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A landscape-scale field experiment reveals the importance of dispersal in a resource-limited metacommunity

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Abstract

Dispersal may play a strong role in driving species diversity across landscapes. Theoretically, dispersal permits species to remain extant within a metacommunity, even if they are periodically excluded from some local communities. Field tests of dispersal effects are difficult, and most non-experimental data suggest that environmental conditions play the predominant role in setting species diversity. However, most such studies cannot differentiate between patterns caused primarily by dispersal constraints vs abiotic factors vs biotic constraints (e.g. priority effects). In

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31 22 km of a sand-bed stream in southeastern Australia, strong longitudinal gradients in the abiotic
32 environment and detritus densities (resources) mean that downstream locations have abiotic
33 conditions that may be physiologically stressful, low resource densities and low species
34 diversities. We experimentally increased the retention of detritus over 40 m stream lengths along
35 the gradient, with other sites acting as controls. If dispersal is constrained, or abiotic or biotic
36 factors primarily control community structure, then we predicted that increasing resources would
37 result in no change in species composition. Alternatively, if dispersal is common, we predicted
38 that species diversity would increase at treatment sites through colonization by species able to
39 tolerate abiotic conditions downstream and able to invade established communities. Invertebrates
40 were sampled prior to manipulation and then four times (1, 4, 9 and 12 months) following
41 manipulation. Detrital standing stocks increased by an order of magnitude at treatment sites. Over
42 one year, invertebrate densities and species richness also increased in treatment sites. Effect sizes
43 were strong in middle and downstream areas, which were colonized by upstream species. Thus,
44 faunal composition of the downstream treatment sites became more similar to upstream locales,
45 and β -diversity across treatment sites declined as α -diversity increased. Out of 54 common taxa,
46 roughly half responded to the experiment; responders and non-responders had similar proportions
47 of upstream specialists and of different functional feeding groups. Contrary to many non-
48 experimental studies, our results demonstrate that extensive dispersal can be very important and,
49 for many species, potentially more important than the abiotic environment or biotic constraints in
50 affecting community structure when adequate resources are available.

51

52 *Key words: community structure, dispersal, field experiment, invertebrates, rivers*

53 INTRODUCTION

54 Central concepts in metapopulation and metacommunity ecology are the notions that local
55 communities and populations are linked by dispersal and that dispersal is essential for some
56 species to remain extant within a metacommunity. Species that are good dispersers can
57 theoretically remain extant regionally, even if they are periodically excluded from some locations
58 (e.g. through colonization-competition tradeoffs or temporal variation in resources: Chesson
59 2000), or if low numbers in marginal locations are sustained by immigration from other locations
60 (e.g. source-sink dynamics, mass effects, spatial storage effect: Chesson 2008). At the
61 metacommunity level, there is considerable interest in understanding how dispersal influences

62 patterns of diversity or species richness in local communities (α -diversity) and the variability in
63 species composition among local communities (β -diversity), and the mechanisms that underlie
64 these patterns. Increased rates of dispersal between local communities are expected to decrease β -
65 diversity as average α -diversity increases, provided that local communities are not saturated
66 (Mouquet and Loreau 2003, Cadotte 2006). In contrast, stochastic dispersal can increase β -
67 diversity if productivity is sufficiently high that multiple stable equilibria can occur within the
68 metacommunity (Chase 2010). Understanding how natural dispersal shapes communities is
69 therefore clearly important to unravel the processes that underpin the variations in community
70 structure and function across diverse ecosystems.

71
72 Despite intense interest, direct tests of these ideas in natural systems remain scarce. The
73 overwhelming majority of studies employ an indirect approach involving variation partitioning of
74 survey data (e.g. species \times site \times environment matrices) to disentangle the roles of dispersal from
75 that of local environmental conditions (review: Logue et al. 2011). However, these methods rely
76 on an assumption that distance between sites is a proxy measure of dispersal, even though few
77 studies have empirical data on dispersal distances or frequencies (Logue et al. 2011).
78 Complementing analyses with information on species traits or expected dispersal abilities (e.g.
79 Brown and Swan 2010, Göthe et al. 2013) is also problematic because independent verification of
80 traits is rare and alleged traits may poorly forecast actual dispersal distances (e.g. Lancaster et al.
81 2011). Additionally, dispersal routes and some environmental variables are often strongly
82 correlated for many ecosystems (e.g. coastal marine habitats, rivers, corridor vegetation), which
83 prevents confident separation of spatial and environmental variation (Gilbert and Bennett 2010,
84 Downes et al. in press). Experimental tests of metacommunity theory occur but most involve
85 artificial arenas (e.g. microcosms or mesocosms), insular communities with discrete boundaries
86 (e.g. phytotelmata), and small-bodied organisms (e.g. protists, bacteria, algae) (reviews: Cadotte
87 2006, Logue et al. 2011). Additionally many experiments lack strong environmental gradients –
88 even though metacommunity theory predicts strong impacts of environmental variation on
89 species diversity – and use artificial movement of individuals as a surrogate for natural dispersal
90 (e.g. sowing of seeds; translocation of plankton) (Cadotte 2006). As a result, extrapolating from
91 mesocosm experiments to natural systems is difficult because species with dispersal constraints
92 cannot be distinguished from those that can disperse but are unable to establish at new sites,

93 either because of environmental constraints (e.g. abiotic conditions that exceed physiological
94 tolerances) or biotic constraints (e.g. priority effects, Belyea and Lancaster 1999, Fukami 2015).
95 These outcomes reflect different ecological processes. There is clearly a need for more diverse
96 empirical approaches to test metacommunity theories, for which dispersal is an essential and
97 integral component, ideally in natural systems and including a wider range of systems and
98 organism types.

99
100 In this study, we present a large-scale field experiment designed to test for changes in the
101 diversity of stream invertebrates that could be attributed unambiguously to successful dispersal,
102 using natural communities and dispersal regimes. Several characteristics of riverine environments
103 make them ideal for such tests. Streams have marked environmental gradients that change with
104 altitude (temperature, channel width and morphology, etc.) and that are associated with, and
105 potential explanations for, changes in species composition along channels (e.g. Statzner and
106 Higler 1986). Stream corridors are major dispersal routes. Some taxa may use water currents to
107 disperse downstream (the ‘drift’) and, although it is unclear how often or how many taxa drift
108 long distances successfully (Lancaster 2008), the drift provides a direct dispersal route along
109 channels. Additionally, many stream invertebrates are insects that have terrestrial adults, many of
110 which fly and often disperse along river corridors (flight over catchment boundaries is also
111 possible) (Hughes et al. 2009). Because dispersal along stream corridors is strongly directional,
112 local communities are directly linked by prospective dispersal routes. This maximizes the
113 possibility that individuals can locate all parts of the study area if there are no dispersal
114 constraints, and will colonize if local conditions are suitable. Finally, the spatial scale of many
115 river systems is sufficiently small that biogeographical processes are unlikely to influence
116 distribution patterns within the metacommunity (Warren et al. 2014).

117
118 One way to test experimentally whether dispersal or environmental constraints drive spatial
119 variations in species diversity is to manipulate the supply of an essential resource
120 (HilleRisLambers et al. 2012). A longitudinal gradient in detritus densities in our study stream
121 (and typical of many streams) was therefore advantageous in providing a means to test
122 hypotheses. The role of detritus as a key resource of rivers is well established; detritus is
123 exploited in diverse ways by the aquatic and terrestrial stages of many invertebrates (e.g. as food,

124 hard substrate to sit on, refuges from predation, etc). The dearth of detritus at downstream
125 locations in our study system afforded an opportunity to boost the density of an essential resource
126 at locations with abiotic conditions that could be physiologically stressful, as a way of testing
127 how dispersal and environmental conditions affect species diversity, (e.g. HilleRisLambers et al.
128 2012), but without altering major abiotic gradients. In defining resources and abiotic variables,
129 we follow classical definitions that are based in ecological theory (e.g. Tilman 1982, Chesson
130 2008). Accordingly, resources are any substance or factor (e.g. food, space) that can be
131 consumed or monopolized by organisms, potentially leading to competition and density-
132 dependent feedback loops on populations. In contrast, the abiotic environment may also influence
133 populations if conditions are sufficiently extreme so as to exceed physiological tolerances; those
134 processes are density independent. Thus, organisms can react to temperature, but cannot control
135 temperature in any strong way, whereas detritus is a resource that can be consumed and
136 monopolized in direct relation to animal density, regardless of whether detritus acts as a source of
137 food, living space, predator refuges, oviposition sites, etc.

138
139 The experimental design entailed creating resource-rich islands along a 22 km stream length and
140 comparing them to control sites over one year. Previous, independent surveys of invertebrates in
141 the benthos and dispersing along this stream revealed longitudinal gradients in species richness
142 with some species apparently restricted to particular locations (e.g. by abiotic factors), but also
143 suggested a strong role of dispersal in this metacommunity (Downes et al. in press). Standing
144 stocks of detritus generally declined with distance downstream, but local variations in detritus
145 abundance along that gradient were high (at scales of 100s m²) and associated with small-scale
146 variations in the riparian zone and channel retention, which can influence local assemblages
147 (Lancaster and Downes 2015). In experimental sites, species that were resource limited were
148 expected to increase in density relative to control sites. Regarding species diversity and
149 composition, two alternative outcomes of the experiment are germane in the context of
150 metacommunity theories, which require there to be significant amounts of successful dispersal
151 that change species composition. (1) If dispersal rates were very low or if the abiotic environment
152 was the primary driver of community composition or if dispersers are unable to invade
153 established communities, then in treatment sites we predicted no change in species richness
154 (mean α -diversity) or community composition, and hence no change in β -diversity. Additionally,

155 no change was expected in the distribution pattern of location specialists (i.e. taxa restricted to, or
156 with highest densities in particular locations, such as upstream sites, before the manipulation). (2)
157 Alternatively, if some taxa could disperse and establish at new locations when sufficient
158 resources were available, irrespective of the abiotic environment, then we predicted increased
159 species richness (i.e. a change in community composition) and decreased β -diversity at treatment
160 sites. Changes in the distribution of location specialists would suggest that their distributions are
161 not determined by the abiotic environment. The first outcome is consistent with the conclusions
162 of most metacommunity studies based on variation partitioning of survey data; the second would
163 suggest a much more significant role for dispersal than demonstrated hitherto.

164

165 METHODS

166 *Study site*

167 The study was carried out in a 22 km length of Hughes Creek, a sandy-bed stream tributary of the
168 Goulburn River in central Victoria, south-eastern Australia (Lancaster et al. 2009, Downes et al.
169 2011). There were no major tributaries along this length and, thus, all sample sites were on the
170 main stem. Sample sites were in the upper reaches of Hughes Ck (36° 59' S; 145° 21' E) where
171 the stream runs off the granite batholith of the Strathbogie Ranges. Stream gradient changed
172 along the study length (Fig. 1) and downstream sites had a gentler gradient than those farther
173 upstream, but all sites were upstream of Goulburn River floodplain. Sand in the stream bed
174 (median grain size = ϕ -0.5 to -1, or 1.7 to 2.0 mm) is sourced from erosion and present naturally,
175 but has increased with bushfires and vegetation clearance, and has caused sand slugs in local
176 streams (Davis and Finlayson 2000). As a result of these changes, active channel width increases
177 greatly from up- to downstream locations, as does the wetted width, and this is associated with
178 decreasing average water depths (Table 1) Heavy sand deposition causes an unstable stream bed
179 and a loss of habitat structure as detritus (the primary source of hard substrate and an important
180 food resource) is buried (Downes et al. 2006).

181

182 Along the study length there were strong longitudinal gradients in the abiotic environment
183 (physicochemistry and channel morphology), resources (standing stocks of detritus in the
184 channel), and also in benthic invertebrate diversity. Many of these gradients are associated
185 (directly or indirectly) with greater impacts of human activities (e.g. tree clearance) in

186 downstream than upstream areas. A brief summary of some environmental variables is provided
187 in Table 1; detailed information is available elsewhere (Downes et al. 2011, Downes et al. 2016,
188 in press). Multivariate analysis demonstrated that the collective effects of all these variables
189 produces a marked change in the environment of Hughes Ck from up- to downstream (Downes et
190 al. in press); a brief description is as follows. Perhaps the most physiologically important abiotic
191 gradient for aquatic invertebrates was a longitudinal increase in water temperature,
192 accompanying increasing channel width, decreasing water depth and lack of shade from an
193 increasingly sparse riparian zone. Water temperatures in excess of 30 °C and up to 36 °C were
194 common in downstream zones in summer (water temperatures >30 °C are considered extreme for
195 most aquatic insects: Lancaster and Downes 2013), and are coincident with low dissolved oxygen
196 concentrations in Hughes Creek at some locations (e.g. <1 mg L⁻¹, Lancaster et al. 2009).
197 Turbidity, conductivity and pH of the water also increased from up- to downstream locations.
198 Other strong gradients were associated with the supply and retention of detrital resources (see
199 Results), which declined markedly downstream with an increasingly narrow and sparse riparian
200 zone, and a loss of retentive structures in the channel, such as large woody debris. Throughout the
201 stream, detritus is derived from riparian vegetation, which is primarily River Red Gum trees
202 (*Eucalyptus camaldulensis*), plus some other species of *Eucalyptus* and *Acacia*. Typical of many
203 Australian streams where *Eucalyptus* spp. dominate the riparian zone, most bark and leaf fall
204 occurs in summer and, combined with seasonally low and stable flows, detrital standing stocks in
205 Hughes Creek are highest in summer, but still very low in the downstream areas compared to
206 many other streams (Downes et al. 2011, Lancaster and Downes 2015). Low standing stocks of
207 detritus have implications for macroinvertebrate density and diversity, because terrestrially
208 sourced detritus forms the main energy source for foodwebs in streams in this region (Reid et al.
209 2008).

210

211 *Experimental Design*

212 We increased standing stocks of detritus by increasing channel retentiveness at treatment sites
213 while leaving control sites unchanged. In total, there were 12 sample sites, four in each of three
214 zones (up-, middle, down-stream) and, within each zone, control and manipulation sites were
215 allocated at random (Fig. 1). Zones reflect major shifts in environmental conditions, which
216 change fairly abruptly rather than smoothly along the channel (Downes et al. 2011, Downes et al.

217 in press). Sites were 40 m channel lengths and selected to be relatively straight, homogeneous
218 stretches with no bedrock outcrops, islands or braiding. The stream-wise distance between sites
219 ranged from 0.6 to 3.7 km (mean 1.6 km).

220
221 To increase stream retentiveness in treatment sites, in early summer 2013, wooden stakes (length
222 120 cm) were hammered into the stream bed in pairs (≈ 25 cm apart, perpendicular to the
223 direction of flow). Stakes protruded above the water surface throughout most discharges and
224 were fully submerged only rarely during winter floods. Detritus transported by water currents
225 became trapped and accumulated on these stakes, thereby increasing standing stocks of detritus in
226 the treatment sites relative to the controls. The density of stake pairs ranged from 1.3 m^{-2} in the
227 upstream sites, which had some natural retentive structures, to 1.9 m^{-2} in the downstream sites,
228 which had virtually no natural retention. To initiate detrital accumulation, we collected leaves,
229 bark and small twigs from the riparian zone. This material was placed in linen bags, submerged
230 in the stream for 48 hours to become water logged, and then released into treatment sites
231 immediately after stakes were installed at the start of the experiment only (for a description of
232 amounts released see Appendix S1). Some stakes were lost or partially buried by shifting sand
233 during winter spates (Appendix S2), but $\geq 80\%$ of the stakes in each site remained *in situ*
234 throughout the experiment. Lost stakes were replaced in spring to maintain treatment effects.

235
236 Altering channel retention can also alter local hydraulics so we surveyed near-bed velocities and
237 water depths at the end of the experiment to characterise possible differences between treatment
238 and control sites. This survey revealed no changes in depth or flow that were likely to be
239 ecologically significant or affect the experimental results or interpretation (for a full description,
240 see Appendix S3).

241
242 All sites were sampled for benthic invertebrates and detritus immediately before manipulation
243 (time 0) and at 1, 4, 9, and 12 months post-manipulation. On each occasion, we collected 10
244 Surber samples (0.09 m^2 , $250 \mu\text{m}$ mesh) per site (increased to 15 samples for 9 and 12 month
245 collections, to ensure adequate sampling effort after winter spates: Appendix S2). Samples were
246 located within the site according to a random stratified design, with roughly one quarter of the
247 samples located within each 10 m segment of the 40 m site. Stream width was measured at 10 m

248 intervals to estimate area. Sites are replicates in our statistical analyses (not individual samples),
249 so samples were composited to provide a single estimate of invertebrate densities per site.
250 Detritus greater than $\approx 5 \text{ cm}^2$ was removed from samples, air dried and weighed to estimate
251 standing stocks per site. Leafy and woody detritus were weighed separately, but these two
252 fractions showed exactly the same patterns across sites and times, so only results for total detritus
253 are reported. Composited samples of invertebrates were split into 100 aliquots using a sample
254 splitter (Marchant 1988), and 20 aliquots were selected at random for enumeration (as per
255 Downes et al. in press). Invertebrates were sorted under a stereomicroscope and identified to the
256 lowest taxonomic level where possible: species for most taxa; genus for most Chironomidae. See
257 Appendix S4 for a list of the major taxonomic references.

258
259 *Numerical and statistical analyses*

260 Spatial structure of the initial metacommunity was described using pre-manipulation data to test
261 for longitudinal patterns in species richness (Spearman's rank correlation) and nestedness of local
262 communities in the 12 sample sites. Nestedness was measured using the metric NODF and
263 calculated by Aninhado 3.0 (Guimarães and Guimarães 2006, Almeida-Neto et al. 2008). Sites
264 were ordered according to their position along the stream gradient. Significance of NODF was
265 determined by Monte Carlo tests (1000 permutations) using an equiprobable-equiprobable null
266 model.

267
268 The experiment was designed to be analyzed by three-way, repeated measures analysis of
269 variance (RMANOVA). Time was the repeated measure and there were two fixed factors,
270 Treatment (control vs treatment) and Zone along the gradient (up-, middle and down-stream). In
271 this statistical model, the tests of our hypotheses involve the Treatment x Time interaction term.
272 If significant, this would indicate a response to the increase in detritus, and changes that became
273 more pronounced with increasing time since the manipulation. A significant three-way
274 interaction (Treatment x Zone x Time) would indicate that the magnitude or speed of response
275 varied spatially along the channel. This statistical model was used for univariate variables
276 (detrital standing stocks, taxon richness, total invertebrate density, densities of individual taxa)
277 and the multivariate data set (multi-species assemblages). Univariate data were log-transformed
278 before analyses to satisfy assumptions of homogeneity of variance. For individual taxa that

279 showed a significant treatment effect, planned contrasts were carried out to determine in which
280 time period the response first became significant. Multivariate data were analyzed using
281 PERMANOVA+ and PRIMER v6 (Clarke and Gorley 2006, Anderson et al. 2008), based on a
282 resemblance matrix constructed from fourth-root transformed species abundance data and Bray-
283 Curtis similarity coefficients. Significance levels of all multivariate tests were determined by
284 9999 permutations. We used non-metric multidimensional scaling (NMDS) solved in two
285 dimensions to display differences among the sites with respect to Zone, Treatment and Time. We
286 tested whether potential spatial autocorrelation between sites compromised statistical tests of the
287 experimental treatment in the multivariate RMANOVA (Underwood 1994). This test and its
288 outcomes are described in Appendix S5 and indicated that such correlations did not compromise
289 tests of the hypotheses of interest.

290
291 We quantified β -diversity as the variability in species composition among sampling units
292 (Anderson et al. 2008) by creating a dissimilarity matrix from the species abundance data using
293 the Jaccard measure, which uses species presence/absence data. We used *t*-tests (and *P*-values
294 created via permutations) within PERMDISP routine of the PERMANOVA+ package to test
295 whether the degree of variability in species composition differed between treatment and control
296 replicates at each sample time.

297

298 RESULTS

299 Pre-manipulation, detritus densities were an order of magnitude higher in the upstream vs
300 downstream zones: on average, densities were 98, 19 and 7 g dry wt m⁻², in up-, middle and
301 down-stream zone sites respectively. Experimentally increasing channel retention produced a
302 significant increase in the standing stocks of detritus in all treatment sites, including the upstream
303 zone which had the highest natural retention (Fig. 2a, Table 2: significant Treatment x Time, non-
304 significant Treatment x Zone x Time). The magnitude of the difference in detritus densities
305 between treatment and control sites increased in a downstream direction and, after 12 months,
306 detritus densities were roughly 3×, 19× and 42× higher in treatment sites, in up-, middle and
307 downstream zones respectively. Thus, after 12 months experimental sites attained approximately
308 the same average density of detritus in all zones. The detritus increase after only 1 month (Fig.
309 2a) partly reflects the experimental addition of detritus at the start of the manipulation, but natural

310 accumulations contributed significantly to high densities in the longer term (Table 2: Treatment x
311 Time). Observations suggested that detritus accumulation was dynamic, with considerable
312 turnover (continuous accumulation and loss) of individual pieces of detritus. Notable
313 accumulations of detritus occurred also on the stream bed between stakes because detritus traps
314 created some areas of low flows (Appendix S3).

315
316 Over the experiment, we recorded 260 taxa of benthic invertebrates, 96% of which were aquatic
317 insects. Pre-manipulation, there was a longitudinal decrease in taxon richness per site ($r_s = -0.74$,
318 $P = 0.006$) with $\approx 50\%$ more species per site in upstream than downstream zones. Local
319 communities were significantly nested (NODF = 55.4, $P < 0.001$) such that the species
320 compositions of downstream sites were proper, nested subsets of sites further upstream.

321
322 Invertebrate taxon richness (α -diversity) and total densities increased significantly in treatment
323 sites and in all zones (Fig. 2b, 2c, Table 2: significant Treatment x Time, non-significant
324 Treatment x Zone x Time). In control sites, despite an overall drop in taxon richness in winter
325 (month 9), numbers of taxa in months 0 and 12 (summer) were similar for each zone. In contrast,
326 taxon richness in treatment sites did not decline but increased noticeably in all zones after nine
327 months. After 12 months, taxon richness was approximately 1.3 \times , 1.9 \times and 1.6 \times higher in
328 treatment than control sites, in up-, middle and downstream zones, respectively. The pattern for
329 total invertebrate densities was broadly similar to that for taxon richness: densities in treatment
330 sites were higher than controls in all zones after only four months (autumn) and seasonal density
331 decreases in winter were more pronounced in control than treatment sites.

332
333 Multivariate analysis revealed significant effects of the experimental manipulation on entire
334 invertebrate assemblages (Table 3: Treatment x Time). The effects varied between zones and
335 over time, as evidenced by a significant 3-way interaction term (Table 3: Treatment x Zone x
336 Time). There were insufficient unique permutations to allow pair-wise contrasts within the three-
337 way interaction, but the multivariate patterns illustrated in NMDS plots (Fig. 3) show that
338 treatment effects were greater at middle and downstream sites than upstream sites, and that these
339 differences varied over time. Pair-wise tests within Treatment x Time indicated that treatment
340 effects first manifest after four months ($t = 1.6$, $P = 0.035$) and remained significant in

341 subsequent sample occasions. Seasonal changes in composition are illustrated by swings in the
342 temporal trajectory of all sites along NMDS axis 1; these swings were most pronounced in the
343 control sites and the downstream sites (Fig. 3a, c, e). Axis 2 is associated with stream zone, with
344 higher values for upstream than downstream sites at each sample time. Between 0 and 12 months,
345 there was little net directional change in the upstream sites (Fig. 3b). In control sites of the
346 middle and downstream zones, net directional change was in the same direction and of similar
347 magnitude over 12 months (Fig. 3d, f), which may reflect inter-annual variation. In treatment
348 sites, the vector direction of change was also similar in the middle and downstream zones, but in
349 roughly the opposite direction to the control sites, suggesting a treatment effect over and above
350 interannual variation. This vector direction indicates that communities in the middle and
351 downstream treatment sites became more similar to communities in the upstream zone.

352
353 Analyses of β -diversity confirmed outcomes of the multivariate analyses. Treatment sites from all
354 three zones became more similar to each other over time, whereas control sites became less
355 similar, partly due to interannual variation (Fig. 4). Thus β -diversity declined across experimental
356 sites as downstream and middle sites acquired species present in upstream locations rather than
357 species from outside the species pool.

358
359 Univariate analyses of common taxa also provided results consistent with the multivariate
360 analyses. Of the 260 taxa, 54 were sufficiently abundant to permit RMANOVA of individual
361 species' densities. The number of taxa with and without Treatment and Zone effects are
362 summarized in Table 4 and species names in Appendix S6 (for brevity, outcomes of the 54
363 analyses are not reported). Approximately half the taxa were not affected by the manipulation;
364 most of these occurred throughout the longitudinal gradient and 25% were location specialists
365 (mainly upstream specialists). All significant treatment effects involved higher densities in
366 treatment than control sites. For location specialists that responded to the manipulation, the zone
367 with highest densities was typically the same for treatment and control sites. However, between-
368 zone differences in density were reduced in treatment sites and these taxa were often absent from
369 controls but abundant in corresponding treatment sites. When treatment effects first became
370 statistically significant varied among taxa: 1, 14, 7 and 4 taxa first showed significant treatment
371 effects after, 1, 4, 9 and 12 months, respectively. Most of the responding taxa occurred

372 throughout the stream gradient; 38% of responders were location specialists pre-manipulation,
373 but were present in new zones post-manipulation. Whether species responded to the treatment
374 was not obviously related to any functional traits, and species within the same genus could
375 respond differently. For example, among the predatory caddisflies *Ecnomus continentalis*
376 responded but *E. cygnitus* did not; among filter-feeding blackflies *Austrosimulium furiosum*
377 responded but *Simulium ornatipes* did not; mayfly grazer/scrapers: *Offadens* sp. responded but
378 *Tasmanocoenis tillyardi* did not; chironomid grazer/scrapers: *Thienemanniella* sp. responded but
379 *Corynoneura* sp. did not.

380

381 DISCUSSION

382 Our landscape-scale field experiment demonstrated that natural dispersal processes within a
383 metacommunity can increase species richness in species-poor sites if essential resources are
384 increased. Such increases are expected if species disperse frequently among sites but are unable
385 to colonize locations where resources are usually scarce or fully monopolized. Our experiment
386 encompassed strong environmental gradients, and resource-poor sites occurred in places with
387 abiotic conditions that may be physiologically stressful (shifting sand, warm water, low dissolved
388 oxygen). Nevertheless, many species colonized these sites once resources had been increased
389 and, after only one year, the number of taxa nearly doubled in some treatment sites. While
390 species diversity may have been increased by various aspects of high detritus levels (e.g. increase
391 in food, living space, refuge etc.), interpretation of the results are not contingent upon identifying
392 which aspects facilitated invasion. The results demonstrate an important role for dispersal in this
393 metacommunity.

394

395 The outcomes of this experiment have two major ecological implications. First, abiotic conditions
396 that are often assumed to be physiologically stressful do not necessarily preclude colonization by
397 many species. Second, dispersal was successful even with well-established communities present,
398 suggesting that priority effects (e.g. Belyea and Lancaster 1999, Fukami 2015) do not necessarily
399 prevent many species from successfully invading established local communities. Other research
400 using retention traps to increase detrital resources have recorded only small increases in species
401 diversity (e.g. Dobson and Hildrew 1992, Koljonen et al. 2012, Palmer et al. 2014), but those
402 studies were not specifically designed to test whether dispersal along river corridors can effect

403 establishment of species at new locations, and may have been unable to detect dispersal from
404 distant locations (e.g. study duration short relative to dispersal rates and/or distances). Our results
405 corroborate indirect evidence from a previous survey in this system (Downes et al. in press) and
406 provide rare experimental evidence of how dispersal drives diversity among local communities at
407 landscape scales.

408
409 Unlike most previous experiments testing ideas in metacommunity ecology, this study tested the
410 effects of natural dispersal rates in a natural system. The manipulation increased detritus
411 markedly, and standing stocks of detritus in treatment sites were very similar across all zones by
412 the end of the experiment, despite a strong longitudinal gradient of resource density at the outset.
413 Additionally, because detritus was naturally sourced, resource type and quality were comparable
414 at all sites. Our experiment ran for sufficient time to include the effects of dispersal over different
415 spatial and temporal scales: aggregation via short-distance movements (e.g. crawling, swimming)
416 and longer-distance dispersal (e.g. drift), or by population growth due to recruitment (e.g. from
417 adults laying eggs, often after adult dispersal by flight). Theoretically, movement and aggregation
418 of aquatic life stages could occur rapidly and at any time of year for any species, but processes
419 involving adult flight and population growth are likely to take longer and vary seasonally.
420 Response times were species-specific, suggesting that all three types of dispersal were at play.
421 Treatment effects in the multivariate data were rapid and apparent after only four months,
422 whereas responses of some individual taxa were not apparent until nine or even 12 months, which
423 likely reflects species-specific life histories and dispersal capabilities. For example, some rapid
424 responders were Chironomidae (midges), which can produce multiple generations per year and
425 could respond rapidly via population growth. In contrast, slow responders included some
426 Trichoptera (caddisflies), which produce only one or two generations a year in this system, and
427 responses via population growth may take longer. Most Plecoptera (stoneflies) in this system
428 enter diapause over summer and are most abundant during spring, the only time that treatment
429 effects were apparent for stoneflies. These variable responses illustrate the importance of
430 incorporating natural dispersal regimes, life-history variability and seasonality into realistic
431 experimental tests.

432
433 The β -diversity of treatment sites declined as average α -diversity increased, as predicted by some

434 models (Mouquet and Loreau 2003, Cadotte 2006). Taxa contributing to increased species
435 richness originated within the species pool of the creek, i.e. 'new' species did not originate
436 outside the metacommunity, and many colonists of treatment sites were previously restricted to,
437 or most abundant in, upstream locations. Post-manipulation, the faunal composition of middle
438 and downstream treatment sites became more similar to that of upstream locations. The pre-
439 manipulation pattern of nested communities further suggest that upstream locations were the
440 source of potential colonists. Among species-specific responses, roughly half of the common taxa
441 responded to the experiment and there were no obvious patterns in the taxonomy or functional
442 traits of species that did or did not respond. Approximately 30% of taxa were location specialists
443 (primarily upstream specialists) before the experiment, and one common interpretation of such
444 restricted distribution patterns is that abiotic conditions limit distributions. However, roughly half
445 these location specialists changed distribution during the experiment and appeared for the first
446 time and/or at high densities in treatment sites in zones outside their 'normal range'. Although we
447 observed changes in α - and β -diversity after one year, an important question is whether these
448 changes will persist or decline as dispersal delivers strong competitors or predators to treatment
449 sites (Mouquet and Loreau 2003); this is the subject of a subsequent paper.

450
451 Alternative models predicting increased β -diversity with successful dispersal in productive
452 environments (e.g. Chase 2010) were not supported by our experiment. In these models,
453 however, dispersal is modelled as a largely stochastic event whereby relatively few successful
454 dispersers produce almost random changes among replicate local communities (as demonstrated
455 using pond mesocosms: Chase 2010, Steiner 2014). Such models may not apply to natural, large-
456 scale metacommunities (regardless of productivity) where dispersal may be strongly directional,
457 occurs on a seasonal (or semi-regular) basis and is therefore not stochastic (Lowe and McPeck
458 2014), even though absolute numbers of dispersers can vary greatly between localities and
459 patches of suitable habitat within metacommunities (e.g. Sams and Keough 2012).

460
461 Evidence that upstream locations have reservoirs of species capable of living in a variety of
462 locations is of strong interest because many restoration projects rely on dispersal from such
463 reservoirs for success (e.g. the Field of Dreams hypothesis: Palmer et al. 1997). Many river
464 restoration projects have failed to deliver increases in biological diversity (Palmer et al. 2014),

465 and one concern is that species in intact areas, which are typically upstream of areas degraded by
466 human impacts, are incapable of inhabiting or reaching restored sites, or may take many years to
467 do so (Parkyn and Smith 2011). Our experiment demonstrates this may not always be the case.
468 Dispersal clearly plays a significant role in the dynamics of communities along Hughes Creek;
469 abiotic variables and priority effects did not block many species from dispersing successfully and
470 establishing at new locations in our experiment.

471
472 Much of the metacommunity literature suggests that environmental gradients and niche-based
473 processes dictate species composition of local communities, with dispersal playing only a minor
474 role (e.g. Logue et al. 2011). However, most of this literature is based upon survey data and
475 indirect numerical methods to estimate whether dispersal is successful – methods that may
476 underestimate true frequencies of successful dispersal (e.g. Gilbert and Bennett 2010). Although
477 some experiments have successfully highlighted the effects of dispersal, most lack realism (see
478 Introduction); large-scale field experiments are rare and much needed (Cadotte 2006, Simonis
479 and Ellis 2014). We are unaware of any studies comparable to this large-scale manipulation.
480 Some experiments do test how boosting essential resources affects species diversity, but the
481 majority have focused on plants (increasing nutrients, water or light: HilleRisLambers et al.
482 2012), rather than animals and across multiple trophic levels. Studies using natural dispersal rates
483 are common in marine studies of community assembly (e.g. Sams and Keough 2012) but usually
484 resources can only be increased over small scales. An exception is the creation of artificial reefs,
485 which increase living space for fish and invertebrates. However, such reefs tend to be constructed
486 away from natural reefs so priority effects cannot be assessed, and the results are more akin to
487 examining re-assembly of communities following disturbance (Schroeter et al. 2015).

488
489 An important goal in community ecology is to link metacommunity or community assembly
490 models with those of species coexistence (Chesson 2000, 2008, HilleRisLambers et al. 2012).
491 Species coexistence models explain how species sharing similar resources and potentially the
492 same predators are able to coexist in the face of competition that might otherwise drive some to
493 extinction (Chesson 2000, 2008). High diversity within guilds is a major source of species
494 richness so understanding how guild members can coexist can explain differences in species
495 diversity between communities. Models that deliver stable coexistence include trade-offs (e.g.

496 colonization/competition trade-off), mechanisms producing spatial niche differences, spatial
497 disturbance effects and others (Chesson 2008). A first step in testing these models is to
498 demonstrate that species can disperse between local communities and successfully establish at
499 locations that have a range of environmental conditions. We have demonstrated this for species in
500 a range of guilds, which now paves the way for a more detailed examination of the mechanisms
501 underlying the coexistence of species in this system.

502

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510

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615 biology: inferring processes from species distributions. *Trends in Ecology and Evolution*
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617

618 Table 1 Summary of some environmental variables (mean values) characterizing upper,
 619 middle and lower sections of the study length in summer. NB: temperature loggers
 620 were deployed in upper and lower reaches only; data are not available for middle
 621 sections. Data from (Downes et al. 2016, in press); see Downes et al. (2016, in press)
 622 for details of instrumentation and collection methods; see Downes et al (in press) for
 623 statistical analyses.
 624

Variable	Upper	Middle	Lower
Active channel width (m)	6.7	8.8	25
Wetted channel width (m)	2.7	4.8	5.3
Water depth (m)	0.53	0.27	0.08
Riparian width (m)	89	39	45
Tree cover in riparian zone (%)	90	50	20
Air temperature (°C): daytime, night time (range)	21.8, 15.8 (3 – 45)	NA	23.4, 16.1 (2 - 46)
Water temperature (°C): daytime, night time (range)	18.8, 18.4 (13 - 29)	NA	21.7, 19.0 (11 - 36)
Water temperature (% of time temperatures exceeded 29 °C)	0	NA	7.11
Conductivity ($\mu\text{S cm}^{-1}$ at 25°C)	177	265	307
Turbidity (NTU)	5	5	11
pH	7.11	7.30	7.42

625

626 Table 2 Summary of RMANOVA comparing standing stocks of detritus, taxon richness and total invertebrate densities between treatments in
 627 different zones on the stream gradient and over time. Subjects in these analyses are sites. See Figure 1 for illustration.
 628

Source	df	Detritus standing stock			Taxon richness			Total density		
		MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>
<i>Between subjects</i>										
Treatment	1	12.1	89.1	0.001	1206	5.221	0.062	1.678	41.25	<0.001
Zone	2	2.37	17.4	0.003	879	3.805	0.086	0.1879	4.618	0.061
Trt*Zone	2	0.558	4.09	0.076	70.1	0.3035	0.749	0.1576	3.873	0.083
Subject	6	0.136			231			0.0407		
<i>Within subjects</i>										
Time	4	0.970	9.81	<0.001	708	12.28	<0.001	1.785	70.04	<0.001
Trt*Time	4	0.748	7.56	<0.001	398	6.894	<0.001	0.1330	5.217	0.004
Zone*Time	8	0.122	1.23	0.322	33.33	0.5777	0.786	0.1621	6.361	<0.001
Trt*Zone*Time	8	0.0694	0.701	0.687	36.41	0.6312	0.744	0.0437	1.714	0.146
Error	24	0.0989			57.68			0.0255		

629 Table 3 Summary of PERMANOVA comparing invertebrate assemblages between
 630 treatments in different zones on the stream gradient and over time. Subjects in these
 631 analyses are sites. See Figure 2 for illustration

632

Source	df	MS	Pseudo- <i>F</i>	<i>P</i>
<i>Between subjects</i>				
Treatment	1	3474	2.446	0.043
Zone	2	5957	4.194	0.013
Trt*Zone	2	974.0	0.6858	0.752
Subject	6	1420		
<i>Within subjects</i>				
Time	4	5434	10.59	<0.001
Trt*Time	4	1356	2.644	<0.001
Zone*Time	8	926.0	1.805	<0.001
Trt*Zone*Time	8	643.4	1.254	0.031
Error	24	513.0		

633

634 Table 4 Summary of univariate responses (3-way RMANOVA) for 54 taxa, showing the
 635 number and percent (in brackets) of taxa with significant (signif.) and non-significant
 636 (ns) treatment and zone effects, and the zone where densities were highest. Taxa with
 637 significant treatment effect (Trt x Time or Trt x Time x Zone) were pooled; all
 638 treatment effects were positive, i.e. increased density in manipulation sites compared
 639 with controls. See Appendix S6 for species names.

640

Treatment effect	Zone effect	Highest densities			
		Up	Mid	Down	
ns	28 (52%)	ns	21 (39%)		
	signif.	7 (13%)	5	0	2
signif.	26 (48%)	ns	16 (30%)		
	signif.	10 (18%)	5	4	1

641

642

643 Figure legends

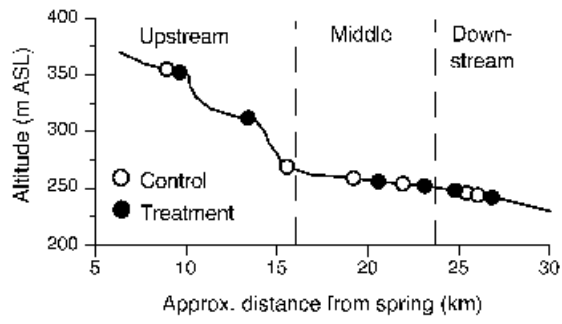
644

645 Figure 1 Altitudinal profile of the study stream showing locations of control and treatment
646 sites in each of the three zones (upstream, middle, downstream).

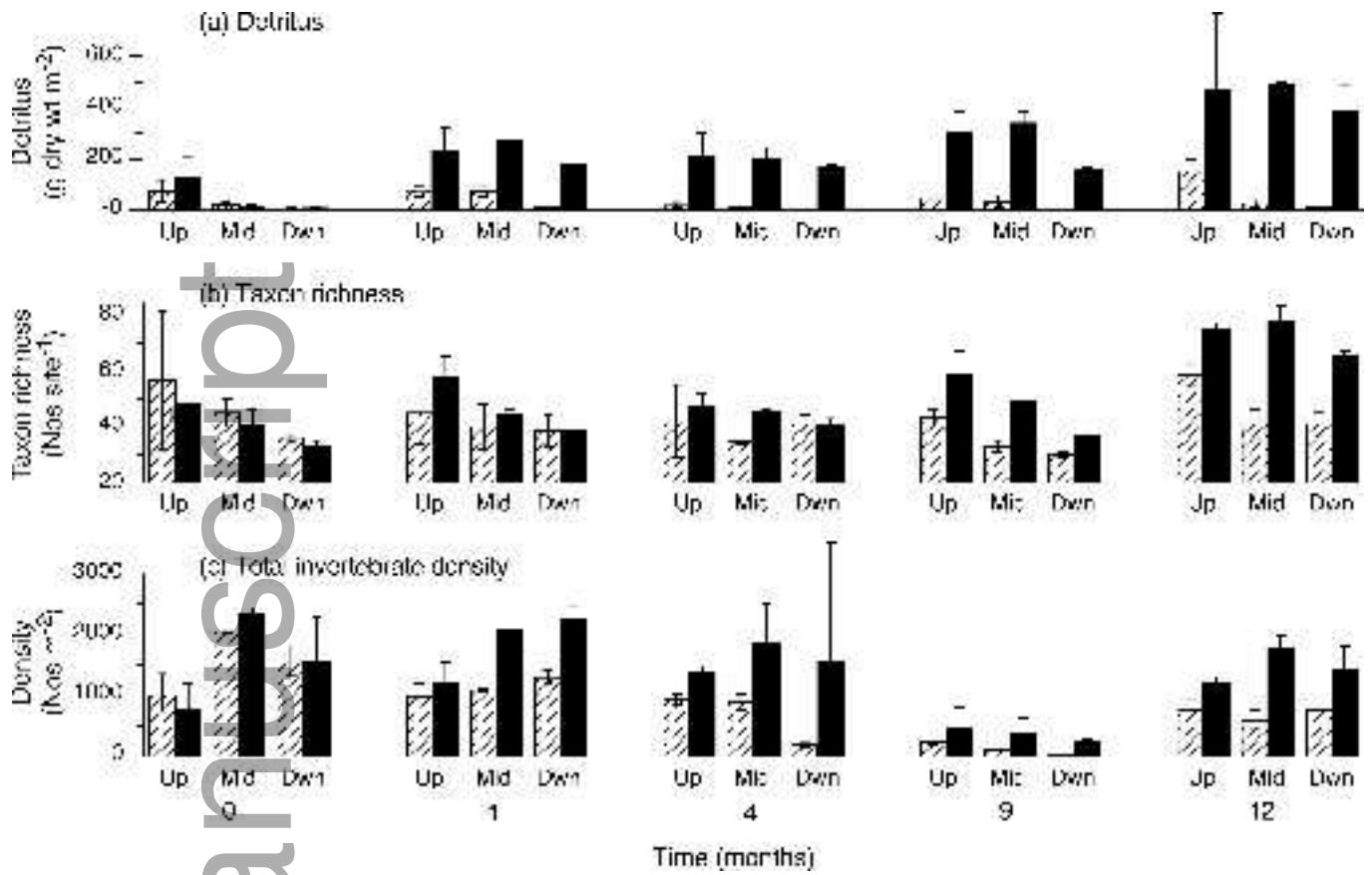
647 Figure 2 Summary of (a) standing stock densities of detritus, (b) taxon richness and (c) total
648 invertebrate densities per site (mean \pm SE), in control and treatment sites (stippled
649 and solid bars, respectively) in relation to stream zone (up, middle, down) and time
650 since the manipulation started (time 0 = pre-manipulation). See Table 2 for
651 summary of statistical analyses.

652 Figure 3 Non-metric multi-dimensional scaling (NMDS) ordination of sites at different
653 times. For convenience, the three zones are shown in separate panels with the same
654 scales, (a) & (b) upstream, (c) & (d) middle and (e) & (f) downstream, although all
655 sites and times were included in the ordination (stress for 2D configuration = 0.17,
656 indicating a good fit to the data). Different sites are indicated by different symbols
657 (circles, squares): open symbols indicate control sites, solid symbols treatment
658 sites; symbols with crosses indicate pre-manipulation samples. (a), (c) & (e) show
659 all sites and times with lines connecting samples from the same site over the
660 temporal trajectory. (b), (d) & (f) show only the pre-manipulation and final, 12-
661 month samples. Arrows with open and closed heads indicate the average direction
662 and magnitude of change in ordination space for control and manipulation sites,
663 respectively. Start and end of each arrow was calculated as the mid point in
664 ordination space between replicate control or treatment sites.

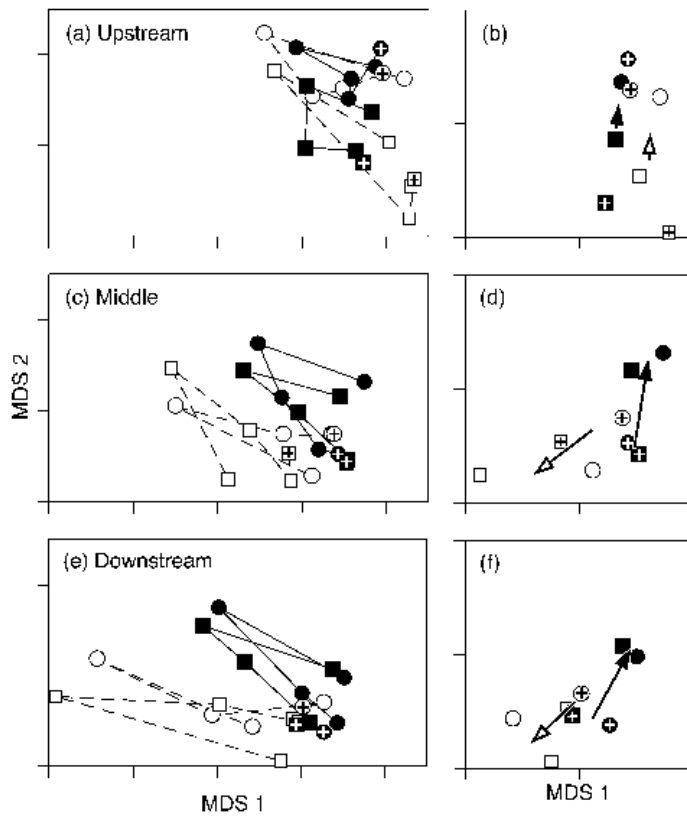
665 Figure 4 β -diversity as described by mean (\pm SE) dissimilarity among replicate control and
666 treatment sites (stippled and solid bars, respectively) in relation to time since the
667 manipulation started (time 0 = pre-manipulation). This measure of dissimilarity
668 (Jaccard's index \times 100) can be interpreted directly as the percent of unshared
669 species. * indicates bars that are significantly different at $P < 0.05$.



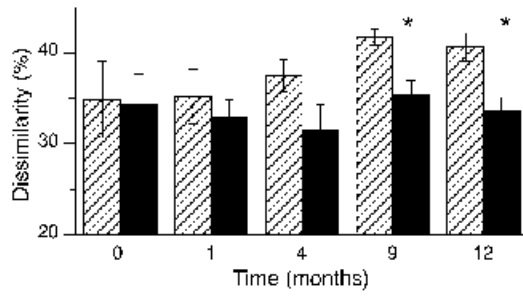
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