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Spatial arrangement or amount? Spatially variable oviposition habitat can determine aquatic insect egg abundance

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Abstract

1. Both the amount and spatial arrangement (configurational heterogeneity) of resources can affect population abundance and community diversity via influence on the growth, survival, reproduction, recruitment and movement of species. However, in most cases, it is difficult to separate the effects of resource amount from arrangement because these two attributes are often naturally correlated. In this study, we examined the configurational heterogeneity of resources (oviposition habitat—emergent rocks, ER) within rivers and decoupled the effects of resource amount from those due to the spatial arrangement on oviposition by eight species of aquatic insects (seven caddisflies and one mayfly).
2. To capture the configurational heterogeneity of resources in 28 sites (riffles) across multiple streams in Australia and Scotland, we calculated fractal dimensions (D_B) using the box-counting technique. We then used simulated riffles to explore how numbers of ER, edginess (the proportion of ER along river margins) and patchiness (clustering of emergent rocks in the middle) separately and together affected the values of D_B using asymptotic regression models. Finally, we used multiple regression to test whether the numbers of egg masses laid in natural riffles of each of the eight species were explained by the number of ER, fractal dimension or both.
3. The distributions of ER in natural riffles were scale-independent, self-repeating patterns (i.e. they were fractal), and values of D_B varied significantly among riffles. Variations in fractal dimensions among simulated riffles were significantly related to the number of ER, edginess and patchiness. However, in natural riffles, only the number of ER and patchiness affected D_B . Egg mass abundances were related to the fractal dimensions of ER distributions in riffles in three species and to the number of ER in five species.
4. The fractal dimensions of riffles are unlikely to be driven by large-scale processes but instead may result from within-riffle variability that influences rock movement, arrangement and emergence. Increased oviposition by aquatic insects in riffles with greater numbers of ER suggests that these species may be limited by

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the amount of oviposition resources. Of the species responding to fractal dimension, two species favoured tightly clustered ER whereas the third favoured ER in much looser clusters. It is feasible that aquatic insects can detect ER clusters from the air by responding to changes in the reflectivity of water (albedo) caused by turbulence around ER.

5. That fractals can capture configurational heterogeneity of resources in streams suggests that this technique is useful to test for general ecological patterns across diverse stream systems. Whether configurational heterogeneity influences adults directly or indirectly, these results showed that the amount and arrangement of suitable oviposition habitat plays a role in determining egg mass densities, with potential consequences for larval densities. These patterns may have important community-level and functional consequences and hence spatial arrangements should be considered when humans manipulate these resources in rivers.

KEYWORDS

box-counting fractal dimension, configurational heterogeneity, emergent rocks, spatial heterogeneity, spatial scale

1 | INTRODUCTION

The amount and spatial arrangement (configurational heterogeneity) of resources can influence species abundance and diversity and have functional consequences in ecosystems. Traditionally, ecologists have focused on the roles of resource quantity (resource concentration hypothesis) and diversity of resource types (compositional heterogeneity) in shaping biological communities (Hutchinson, 1957). However, configuration can influence the growth, survival, reproduction, recruitment and movement of species (Fahrig & Paloheimo, 1988; Hansson et al., 2012; He et al., 2019). For example, the spatial arrangement of leaf packs affects the emergence (completion of life cycle) of aquatic insects likely due to increased local population densities (hence intraspecific competition) with aggregation of resources (Palmer et al., 2005). Separating the effects of resource amount from spatial arrangements can be difficult, particularly in natural systems (Gardner & O'Neill, 1991). For example, leaf pack aggregation can increase in autumn when fallen leaves are abundant (Palmer et al., 2005). Nevertheless, separating these two phenomena is important to understand natural and human-modified patterns of species abundances, that is, why do some patches have far more animals than others of similar size? In this study, we examine the configurational heterogeneity of resources (oviposition habitat) within rivers and decouple the effects of resource amount from spatial arrangement to test for associations between resources and recruitment.

In rivers, emergent rocks (ER) are essential resources for a variety of aquatic insects that use them for oviposition (e.g. Reich & Downes, 2004). Both the amount and spatial arrangement of ER can influence the recruitment of some stream insects. Low numbers of ER can limit the number of egg masses laid, that is, create resource

limitation ('habitat limitation', examples in Downes et al., 2021), whereas high numbers of ER may exceed the number of available gravid females ('supply limitation'). The spatial arrangement of ER may also affect egg mass abundances by altering inter- and intra-specific interactions (Lancaster, Downes, Lester, & Rice, 2020) or by altering the relative abundance of resources in different micro-environments (Lancaster et al., 2003). For example, some aquatic insect species prefer ER in slow flows, which typically are found along channel margins where riverbank roughness reduces local velocity, whereas other species prefer ER in fast flows, which are typically clustered in the middle of channels where velocity is higher (Lancaster et al., 2003). The subsequent hatching success of eggs can depend on whether females oviposit on preferred ER (Bovill et al., 2013). Thus, if preferred oviposition resources are limited, due to unfavourable spatial arrangements, for example, females may opt for less preferred ER, move to alternative locations or fail to oviposit. Importantly, understanding whether mortality rates of other stages in the life cycle are influenced by the density patterns that result from oviposition preferences and behaviours is key to understanding the implications of oviposition patterns on populations and community composition.

Finding a measure of configurational heterogeneity and determining the appropriate spatial scale for measurement is crucial for detecting and interpreting relations between the arrangement of resources and species' responses (Kotowska et al., 2022; Loke & Chisholm, 2022). One such measure, fractal dimension, is widely used as a measure of complexity because it is applicable and comparable across most subject matter (rather than using measures that are intrinsic to particular subjects or ecosystems) and is independent of spatial scale. Being scale-independent, fractal dimensions are theoretically valid at scales outside their measured range. Measures of fractal dimension

often fall between the well-known dimensions of 1, 2 and 3 for a line, surface and volume, respectively, and represent the extent to which the space is filled (see Dwyer et al., 2021). In a previous study, we found that ER distributions along long stream lengths were fractal (i.e. had scale-independent repeating patterns) and had fractal dimensions that reflected ecologically meaningful aspects of the environment, including pool–riffle spacing, sediment size, and channel slope (Dwyer et al., 2021). Accordingly, these fractal dimensions may also reflect the spatial arrangement of ER at smaller scales, for example, within riffles (Papanicolaou et al., 2012), and provide insight into the egg-laying patterns of insects that oviposit on ER. For example, positive associations were found between fractal dimensions and animal abundance and diversity in some other ecosystems (e.g. seaweeds, Mancuso et al., 2023 and references within; coral reefs, Torres-Pulliza et al., 2020).

In this study, we divide our questions, analyses and discussion into two sections: the first explores the patterns of configurational heterogeneity of oviposition resources and the second relates resource configurational heterogeneity to oviposition patterns. First, to explore patterns of resource configurational heterogeneity, we tested whether the spatial arrangements of ER in riffles were scale-independent and could be described by fractal dimensions (Q1), and whether variation in fractal dimensions is driven by particular spatial scales (riffle, river and region scales) (Q2). The latter may elucidate whether fractals effectively characterise configurational heterogeneity outside the range over which they are measured. Because we cannot control the values of all variables in natural systems, we also use numerical simulation to better understand how fractal dimensions describe spatial arrangement of resources (Q3) and how these relations compare with real riffles (Q4). This is particularly critical in systems where elements of configurational heterogeneity vary systematically with others (e.g. the number of ER may be associated with the patchiness of ER distribution).

Second, to understand how configurational heterogeneity of resources influences oviposition at the riffle scale, we first tested for associations between egg mass abundances and ER characteristics at the rock scale (preferences for water velocity, water depth and rock size) and at the within-riffle scale (preferences for ER in the margins or middle of riffles) (Q5). As detailed above, these ER characteristics are related to the arrangement at the riffle scale and consequently may explain relations of egg mass abundances with fractal dimension. Finally, we tested whether the numbers of ER and fractal dimensions of riffles were associated with egg mass abundances of seven caddisflies and one mayfly species (Q6). A linear association between the number of egg masses and ER across the full range of ER densities implies that numbers of ER limit the number of oviposited eggs, that is, that some females must either move to other sites or fail to oviposit (resource limitation). Alternatively, an asymptotic relation implies that high numbers of ER exceed the local supply of gravid females ('supply limitation'—see Downes et al., 2021). If the spatial arrangement of

ER matters, then we expect species to show a relation with fractal dimension, independent of the number of ER.

2 | METHODS

2.1 | Field sites and survey protocols

To capture a wide range of spatial arrangements in oviposition resources, our field sites included three streams in the Goulburn River catchment, SE Australia (Little River, Snobs Creek and Steavenson River) and two streams in the Lammermuir Hills in SE Scotland (Dye Water and Faseny Water). These streams and study sites have been described in detail elsewhere (Lancaster et al., 2010; Lancaster, Downes, Lester, & Rice, 2020). For each stream, 5–7 riffles within a 1 km stretch were surveyed. Surveys of the Australian and Scottish streams were conducted in the austral summer 2017 and the European spring 2007, respectively. Riffles were discrete lengths of river that were steeper, with higher average velocities and low relative roughness (low ratio of depth to substrate sediment size), distinguishable from flatter sections upstream and downstream that had slower, deeper flows (lower Froude numbers) and higher relative roughness. Riffles had relatively high densities of ER compared to the adjoining areas that had few or no ER. In Australia, riffles were selected to encompass a wide range of sizes and emergent rock densities to capture the natural range of conditions; in Scotland, we sought to achieve a range of ER spatial arrangements, because a positive association between ER and egg mass numbers had been established previously (Lancaster et al., 2010) (Table 1). In each riffle, the spatial coordinates (X, Y) were mapped for every potential oviposition site using a total station (Leica TC803; see Figure S1, for example maps of riffles). Potential oviposition sites were ER ≥ 5 cm in size (b-axis dimension) in ≥ 5 cm of water and not embedded in fine sediments (Lancaster, Downes, Lester, & Rice, 2020). At every ER, we measured several environmental variables (ER size, water velocity, depth) and egg masses of the aquatic insects were counted and identified. For a more detailed description of survey protocols, see Lancaster, Downes, Lester, and Rice (2020).

2.2 | Study organisms

Our study organisms were insect species that obligately use ER for oviposition. In the Australian streams, there were six species of caddisflies

TABLE 1 Summary of riffle morphological characteristics.

| | Australian streams | Scottish streams |
|--|--------------------|------------------|
| Range of riffle lengths (m) | 8–49 | 17–213 |
| Range of the number of ER in riffles | 57–765 | 127–208 |
| Range of ER densities in riffles (ER m ⁻²) | 0.40–4.32 | 0.13–1.20 |

Abbreviation: ER, emergent rock.

in the family Hydrobiosidae [*Apsilochorema gisbum* (Mosely), *A. obliquum* (Mosely), *Ulmerochorema rubiconum* (Neboiss), *U. seona* (Mosely), *Ethochorema turbidum* (Neboiss) and *Taschorema evansi* (Mosely)] and one in the family Tasimiidae [*Tasimia palpata* (Mosely)]. In Scotland, there was one species of mayfly [*Baetis rhodani* (Pictet), Baetidae]. These species have similar oviposition habits: a gravid female lands on an ER, walks down the sides under the water and lays her entire clutch of eggs as a single mass attached to the underside of the ER (Lancaster et al., 2010; Lancaster & Glaister, 2019). Species identification of caddisfly egg masses followed Lancaster and Glaister (2019); egg mass identification of *B. rhodani* is well known (e.g. Lancaster et al., 2010 and references therein). Several species of *Ulmerochorema* [*U. stigmum* (Ulmer), *U. onychion* (Neboiss) and *U. membrum* (Neboiss)] occur in the study streams and have morphologically similar egg masses to *U. rubiconum* (Lancaster & Glaister, 2019), but adults of these were rare (Lancaster, Downes, & Dwyer, 2020), and we assume that the majority of egg masses of this type were *U. rubiconum*.

While our study species all use the same oviposition habitat, species-specific behaviours can lead to patchy patterns at different scales. For instance, *A. obliquum* and *A. gisbum* avoid ovipositing on emergent rocks where egg masses of congeners or conspecifics are present (Lancaster, Downes, Lester & Rice, 2020). In contrast, *U. rubiconum* and *U. seona* aggregate egg masses onto individual rocks as well as aggregate in places where emergent rocks are clustered (Lancaster et al., 2003; Lancaster, Downes, Lester, & Rice, 2020). Furthermore, preferences for rock size, water depth and velocity differ between the species (Lancaster, Downes, Lester & Rice, 2020). *Apsilochorema* spp. select ER in slow-flowing water, whereas *Ulmerochorema* spp. select ER in fast-flowing water, and *U. seona* exploits a subset of the ER used by *U. rubiconum* (the largest ER in the fastest flows and deepest water). The present study includes three additional species, *E. turbidum*, *T. evansi* and *T. palpata*, for which rock and flow preferences have not previously been documented. We used data from the field survey to establish ER preferences for these remaining species. We also categorised all species as 'margin' or 'middle' species, depending on how far egg masses were from stream banks. Margin species showed a skewed relationship, with most egg masses deposited at shorter distances from the bank, whereas all other taxa were defined as middle species (explained in the Methods below).

2.3 | Calculating fractal dimensions

We used the box-counting fractal dimension (D_B) to measure the configurational heterogeneity of ER in riffles. D_B was calculated using methods prescribed by Seuront (2009) and the R scripts in Dwyer et al. (2021). This involved dividing the riffle into a set of nested equal-sized 'boxes' of size δ . The number of occupied boxes (N_B) (i.e. those containing at least one ER) were then counted for the range of δ . Thus, the box-counting method produced a binary measure of ER versus no ER. Box sizes ranged from 0.4 to 71.2m. All possible box sizes were used, however, the data set excluded box sizes

that did not result in a change in N_B and so box sizes varied among riffles. The slope of $\log_e(\delta)$ versus $\log_e(N_B)$ plots provides estimates of the fractal dimensions, and a linear relationship between these variables indicates the possible presence of self-similarity (fractal structure). To determine whether the spatial arrangements of ER in riffles were scale-independent and could be described by fractal dimensions (Q1), we followed Seuront's (2009) three-step procedure to detect fractal-like properties in natural patterns (Table S1). Reported estimates of the fractal dimension (D_B) are taken from the third of these steps (the compensated slope procedure) because this estimate is most robust to random non-fractal structure (i.e. artefacts of the data).

2.4 | Quantifying edginess and patchiness

Because the target insect species vary in whether they lay egg masses predominantly either on ER along the margins or on ER in the middle of riffles (Lancaster et al., 2003), we quantified lateral accumulations of ER at the margins (edginess) and clustering of emergent rocks in the middle (patchiness). Riffle margins were defined as the distance from the bank that captured 70% of egg masses of species that typically oviposit close to the stream banks ('margin species') (Figure S2). The margins were mapped onto the spatial coordinates of the banks and ER of each riffle (e.g. Figure S1), and the number of ER that fell inside and outside the margins (in the middle) was counted. Edginess was then calculated as the proportion of ER inside the margins. Patchiness was quantified as per Lloyd's patchiness equation (Lloyd, 1967) using ER in the middle area. This index is a density-independent ratio (Pielou, 1974). Patches comprised 1×1 m cells in a grid laid over the riffles, excluding the margins (e.g. Figure S1).

2.5 | Simulations

Multiple variables that likely affect fractal dimension were correlated with each other (i.e. numbers of ER and edginess; Table S2), hence, we simulated riffles using a numerical model. These simulated riffles allowed ER number and aspects of arrangement (edginess and patchiness) to be manipulated individually and with greater replication to test how each aspect influences fractal dimensions. Simulations were carried out in the open-source software R (R Core Team, 2020) based on empirical measurements of morphological characteristics (riffle length and width) that allowed us to create synthetic riffles that varied systematically in ER number, edginess and patchiness (see Appendix S1 for details).

2.6 | Statistical analyses

To determine whether variation in fractal dimensions is driven by particular spatial scales (riffle, river and region scales) (Q2), two

sets of analyses were performed: nest two-way ANOVA was used to determine whether fractal dimensions of ER in riffles (D_B) varied between riffles, rivers or countries; and Pearson's product-moment correlation test was used to test for correlations between the fractal dimensions of ER arrangements in 2D riffles and 1D longitudinal stream segments (data from Dwyer et al., 2021).

Simulated riffles were used to separate the influence of ER number and arrangement (edginess and patchiness) on fractal dimension (Q3). Asymptotic regression models were fitted to the fractal dimensions of simulations grouped by edginess or patchiness, which included a range of ER densities. This was achieved using the self-starting *SSasympt* function in R, which estimates the upper asymptotic value (*Asym*), the natural logarithm of the rate constant (*Lrc*) and the *y*-intercept (*R0*) parameters of the models. Type II model regression tests were then used to assess whether the parameters of asymptotic regression models varied with edginess or patchiness. Multiple regression was then used to test which elements (number of ER, edginess and patchiness) were related to 2D real riffle fractal dimensions (Q4). Model terms were entered in different orders to test whether the order of addition influenced the results. Correlations among model terms were tested using Spearman's rank correlation tests.

For the egg mass data, we first characterised the types of ER preferred by *E. turbidum*, *T. evansi* and *T. palpata* (which have not previously been described) (Q5). For each species, we contrasted ER with egg masses (exploited ER) to those without egg masses (unexploited ER) across four, co-measured environmental variables (water velocity at the upstream side of each ER, water depth, height of ER above water's surface, *b*-axis; see Lancaster, Downes, Lester, & Rice, 2020 for details) using distance-based redundancy analysis (dbRDA) and PERMANOVA (Anderson, 2008). Data were normalised, and resemblance matrices were created using Euclidean distance. To determine which environmental variables were associated with a non-random selection of ER, distance-based linear modelling (DistLM) was used for marginal (single predictor) and conditional (multiple predictor) tests of which environmental variables explained patterns in resemblance matrices for each species. For *B. rhodani*, the DistLM analysis was carried out separately for the two Scottish rivers due to a significant river interaction in the initial PERMANOVA.

Finally, multiple regression tested whether egg mass abundances of each species were related to the number of oviposition resources (total number of ER in the riffle) and the spatial arrangement of resources as described by fractal dimension (D_B) (Q6). Where neither independent variable was significant, a more parsimonious model was run that included only the total number of ER. For species with significant linear relationships with the total number of ER, asymptotic models were also fit to log-transformed egg abundance data to inspect for habitat and supply limitation (linear vs. asymptotic relationships, respectively). The Akaike information criterion (AIC) was used to evaluate model fits. Computations and analyses were undertaken using packages *ggpmisc*, *stats*, *lmodel2* and *dplyr* in R.

3 | RESULTS

3.1 | Resource configurational heterogeneity (Q1-Q4)

The 2D spatial arrangements of ER in all 28 riffles were fractal-like using the box-counting method (Q1). All riffles satisfied at least two of the three tests developed by Seuront (2009); this is sufficient to illustrate fractal behaviour (Table S1). Coefficients of determination for all streams ranged from 0.94 to 0.99, indicating a good fit in all cases (Figure S3). Fractal dimensions varied among the five streams in Australia or Scotland (i.e. nested in Country) (Q2) (Table 2) but the only significant pairwise comparison occurred between Little River and Dye Water (Tukey HSD: difference = -0.35, adjusted $p = 0.033$), which are located in Australia and Scotland, respectively. The term River explained 33% of the variability in D_B ; Country explained 3%; and the remaining 63% of the variance was due to within-river variation plus error. The 2D fractal dimensions of ER in riffles were unrelated to the 1D fractal dimensions (longitudinal) of ER over long stream lengths up to a kilometre (Figure 1; Model II regression: $df = 26$, $r = -0.05$, $p = 0.804$).

The fractal dimensions of simulated riffles increased with the number of ER but decreased with both edginess (Figure 2) and patchiness (Figure 3) because both attributes create patterns in rock distributions (i.e. greater spatial order, which results in lower D_B) (Q3). The nature of the relationships between each of these attributes and fractal dimension varied. For edginess, the rate of change and the asymptote of its relationship with fractal dimension declined such that riffles with the most edginess exhibited the smallest rate of change in fractal dimension with increasing ER numbers and the smallest asymptote (Figure S4). Thus, edginess had a strong effect on D_B . Over the range of edginess seen in the real riffles (Figure 2), fractal dimension was reduced by 0.64 (mean difference between highest and lowest edginess simulations). In contrast, patchiness did not interact with the number of ER because the shape of that relationship was maintained (i.e. there was no change in the rate of increase; Figure S4). Thus patchiness has a real but smaller effect on fractal dimension. Over the range of patchiness seen in the real riffles (Figure 3), fractal dimension was reduced by 0.12 (mean difference between highest and lowest patchiness simulations).

TABLE 2 Nested ANOVA to determine whether fractal dimensions of ER in riffles (D_B) varied between rivers or countries.

| | <i>Df</i> | Sum of squares | Mean square | <i>F</i> | <i>p</i> |
|-----------|-----------|----------------|-------------|-------------|-------------|
| Country | 1 | 0.04 | 0.04 | 1.01 | 0.33 |
| River | 3 | 0.43 | 0.14 | 3.97 | 0.02 |
| Residuals | 23 | 0.83 | 0.04 | | |

Note: Bold text indicates significant model terms ($p < 0.05$).

Abbreviation: ER, emergent rock.

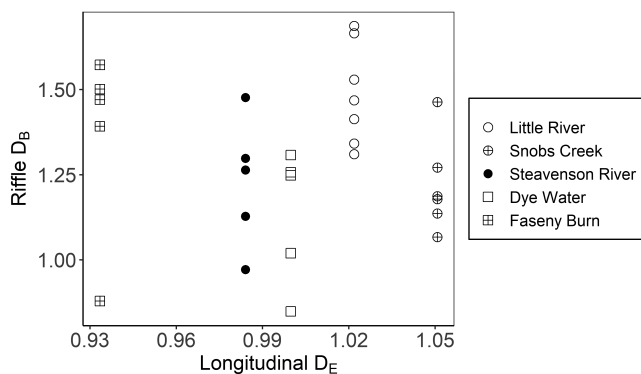


FIGURE 1 The fractal dimensions of the 2D arrangement of ER in riffles (riffle D_B) plotted against 1D fractal dimension (longitudinal D_E) for stream segments up to 1 km long in each of three Australian rivers (Little R., Snobs Ck, Steavenson R.) and two Scottish rivers (Dye Water, Faseny Water) from Dwyer et al. (2021). Values of riffle D_B were not correlated with longitudinal D_E . Riffle D_B varied greatly between riffles (63% of variance explained) and rivers (33% of variance explained) but not between countries (3% of variance explained).

For the real riffles, multiple regression indicated that fractal dimensions were positively related to the number of ER (log-transformed; $R^2=0.49$; slope=0.60, $t=4.80$; $p<0.001$) and patchiness ($R^2=0.37$; slope=-0.04, $t=3.78$; $p=0.001$) but not edginess ($R^2=0.05$; slope=-0.18, $t=1.07$; $p=0.293$; Figure 4) (Q4). Potential interactions between country and patchiness or edginess did not influence significance tests (Table S3) nor did the order of predictor variables (not reported). While model terms were uncorrelated (i.e. $p>0.05$) for streams from both countries, edginess and number of ER had a moderate but non-significant, negative association in Scottish streams (Table S2). Additionally, there were other differences between the two sets of streams. In Australian streams, the ER numbers in the middle and margins increased with the total numbers of ER. In contrast, in Scottish streams, the ER numbers in the margins declined with increasing total ER and declined also with increasing number of ER in the middle (Table S2).

3.2 | Oviposition patterns (Q5 and Q6)

The species *E. turbidum*, *T. evansi*, *T. palpata* and *B. rhodani* all occupied ER that differed in their environmental characteristics from unexploited ER (Figure 5, Tables S4–S6, Figure S5) (Q5). *Ethochorema turbidum* occurred predominantly on the largest and most protruding ER in relatively fast, deep water. *Taschorema evansi* occurred on highly protruding ER in deep water but evidence of a preference for large ER or fast-flowing water was weak (both variables were only significant when entered in a particular order: Table S5). *Tasimia palpata* occurred on highly protruding ER but exhibited no preference for water velocity. Evidence for a preference for large ER or shallow water by *T. palpata* was weak (only significant in conditional tests contingent on order of entry). *Baetis rhodani* occurred predominantly on large ER in relatively fast, deep water (noting that exposed rock height was not measured in the Scottish streams).

Four species were defined as margin species, namely *A. gisbum*, *A. obliquum*, *T. evansi* and *T. palpata* (Figure S2a), that is, these species oviposited at least 70% of their egg masses close to the banks of the streams (within a margin of 1.17 m). The remaining four species largely oviposited in the middle zone of the streams (Figure S2b; per cent oviposition in middle: *U. seona*=88%, *U. rubiconum*=85%, *E. turbidum*=94% and *B. rhodani*=79%). We acknowledge this definition of the margins is an arbitrary break to produce a categorical variable from a continuous variable and this should be considered when interpreting the results. The margins did not overlap in any riffle in the present study because all riffles were at least 2.35 m (2 x margin width) wide in any section.

Of the margin species, *A. gisbum* and *T. palpata* had higher numbers of egg masses in riffles with high numbers of ER, as did *A. obliquum* but the latter was only significant using the parsimonious test that included only the number of ER and not riffle D_B (Table 3, Table S7, Figure 6a,c,g). *Taschorema evansi* abundances were unrelated to the total number of ER (Table 3, Figure 6e). No margin species were related to riffle D_B , although the test for *T. palpata* was marginally non-significant ($p=0.051$; Figure 6h) (Q6). For *A. obliquum* and *A. gisbum*, linear models best fit the abundance data indicating possible habitat limitation (Figure S6). For *T. palpata*, an asymptotic model best fit the data suggesting this species may be supply limited but only at sites with particularly high numbers of ER. Asymptotic regression models were not fit to the abundances of *T. evansi*.

The abundances of the middle species *U. rubiconum* and *E. turbidum* were both positively related to the number of ER in riffles (Table 3, Figure 6i,m) but negatively related to riffle D_B (Figure 6j,n). In contrast, abundances of *U. seona* were not related to the number of ER in riffles and were positively related to riffle D_B (Figure 6l). Abundances of the mayfly, *B. rhodani*, were not related to riffle D_B . A test relating egg mass abundance of *B. rhodani* to the number of ER was not completed due to the sampling design in the Scottish streams, but previous studies found a significant relationship with the amount of oviposition resources (Lancaster et al., 2010). For *U. rubiconum* linear models best fit the abundance by number of ER indicating habitat limitation (Figure S6). Asymptotic regression models were not fit to the abundances of *U. seona*, *E. turbidum* or *B. rhodani*.

4 | DISCUSSION

Whether, and how, the spatial arrangement of resources affects species is an enduring problem in ecology and difficult to address because, in part, finding an appropriate measure of configurational heterogeneity is critical but often elusive (Loke & Chisholm, 2022). We used fractal dimensions to describe the spatial heterogeneity of oviposition resources (ER) in multiple riffles from five rivers. We found that the spatial distribution of ER exhibited fractal behaviour, which means that ER exhibited scale-independent patterns of distribution within riffles. Moreover, we found significant associations between fractal dimension and egg mass abundances for some species as well as positive relationships between the number of ER and

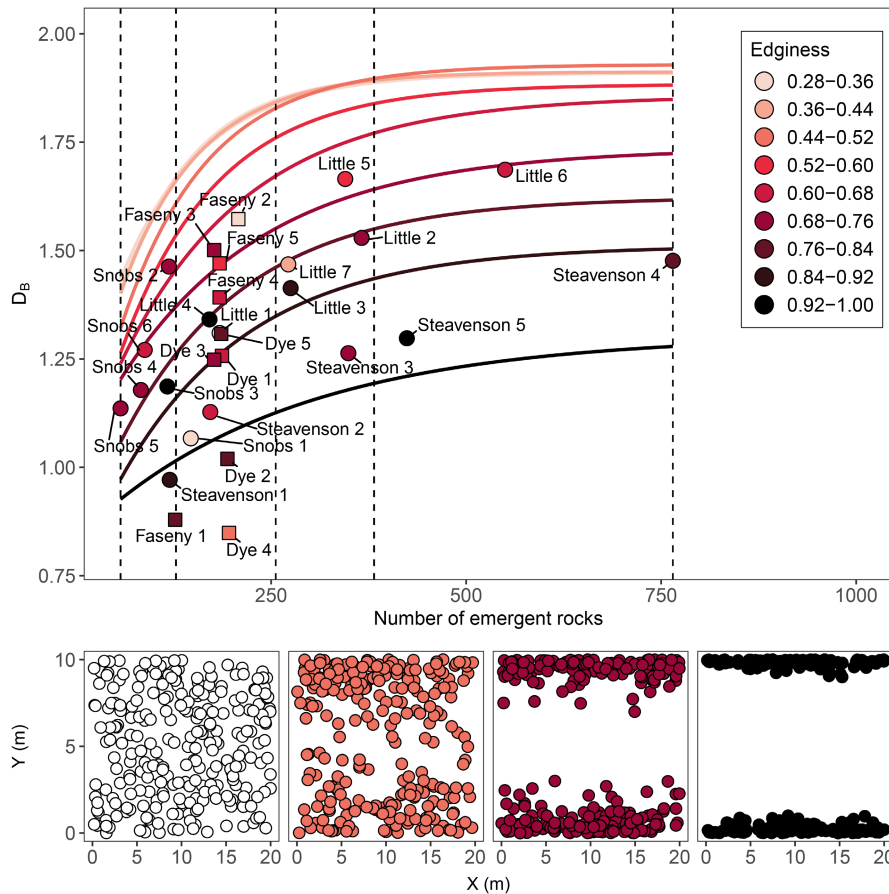


FIGURE 2 Fractal dimension (D_B) of simulated riffles varied with the number of ER and the edginess (the proportion of emergent rocks (ER) in the margins) of the ER arrangements. Lines illustrate asymptotic regression models fit to groups of simulations with different levels of edginess and varying in the number of ER. Dashed lines illustrate the minimum, half mean, mean, half maximum and maximum of the numbers of ER observed in the real riffles, which were used to produce the simulations. The upper asymptotic value (Asym), the y-intercept (RO) and the natural logarithm of the rate constant (Lrc) parameters of the models decrease with edginess (Figure S4a–c). Points show the fractal dimension and number of ER for the real riffles to illustrate how their values relate to trends in the simulations. The simulation points are not shown. Point and line colour illustrates edginess as increasing from white to red to black fill. Examples of simulated riffles are shown in bottom panels with the mean ER density of the Australian riffles.

egg mass abundances for most taxa, which aligns with results for some other aquatic insects (Downes et al., 2021). Together these results suggest that the amount and the arrangement of suitable oviposition habitat can determine egg mass densities of insects that oviposit on ER, and potentially subsequent larval and adult densities (depending on density-dependent processes).

The idea that fractal dimensions can capture elements of spatial heterogeneity has featured in previous ecological research, including in freshwater systems (Barnes et al., 2013; Jeffries, 1993; McAbendroth et al., 2005). However, our evidence that fractals can capture configurational heterogeneity of resources (ER) in stream riffles is novel and exciting because it provides a technique to test for general ecological patterns across diverse stream systems. The distributions of ER in 2D space are fractal, that is, riffles exhibited scale-independent, self-repeating patterns of ER distribution. Thus, fractal dimensions are applicable to the range of scales used in this study and potentially outside that range. Notably, these patterns held over riffles in multiple streams with different geomorphological and

hydrological contexts (Lancaster et al., 2021), which consequently offers an explanation for the consistency of egg-laying behaviour by individual species despite wide variability in numbers and spatial arrangements of ER (e.g. Lancaster, Downes, Lester, & Rice, 2020).

4.1 | Resource configurational heterogeneity

While all riffle-scale ER distributions were fractal, the actual values of D_B varied considerably among riffles. We can only speculate about the physical causes of these self-repeating patterns because our study was not designed to reveal the processes that allow riffle-scale bed structures to develop. However, differences in average D_B among rivers and countries were essentially zero, and values of D_B were unrelated to the longitudinal values of D_E for each stream. Those two findings suggest that the large-scale physical processes that shape river channels and distribute ER (e.g. recruitment, dispersal and sorting of large rocks into morphological

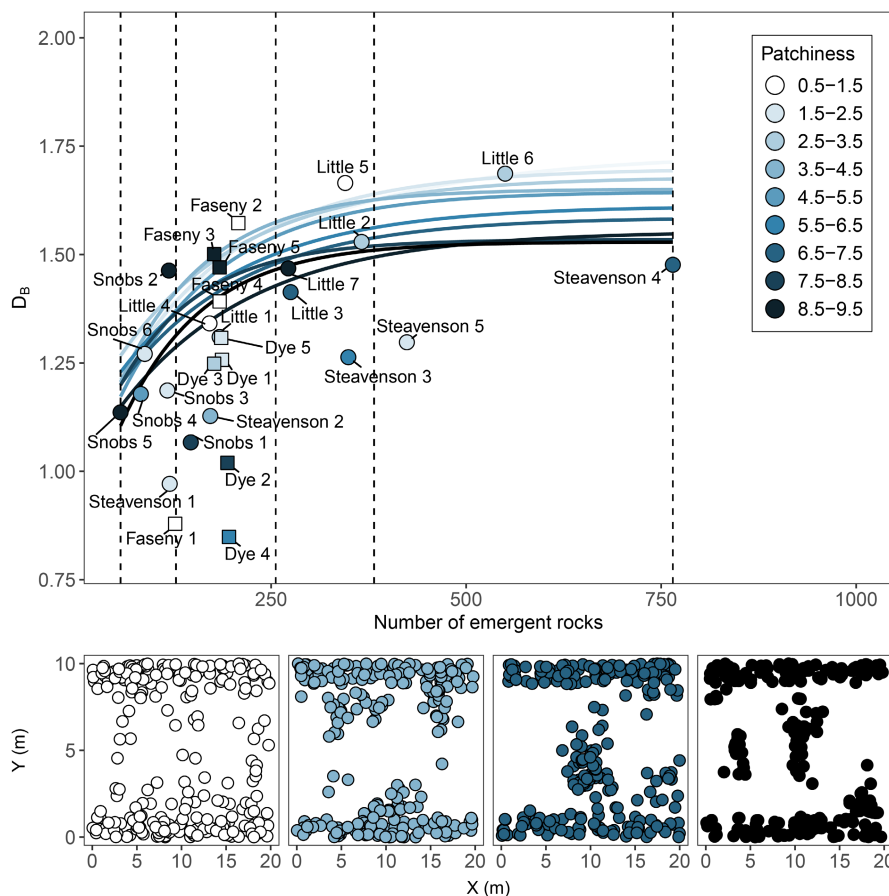


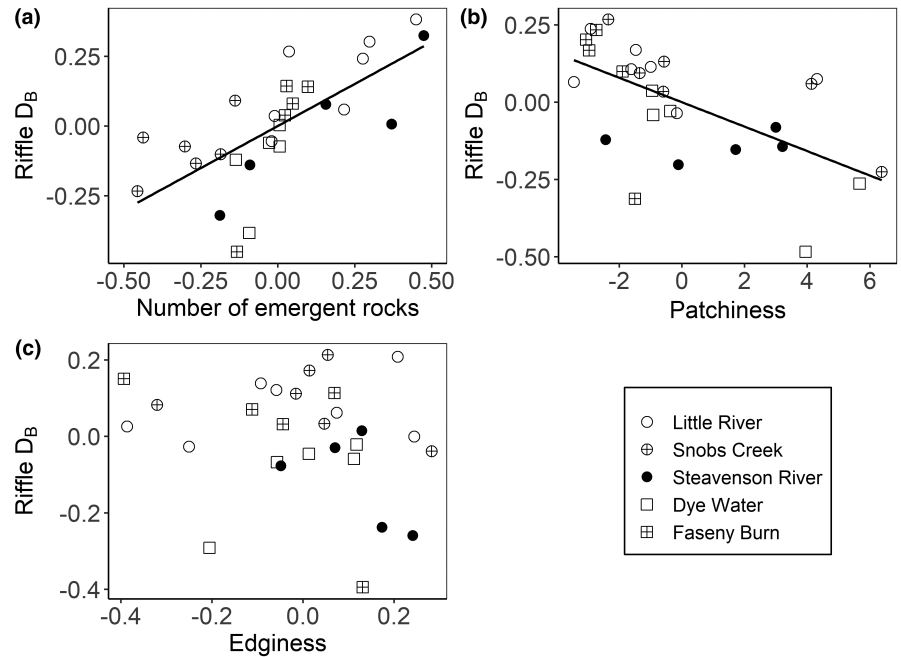
FIGURE 3 Fractal dimension (D_B) of simulated riffles varied with the number of emergent rocks (ER) and the patchiness (the degree of ER clustering in the middle) of the ER arrangements. Lines illustrate asymptotic regression models fit to groups of simulations with different levels of patchiness and varying in the number of ER. Dashed lines illustrate the minimum, half mean, mean, half maximum and maximum of the numbers of ER observed in the real riffles, which were used to produce the simulations. The upper asymptotic value (Asym) of the models was found to decrease with patchiness; the y-intercept (R_0) and the natural logarithm of the rate constant (Lrc) parameters were not related to patchiness (Figure S4d-f). Points show the fractal dimension and number of ER for the real riffles to illustrate how their values relate to trends in the simulations. The simulation points are not shown. Point and line colour illustrates patchiness as increasing from white to blue to black fill. Examples of simulated riffles are shown in bottom panels with the mean ER density of the Australian riffles.

units along channel reaches; Rice & Church, 1998, Church, 2006, Buffington & Montgomery, 2013, Dwyer et al., 2021) and that are likely to differ between continents are not the primary cause of patterns in ER distribution within riffles. That conclusion accords with research showing that the development of within riffle-scale bed structures (e.g. pebble clusters, transverse ribs, stone lines and nets; Hassan et al., 2007) is complex and related to interactions between local sediment supply, high bed stability (references in Hassan et al., 2007), duration between disturbance events, surface microtopography and hydraulic conditions causing particle rearrangement and fabric development over small spatial scales (e.g. Robert, 1993). The disconnection between fractal dimensions at different scales also demonstrates the limit to their scale-independent nature. The complexity of riffles does not adequately describe the complexity of the rivers and vice versa.

Simulations to explore the source of variation in D_B revealed a strong effect of ER numbers and two aspects of ER spatial distribution (edginess and patchiness). Values of D_B increased with the

number of ER because the addition of even a few ER to a vacant 2D plane increases spatial disorder. However, the rate of increase gradually levelled off because increasing numbers of ER have progressively less impact on 'filling in' the 2D space (i.e. they are more likely to occupy an already-filled box than a vacant box and so will not change D_B). Thus, real riffles that contain very few ER should have lower D_B than those that have either intermediate numbers or many. In terms of spatial arrangement, riffles varied naturally in edginess (the proportion of total ER in the margins) and high edginess comes with greater spatial order. Accordingly, edginess was inversely related to D_B in our simulations. However, this effect on D_B was disproportionately larger when overall numbers of ER were low. In that case, a high proportion of ER in the margins left only a few ER in the middle and much empty space. With increasing numbers of ER, the effect of high edginess on D_B declined because the absolute numbers of ER in the middle were sufficient to 'fill in' much of the 2D space, as described above. In contrast, patchiness reflects the degree of clustering of ER in the middle of the river. In natural

FIGURE 4 Added variable plots (with each variable adjusted to account for other predictors) relating the fractal dimension (D_B) of riffles to three predictor variables, (a) the number of emergent rocks (ER), (b) patchiness and (c) edginess of riffles, while holding the other two predictor variables constant. Solid lines illustrate significant relationships ($p < 0.05$); see Table S3 for test results. The numbers of ER were log-transformed.



riffles, ER are very often clustered, but the distances between clusters (i.e. the density of clusters) varies between riffles (e.g. Lancaster et al., 2003). In simulations, patchiness was also inversely associated with D_B because it created greater spatial order away from the edges. However, the effect on D_B was modest compared to that of edginess and did not vary with the total number of ER. Consequently, we expected patchiness to play a smaller role than edginess in explaining D_B of natural riffles.

In real riffles, D_B increased with the numbers of ER and declined with increased patchiness as expected from the simulation results, but edginess had no effect on D_B . This surprising outcome reflected that edginess was correlated with variables that masked its effects (Table S2). In the Australian riffles, the numbers of ER in the margins were strongly related to the total number of ER and, consequently, there was little independent variation in edginess. In the Scottish riffles, higher total numbers of ER were associated with greater proportions of rocks in the middle, leading to a small, negative relation between edginess and total numbers of ER. These contrasting differences between regions were too weak to create a statistically significant interaction between Country and Edginess in the analysis but collectively meant that edginess played no role in explaining D_B in real riffles. Differences in the numbers of ER in river margins likely reflect variability in floodplain sedimentology (including the incorporation of relict, e.g. glacial or flood deposits), the degree of coupling between the channel and coarse hillslope sediments and river-bank stability. Together these determine the availability of large rocks and their potential recruitment to the river. Additionally, channel cross-sectional shape is important because if banks are gently sloped, this increases the propensity for rocks to be emergent compared to steeply sloped banks. River bank steepness is a function of variables including vegetation density and bank-material particle size. We did not measure bank characteristics, but our field observations do not suggest any systematic differences between sites or countries. It is

unlikely we would have discerned the role of edginess in fractal dimension by examining only real riffles.

4.2 | Oviposition patterns and potential mechanisms

Overall, the arrangement and the amount of resources frequently affected oviposition, with only one species (*T. evansi*) failing to respond to either ER number or arrangement, possibly because it is much less common than all other taxa. Firstly, six of eight species laid significantly more egg masses in riffles containing high numbers of ER. This total includes *B. rhodani* and reflects an outcome seen previously for that species using different data (Lancaster et al., 2010). There was no sign that egg mass numbers of most of these species (except one) plateaued at the highest numbers of ER. Thus, the more ER were present, the more egg masses were laid. This outcome implies that the supply of gravid females at sites often outstripped the amount of suitable oviposition habitat, that is, that oviposition was habitat-limited (Downes et al., 2021). For the exception, *T. palpata*, abundances may plateau when ER numbers exceed ~200. It is feasible that suitable oviposition habitat usually exceeds the number of gravid females of this species, in which case egg mass densities may be supply- rather than habitat-limited (Downes et al., 2021). However, a proviso for these conclusions is that we have no independent information on the supplies of females for any species. Those data are needed to test whether riffles with fewer ER and egg masses actually have fewer females, in which case the supply of gravid females may be just as important as the supply of ER.

Secondly, three species responded to the arrangement of ER as captured by fractal dimension. All were middle species (likely to oviposit on ER in the middle of stream channels), but we cannot conclude much about the lack of effect of D_B on margin species.

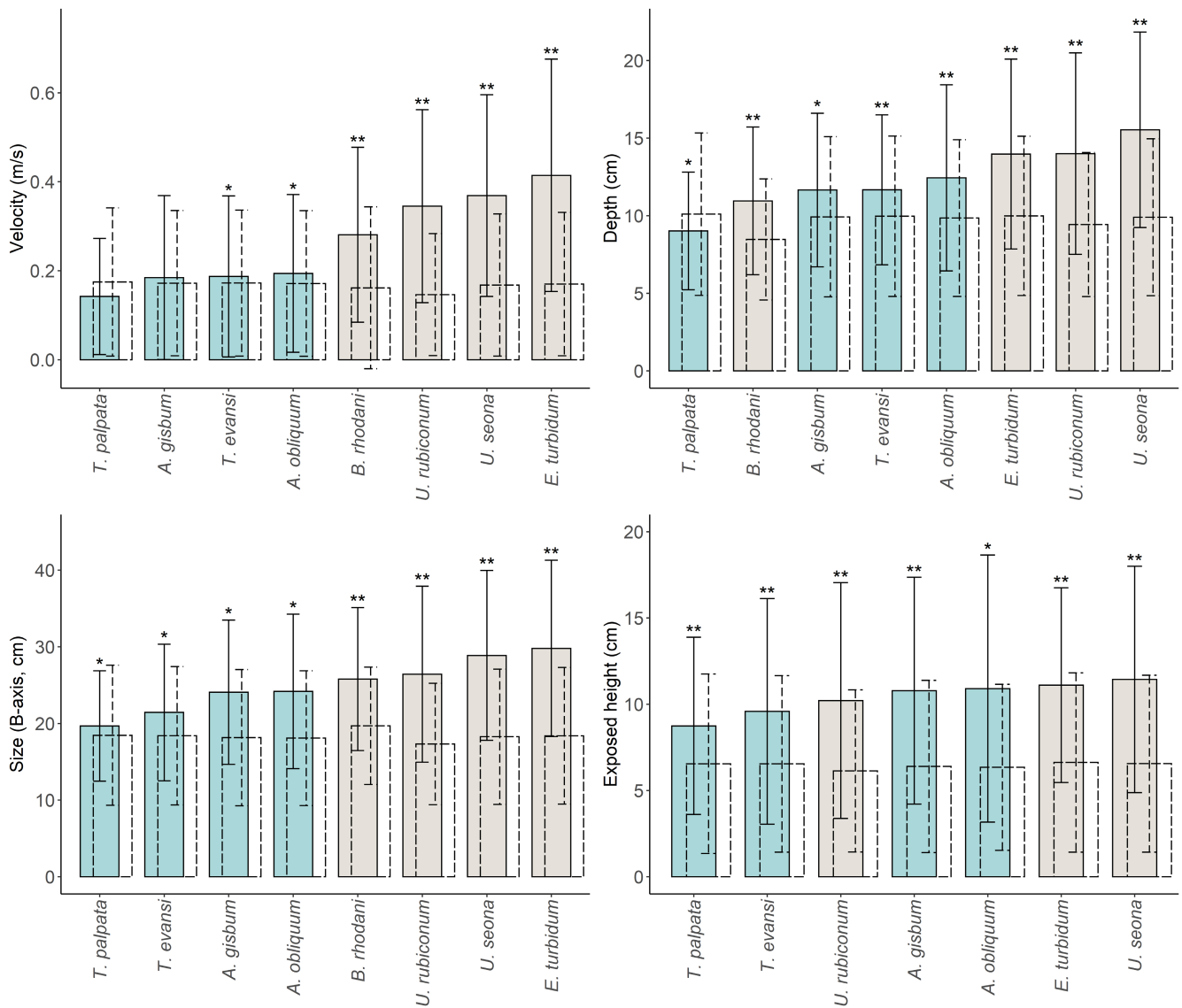


FIGURE 5 Summary of emergent rock (ER) preferences according to four environmental variables (water velocity, water depth, rock size, exposed height of rock) for seven species of Australian Hydrobiosidae caddisflies and one Scottish Baetidae mayfly (*Baetis rhodani*). Species are arranged in order of the magnitude of the variable on the exploited rocks, which changes between panels. Margin (blue) and middle species (grey) are highlighted. Data from three Australian rivers (Little R., Snobs Ck and Steavenson R.) and two Scottish rivers (Dye Water and Faseny Water) are summarised (mean \pm SD). Asterisks indicate strong (** $p < 0.05$ in all tests) or weak (*inconsistent results depending on test) evidence that the environmental variable is significantly different between exploited (solid lines) and unexploited ER (dashed lines) from DistLM marginal (Table S5) and conditional tests (Table S6) or sequential MANOVA tests (Table Electronic Supplementary Material 1 in Lancaster, Downes, Lester, & Rice, 2020) for four previously published species (*Ulmerochorema* spp. and *Apsilochorema* spp.).

As acknowledged above, our riffles had little, independent variation in edginess. It is unsurprising therefore that margin species did not respond to fractal dimension, although it is interesting that *T. palpata* was only marginally non-significant. Feasibly, ER arrangement does affect margin species, but this would require tests with riffles that vary systematically in edginess or other characteristics that change spatial arrangements in margins. Of the three species responding to the arrangement of resources, two (*U. rubiconum*, *E. turbidum*) favoured riffles with lower fractal dimensions, that is, higher patchiness (although the test for *E. turbidum* should be regarded with caution, owing to an outlier that was included in the

test). A negative response to fractal dimension suggests more egg masses were laid in riffles where ER in the central part of the channel were densely packed together. In contrast, *U. seona* laid more egg masses in riffles with higher fractal dimensions, where clusters of ER in the central part of the channel were less densely packed together. Additionally, *U. seona* did not respond to total ER. These results are intriguing because *U. seona* exploits a subset of ER used by *U. rubiconum* (Lancaster, Downes, Lester, & Rice, 2020) and are also of similar characteristics to those exploited by *E. turbidum* (highly protruding large ER in deep, fast-flowing water). We consider each species in turn.

TABLE 3 Multiple regression tests of species' egg mass abundances as a function of the number of ER (n ER) and the fractal dimension (D_B) of riffles.

| Species | Riffle variable | Slope | t | p |
|---|-----------------|-----------------|-------------|------------------|
| Margin species | | | | |
| <i>Apsilochorema obliquum</i> ^a | n ER | 0.07 | 2.51 | 0.023 |
| <i>A. gisbum</i> | n ER | 0.10 | 5.08 | <0.001 |
| | Riffle D_B | -12.19 | 0.68 | 0.505 |
| <i>Taschorema evansi</i> ^a | n ER | 0.04 | 1.52 | 0.150 |
| <i>Tasimia palpata</i> | n ER | 0.11 | 4.57 | <0.001 |
| | Riffle D_B | -49.90 | 2.12 | 0.051 |
| Middle species | | | | |
| <i>Ulmerochorema rubiconum</i> ^b | n ER | 6.99 | 7.16 | <0.001 |
| | Riffle D_B | -2778.48 | 3.04 | 0.008 |
| <i>U. seona</i> | n ER | -0.10 | 1.92 | 0.074 |
| | Riffle D_B | 201.12 | 4.25 | 0.001 |
| <i>Ethochorema turbidum</i> ^c | n ER | 0.09 | 5.47 | <0.001 |
| | Riffle D_B | -40.45 | 2.59 | 0.021 |
| <i>Baetis rhodani</i> ^d | Riffle D_B | -0.30 | 0.93 | 0.378 |

Note: Where neither independent variable was significant, a parsimonious model including only n ER is presented. Significant tests are in bold ($p < 0.05$).

Abbreviation: ER, emergent rock.

^aParsimonious model including only n ER; see Table S7 for full multiple regression tests.

^bOne datum was an outlier but its removal had no effect on the significance of tests.

^cOne datum was an outlier; its removal changed the p -value of Riffle D_B to 0.08.

^dTests of *B. rhodani* abundances including the number of emergent rocks are not appropriate with our data set, however, Lancaster et al. (2010) demonstrated that *B. rhodani* abundances were positively related to the number of oviposition resources.

How and why do *U. rubiconum* respond to clusters of ER? *U. rubiconum* oviposit on ER in a wide range of flow velocities above a minimum threshold of approximately 0.3 m/s (Bovill et al., 2013; Reich & Downes, 2003). Additionally, both male and female *U. rubiconum* are able to locate suitable ER from the air (Reich & Downes, 2003). It is possible that adults of this species detect the changes in reflected, polarised light caused by fast, chaotic flows around ER. Relatively tight clusters of ER may produce larger areas of broken water than loose clusters and hence a greater chance of adult visitation and oviposition. If so, then *U. rubiconum* can detect and respond to whole clusters of suitable ER. This reasoning also helps explain why females consistently favour some ER over other seemingly suitable ER (Reich et al., 2011). Based on this reasoning, individual ER within relatively tight clusters of other suitable ER would then be favoured more than lone ER or those in loose clusters. Additionally, ER with egg masses of *U. rubiconum* are always more spatially clustered than the background distribution of suitable ER (Lancaster et al., 2003;

Lancaster, Downes, Lester, & Rice, 2020). That outcome could arise if *U. rubiconum* targets relatively tight clusters of ER, which would result in ER with *U. rubiconum* eggs being more spatially clustered than the background.

In contrast, there is no evidence that *E. turbidum* can detect suitable ER from the air. Rather, they land on suitable and unsuitable ER at the same frequency (Reich & Downes, 2003). Females of this species have been observed in the laboratory to land on an individual rock, walk underwater and then emerge and fly to a new rock and repeat the behaviour before making a final choice for oviposition (Reich & Downes, 2004). This behaviour of serially landing on and rejecting unsuitable ER can still produce a relationship between egg mass numbers and fractal dimension. If many suitable ER are within tight clusters, then egg mass numbers will correlate with patchiness, which of course, is reflected in D_B . In this case, however, the correlation between egg mass numbers and D_B is a consequence of the way suitable ER are distributed in streams, not because females can detect clusters of suitable ER. Thus, *E. turbidum* likely do not have to be able to detect and respond to different types of ER clusters from the air to be affected by fractal dimension. While speculative, this reasoning suggests we might expect to see different egg mass abundances for *U. rubiconum* and *E. turbidum* in rivers with radically different arrangements of ER to those in this study.

Ulmerochorema seona predominantly oviposit on the largest ER in the fastest and deepest water, which are a narrow subset of the ER used by *U. rubiconum* (Lancaster, Downes, Lester, & Rice, 2020). Remarkably, *U. seona* did not lay more egg masses in riffles with high numbers of ER, even though suitable ER were strongly correlated with the total number of ER in riffles (Lancaster, Downes, Lester, & Rice, 2020—Electronic Supplementary Material 5). Some riffles even had zero egg masses of this species despite the presence of suitable ER. There is no information on how females locate oviposition habitat, but the strength of response by *U. seona* to fractal dimension suggests that females may predominantly search for riffles with ER in loose clusters. Tightly clustered ER may often abut one other and ER in the middle of such clusters are likely to be sheltered from water flow. As such, perhaps tight clusters of ER offer fewer suitable places for oviposition for this species, given its strong preference for oviposition sites in high velocities.

Where and how many egg masses are laid can affect subsequent larval densities. For two species of *Baetis* and the caddisfly *Rhyacophila dorsalis* (Curtis), more egg masses were laid in riffles or rivers with high densities of suitable oviposition habitat and this resulted in persistently higher larval densities, even after density-dependent losses (Encalada & Peckarsky, 2012; Lancaster et al., 2010; Lancaster & Downes, 2014). Links between hydrobiosid egg mass numbers and subsequent larval densities are little studied, but Reich and Downes (2004) reported that larval densities of *A. obliquum*, *E. turbidum* and *U. rubiconum* varied little between sites having either plentiful or zero ER. Moreover, average first instar larval densities were a tenth of typical egg densities, suggesting considerable mortality at, or dispersal from, natal sites early in larval life. In the case of *T. palpata*, a comprehensively studied population

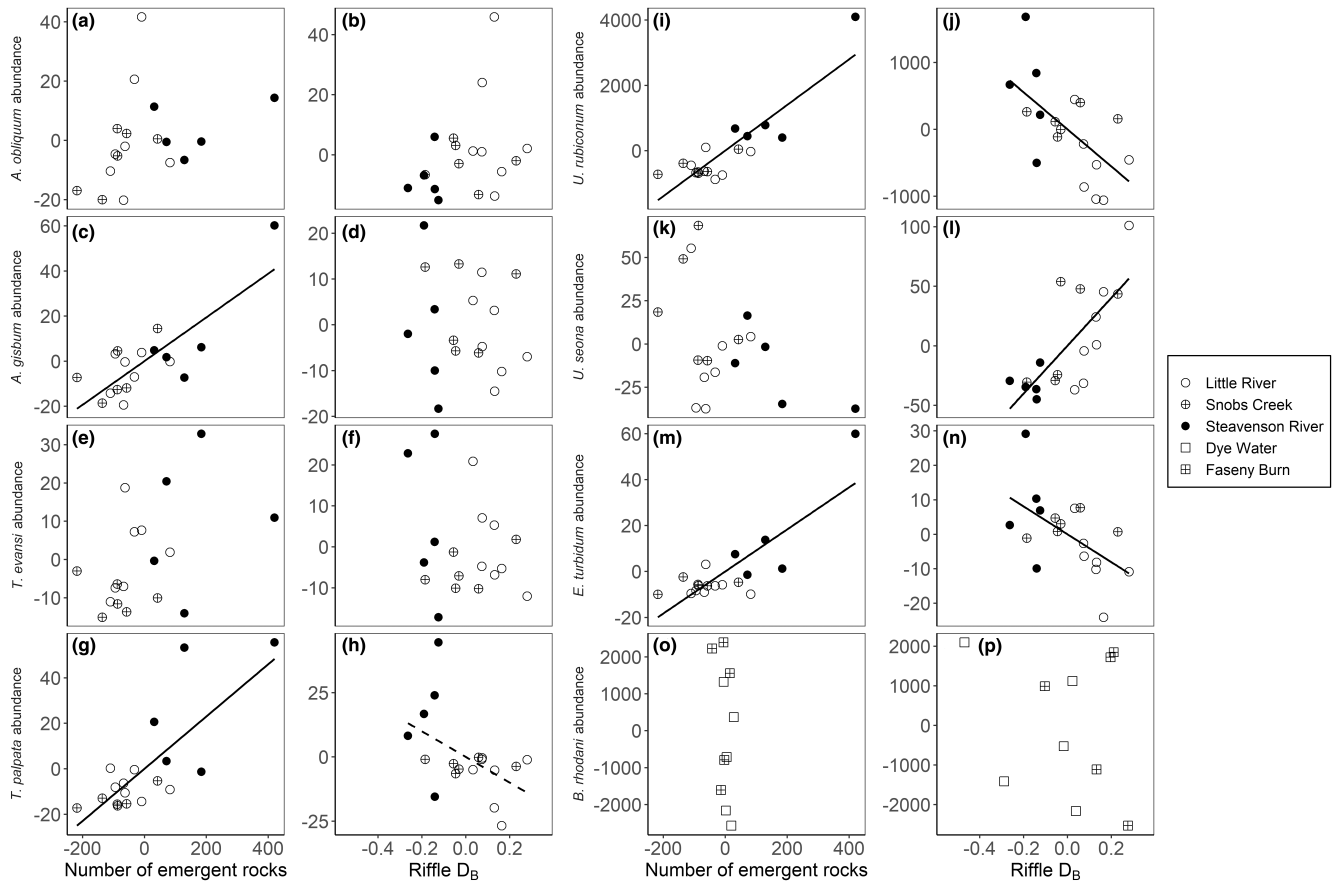


FIGURE 6 Added variable plots (with each variable adjusted to account for other predictors) relating the egg mass abundances of margin species (*Apsilochorema obliquum*, *A. gisbum*, *Taschorema evansi* and *Tasimia palpata*: two left-hand columns) and middle species (*Ulmerochorema rubiconum*, *U. seona*, *Ethochorema turbidum* and *Baetis rhodani*: two right-hand columns) to two predictor variables [the number of emergent rocks and fractal dimension (D_B) of riffles] while holding the other predictor variable constant. Solid lines illustrate significant relationships ($p < 0.05$) and dashed lines illustrate marginally non-significant relationships ($p = 0.051$); see Table 3 for multiple regression test results. Symbols are consistent with Figure 4.

suffered density-dependent losses between the egg and first instar stage, that is, eggs failed to hatch or first instars died disproportionately more frequently in places where egg densities were high (Marchant, 2021). These studies and others (e.g. Hildrew et al., 2004) suggest that oviposition and survivorship of first instars are key stages where populations of aquatic insects may be regulated by density dependence—but this is not always the case (e.g. Marchant, 2021; McIntosh et al., 2022). Such disparate outcomes show that we need a far better understanding of when and where in the life-cycle density dependence occurs in populations of aquatic insects to understand the likely implication of oviposition patterns on population densities.

5 | CONCLUSION

Our results show that the arrangements of resources (ER) in 28 riffles across multiple streams are fractal, with fractal dimensions largely capturing the tightness of ER clusters in the middle of the stream (patchiness) rather than the lateral distribution of ER in

the margins (edginess). Clustering of larger particles is common in rivers as a result of small-scale sorting and bed stabilisation processes. Further, this study shows that the amount and arrangement of resources at the riffle scale can influence where aquatic insects deposit their eggs. This adds further evidence that the amount of suitable oviposition habitat can play a strong role in determining egg mass densities (Downes et al., 2021) but also provides new evidence that configurational heterogeneity can be important independently of the number of resources (*U. seona*). Configurational heterogeneity of resources may influence adults directly if they can detect and respond to spatial patterns (*U. rubiconum*) or indirectly if spatial patterns are correlated with suitable resources (*E. turbidum*). Spatial arrangements should be considered when humans manipulate these resources in rivers (e.g. extraction of gravel and rock, creation of sand slugs that cover rocks, addition of rocks to replace dams, prevent erosion, or to create oviposition habitat). Our simulations provide clear examples of how riffle fractal dimensions could be manipulated; this method could be adapted for use in restoration projects. Adding oviposition habitat has been a focus of several restoration

projects, which have successfully increased the recruitment of eggs (and later life stages) of aquatic insects in previously degraded streams (Dilworth & Taylor, 2023; Jordt & Taylor, 2021). Our results suggest that species responses vary with emergent rock arrangement, and so the arrangement of these resources within an ecosystem could also have important community-level and functional consequences.

AUTHOR CONTRIBUTIONS

Conceptualisation and development of methods: RL, JL, BD, GD, SR and LS. Data analysis, data interpretation and preparation of figures and tables: GD and BD. Conducting the research and writing: GD, BD, JL, SR, RL and LS.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interests.

DATA AVAILABILITY STATEMENT

Data analysed in this work are available from the authors upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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