biogeographic processes (e.g. range extensions) rather than community dynamics.

Our data also suggest that the characteristics used to form traits need to be used with some caution. For example, it is well known that presence in the drift, even when that is common, does not automatically signify that species travel long distances, even for “champion” dispersers such as the mayfly *Baetis* (Elliott, 1971; Lancaster, Hildrew & Gjerlov, 1996; Downes & Lancaster, 2010; Lancaster *et al.*, 2011). Here, late instar specimens of the cased caddisfly *Triplectides cuiskus* drifted, and drift numbers were significantly associated with benthic densities. Nonetheless, drifting *T. cuiskus* were nomads, not invaders. Mature specimens were never found in the drift outside of the upstream zone where this species is largely restricted (Downes *et al.*, 2017; Lancaster & Downes, 2017b).

Observations on morphology and behaviour, especially in a laboratory setting, may also mislead. For example, molluscs are commonly observed to move by crawling (as do many other species, such as cased caddis). We found that snails and the limpet *Ferrisia petterdi* routinely drifted and that drift numbers were related to benthic densities, suggesting that this is how these species disperse in Hughes Creek; they were not poor dispersers. It is clearly imprudent to assume that molluscs disperse only by crawling in all systems, and this example serves to emphasise that dispersal traits need to be tested, i.e. evidence-based.

Is the level of influence of dispersal success on invertebrate densities in Hughes Creek unusual? We cannot answer this question because we have not located any other studies that have quantified how dispersal success affects stream invertebrate densities at relevant spatial and temporal scales. Most empirical studies are surveys that use indirect methods for quantifying dispersal that are problematic (as discussed in the introduction) or are experiments done in micro- or mesocosms (e.g. artificial stream channels), which cannot emulate the effects of drift dispersal occurring over many kilometres and months, and do not examine adult dispersal at all. One important source of information comes from genetic studies; these suggest that flight is the major dispersal mechanism for insects having winged adults, while in-channel dispersal (e.g. via the drift) is more critical for species that are fully aquatic (Hughes *et al.*, 2008). Of course, dispersal that creates genetic homogeneity may be insufficient to influence population densities, but genetic studies have identified geographic features that are barriers to adult dispersal (e.g. deep canyons, large lowland areas, mountain ranges: Hughes, Huey & Schmidt, 2013). Likewise, a small group of studies have identified features that can block drift dispersal such as waterfalls: (Hughes *et al.*, 1995) and pools (Brooks *et al.*, 2017). Rivers may vary in the frequency or existence of such barriers, and this variation could result in systematic differences between rivers in dispersal success. Hughes Creek is a predominantly sandy bed stream with some pools and bedrock outcrops throughout the sections we studied (Erskine, 2016). We do not know how geomorphology influenced the outcomes of our experiment, but it would be fascinating to know how channel morphology interacts with dispersal abilities to influence the colonisation success of fauna.

In this vein, it is interesting to note that, like freshwater ecologists, marine ecologists also assumed that traits (e.g. larval morphology, longevity) should deliver different dispersal abilities that would explain the densities of species in different places (stimulated by a comprehensive review of larval biology by Thorson, 1950). While some of these dispersal traits have proven somewhat useful in capturing dispersal ability, local oceanographic features are often influential in determining which dispersers arrive at a location. Additionally, colonisation failure is often more important, because many successful dispersers fail to settle or settle but do not survive (review: Schiel, 2004). It seems feasible that colonisation failure among river fauna is also common, but we need many more, purpose-designed studies reporting data that can test such hypotheses directly.

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Conflict of interest

Neither author has a conflict of interest.

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Table 1 Summary of PERMANOVA for two data sets: (a) Drift & Benthos: a 4-factor, repeated measures design comparing larval invertebrate assemblages between sample types (drift vs benthic samples), experimental treatments, zones on the stream gradient, and over time (a repeated measure). Subjects in these analyses are sites. (b) Adults: a 3-factor, crossed design comparing adult insects between experimental treatments, zones on the stream gradient, and times. Lines in bold are referred to in the text. See Figures 2 and 3 for illustrations.

Data set	Source	df	MS	Pseudo-*F*	*P*
(a) Drift & Benthos	*Between subjects*				
	Sample type	1	15385	24.8	<0.001
	Treatment	1	2882	1.88	0.094
	Zone	2	6658	4.35	0.010
	Sa × Trt	1	2704	4.35	0.011
	Sa × Zone	2	1555	2.50	0.024
	Trt × Zone	2	1166	0.762	0.691
	Sa × Trt × Zone	2	666	1.07	0.415
	Sa × Subject (Trt × Zone)	6	621	1.14	0.218
	Subject (Trt × Zone)	6	1531		
	Within subjects				
	Time	3	9694	12.8	<0.001
	Sa × Time	3	2542	4.68	<0.001
	Trt × Time	3	1010	1.33	0.078
	Zone × Time	6	1267	1.67	0.002
	Sa × Trt × Time	**3**	**893**	**1.64**	**0.018**
	Sa × Zone × Time	6	936	1.72	0.002
	Trt × Zone × Time	6	686	0.904	0.733
	Subject (Trt × Zone) × Time	18	758	1.40	0.002
	Sa × Trt × Zone × Time	6	650	1.20	0.146
	Error	18	543		
(b) Adults	**Treatment**	**1**	**415**	**1.01**	**0.445**

	Zone	1	4563	11.1	0.001
	Time	1	2967	7.24	0.002
	Trt × Zone	1	396	0.967	0.469
	Trt × Time	1	237	0.578	0.792
	Zone × Time	**1**	**1195**	**2.91**	**0.010**
	Trt × Zone × Time	1	393	0.959	0.503
	Error	8	410		

Table 2. Classification of 54 responding or non-responding taxa into one of three types of drift disperser, reflecting outcomes of tests for relationships between benthic densities and drift rates (see text). The proportions in different classes did not differ between responding and non-responding taxa (Fisher’s exact test: $P = 0.999$). Successful dispersers were then subdivided into nomads and invaders, as defined in the text. Five successful dispersers could not be classified into either category (“unclass.” - see Table S1). The proportions in different classes differed significantly between responding and non-responding taxa (Fisher’s exact test: $P = 0.003$). Table S1 lists which taxa belonged in each group.

	All groups				Successful dispersers			
	Poor	Itinerants	Successful	Total	Nomads	Invaders	Unclass.	Total
Responders	1	9	16	26	2	12	2	16
Non-responders	1	9	18	28	11	4	3	18

Table 3 Frequency of responder and non-responder taxa with three traits commonly assumed to reflect the potential for successful dispersal, and with the three "best" traits combined. *P*-values are outcomes of Fisher's exact test comparing frequency of taxa that were responders or non-responding. Voltinism: M = multivoltine, BUS = bi- uni- or semivoltine. MDF = multivoltine, common in drift and capable of adult flight. Table S1 lists which taxa belong to which group.

	Voltinism (P = 0.404)		Drift (P = 1)		Adult flight (P = 0.999)		Combined (P = 0.405)	
	M	BUS	Common	Rare	Yes	No	MDF	Others
Responders	12	14	25	1	23	3	11	15
Non-responders	15	10	27	1	24	2	14	11

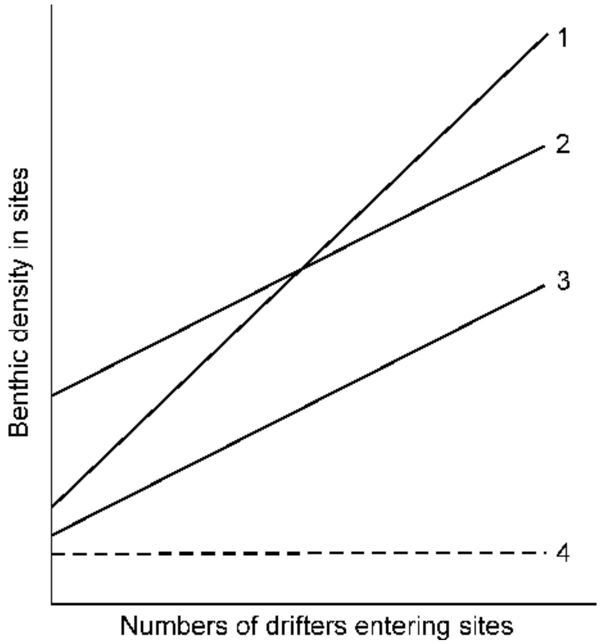
Figure captions

Figure 1 Illustration of expected outcomes from relating benthic densities to drift numbers that were measured at commensurate times and just upstream of where benthic samples are collected. If drift dispersal of a species drives changes in benthic densities, then we expect a relation between drift numbers and benthic density (line 1, 2 or 3), whereas if drift is not a source of colonists or dispersers are unsuccessful, then we expect no such relation (line 4, dashed to indicate no relationship). If the relationship for manipulation sites achieves a greater *slope* than that for controls (line 1 vs line 3), then this suggests that detritus increases the rate at which drifters contribute to benthic densities; this effect could also occur where control sites receive no increases via the drift at all (line 1 vs line 4). Alternatively, if manipulation sites have a similar slope to controls site but a higher *y*-intercept (e.g. line 2 vs line 3), then this suggests that, while the rate at which drifters contribute to benthic densities is consistent between manipulation and control sites, benthic densities build up at manipulation sites. This latter increase may be caused by drift or by new recruits following adult oviposition.

Figure 2 NMDS plots comparing drift and benthic assemblages from control and manipulation sites 1, 4, 9 and 12 months after the start of the experiment (February, May, October 2013 and January 2014, respectively). Data were analysed together but each date is plotted on a separate graph to illustrate patterns. The numbers in the bottom left corner of each graph indicate for control and manipulation sites the average similarity between benthos and drift on that date, with an asterisk indicating whether the difference was statistically significant.

Figure 3 An NMDS plot of adult data comparing species compositions between up- (Up) and downstream (Down) sites from one month after the start of the experiment (Feb 2013) to 12 months after the start (Jan 2014).

Figure 4 The benthic density (number per m^2) of four invaders, (A**)** all snails, (B) all Gripopterygidae (other than *Dinotoperla*) (Plecoptera), (C) *Atalophlebia* spp. (Ephemeroptera) and (D) *Austrosimulium furiosum* (Diptera, Simuliidae), at control (open circles, dotted line) and manipulation (closed circles, solid line) sites *versus* the number of individuals of these species drifting into sites (over two hours at sunset) at dates commensurate with benthic samples. All values had one added to enable plots on $\log_{10}$ scales. Lines represent outcomes of regression analyses as reported in the text (see Results) and relevant tests are reported in each panel. In (A) and (B), the slopes of lines differ significantly between manipulation and controls sites, whereas in (C) and (D), the slopes are the same but the y-intercept is greater at manipulation sites than controls. Tr x D = Treatment x Drift covariate interaction; D = Drift covariate (Tr x D is insignificant); *y*-int = test for difference in y-intercepts for manipulation and control sites; *F* = value of F-statistic; *P* = probability; R^2 = value of R^2 for full model.



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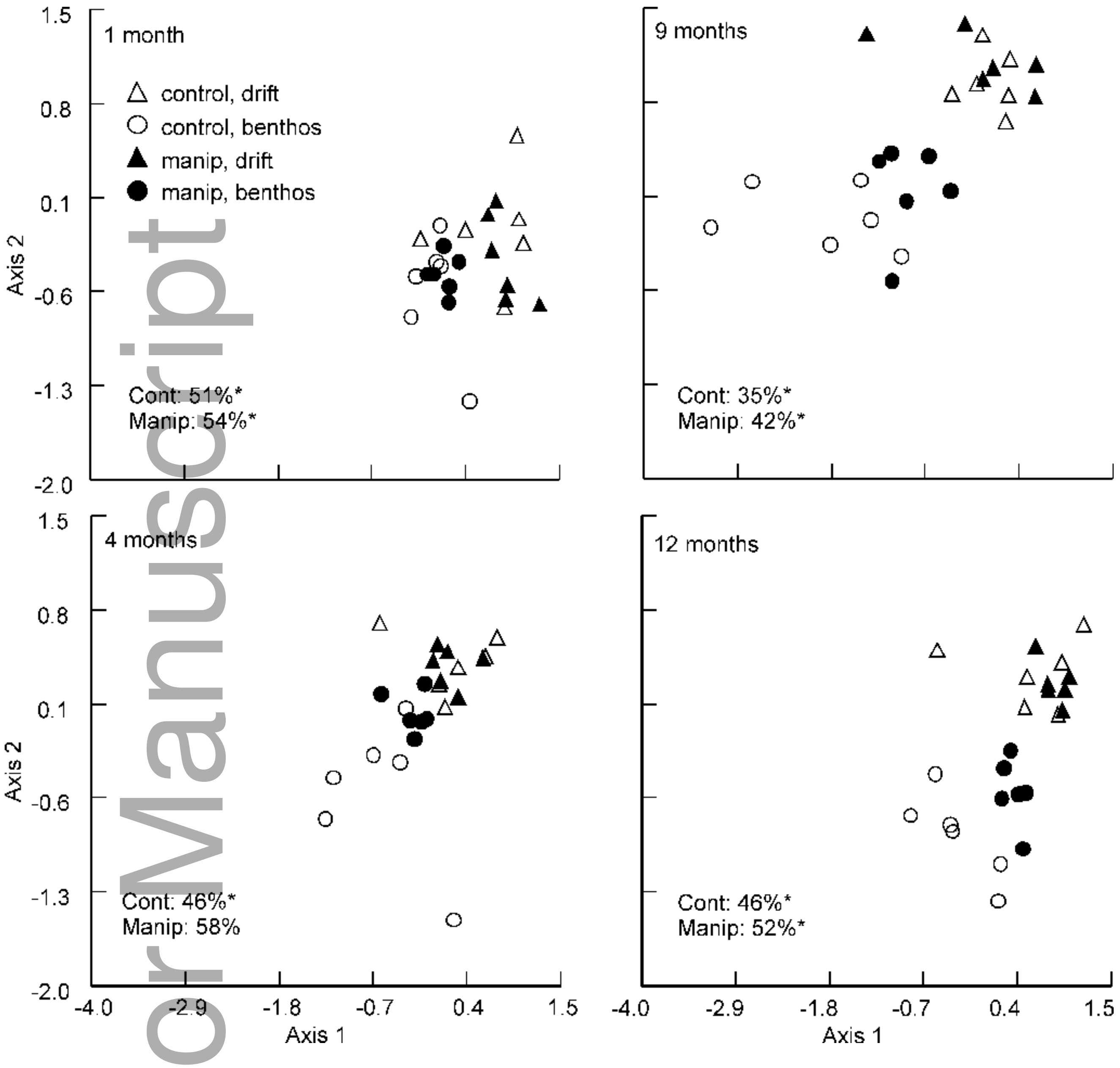

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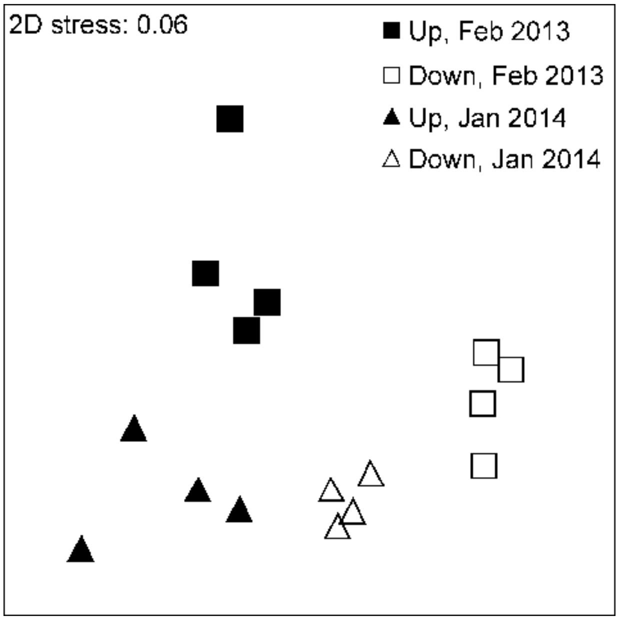

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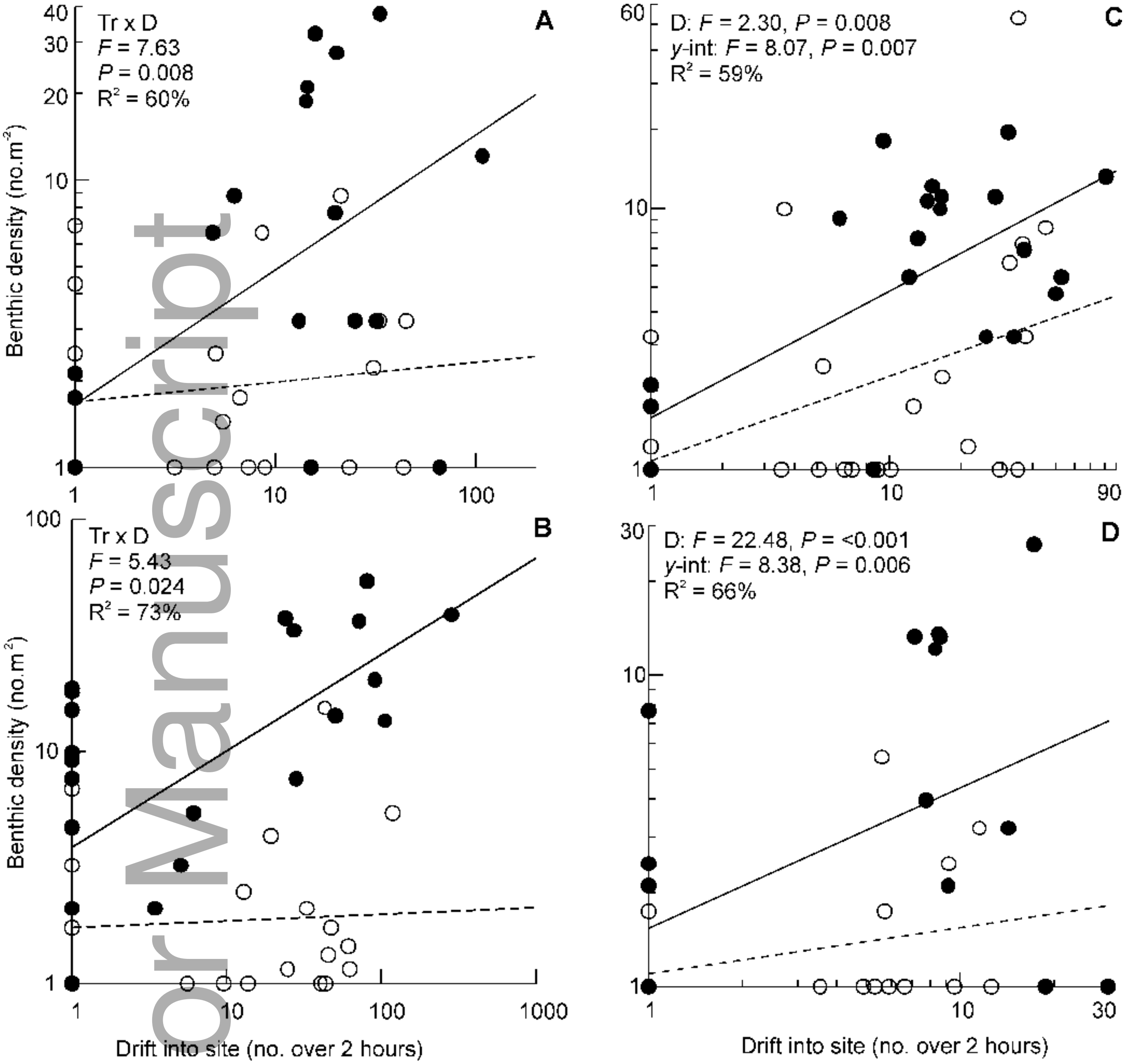

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