COMMUNITY ECOLOGY

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Disturbance, biological legacies and community development in stream mesocosms

Abstract Disturbances reduce the biota in stream ecosystems, and leave biological legacies, including remnant species, which potentially influence post-disturbance community development but are poorly understood. We investigated whether three remnant species, the snail *Radix peregra*, the mayfly *Serratella ignita* and the freshwater shrimp *Gammarus pulex*, affected community development in mesocosms that mimicked disturbed habitat patches in streams. Following 21 days of colonisation, we found that the occurrence of legacy effects depended on the identity of the remnant species. *Radix* had the strongest effect. By bulldozing epilithon, the snails acted as ecological engineers that promoted settlement of filter feeders (Simuliidae) and invertebrate predators (especially *Pentaneura* and *Aphelocheirus*) and strongly deterred settlement of non-predatory chironomids (e.g. *Heterotrissocladius* and *Microtendipes*). *Gammarus* increased in density (by 665%) where remnant, probably through rapid reproduction. *Baetis* and *Pentaneura* were scarce, and *Asellus* absent, in remnant *Gammarus* treatments, as a consequence of interference and/or predation by the amphipods. In contrast, *Serratella* tolerated the colonisation of immigrant species and did not affect the structure of the developing benthic community. Despite the observed effects on the presence and abundance of benthos, remnant fauna had no significant effect on assemblage taxon richness, or that of any specific trophic group. The contrasting effects of remnant species on immigrant colonisation echoed differences in their life-history traits and foraging behaviours. Our results indicate that biota can generate spatial patchiness of epilithon and benthic invertebrates in stream ecosystems.

Keywords Community structure · Patchiness · Perturbation · Recovery · Spatial heterogeneity

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Introduction

Natural disturbance is integral to the organisation of ecosystems (e.g. Sousa 1984a; Pickett and White 1985). Catastrophic disturbances, which eliminate biota from habitats, are rare in nature (Connell and Slayter 1977). Most natural disturbances are non-catastrophic events (Platt and Connell 2003) that leave biological legacies: "the organisms, organic materials, and organically generated patterns that persist through a disturbance and are incorporated into the recovering ecosystem" (Franklin et al. 2000; Keeton and Franklin 2005). As historical artefacts of disturbance, biological legacies have the potential to govern the development of communities in the post-disturbance environment (Platt and Connell 2003; Keeton and Franklin 2005), but are poorly understood.

The importance of ecological history in community development has long been recognised by theoreticians and empirical ecologists (Drake 1990; Samuels and Drake 1997). For example, research has revealed that endpoint community structure depends upon the sequence in which species arrive in disturbed habitat patches (e.g. Robinson and Edgemon 1988; Fukami 2001; Price and Morin 2004), and that sites with small differences in initial conditions can follow divergent trajectories of community development (Berlow 1997;

Samuels and Drake 1997). However, despite the apparent ubiquity of biological legacies in disturbed environments, research has centred largely on terrestrial ecosystems, addressing, for example, the influence of remnant trees on the structure and function of northern temperate forests (e.g. Zenner 2000; Keeton and Franklin 2005). More research is needed to explore the effects of persistent 'remnant species' on community dynamics in a variety of ecosystems, particularly freshwaters.

As key players in early succession, remnant species potentially facilitate or inhibit the settlement and establishment of colonists, either directly, through species interactions, or indirectly, through ecosystem engineering (e.g. Dean and Hurd 1980; Cardinale et al. 2001; Mullineaux et al. 2003). However, community development may also advance independently of remnant species where interactions with colonists and habitat features are weak or absent. Ultimately, legacy effects may hinge on the particular traits, and thus the identity, of remnant species.

In physically complex environments like rivers and streams, the benthic fauna is diverse, with species composition often varying significantly among habitat patches (Giller and Malmqvist 1998). Episodic disturbances, especially floods, displace and eliminate invertebrates by scouring and overturning mineral substrata and uprooting macrophytes (Resh 1988). The post-disturbance environment typically consists of a mosaic of disturbed patches (Hildrew and Giller 1992; Lancaster 2000) containing a remnant fauna (e.g. Matthaei et al. 1997). Invertebrates rapidly colonise these patches (Mackay 1992) by several routes, principally by crawling or drifting from local (sub-)surface sediments and the vegetated margins that provide refuge during floods (e.g. Williams and Hynes 1976). Where patches are disturbed in close proximity to refugia, a community can re-establish within days or weeks (Milner 1994). The species composition of recovering patches may hinge on the outcome of interactions between colonist and remnant faunas. However, the extent to which survivors of disturbance affect community recovery in streams has not been specifically examined.

In this study, we considered whether and how remnant species affect community development in a disturbed freshwater ecosystem. Our research was based on observations in lowland chalk streams in the southern United Kingdom in which the substratum forms visually distinct patches of contrasting structure that contain assemblages of different species (Pardo and Armitage 1997; Armitage and Cannan 2000). Where such faunal heterogeneity persists through floods, patches of different remnant species could provide 'threads of continuity' (sensu Franklin et al. 2000) that have the potential to guide community recovery, thereby creating spatial patterns on the river bottom. We focus on three taxa, pulmonate snails, mayfly larvae and amphipods, which are abundant in the stream benthos of chalk streams, that can survive disturbance (Armitage 1995) and therefore form part of a remnant fauna. We conducted a field experiment in artificial streams to test two related hypotheses: first, that remnant species affect taxonomic composition of endpoint communities in post-disturbance habitat patches, and second, that endpoint community structure depends on the identity of the remnant species.

Materials and methods

Remnant species

Three species that differ in behaviour and morphology were selected as remnant species for the experiment. They all have patchy distributions in chalk streams, and can attain densities of 1,000–10,000 individuals m^{-2} (Pardo and Armitage 1997; Armitage and Cannan 2000; M.E. Ledger, unpublished). *Serratella ignita* (Poda) is a herbivorous mayfly that feeds on attached algae and associated detritus (epilithon) (Rosillon 1988). Its larvae are fusiform and adopt a clinging and sprawling habit on mineral surfaces (Elliott et al. 1988). *Gammarus pulex* L. is an omnivorous amphipod that consumes decomposing leaf litter, algae and other invertebrates (Welton 1979). *Radix peregra* (Muller) is a pulmonate snail that grazes epilithon from the surfaces of stones (Macan 1994).

Experimental design

The experiment was conducted over a 28-day period in May and June 2002 in streamside channels located at the Freshwater Biological Association River Laboratory (50°40′48″N, 2°11′06″W) in Dorset, UK. Stream water (containing suspended algae, detritus and invertebrates), rerouted from a side channel of the River Frome through a branching 110-mm pipe, fed four blocks of 4 channels (16 channels in total). Each block of channels consisted of a head tank (0.4 m wide, 0.6 m long, 0.4 m deep) with four equally spaced ducts (4 cm diameter) that fed stream water into four linear channels (each 1 m long, 0.13 m wide, 0.15 m deep). The ends of the channels were closed, except for an outflow duct (4 cm diameter) that allowed water and suspended particles, including invertebrates, to discharge freely into a drainage pipe. The channels were positioned 5 cm below the inflow ducts and 10 cm above the drainage pipe to prevent cross-contamination of channels during the experiment. Current velocities in the channels (30-day mean, 9.5 cm s^{-1}), measured using a small bucket wheel flow meter, were equivalent to flows in headwater chalk streams (e.g. Pardo and Armitage 1997). Water flow into each head tank was controlled precisely by a series of valves, ensuring an equal flow across blocks, among treatments and through time (ANOVA, $P > 0.05$). Channels filled to 6 cm depth with newly washed flint gravel (volumetric proportions of particle sizes: 85%, 25–11 mm; 8%, 11–2 mm; 7%, 2–0.35 mm), closely matching that of local streams, mimicked disturbed patches of

streambed. Water depth over gravel ranged between 3 and 5 cm across the channels, and short residence times (< 5 min) ensured water temperature did not deviate from that in the river (30-day minimum, 12.3°C; maximum, 20.7°C; mean, 16.1°C). Inflowing stream water was alkaline (pH 7.9) and nutrient rich (NO₃, 3.67 mg l^{-1}; PO₄, 1.09 µg l^{-1}). We conducted a pilot study to test whether invertebrate immigration by drift varied among the blocks of channels, or with channel position within a block (i.e. each quartet of channels). Using drift nets placed over channel inlets, we collected invertebrates for 7 days immediately prior to the onset of the main experiment, and ascertained that neither the richness nor abundance of immigrants differed significantly within (two-way ANOVA, $P = 0.785$) or across blocks ($P = 0.770$).

The main experiment consisted of four treatments in which we investigated the effect of the three remnant species, *S. ignita*, *G. pulex* and *R. peregra*, and no remnant species (control), on subsequent community structure. Treatments were replicated four times in a randomised complete block design. Unfiltered water from the feeder stream was diverted into each channel to enable colonisation by benthic algae (from day 1) before remnant species were introduced on day 3. Immigration by invertebrates from the local species pool (stream and aerial sources) was prevented up to day 7 by placing drift nets (200 µm mesh) below the inlets of each head tank and channel, and by fitting clear Perspex lids to each channel to prevent oviposition by adult insects. No invertebrates other than remnants were found during periodic examination (using a dissecting microscope) of channel sediments collected up to day 7, although it is possible that some very small larvae (e.g. 1st instar chironomids) passed through the drift nets.

On day 3, we introduced one of the three remnant species (30 individuals equivalent to 240 m^{-2}) of similar body size (range 6–8 mm body length for all three species) to respective treatment channels, but not controls. This density, equivalent to approximately one-tenth of that in local chalk streams (e.g. Pardo and Armitage 1997), was held constant across treatments between days 3 and 7 to mimic persistence of a reduced population in post-disturbance patches. Standardisation of treatments by numbers was necessary to ensure later colonists encountered an equal number of residents across replicates and treatments. Standardisation by body size was necessary to unambiguously determine species-specific legacy effects. The three taxa added to the channels were collected from a local stream where they were abundant. Any individuals found in drift nets at the channel outlets were replaced. The percentage of drifting individuals reintroduced was low: 0.25% *Radix*, 2.25% *Gammarus* and 6.25% *Serratella*. On day 7, the barriers to colonisation of the channels were removed to enable community development to proceed unimpeded for 21 days during which emigrating remnant species were not replaced. At the end of the experiment on day 28, endpoint assemblages (both algae and invertebrates) were collected from each channel (see below).

Sampling and processing

Eplithon on the upper surfaces of three stones (mean upper surface area 5.2 cm²) was sampled on days 7, 14 and 28, by scrubbing the upper surface with a toothbrush and concentrating the loosened material in 25 ml of water. Two aliquots (10 ml each) of thoroughly shaken samples were drawn on to separate pre-ashed glass fibre filters (GF/C) for chlorophyll and ash free dry weight (AFDM) determination. Chlorophyll pigments were extracted from filters in 90% acetone for 24 h at 5°C. Absorbance of the extract was read at 750 (turbidity), 664, 647 and 630 nm on a spectrophotometer, and concentrations of chlorophylls *a*, *b* and *c* calculated using the equations of Sterman (1988). Epilithon AFDM was estimated as the difference in mass between freeze-dried and ashed filters (550°C for 5 h) (Ledger and Hildrew 1998, 2000). To collect invertebrates, the downstream end of each channel was removed and all gravel and invertebrates were washed into a bucket. Invertebrates and detritus were separated from gravel by elutriation and hand searching, and preserved in 70% ethanol. Invertebrates were sorted from debris, identified to the lowest practicable taxonomic unit and counted. Juvenile (< 4 mm), immature (4–6 mm) and mature (> 6 mm) *Gammarus* individuals (see Welton and Clarke 1980) were enumerated to compare their contrasting responses to the treatments.

Statistical analysis

We used repeated measures analysis of variance (ANOVA) to test the effect of remnant species treatment, block (between-subject factors) and time (within-subject factor) on epilithon biomass (chlorophyll *a* and AFDM). Data were log-transformed and *P*-values corrected for departure from sphericity using the Huynh–Feldt adjustment. One-way ANOVA was used to determine when (day 7, 14, 28) treatment effects were significant. Two-way ANOVA was also used to determine the effect of remnant treatment and block on: (1) final densities of remnant species, (2) taxon richness and absolute density (log-transformed) of all invertebrates, (3) taxon richness, absolute (log-transformed) and relative abundances (arcsin square root-transformed) of trophic groups (primary consumers, intermediate and top predators) at the end of the experiment, and (4) final densities of selected component taxa. Assignment of species to trophic levels was based on analysis of gut contents and food web metrics (M.E. Ledger, unpublished), and reference to Moog (1995) (see Appendix). Data were log-transformed to ensure normality and homogeneity of variances. Tukey HSD tests were used to identify significant differences between treatment means. Sequential Bonferroni corrections were applied to groups of tests to preserve an alpha of 0.05 (Rice 1989).

Linear constrained ordination (partial redundancy analysis, partial RDA) was performed using CANOCO 4.5 (ter Braak and Smilauer 2002) to determine the

response of the community, and component species, to remnant treatments (Leps and Smilauer 2003). Treatments and blocks were coded as dummy environmental variables and covariables, respectively. RDA was used because dummy environmental variables were categorical (0 or 1), and gradient lengths on axis 1 (0.824 SD) and 2 (0.746 SD) of a preliminary DCA were short (Leps and Smilauer 2003). Ordinations were performed on invertebrate species data as absolute densities (in the CANOCO analysis, 'non-standardised') and as proportions of total abundance (i.e. 'standardised by sample norm'). To investigate the extent to which among-treatment differences in invertebrate community structure were attributable to the presence of the remnant species, two ordinations (based on absolute and relative abundances) of the full invertebrate species data matrix, including all the remnant species (*Serratella*, *Gammarus*, *Radix*), were compared with two in which all remnant species were fitted passively (made supplementary) in the model. When supplementary, species are added post hoc to the ordination by projection and do not influence the definition of ordination axes (ter Braak and Smilauer 2002). A Monte Carlo permutation test (999 permutations, with treatments permuted randomly within blocks) was used to test the significance of each model.

Results

Epilithon

An algal mat, dominated numerically by filamentous and unicellular diatoms (*Melosira varians*, *Nitzschia perminuta* and *Navicula menisulus* dominant), developed rapidly on the gravel substratum of each channel. Repeated measures ANOVA revealed that chlorophyll *a* concentration varied with specific remnant treatment and time. The main effects of time ($P=0.0001$) and remnant treatment ($P=0.002$) were significant as was their interaction ($P=0.001$), but there was no block effect ($P=0.225$) nor any interaction between block and time ($P=0.262$). Control channels had high chlorophyll *a* biomass on days 7 (Plate 1, Supplementary material) and 14, after which algal filaments became detached and were washed downstream, decreasing biomass by day 28 (Fig. 1a). Chlorophyll biomass was reduced significantly in *Radix* patches (Tukey HSD, $P<0.05$). One-way ANOVA demonstrated that *Radix* effects were evident on day 7 and persisted up to day 14 (Tukey HSD, $P<0.05$ in both cases), but were annulled thereafter as algal sloughing occurred during the final 2 weeks of the experiment ($P>0.05$; Fig. 1a). Effects of *Serratella* and *Gammarus* on chlorophyll biomass were weak by comparison (Tukey HSD, $P>0.05$) and temporal trends (over 21 days) in these two treatments were similar to controls (Fig. 1a).

Epilithon AFDM varied significantly with time ($P=0.0005$), remnant treatment ($P=0.008$) and their interaction ($P=0.031$), but there was no block effect
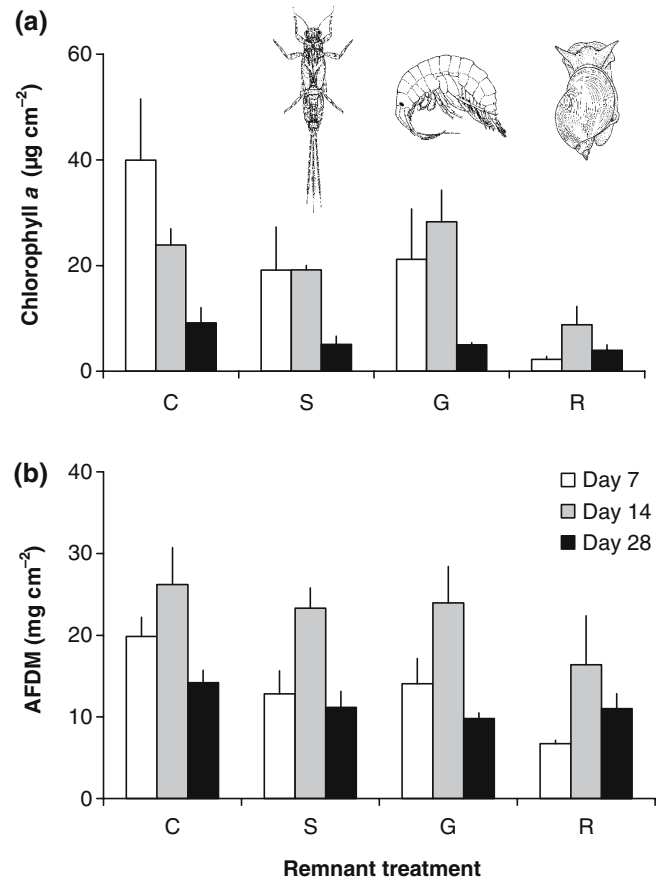
Fig. 1 Mean (+1 SE) epilithon chlorophyll *a* concentration (**a**) and ash-free dry mass (**b**) in remnant treatments. Abbreviations on the *x*-axis are *G*, *Gammarus*; *S*, *Serratella*; *R*, *Radix* and *C*, control

($P=0.460$), nor any interaction between block and time ($P=0.177$). In controls and treatments where remnant species did not depress or dislodge the epilithon (*Serratella* and *Gammarus*), AFDM peaked in the middle of the experiment (day 14; Fig. 1b) when the epilithon layer included a considerable amount of non-algal organic matter. In *Radix* treatments, AFDM was significantly lower than in controls on day 7 (one-way ANOVA, $P<0.05$; Fig. 1b), but increased thereafter to levels not significantly different from those in the other treatments ($P>0.05$).
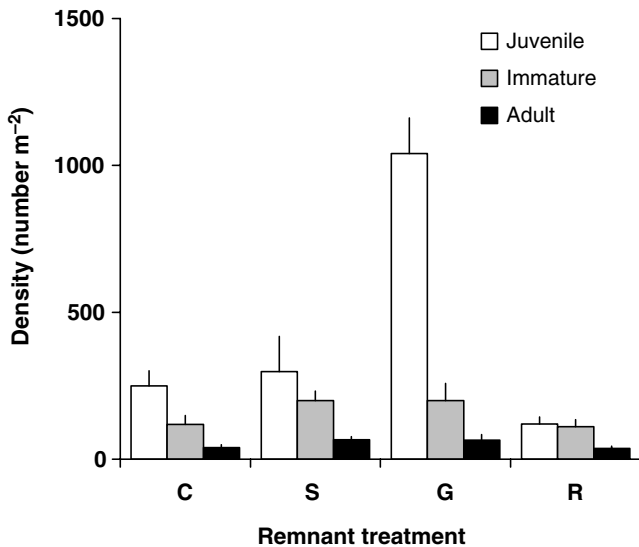
Trends in the abundance of remnant species

At the end of the experiment, densities of remnant *Serratella* (mean 218 m^{-2}, SE 38) and *Radix* (mean 223 m^{-2}, SE 26) were not significantly different from initial densities (240 m^{-2}) (*t*-tests, $P>0.05$), nor from final densities in other treatments, and did not differ significantly among blocks (two-way ANOVA, $P>0.05$). In contrast, *Gammarus* densities increased significantly (on average by 665% to 1,838 m^{-2}, SE 162) by day 28 (*t*-test, $P<0.05$) in remnant *Gammarus* patches. However, the final abundance of *Gammarus* differed with size-class (two-way ANOVA, $P=0.0002$; juvenile > immature > mature,

Tukey's HSD, $P < 0.0005$) and treatment ($P = 0.0004$; *Gammarus* > other remnants, Tukey's HSD, $P < 0.0005$; Fig. 2). A significant interaction between size-class and treatment ($P = 0.0005$) denoted a greater density of juvenile (<4 mm, predominantly <1 mm), but not immature (4–6 mm) or mature (>6 mm) individuals, where *Gammarus* was the remnant species (Fig. 2).
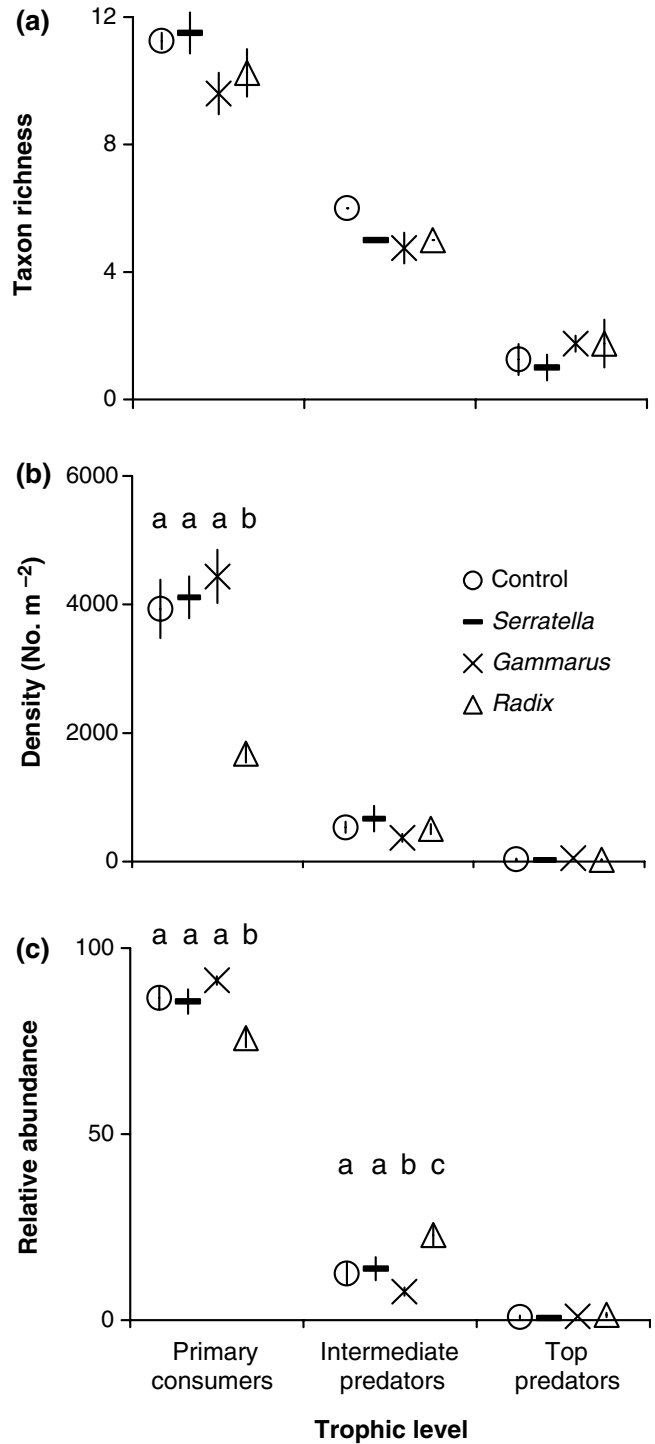
Endpoint community structure

By the end of the experiment, 34 invertebrate taxa had colonised the channel array (Appendix, Supplementary material). Taxon richness increased from the highest to the lowest trophic level in all channels (Fig. 3a), but there was no significant effect of remnant treatment, either on total invertebrate taxon richness, or richness at any individual trophic level (Fig. 3a; Table 1). In contrast, total invertebrate density was lower in *Radix* patches ($2,216 \pm 398\ \mathrm{m}^{-2}$) than in controls ($4,500 \pm 398\ \mathrm{m}^{-2}$), or where *Serratella* ($4,802 \pm 305\ \mathrm{m}^{-2}$) and *Gammarus* ($4,858 \pm 446\ \mathrm{m}^{-2}$) were remnant species (Table 1). Primary consumers were numerically (42% of controls) and proportionately least abundant (76%, compared with 87% in controls) in the *Radix* treatment (Fig. 3b, c, Table 1). Treatment effects on the absolute and relative abundance of top predators, and on the absolute abundance of intermediate predators, were all non-significant (Fig. 3b, c, Table 1). However, the relative abundance of intermediate predators was greater in remnant *Radix* treatments (22.9%, control 11.9%) but lower (7.6%) where *Gammarus* was the remnant species (Fig. 3c, Tukey HSD $P < 0.05$; Table 1).

Partial redundancy analysis revealed a significant overall effect of treatment on invertebrate community structure, based on both the numerical (non-standardised partial RDA, axes 1 and 2 explained 55.8% of total

Fig. 3 Mean (± 1 SE) taxon richness (**a**), numerical (**b**) and relative abundance (**c**) at three trophic levels in the four remnant treatments. Significant treatment effects (Tukey HSD, $P < 0.05$) are denoted by *different letters* above the symbols

variance in species data, $P = 0.002$; Fig. 4a) and relative abundance (standardised partial RDA, axes 1 and 2 explained 51.3% variance, $P = 0.002$; Fig. 6a) of component species, that was additional to that caused by the presence of remnant individuals (non-standardised

Fig. 2 Mean (+1 SE) abundance of juvenile (<4 mm), immature (4–6 mm) and mature (>6 mm) *Gammarus* in remnant treatments at the end of the experiment

Table 1 Effect of remnant treatment and block on invertebrate assemblage structure

Taxon	Species richness		Absolute density		Relative abundance	
	Treatment	Block	Treatment	Block	Treatment	Block
All metazoans	0.15	0.58	**0.0002**	0.74		
Top predators	0.34	0.11	0.16	0.78	0.32	0.61
Intermediate predators	0.23	0.45	0.14	0.46	**0.009**	0.33
Primary consumers	0.26	0.52	**0.0004**	0.49	**0.005**	0.16

Numbers are ANOVA P-values, corrected using the sequential Bonferroni procedure, with statistically significant ($P < 0.05$) results in bold. Degrees of freedom were 3,16 for both treatment and block

partial RDA, remnant species supplementary, axes 1 and 2 explained 45.5% variance, $P = 0.002$; Fig. 4b; standardised partial RDA, remnant species supplementary, axes 1 and 2 explained 40.4% variance, $P = 0.002$; Fig. 6b). Partial RDA based on numerical abundance of all invertebrate species revealed that remnant *Radix* patches supported more filter feeding simuliids (688% of control density; Fig. 5e) and fewer non-predatory chironomids (*Heterotrissocladius* and *Microtendipes*) than any of the other treatments (Fig. 4). In *Radix* patches, densities of *Heterotrissocladius* and *Microtendipes* were 29% and 33% of controls, respectively (Fig. 5a, b). *Aphelocheirus* nymphs (hemipteran predators) occurred only in the *Radix* treatment and were uncommon (11 m^{-2}) (Fig. 5g). *Gammarus* was most abundant, and *Pentaneura* scarcest, in the remnant *Gammarus* treatment (Figs. 4a, 5c). Higher densities of *Asellus*, *Baetis* and non-predatory chironomids characterised early *Serratella* treatments and the control, the former taxon being absent from channels where *Gammarus* was the remnant species (Figs. 4a, 5d, f). Contrasts in the relative abundance of species among treatments reflected those for numerical abundance, reported above, with the addition that *Procladius* and *Macropelopia* (both predatory chironomids) were also proportionately most abundant in the *Radix* treatment (Fig. 6a). The effects of treatment on colonists revealed by RDA were confirmed by ANOVA and Tukey HSD tests ($P < 0.05$ in all cases, following sequential Bonferonni correction for groups of tests; Fig. 5).

We assessed whether among-treatment differences in community structure were attributable to the presence of the remnant species by comparing the position of treatment centroids in ordinations of the full data matrix, including remnant species, with one in which all remnants were fitted passively in the model. *Radix* and *Serratella* treatment centroids in ordinations based both on numerical (Fig. 4a) and relative abundance (Fig. 6a) did not noticeably change position when the remnant fauna was made supplementary in the models, indicating that these species did not contribute to observed differences in community structure. However, the remnant *Gammarus* centroid migrated markedly towards the origin in ordinations based on numerical abundance (Fig. 4b) but not relative abundance (Fig. 6b). Thus, both high *Gammarus* numbers (predominately juveniles) and low relative abundance (*Baetis*, *Pentaneura*) or absence (*Asellus*) of colonists differentiated community composition in remnant *Gammarus* patches.
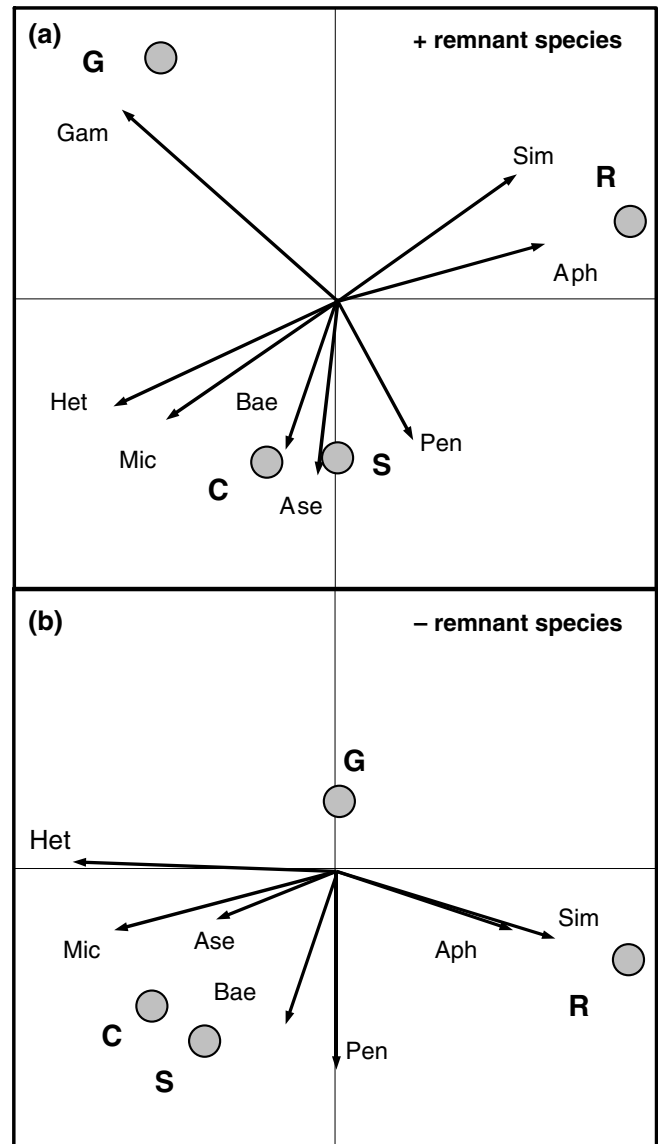
Fig. 4 Partial RDA ordination diagrams demonstrating differences in invertebrate community structure, based on absolute abundance of component species, in treatments where *Serratella* (S), *Gammarus* (G) and *Radix* (R) were remnant species, and C was the control. Remnant taxa were either fitted actively (**a**) or passively (**b**) in the partial RDA model. The direction and length of species vectors indicate the trend, and extent, of increase in abundance among the treatments. Taxa are abbreviated on vector labels: *Aphelocheirus* (Aph), *Asellus*, (Ase), *Baetis* (Bae), *Gammarus* (Gam), *Heterotrissocladius* (Het), *Microtendipes* (Mic), *Pentaneura* (Pen) and Simuliidae (Sim)

Fig. 5 Mean (+ 1 SE) density of seven metazoan colonists in treatments where *Serratella* (S), *Gammarus* (G) and *Radix* (R) were remnant species, and C was the control. Significant differences (Tukey HSD, $P < 0.05$) between treatments are denoted by *different letters* on bars. Note different scales on *y*-axis
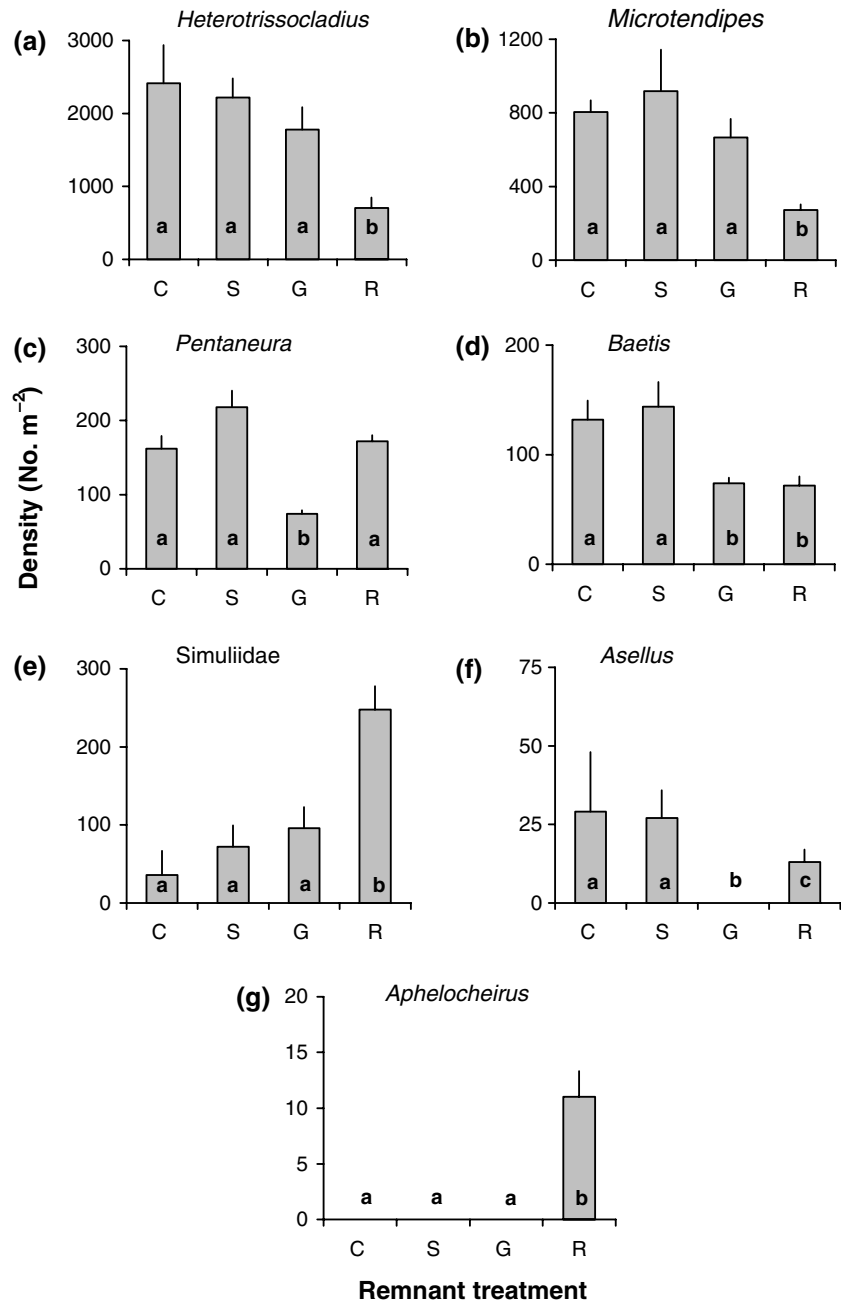

Discussion

Disturbances in benthic habitats create mosaics of patches with different characteristics (Sousa, 1984b), including areal extent and remnant species occupancy. In this study, model patches (mesocosms) were manipulated in order to test whether invertebrates surviving disturbance function as 'biological legacies' that influence the reestablishment and restructuring of benthic assemblages. Realistic colonisation dynamics were observed by conducting the experiment in mesocosms at the spatial scale of small substratum patches created by floods in streams (see Englund and Cooper 2003). Our results indicate that legacy effects can influence the structure of developing assemblages, but depend on the identity of remnant species in patches.

Radix patches differed markedly from those in the other treatments. Snails strongly reduced the density of epilithic mats, exposing stony gravels to the flow. Consequently, fine particulate organic matter (FPOM) was flushed from the upper surfaces of stones and from the interstices between them, thereby increasing the availability of these microhabitats within experimental patches. These substantial alterations to the physical environment strongly affected the developing invertebrate community. Thus, through their foraging activities, the snails facilitated the colonisation of filter feeding
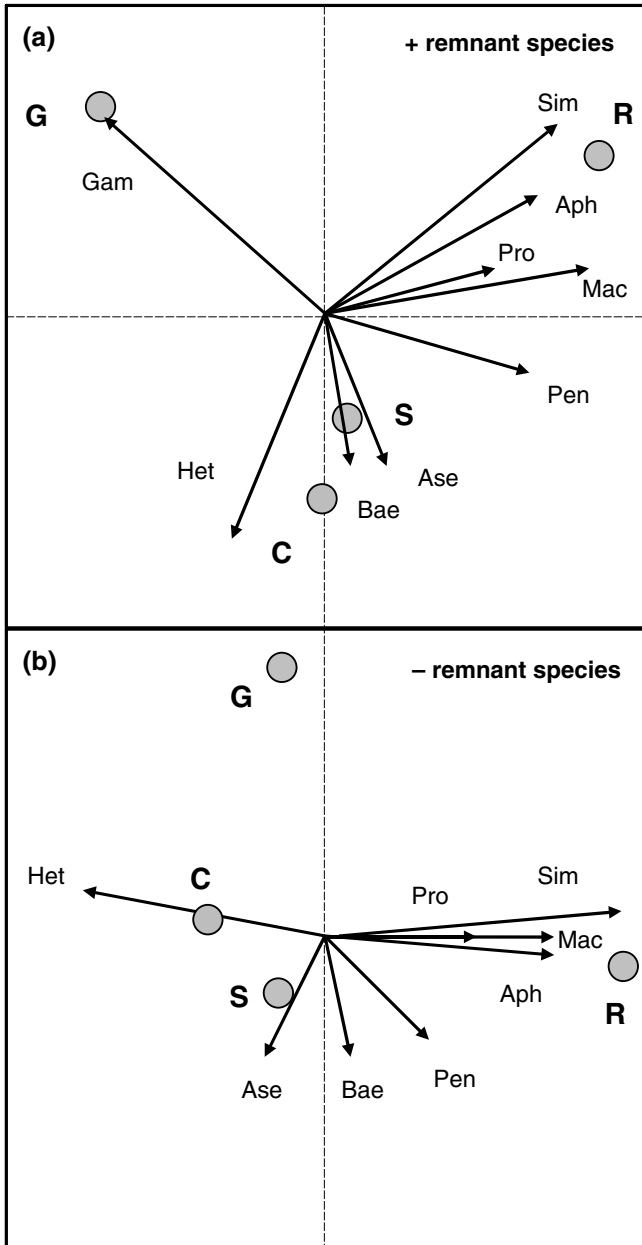
Fig. 6 Partial RDA ordination diagrams demonstrating differences in invertebrate community structure, based on the relative abundance of component species, in treatments where *Serratella* (S), *Gammarus* (G) and *Radix* (R) were remnant species, and C was the control. Legacies were either fitted actively (**a**) or passively (**b**) in the partial RDA model. Abbreviations as in Fig. 4 and also *Macropelopia* (Mac) and *Procladius* (Pro)

simuliids by increasing the availability of bare stony surfaces, to which they could attach, and, of the predators (*Pentaneura* and *Aphelocheirus*) by initiating FPOM clearance from the interstitial spaces they occupy. In contrast, snails strongly inhibited the colonisation of non-predatory chironomids that feed on algae and build retreats within the epilithon itself (especially *Heterotrissocladius*) or on stones (*Microtendipes*). The strong inhibition of herbivorous chironomids by *Radix* decreased overall invertebrate abundance to 49% of controls and

lowered the absolute and relative abundance of primary consumers as a group (although filter feeders increased markedly), thereby skewing trophic structure in favour of invertebrate predators. Although the reduction of algae by *Radix* was transient, and was not evident on day 28, habitat changes, including dislodgment of algae and sediment, occurred rapidly (within 7 days) during community recovery. The effect of *Radix* on community structure was consequently substantial, and demonstrated that remnant biota can influence community development at small spatial scales.

In contrast to *Radix*, the other two remnant taxa, *Serratella* and *Gammarus*, had little demonstrable effect on the epilithon. Although both *Serratella* and *Gammarus* consume algae in chalk streams (Welton 1979; M.E. Ledger, unpublished), detritus forms a substantial part of their diets (Rosillon 1988; Moog 1995), and *Gammarus* also sometimes predates other invertebrates (Gledhill et al. 1993; Moog 1995). Although leaf particles were scarce, FPOM and other invertebrates were abundant in the channels after the first week of the experiment, providing alternative food sources for both species. *Serratella* and *Gammarus* foraged within the epilithon but did not dislodge it. In contrast, high algal exports from *Radix* patches (M.E. Ledger, personal observations), caused by the bulldozing action of snails at the base of algal filaments, revealed a sizeable non-consumptive element to epilithon reduction not observed in the other treatments.

Algal resource depression by pulmonate snails is commonly reported in streams (e.g. Underwood and Thomas 1990; Bronmark et al. 1991; Hill et al. 1992), but to our knowledge the effect of this form of habitat modification on the metazoan community has not been considered within the context of successional dynamics in streams. However, Bertness (1984) demonstrated that when snails (*Littorina littorea*) were removed from a marine rocky shore, algal biomass and sediment accumulation increased, enabling marsh grass (*Spartina alterniflora*) to extend its supra-littoral distribution. Consequently, the structure of the invertebrate community changed with biota characteristic of soft-sediments (especially polychaetes, amphipods, mud crabs and mud snails) increasing in abundance at the expense of barnacles and encrusting algae. As in our study, Bertness (1984) attributed the influence of snails to their bulldozing of algae and sediment, an activity that in both studies can be described as 'ecosystem engineering', sensu Jones et al. (1994). Several recent studies report other examples of engineering by freshwater species, including blackflies (Wotton et al. 2003), caddisflies (Cardinale et al. 2004), crayfish (Usio and Townsend 2004) and fish (Flecker and Taylor 2004). These taxa alter their environment in different ways. Suspension feeding blackfly larvae (Simuliidae) transform dissolved and very fine particulate material in to much larger faecal aggregates, thereby promoting the local retention of organic matter (Wotton et al. 2003). Caddisflies (Hydropsychidae) spin food-capture nets that bind substratum particles together,

increasing the stability of the streambed (Cardinale et al. 2004). Grazing fishes (Parodontidae) bulldoze sediments in tropical streams, creating spatial mosaics of organic matter, and affect the diversity of benthic invertebrates (Flecker and Taylor 2004). Usio and Townsend (2004) reported that New Zealand crayfish (*Paranephrops zealandica*) bioturbate sediment, reducing the abundance of orthoclad chironomids, worms and mites. In our study, pulmonate snails influenced the numerical and relative abundance of invertebrates, but not taxon richness, by reducing algae and FPOM, and creating epilithic and interstitial space.

Like *Radix*, *Gammarus* had a marked effect on community structure in the channels. In contrast to *Radix* patches, however, where only substantial shifts in the abundance of species other than the remnant species were observed, differences in *Gammarus* treatments were due to both increased numerical abundance (665% of initial densities) of the remnant species itself, predominantly juveniles, and reduced abundance (*Baetis* and *Pentaneura*) or exclusion (*Asellus*) of colonists. Our experiment was conducted in May and June during the gammaridean breeding season when water temperature was relatively high (30-day mean, 16.1°C) and brood development time was correspondingly short (approximately 20 days; Welton and Clarke 1980). While small numbers of *Gammarus* colonised all the channels by drift, the substantial increases in juveniles in remnant *Gammarus* patches probably reflect reproduction and the release of brood by the mature individuals we introduced as remnants. Interference from *Gammarus*, and their preemption of limited interstitial space, probably accounted for the reduced abundance of colonising *Baetis* and *Pentaneura*, and the non-establishment of *Asellus*, although predation by adult shrimps cannot be discounted, and has been demonstrated for some congeners (Dick et al. 1993).

In contrast to the legacy effects of *Radix* and *Gammarus*, *Serratella* had no detectable influence on the development of invertebrate communities in our experimental habitat patches. These nymphs are weak swimmers and cling to algal filaments and stones to avoid displacement by the flow (Elliott et al. 1988). Thus, while *Serratella* persisted in the channels throughout the experiment, habitat architecture was conserved by the refuge-seeking traits of the nymphs. Furthermore, the high similarity of invertebrate communities in *Serratella* treatments and controls demonstrated that these mayfly larvae also had a neutral effect on the settlement of other invertebrate colonists. We suggest that benthic invertebrate species, whose small-scale distributions are continually changing in response to disturbance and resource heterogeneity, are likely to be mutually tolerant in general (Diamond and Reice 1985). Nevertheless, when abundant early in successional sequences, taxa that modify the environment, reproduce rapidly, or are strong competitors or predators, are likely to affect the subsequent pathway of community development after disturbance events (Platt and Connell 2003).

Disturbances frequently reduce or destroy pre-existing patterns in the distribution and abundance of algae, organic matter and invertebrates on the riverbed. Our research suggests remnant species may play a key role in the renewal of heterogeneity in the post-disturbance environment, via both trophic and non-trophic processes. Remnants may therefore be perceived as 'threads of continuity' (sensu Franklin et al. 2000) in stream communities. This interplay between episodic disturbance and biotic processes potentially influences patchiness in community structure at different spatial scales, ranging from individual substratum particles to river reaches. However, the precise role of biota, including remnant species, in community organisation is ultimately characterised by the size and composition of the local species pool, which is in turn regulated by abiotic landscape scale factors, including climate and water quality (e.g. Poff 1997).

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