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3	Population densities and density-area relationships in a community with advective dispersal and
4	variable mosaics of resource patches
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 $\,$ JL analyzed the data. JL and BJD wrote the manuscript.

28 Abstract

29 Many communities comprise species that select resources that are patchily distributed in an 30 environment that is otherwise unsuitable or suboptimal. Effects of this patchiness can depend on the 31 characteristics of patch arrays and animal movements, and produce non-intuitive outcomes in which 32 population densities are unrelated to resource abundance. Resource mosaics are predicted to have 33 only weak effects, however, where patches are ephemeral or organisms are transported advectively. 34 The running waters of streams and benthic invertebrates epitomize such systems, but empirical tests of resource mosaics are scarce. We sampled 15 common macroinvertebrates inhabiting distinct detritus 35 patches at four sites within a sand-bed stream, where detritus formed a major resource of food and 36 living space. At each site, environmental variables were measured for 100 leaf packs; invertebrates 37 38 were counted in 50 leaf packs. Sites differed in total abundance of detritus, leaf pack sizes and 39 invertebrate densities. Multivariate analysis indicated that patch size was the dominant environmental 40 variable, but invertebrate densities differed significantly between sites even after accounting for patch size. Leaf specialists showed positive and strong density-area relationships, except where the patch 41 42 size range was small and patches were aggregated. In contrast, generalist species had weaker and 43 variable responses to patch sizes. Population densities were not associated with total resource 44 abundance, with the highest densities of leaf specialists in sites with the least detritus. Our results 45 demonstrate that patchy resources can affect species even in communities where species are mobile, 46 have advective dispersal, and patches are relatively ephemeral.

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49 **Key words:** detritus, patch dynamics, patch size, stream invertebrates

51 Introduction

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53 Many communities occur in complex landscapes in which high quality resources (or habitat) are 54 distributed across an array of multiple patches embedded in a lower quality matrix. The total amount 55 of resource as well as the heterogeneous nature of these landscapes can affect populations and 56 communities in diverse ways and, thus, are important to habitat management and conservation, 57 particularly for mobile organisms that actively search for resource patches (e.g. Fahrig 2003). At the population level, density at the landscape scale may vary with total resource abundance and array 58 characteristics (e.g. contagion, patch shape). Densities within patches are a function of movement rates 59 60 into and out of patches, which depend strongly on movement behaviour (Bowman et al. 2002). For 61 example, when patches are clumped, landscape-scale densities can be lower than when patches are 62 distributed randomly, because distances between clumps may exceed the movement capacity of 63 animals (Cain et al. 1985). Density within a single patch may vary also with patch shape and size (e.g. 64 a density-area relationship, DAR). Density-area relationships have been described for diverse 65 animals, especially in terrestrial environments. The underlying mechanisms are less well understood, 66 but generally relate to either the movement of individuals between patches or within-patch variations 67 in individual fitness (Connor et al. 2000; Hambäck et al. 2007; Jackson et al. 2013). Modeling studies 68 suggest, however, that the direction of the DAR (positive, negative or neutral) and how it interacts 69 with total habitat amount and with the spatial arrangement of patches in an array can result in variable 70 and potentially unexpected outcomes for populations (Donovan and Lamberson 2001; Matter 2000). 71 Some empirical studies also support this notion of context-dependency (Püttker et al. 2011; Resetarits 72 Jr. and Binckley 2013).

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Strong effects of resource patchiness are predicted in systems where animals move under their own power, search for and select resource patches, and where the matrix between patches is high risk or dispersal is costly. In contrast, ecosystems with ephemeral patches or advectively transported organisms should display weak or no patterns related to patch arrays (Bowman et al. 2002; Palmer et al. 2000). Streams and rivers epitomize such systems, where flowing water facilitates advective

79 movements, and may also influence the longevity and character of habitat patches. Perhaps as a result, 80 landscape studies in freshwater systems focus overwhelmingly on the spatial arrangement of 81 freshwaters within an uninhabitable terrestrial matrix (e.g. river drainage networks and pond 82 complexes). Fewer examine the smaller scale landscapes within freshwater environments, so many 83 hypotheses about habitat patchiness are untested at landscape scales relevant to the movements of 84 aquatic life stages (Wiens 2002). This is surprising given the recognized importance of habitat 85 heterogeneity within stream channels (e.g. Downes et al. 1993; Palmer 1995) and of particular patch 86 types that may be essential for species persistence, such as disturbance refugia (Lake 2000; Lancaster 87 and Belyea 1997) and egg-laving sites (Encalada and Peckarsky 2012; Lancaster et al. 2010). The few 88 empirical studies of resource patch arrays in streams have shown, for example, that the spatial 89 arrangement of patches can influence the survival and abundance of species (Palmer et al. 2000; Silver 90 et al. 2000), recruitment rates (Lancaster et al. 2010; Lancaster et al. 2003) and movement behaviours 91 (Olden 2007; Olden et al. 2004). Importantly, such results contradict the notion that the effects of 92 resource patchiness are weak in systems with advective movement and ephemeral patches.

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94 Terrestrial detritus is an important resource in many aquatic systems (e.g. citations in Mancinelli et al. 95 2005). Bulk changes to densities of detritus between systems can affect communities, food webs and 96 ecosystem processes in diverse ways (e.g. Dobson and Hildrew 1992; Wallace et al. 1999). Detritus 97 often occurs in discrete patches within sites, which may affect the capacity of animals to locate and 98 exploit it. In many streams, detritus is aggregated in depositional areas or trapped around retention 99 structures, thus creating a mosaic of patches against a matrix of the dominant bed material. Such 100 patches vary in size and quality, and also in temporal persistence through decomposition, physical 101 abrasion and transport downstream. Stream invertebrates that exploit detritus are typically mobile and 102 may use multiple resource patches during their aquatic life, or reside in one or a few patches that 103 satisfy organisms' life-time requirements (Robertson et al. 1995). It is well documented, especially 104 for artificially created leaf packs, that species composition can vary with the type of detritus (e.g. leaf 105 vs woody material, leaf species, stage of decomposition), and there is also some evidence that the

106 location of detritus within a channel may be important (Kobayashi and Kagaya 2002; Kobayashi and107 Kagaya 2004).

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109 Little empirical research investigates stream invertebrate responses to multiple resource patches within 110 a mosaic landscape, such as DARs, or whether such relationships are context-sensitive or vary with 111 species traits. More generally, whether stream invertebrate communities and populations are 112 influenced by entire arrays of *natural* detrital patches is largely untested (but see Palmer et al. 2000). 113 For many aquatic taxa, patch connectivity may be a combination of movements on the substrate surface (walking and crawling) and via the water column (many stream invertebrates can swim or drift 114 115 with currents), and largely unidirectional if currents are strong (anisotropic movement). The outcomes 116 of movement behaviours, such as DARs, may be a complex mix of patterns predicted for advective 117 dispersers and species moving at ground level (Bowman et al. 2002) and, therefore, these distinctive 118 environments may provide particularly robust tests of theory. Such models may also provide 119 alternative explanations for phenomena that cannot be explained by commonly measured variables, 120 such as total resource abundance or quality. Human impacts commonly result in the loss of riparian 121 vegetation and in-stream detritus, and almost certainly change the spatial and temporal dynamics of 122 detrital patch arrays. Local species extinctions associated with such habitat changes may arise simply 123 if species' movement behaviours are not suited to the spatial structure of altered landscapes (Fahrig 124 2007).

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126 In a field survey of natural detrital patches in replicate stream lengths, we tested whether variations in 127 the structure of resource patch arrays can explain variations in (1) an assemblage comprising common, 128 macroinvertebrate taxa (predominantly aquatic insects) and (2) patch- and landscape-scale densities of 129 species with different ecological traits. The mechanisms underlying any responses were likely to arise 130 from movement behaviours rather than long-term variations in fitness and reproduction, because the 131 patches are often short-lived relative to invertebrate generation times. We studied a sand-bed stream 132 with a sparse and patchy riparian zone, where site-to-site variations in patch arrays were likely to be 133 high, (Downes et al. 2011). The sand substrate was inherently unstable and constantly shifting – the

134 largest and most stable bed particles were typically detritus, and detrital packs were often short-lived. 135 We focused on 15 common taxa inhabiting detritus and that included leaf specialists, which we 136 predicted to respond strongly to detrital densities and patch sizes, and substrate generalists, which 137 should show weaker or mixed responses. First, we explored how detrital densities, patch sizes and 138 distributions varied among four sites, and then tested whether the composition of species assemblages 139 in entire arrays varied between sites and in accordance to the relative abundance of patches classified 140 according to size, water depth, decomposition, etc. If local population densities are strongly 141 influenced by patch size, we expected size to be important in explaining variations in species 142 composition. At the species level, we tested for DARs within multiple patch arrays and whether they 143 varied between arrays (i.e. context-dependence) and with species traits, with strong relationships 144 predicted for leaf specialists. At the landscape scale, we tested whether densities were associated 145 simply with total resource abundance, as commonly assumed, or whether the characteristics of 146 resource patch arrays mediate such relationships.

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148 Methods

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150 Study sites and sampling protocols

151 The study was carried out in Hughes Creek, a sandy-bed stream in central Victoria, south-eastern 152 Australia (see Downes et al. (2011)). Sample sites were in the mid-reaches (36° 59' S; 145° 21' E) (the 153 two most downstream sites of Downes et al. 2011) where the valley and stream channel were 154 relatively wide, the riparian zone was narrow and patchy due to agricultural activities. Large woody 155 debris was absent and retention structures were scarce. In-stream detritus, coarse particulate organic 156 matter (CPOM), was derived from the riparian vegetation: primarily from River Red Gum trees 157 (Eucalyptus camaldulensis), plus some other species of Eucalyptus and Acacia. Detritus was 158 aggregated into discrete packs scattered across the sand bed, mainly in depositional areas or 159 depressions of deeper water. We will call these 'leaf packs', even though many contained a mix of 160 leaves, bark and small woody debris. Leaf packs were often-short lived through displacement by 161 flowing water or burial in shifting sands. Typical of many Australian streams where *Eucalyptus* spp.

dominate the riparian zone, most leaf fall occurs in summer and, combined with seasonally low and
stable flows, detrital standing stocks in Hughes Creek are highest in summer. Nevertheless, detrital
standing stocks were low, <6 % areal cover; <400 g dry weight m⁻² (Table 1), compared with values
for many other streams types (Cariss and Dobson 1997), but not unusual for sand-bed streams in some
seasons (Palmer et al. 2000).

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168 In summer, leaf packs and their associated benthic invertebrates were sampled in four stream stretches 169 within a 3 km length (longitudinal environmental gradients are not discernible over this stream length, 170 unpublished data). Sampling protocols (described below) focused on sampling all the leaf packs in a 171 site, i.e. the entire array of resource patches, and sampling the same number of leaf packs per site 172 rather than the same area of stream bed. Therefore the length and area of each stretch varied, but each 173 encompassed channel lengths of several 10s of meters (Table 1). The minimum distance between 174 stretches was >300 m. The sampling period (January 2009) coincided with the end of a prolonged, 10year drought so water levels were relatively low, but this part of Hughes Creek flowed continuously 175 throughout the drought. In summer, near-bed velocities typically range from 0 to 55 cm s⁻¹ (Lancaster 176 177 et al. 2009). Sample stretches were sufficiently long to encompass multiple bedform shapes 178 characteristic of narrow, sand-bed streams with low flow regimes and Froude numbers less than 1 179 (Simons and Richardson 1961). Wildlife and domestic livestock had free access to the stream and 180 bedforms were often broken by pugmarks, which could persist in slow flow areas.

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182 Starting at a randomly selected position along the stream, we surveyed all leaf packs up to a total of 183 100 leaf packs for each site. Leaf packs were defined as accumulations of leaves, small twigs, bark and other small detritus (e.g. gum nuts), that covered at least 70 cm² of the stream bed. For each leaf 184 185 pack, we measured pack area (length \times width), water depth in the centre of the leaf pack, percent 186 decomposition, and mapped its spatial position. Decomposition was estimated visually as 0, 25, 50, 187 75 or 100%: 100% denoted leaf packs in which most leaves were dark in colour with a well-developed biofilm, and often broken or partially skeletonised; 0% denoted leaf packs comprised primarily of 188 189 leaves that had recently entered the stream (i.e. entire, 'clean' leaves with no obvious biofilm or

attached silt). Freshly dropped, green leaves tended to be scattered singly or in very small clusters
below the threshold size, and these were not sampled. We used a total station to map *X-Y* coordinates
for the centre of each leaf pack, and map the channel boundaries to calculate stream bed area.

The first 50 leaf packs in each site were sampled (Surber sampler, 0.09 m^2 , 250 µm mesh) to 194 195 enumerate invertebrates and quantify CPOM biomass. For leaf packs smaller than the Surber sampler, 196 we collected all the detritus and associated invertebrates, but not the surrounding or underlying sand. 197 For larger leaf packs, samples were collected from the centre of the leaf pack, taking care to collect 198 only detritus and not the underlying sand. Invertebrates of 15, common taxa that could be identified 199 live and were present at all sites were enumerated on the stream bank and then returned to the stream, 200 barring a few specimens that were preserved to confirm identifications. In the laboratory, CPOM from 201 each sample was separated into heavy and light fractions (wood, twigs, barks vs leaves), air dried and weighed. Species were categorized as leaf specialists vs generalists or sand-specialists according to a 202 203 previous, independent study in this stream (Downes et al. 2011). Generally, leaf specialists were more 204 abundant on detritus than sand and had a foraging mode or diet clearly associated with detritus 205 patches.

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207 Numerical and statistical analyses

208 In each site, X-Y spatial coordinates were used to calculate the 1st, 3rd and 5th nearest neighbour 209 distances, as a measure of inter-patch distances. The overall spatial pattern of leaf pack arrays was 210 analyzed using one-dimensional, point pattern analysis of the map data. Although leaf packs were 211 mapped in two dimensions, the sites were long and thin so the spatial data were transformed and 212 represented as linear distances along the thalweg. Our point pattern analysis (method detailed in 213 Lancaster and Downes 2004) is based on univariate spatial point pattern analysis using Ripley's K-214 function and its linearized form the L-function, and the related functions of second-order 215 neighbourhood analysis (Ripley 1981). First, the observed spatial pattern of leaf packs was compared 216 with a null hypothesis of complete spatial randomness (CSR), thereby testing whether leaf packs were 217 spatially clumped, random or over-dispersed. Second, we used marked point pattern analysis

(Lancaster 2006) to test whether there was any association between leaf packs of different sizes, e.g.
were small leaf packs more likely to occur together, or were small leaf packs most likely to be close to
large leaf packs. All significance tests were based on 999 Monte Carlo permutations.

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222 Multivariate permutation tests were used to compare the invertebrate species composition between 223 sites and with variables describing leaf pack characteristics (using PERMANOVA+ and PRIMER v6, Anderson et al. 2008; Clarke and Gorley 2006). All analyses were based on a resemblance matrix 224 225 constructed from fourth-root transformed species abundance data and Bray-Curtis similarity 226 coefficients; environmental variables (leaf pack characteristics) were transformed where necessary to 227 remove skew. Significance levels of all tests were determined by 9999 permutations. As a first step, 228 one-way multivariate analysis of variance (PERMANOVA) was used to test for differences between 229 sites. If sites are significantly different, we must first determine which, if any, patch characteristics 230 (environmental variables) influence species composition within a patch and, second, then test whether 231 site-scale differences in species composition can be attributed to variations between arrays in patch 232 characteristics (see Anderson et al. 2008). We examined the relationships between species and 233 environmental variables using a distance-based linear model (DISTLM). This procedure yields the 234 best combination of environmental predictor variables that explain the largest percentage of the 235 variation in the resemblance matrix of the species data. Models were fit using step-wise selection and 236 the most parsimonious model chosen by AIC selection criteria within the DISTLM routine. 237 Environmental variables tested included leaf pack area, dry weight of woody debris, dry weight leafy 238 debris, total CPOM dry weight, % decomposition and water depth. To illustrate the model 239 graphically, we used distance-based redundancy analysis (dbRDA) in which the ordination axes are 240 constrained to be linear combinations of the environmental variables that maximally explain variations 241 in the species data. Environmental variables were superimposed onto the dbRDA plot as vectors 242 whose directions and lengths are related to their correlation with the ordination axes and, hence, their role in generating the ordination. Spearman's rank correlations were used to identify correlations 243 244 between species and the ordination axes. Finally, to test whether sites differed in species composition 245 over and above any variation that could be explained between site differences in leaf pack arrays, we

246	used one-way PERMANOVA with environmental variables that were selected in the DISTLM
247	procedure included as covariates, analogous to a univariate ANCOVA. The model used sequential
248	(Type I) sums of squares with covariates (and their interactions) fit before the main factor.

250 For each site and species, we used ordinary least squares regression and log-transformed data to test 251 for DARs. To test whether average patch density varied with total detrital abundance in an array, we 252 used ANCOVA with site as the categorical variable and leaf pack size as a covariate, and used 253 planned comparisons to test for differences between pairs of sites with the highest vs lowest total 254 detritus. The model used Type I sequential sums of squares with the covariate fit first, to account for 255 any DARs before testing for site differences. We could not estimate landscape-scale densities of 256 generalists because the sand matrix between leaf packs was not sampled and many generalists occur 257 on sand and detritus (Downes et al. 2011). For leaf specialists, we assumed that the majority of 258 individuals in a site occurred in leaf packs, and combined information on average densities per leaf 259 pack with measures of total detritus abundances and of site areas to estimate landscape-scale densities.

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261 **Results**

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263 Sites differed in the total amount of detritus, expressed as total surface area or CPOM biomass, in the 264 size frequency distribution of leaf packs, and the nearest-neighbour distances between leaf packs 265 (Table 1, Fig. 1). Variations in site characteristics, such as total CPOM, did not follow a longitudinal 266 gradient. Leafy detritus dominated the leaf packs (63-80%); woody material, such as twigs, bark and 267 seed capsules, made up a smaller fraction that was not correlated with total CPOM. The overall 268 spatial distribution pattern of leaf packs differed between sites: random in sites B and D, weakly 269 clumped at approx. 0-12 m in site C and strongly clumped at 0-6 m in site A (Fig. 1). At one extreme, 270 Site A was characterized by small leaf packs clumped close together; at the other extreme, Site D had 271 larger leaf packs randomly spread over a longer stream length. Preliminary tests using marked point pattern analyses indicated that there was no spatial association between leaf packs of different sizes 272 273 (test results not reported for brevity).

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275 Of the 15 invertebrate taxa, seven were categorized as leaf specialists (Table 2). The relative 276 abundances of species were significantly different between the four sites, even though analyses 277 focused on common taxa present in all sites (one-way PERMANOVA with partial sums of squares: df 278 = 3,196; Pseudo-F = 8.87; P = 0.0001). Of all the environmental variables describing leaf pack 279 characteristics, four were included in the best model and together explained 27% of the variability in 280 the species composition (DISTLM; Table 3). The strongest explanatory variable was leaf pack area 281 (in marginal tests and in the full model) with other variables making smaller contributions. The first 282 two axes in distance-based RDA ordination (Fig. 2) captured about 95% of the variability in the fitted 283 model, and about 26% of the total variation in the species assemblage. Thus, the first two axes 284 explained almost all of the variation in the fitted model, but considerable residual variation was 285 unexplained. The first dbRDA axis was strongly associated with leaf pack area and total CPOM, and 286 the second axis with water depth and % decomposition of the leaf pack. Only a few species were 287 associated with small leaf packs (e.g. the baetid mayfly Offadens MV4) or low decomposition leaf 288 packs in shallow water (e.g. the filter-feeding caddisflies *Cheumatopsyche* spp.) as indicated by 289 correlations between individual species and the dbRDA ordination axes (Table 2). No species was 290 strongly associated with highly decomposed leaf packs in deep water. Several species were associated 291 with large leaf packs, particularly the net-spinning caddisfly Ecnomus continentalis and the cased 292 caddisfly Triplectides ciuskus.

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Once all the variation in the species assemblages explained by the leaf pack array was taken into account, there was still a significant difference between sites (Table 4). Estimated components of variation in the PERMANOVA model indicated that the greatest variation in species composition (24%) was at the level of individual leaf packs (according to the residual term). Over and above that, an additional 12% of the similarity in species composition could be attributed to leaf pack size. Notably, the next highest estimated component of variation was between sites (10% of similarity) and that was after all environmental variables had been fitted in the model (Table 4).

301

302 At the leaf-pack scale, 11 of the 15 taxa were sufficiently abundant at all sites for meaningful analyses of species-specific responses to patch size. Reported analyses use patch densities (nos animals m⁻² of 303 leaf pack); expressing the data as nos g⁻¹ biomass of CPOM yielded the same outcomes. Density-area 304 305 relationships (Table 5) were not significant for any species in Site A, the array dominated by small 306 leaf packs (Fig. 1). Density of one species (*Triaenodes* sp.) was not related to patch area at any site. 307 DARs were positive for eight taxa at two or typically three sites, and preliminary ANCOVA indicated 308 that regression coefficients (DAR slopes) did not differ between sites with significant relationships. These associations were generally stronger for leaf specialists than generalist, based on high R²-values 309 310 and regression coefficients. Relationships for the generalist *Economus continentalis*, however, were 311 comparable to those of most leaf specialists. Two species, Offadens MV4 and Cheumatopsyche spp., 312 had negative density-area relationships at some sites.

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314 Average densities in leaf packs were significantly higher in the pair of sites with the lowest overall detritus (sites A and B) for four of the five leaf specialists (Fig. 3). The probability that the predicted 315 pattern would occur by chance in four out of five species is very low ($P < 1 \times 10^5$ given likelihood 316 317 according to numbers of possible permutations). This pattern occurred in only one generalist species, 318 two had higher densities in sites with high total detritus and three showed no association. At the 319 landscape scale, there was no clear association between density and total detrital abundance for any 320 leaf specialist species (Fig. 4). Site B had the second lowest total detritus abundance, but had the 321 highest densities for four of the five leaf specialist species; the exception (Ferrissia petterdi) had the 322 second highest density in Site B.

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324 Discussion

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A link between faunal abundance and the spatial arrangement of patches is not necessarily expected if there is a high degree of advective movement, as is often the case for drifting or swimming stream invertebrates, and if patch structure changes frequently, as is often the case for leaf packs in streams. This study provides evidence, however, that mosaic landscapes created by natural resource patches in

330 stream channels can vary significantly over relatively short stream lengths and that these differences in 331 patch arrays produced unexpected outcomes on macroinvertebrate populations. The importance of 332 patch array characteristics to various ecological processes is well-established, especially in terrestrial 333 systems, but this is one of only a few empirical studies of the relatively small-scale mosaic landscapes 334 within natural freshwater systems (e.g. Palmer et al. 2000). At the community level, the relative 335 abundance of different patch types within an array was a major factor influencing the relative 336 abundances of common species, and these can have the biggest impact on community and ecosystem 337 dynamics (Dangles and Malmqvist 2004; Gaston 2011; Lancaster et al. 2008), so such shifts in species 338 composition could have larger-scale ecological consequences for events such as detritus processing 339 rates and nutrient dynamics. At the population level, most leaf specialists had positive density-area 340 relationships at most sites, whereas generalist species showed positive, negative and neutral 341 relationships. We found evidence of context-dependence, in terms of total resource abundance, with 342 the highest average patch densities in arrays with the lowest total resource abundance. Consequently, 343 population densities at the landscape scale were not closely related to total resource abundance, as is 344 commonly assumed.

345

346 Over a relatively short stream length (3 km), we found significant between-site differences in the 347 overall density of detritus and the distribution of leaf pack sizes, and the invertebrate fauna responded 348 to these differences. The assemblage of 15 species responded to this variation, with leaf pack area the 349 most significant environmental variable explaining variations in species relative abundances between 350 leaf packs, whereas other environmental variables (e.g. water depth, decomposition of leaves) were 351 less important. Of course, potentially important leaf pack characteristics that we did not measure 352 might explain some further variation, such as the leaf species and species mix (Leroy and Marks 353 2006), hydraulic conditions and oxygen availability (Kobayashi and Kagaya 2002; Kobayashi and 354 Kagaya 2004), and the degree of burial by sand (Tillman et al. 2003). It seems unlikely, however, that additional variables would substantially increase the explained variance or, importantly, alter the result 355 356 that patch size was the most important factor. Generally, small leaf packs were dominated by highly 357 mobile organisms whereas some, but not all sedentary taxa were associated with large packs. For

358 example, among the net-spinning caddisflies, *Ecnomus continentalis* (Ecnomidae) was positively 359 correlated with leaf pack size, whereas Cheumatopsyche spp. (Hydropsychidae) were most strongly 360 associated with shallow water. In many rocky-bed streams, leaf packs are considered to be unstable 361 and unsuitable for filter-feeding hydropsychids (Dobson 1994; Dobson and Hildrew 1992), but leaf 362 packs may be the most stable substrates available for net construction in this sand bed stream and some clearly have suitable hydraulic conditions. Species associated with large leaf packs included leaf 363 364 specialists (e.g. the cased caddisfly *Triplectides ciuksus*, which is strongly detritivorous (St. Clair 365 (1994)), whereas others were generalists that also exploit the sand matrix between leaf packs (e.g. the 366 predatory caddisfly E. continentalis (Lancaster et al. 2009)).

367

368 In contrast to some common expectations about advective systems with high patch turnover, most 369 species had significant density-area relationships. In our system, significant DARs are likely to result 370 from movement behaviours, as shown in some other insects (e.g. Cronin et al. 2004; Jackson et al. 371 2013), perhaps coupled with size-specific variations in the longevity of leaf packs. With survey data, 372 we can only speculate about these behaviours. However, all but one of the patch specialists showed 373 stronger and more consistent responses than generalist species, and this suggests that our DARs are 374 not chance outcomes. Positive DARs for most leaf specialists contradicts the predicted negative or 375 neutral relationships for advective dispersers if immigration rates drives the relationship (Bowman et 376 al. 2002). Positive relationships are, however, consistent with Root's (1973) resource concentration 377 hypothesis (longer residence time in larger, resource-rich patches) and with a negative relationship 378 between emigration and patch size. This may be reinforced by the vulnerability of small patches to 379 disturbance (high flows, wildlife disturbance), such that some small patches are always in the early 380 stages of colonization. Positive, although sometimes weaker, DARs in some generalist species are 381 consistent with suggestions that DAR slopes should be more positive for specialists (Hambäck et al. 382 2007). The observed negative DARs for two generalists might be expected if immigration rates 383 dominate patterns or if density compensation is in operation, i.e. the density of some species decreases 384 in association with an increase in others (Connor et al. 2000; Nee and Cotgreave 2002). In this case, 385 however, we speculate that small patches were simply more similar to the between-patch matrix or the

386 'preferred' substrates of *Cheumatopsyche* spp. (high flows for filter-feeding) and *Offadens* MV4 387 (sufficiently high flows to ensure gas exchange) and, indeed, these taxa are often very abundant on 388 sand in this stream (unpublished data). Furthermore, species abundances in small patches are 389 expected to reflect species typical of the matrix more strongly than the patch habitat (Hambäck et al. 390 2007; Summerville and Crist 2004). Neutral DARs for the leaf specialist Triaenodes sp. at all sites is 391 curious. In this stream system, most leaf specialists are most abundant further upstream where the 392 riparian zone is more extensive and detritus densities are high (Downes et al. 2011). *Triaenodes* sp. is 393 an exception with highest densities where the riparian zone is sparse. Members of this genus are adept 394 swimmers (Gall et al. 2011; Tindall 1964) and may track resource patches more effectively than the 395 other, slower-moving leaf specialists, resulting in neutral DARs. Human impacts have reduced the 396 riparian zone and detrital densities at these study sites and inter-patch distances may affect the 397 movement capacity of some species (Fahrig 2007). It is tempting to speculate that *Triaenodes* is 398 abundant in sandy areas because its movement ability allows it to overcome the highly patchy nature 399 of resources.

400

401 Despite this strong influence of patch size, there were still significant differences in species 402 composition and densities between sites even after accounting for leaf pack area. Some of this 403 variation may be explained by the responses of species to other characteristics of patch arrays, (e.g. 404 resources related to mating and egg-laying behaviours of terrestrial adults: (Encalada and Peckarsky 405 2012; Lancaster and Downes 2014; Lancaster et al. 2011) but also to variations in patch aggregation 406 (Lancaster et al. 2003; Palmer et al. 2000). At one site (Site A), DARs for all species were neutral and 407 this may reflect the small range of patch sizes (Bowers and Matter 1997) but also the significant 408 clumping of resource patches. Aggregation creates high variance in between-patch distances – short 409 distances within clumps but long distances between clumps (Cain 1985) – and if between-clump 410 distances exceed the search capacity of animals, then significant mortality can occur (Cain et al. 1985) 411 and this may obviate DARs. The results for Site A contrast with those of Site B, which had a similar 412 extent of patch sizes but no clumping, and suggests that context-dependence is important in our 413 system.

415	This context-dependence (i.e. interactions between total resource abundance and patch array
416	characteristics) resulted in the highest patch densities of leaf specialists occurring at sites with the least
417	detritus and smallest patches, and thus overall site-scale densities were not associated with total
418	resource abundance. This is despite a four-fold difference in areal cover of detritus and more than two
419	orders of magnitude difference in dry weight biomass among sites. Individual patches are the units
420	within which many interspecific (e.g. trophic) interactions occur and thus patch-level density is
421	germane to a variety of hypotheses about the effects of resource density. In particular, there is strong
422	interest in modeling the effects of detrital resource densities on food webs (references above). Our
423	results illustrate that tests of such models may be strengthened if they take account of the way in
424	which detrital resources are deployed at sites, not just the overall density of such resources.
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427	
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551 Figures legends

553	Fig. 1.	Leaf pack arrays in the four sites. $(a - d)$ Size-frequency histogram of leaf packs
554		according to surface area. $n = 100$ for each histogram. Note the logarithmic scale of the
555		X-axes. (e – h) One-dimensional, point pattern analyses of the spatial distribution of leaf
556		packs. Solid line indicates the mean difference between the observed L-function and the
557		L-function under CSR (complete spatial randomization); dotted lines indicate 95%
558		confidence envelope for the difference; dashed line indicates the null hypothesis of no
559		difference. If the mean difference and its confidence envelope lie above the null
560		hypothesis of no difference, i.e. values >0, then leaf packs are more clumped than
561		expected by chance. If the observed difference is negative, then the leaf packs are evenly
562		spaced. If the null hypothesis lies within the confidence envelope, this indicates a random
563		spatial pattern
564	Fig. 2.	Distance-based redundancy analysis (dbRDA) ordination relating environmental
565		variables to the invertebrate assemblage. Sites A and B are represented by open and
566		closed circles, respectively; sites C and D closed and open triangles, respectively.
567		Environmental variables are shown as vectors whose direction and length indicate the
568		strength and sign of their correlation with the dbRDA axes. The relative size and position
569		of the unit circle is arbitrary with respect to the underlying plot. Each vector begins at the
570		circle origin and terminates at the coordinates describing its correlation with the two axes
571	Fig. 3.	Within-leaf pack density (mean \pm SE), adjusted for effect of leaf pack area, of some leaf
572		specialist species $(a - e)$ and generalists $(f - k)$ at each site. <i>F</i> -statistics for planned
573		comparisons between pairs of (sites A and B vs C and D) are shown in each panel. df =
574		1, 192 for each test. 'ns' denotes $P > 0.05$, * $P < 0.05$, ** $P < 0.01$. <i>F</i> -values that are
575		underlined indicate significant differences opposite in direction than those predicted.
576		Note: y-axes are logarithmic and scales differ between taxa. See Table 2 for full species
577		names

- 578 **Fig. 4.** Site-scale density (mean \pm SE) of some leaf specialists (a e) at each site. Note: y-axis
- 579 scales differ between taxa. See Table 2 for full species names







 Table 1. Characteristics of detrital resources in the four study stretches based on 100 leaf packs and, in parentheses, the 50 leaf packs used to enumerate invertebrates. Dry weight biomass

estimates based on 50 leaf packs. Nearest neighbour distances calculated from *X*-*Y* coordinates of the centre of each leaf pack. Mean values based on 50 and 100 leaf packs did not differ; values shown are for 100 leaf packs.

	Site					
	А	В	С	D		
Order from upstream, to down stream	2	1	4	3		
Length (m)	70 (30)	88 (39)	117 (74)	122 (63)		
Area (m ²)	264 (110)	251 (111)	496 (271)	429 (200)		
Surface area detritus (cm ² CPOM m ⁻² stream	106 (112)	258 (430)	340 (407)	429 (632)		
bed)						
Areal cover detritus (%)	1.1 (1.1)	1.1 (1.1) 2.6 (4.3)		4.3 (6.3)		
Total CPOM biomass (g dry weight m ⁻² stream	1.8	77	109	399		
bed)						
Leafy CPOM as % of total in each leaf pack,	80 ± 3	63 ± 4	66 ± 4	73 ± 4		
mean \pm SE						
Nearest neighbour (m), mean \pm SD	0.8 ± 0.7	0.7 ± 0.8	1.2 ± 1.1	1.2 ± 1.8		
3rd nearest neighbour (m), mean \pm SD	1.5 ± 1.8	1.6 ± 1.3	2.5 ± 1.3	2.3 ± 2.2		
5th nearest neighbour (m), mean \pm SD	2.3 ± 2.3	2.3 ± 1.4	3.6 ± 1.7	3.5 ± 2.6		

Table 2. List of taxa enumerated in leaf pack samples and their substrate associations: L = leaf specialist, G = generalist, S = sand specialists, na = no information. Spearman's rank correlations between species and the dbRDA axes. Numbers in bold indicate correlation where |r| > 0.20.

Order or Family	Species	Substrate	dbRDA1		dbRDA2		
Ephemeroptera	Offadens MV4	G	small leaf packs	0.23	Shallow; low decomp.	0.26	
Trichoptera	Cheumatopsyche spp. ^a	G		0.06	I	0.48	
Coleoptera	Berosus larvae ^b	S		-0.07		0.14	
Tricladida	Tricladida	na		-0.11		0.29	
Planorbidae	Physella acuta	G		-0.13		0.26	
Trichoptera	Anisocentropus sp.	L		-0.19		-0.02	
Trichoptera	Coenoria AV1 ^c	G		-0.21		0.30	
Trichoptera	Triaenodes sp. ^d	L		-0.22		0.15	
Trichoptera	Oecetis spp. ^e	L		-0.34		0.05	
Trichoptera	Notalina fulva	L		-0.35		0.05	
Ephemeroptera	Tasmanocoenis tillyardi	G	\checkmark	-0.42	\checkmark	-0.05	
Trichoptera	Lectrides varians	L		-0.42		0.05	
Planorbidae	Ferrissia petterdi	L		-0.46		-0.01	

Trichoptera	Ecnomus continentalis	G		-0.69		0.06
Trichoptera	Triplectides ciuskus	L	large leaf packs	-0.72	Deep; high decomp.	-0.01

^a *Cheumatopsyche* AV1, AV2 and AV4 are present at these sites and could not be separated as live specimens

^b Berosus involutus and B. australiae are present at these sites but larval identification is not possible

^c Possibly Coenoria boera

- ^d No key to larvae; only *Triaenodes volda* has been identified in adult specimens from this stream
- ^e No key to larvae; at least six species of adult have been identified from this stream

 Table 3. Summary of a distance-based linear model (DISTLM) relating species data with

 environmental variables in a step-wise selection procedure. Table shows the best model

 according to AIC selection criterion.

Variable	Pseudo-F	Р	Variance	Cumulative
			explained (%)	variance (%)
Leaf pack area	39.9	0.001	16.8	17
Decomposition	15.8	0.001	6.2	23
Depth	6.03	0.001	2.3	25
СРОМ	5.12	0.001	1.9	27

Table 4. Summary of one-way PERMANOVA comparing species assemblages between sites (fixed factor) and including environmental variables (covariates) that were identified in the DISTLM model (Table 3). The test used 9999 permutations and sequential sums of squares (Type I). Covariates and interactions among covariates were entered into the model before the main factor (site) and any interactions between the main factor and the covariates. Non-significant interaction terms identified in preliminary analyses have been omitted from the model. Estimated components of variation are expressed as square roots and are akin to a standard deviation in a traditional univariate analysis. The three largest values are in bold.

	Source	df	MS	Pseudo-F	Р	Components
						of variation
Covariates	Area	1	30115	53.5	0.0001	12.2
	Decomposition	1	11111	19.7	0.0001	7.35
	Depth	1	4135	7.34	0.0001	4.95
	СРОМ	1	3439	6.11	0.0001	8.16
	Depth x decomp.	1	2987	5.30	0.0001	3.66
	Area x CPOM	1	3638	6.46	0.0001	3.12
Main factor	Site	3	4790	8.51	0.0001	10.4
	Depth x site	3	1534	2.73	0.0004	5.23
Residual		187	563			23.7

Table 5Summary of regression analyses testing for associations between density and leaf pack area for leaf specialists and substrate generalists in each of
the fours sites. Data were log-transformed before analyses. Regression coefficients (slopes) and associated standard errors, are shown for
significant tests only. d.f. = 1,48 in all cases. See Table 2 for full species names.

Leaf specialists						Generalists					
Species	Site	F	Р	$r^{2}(\%)$	Coeff. (SE)	Species	Site	F	Р	$r^{2}(\%)$	Coeff. (SE)
Triplectides	А	0.010	0.922	0.0		Offadens	А	0.559	0.459	1.2	
	В	26.8	< 0.001	35.8	3.92 (0.75)		В	3.39	0.072	6.6	
	С	19.5	< 0.001	28.9	4.85 (1.10)		С	7.02	0.011	12.8	-3.95 (1.49)
	D	32.4	< 0.001	40.3	4.75 (0.83)		D	14.5	< 0.001	23.2	-4.24 (1.11)
Triaenodes	А	0.657	0.422	1.3		Ecnomus	А	1.89	0.175	3.8	
	В	0.736	0.395	1.5			В	10.2	0.003	17.5	6.38 (2.00)
	С	3.96	0.052	7.6			С	11.1	0.002	18.7	3.82 (1.15)
	D	2.79	0.101	3.2			D	23.7	< 0.001	33.0	3.32 (0.68)

Notalina	А	2.86	0.098	5.6		Tasmanocoenis	А	0.102	0.751	0.2	
	В	5.79	0.020	10.8	5.20 (2.16)		В	4.98	0.030	9.4	2.07 (0.93)
	С	10.1	0.003	17.4	4.05 (1.27)		С	8.03	0.007	14.3	1.54 (0.54)
	D	22.3	< 0.001	31.7	5.21 (1.10)		D	6.53	0.014	12.0	2.14 (0.84)
Lectrides	А	0.068	0.795	0.1		Cheumatopsyche	А	1.41	0.241	2.9	
	В	15.9	< 0.001	24.9	8.12 (2.04)		В	4.74	0.034	9.0	-5.38 (2.47)
	С	17.7	< 0.001	26.9	2.80 (0.67)		С	0.288	0.594	0.6	
	D	17.8	< 0.001	27.0	3.39 (0.81)		D	0.026	0.872	0.1	
Ferrissia	А	0.497	0.484	1.0		Physella	А	0.277	0.601	0.6	
	В	10.5	0.002	18.0	6.48 (2.00)		В	8.61	0.005	15.2	5.78 (1.97)
	С	20.1	< 0.001	29.5	4.73 (1.06)		С	4.93	0.031	9.3	2.58 (1.16)
	D	0.009	0.926	0.0			D	5.49	0.023	10.3	2.20 (0.94)
						Coenoria	А	0.529	0.470	1.1	
							В	0.563	0.457	1.2	
							С	4.57	0.038	8.7	2.80 (1.31)
							D	8.37	0.006	14.8	3.42 (1.18)