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Aquatic and terrestrial invertebrate community responses to drying in chalk streams

George Bunting[1], Judy England [2], Kieran Gething [1], Tim Sykes [2], Jon Webb[3] & Rachel Stubbington [1]

[1]School of Science and Technology, Nottingham Trent University, Nottingham, UK; [2]Environment Agency, Bristol, UK; and [3]Natural England, Peterborough, UK

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Correspondence
Rachel Stubbington, School of Science and Technology, Nottingham Trent University, Nottingham, UK.
Email: rachel.stubbington@ntu.ac.uk

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Abstract

Temporary streams are dynamic ecosystems that shift between wet and dry states and include the 'winterbourne' chalk streams of south England. Our understanding of temporary stream biodiversity is biased, with most research to date exploring aquatic invertebrate communities in benthic sediments during flowing phases. We surveyed the invertebrate communities of the Candover Brook chalk stream, comparing aquatic (benthic, hyporheic) and terrestrial communities in reaches with different flow permanence regimes. We used kick and Bou–Rouch sampling methods to collect aquatic invertebrates, and compared the terrestrial communities characterised by pitfall traps and ground searches and in different seasons. Although aquatic taxa richness was lower in temporary compared to perennial reaches, the total biodiversity of temporary stream channels was enhanced by contributions from both aquatic and terrestrial species, including several of conservation interest. We recommend that both aquatic and terrestrial communities should be considered in research and monitoring to characterise the biodiversity and ecological quality of temporary streams.

Introduction

Temporary rivers are those in which flow sometimes ceases, and many lose most or all surface water (Leigh *et al*., 2016). As such, temporary streams are aquatic–terrestrial ecosystems in which profound differences in habitat availability during wet and dry phases influence biodiversity (Stubbington *et al*., 2017). Temporary streams typically support fewer species than perennial streams when the local-scale taxonomic richness of aquatic communities is compared (Datry *et al*., 2014). However, the total biodiversity of temporary stream channels reflects contributions from both terrestrial and aquatic communities (Corti and Datry, 2016), and ecological assessments of temporary streams should thus characterise both communities. Such assessments are particularly needed in temporary streams protected by legislation, including the 'winterbourne' reaches of chalk streams in south England, United Kingdom (JNCC, 2019). However, methods enabling effective temporary stream assessments still require development (Stubbington *et al*., 2018).

The biodiversity of temporary streams can be increased by the occurrence of specialist species, including some of conservation concern. For example, Armitage and Bass (2013) recorded aquatic juveniles of the rare blackfly *Metacnephia amphora*, mayfly *Paraleptophlebia werneri* and stonefly *Nemoura lacustris* at winterbourne sites on one chalk stream. This *N. lacustris* record followed its initial UK description by Hammett (2012), and it is now known from 16 winterbourne sites in south England (Tapia *et al*., 2018) and is designated as nationally rare (Macadam, 2015). Such species elevate the conservation status of aquatic communities in temporary streams compared to perennial streams (White *et al*., 2018). Temporary streams may also support terrestrial species of conservation interest during dry phases, but terrestrial communities remain very poorly documented in temporary rivers (Stubbington *et al*., 2019a), and no study has quantified those in winterbourne reaches (but see Moon, 1956).

The regulatory agencies responsible for biomonitoring require robust methods that efficiently characterise biological communities, with appropriate adaptation to reflect environmental conditions in temporary streams (Stubbington *et al*., 2018). During wet phases, benthic fauna may be sampled using standard kick sampling supplemented by manually disturbing sediments beneath shallow water and capturing displaced invertebrates (England *et al*., 2019). After the water table declines beneath the bed, aquatic invertebrates may seek refuge in the subsurface (i.e. hyporheic) sediments (Stubbington, 2012). Hyporheic communities may be collected using pump-sampling methods (Bou and Rouch, 1967; Stubbington *et al*., 2016a), the performance of which has not been tested in dry conditions. Terrestrial communities can be sampled using pitfall traps (Corti and Datry, 2016) but leaving traps *in situ* for standard periods (2–4 weeks; Natural England, 2007) is logistically difficult for managers with responsibility for ecological statusassessments. Alternatives include ground searching, which produces immediate results, but remains untested in dry channels.

We characterised benthic, hyporheic and terrestrial invertebrate communities at sites with perennial and winterbourne flow permanence regimes on a chalk stream. We assessed the taxa richness, abundance and conservation status of each assemblage in relation to flow permanence and other habitat characteristics. To inform future development of regulatory biomonitoring programmes, we compared the performance of standard ecological quality indices at sites with different flow permanence regimes; aquatic and terrestrial communities sampled by different techniques; and terrestrial communities sampled in two seasons.

Method

Study area

The Candover Brook, a tributary of the River Itchen, is a 12-km chalk stream in Hampshire, United Kingdom (Fig. 1). Its catchment drains a 71.2 km^2 section of Cretaceous chalk in central southern England (NRFA, 2019). Permeable geology limits surface runoff and the stream is thus principally groundwater-fed (base flow index = 0.96; NRFA, 2019). The region has a temperate oceanic climate, with mean annual minimum and maximum air temperatures of 5.8 ± 3.9 and 14.6 ± 5.8°C, respectively (Met Office, 2019). Mean annual precipitation of 746.5 mm is evenly distributed across seasons (Met Office, 2019). The catchment is predominantly rural, including arable (51%), grassland (mainly pasture; 28%), woodland (14%) and urban (4%) land uses (NRFA, 2019). Regulatory monitoring done to assess Water Framework Directive (WFD) status at the downstream perennial site (Fig. 1) indicates that physico-chemical and hydromorphological quality are good to high, whereas the WFD macrophyte and phytobenthos quality element is of moderate quality, which is attributed to groundwater abstraction and drought (Environment Agency, 2019).

The stream's perennial head is 6.5 km from its source, downstream of which the stream flows continuously for 5.5 km to its confluence with the River Itchen (Fig. 1). A discharge gauging station is located in a perennial reach 50 m upstream of the confluence. In addition, the Environment Agency (the regulatory agency for England, United Kingdom) have recorded the presence or absence of water at 13 sites in the winterbourne reaches at monthly intervals since 1997. These observations show that, at

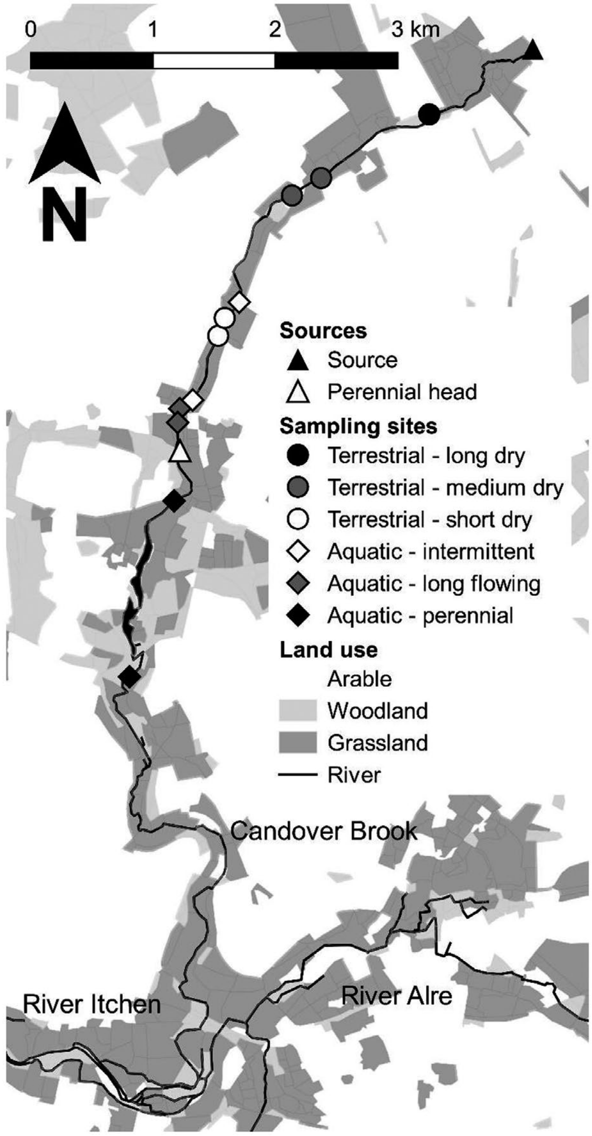

Fig. 1. The location of the study sites along the Candover Brook, Hampshire, United Kingdom. Land cover data from Rowland *et al*., (2017).

the time of the study, the 0.5 km immediately downstream of the source had been dry for 5 years, and the next 2 km for 3 years. Downstream of this, a winterbourne section extends 4 km upstream from the perennial head. Here, flow typically returns in autumn and water levels drop below the sediment surface in spring. Conditions in 2019 followed this pattern, with an increasing stream length drying between May and September in response to receding groundwater levels. Discharge at the downstream gauging station declined from 0.71 to 0.24 m^3/s and was below the long-term average (mean 0.41 m^3/s compared to 0.54 m^3/s; 1970–2020) throughout the study period (19 March to 19 September 2019).

Environmental data collection

The physical environment at each site was characterised using the Modular River Survey (MoRPh), an ecologically relevant habitat-scale survey that assesses habitats in the river channel and riparian zone (Shuker *et al*., 2017). The survey length was 10 and 20 m at sites with channel widths of <5 and 5–10 m, respectively. Each survey encompassed the riparian zone extending 10 m from the bank top, the banks and channel bed, and considered channel dimensions, flow types, substrate materials, riparian and aquatic vegetation types, surrounding land use and channel reinforcement. Surveys of aquatic and terrestrial sampling sites were done during flowing and dry phases, respectively.

At each aquatic sampling site, 10 water depth and flow velocity measurements were taken at regular intervals across the channel using a flow meter and used to calculate discharge. Dissolved oxygen concentrations (mg/L), water temperature (°C) and pH were also measured (Hanna Instruments, Leighton Buzzard, United Kingdom).

Invertebrate community sampling

Aquatic invertebrates

Benthic and hyporheic invertebrate communities were sampled in March and April (i.e. spring) 2019. Six sites were selected to represent the stream's three major flow permanence regimes: two perennial, two long flowing and two intermittent (Figs. 1 and S1). Based on Environment Agency data from 1997 to 2019, perennial sites are defined as those which neither cease to flow nor dry, and long flowing and intermittent sites have typical annual flowing phases of 3.1 ± 2.4 and 2.5 ± 2.0 months, respectively.

Benthic invertebrate samples were collected following a standard kick sampling procedure, with adaptations to promote effective characterisation of temporary stream communities, following England *et al*. (2019). At each site, 3 min were spent sampling each habitat in proportion to its occurrence. Areas covered by shallow water were sampled by splashing sediments with water and collecting displaced invertebrates. A 1-min manual search was also done to collect invertebrates attached to stones and vegetation.

Four replicate hyporheic invertebrate samples were collected from the dominant habitat type present at each site using the Bou–Rouch pump-sampling method (Bou and Rouch, 1967; Stubbington *et al*., 2016a). Samples were collected from downstream to upstream and each obtained ≥2 m from other sampling points, to minimise any disturbance caused by sampling on subsequent samples. At each sampling point, a 125-cm steel standpipe was hammered into the bed so that the top of the perforated section (15-cm length with 5-mm diameter perforations) was 15 cm below the substrate surface (Fig. S1e). A pump was placed on top of the standpipe, primed with 0.5 L of filtered stream water, and operated to collect 6.5 L of hyporheic water and associated invertebrates. Water was poured through a 250-μm sieve to retain invertebrates, and samples preserved in 70% industrial methylated spirits.

Terrestrial communities

Terrestrial invertebrates were surveyed at five in-channel sites in two seasons: early summer (i.e. mid-June to mid-July) and autumn (mid-September) 2019 (Fig. S2). Sites were allocated to *short-*, *medium-* and *long-dry* categories according to the duration of the preceding dry period (Fig. 1). In summer, sites in these categories had been dry for an estimated 2, 63 and 168 weeks, respectively. Accordingly, in autumn, short, medium and long-dry sites had dried 11, 76 and 181 weeks earlier. The two short-dry sites were at an equivalent location to the upstream intermittent aquatic invertebrate sampling site (Fig. 1).

Samples were collected using the ground searching and pitfall trapping methods described by Natural England (2007). Ground searches and 7-day pitfall trapping were done at all sites, and 24-hour pitfall trapping was tested at both short-dry sites and the downstream medium-dry site. We selected 24-hour and 7-day durations instead of standard 2–4-week periods (Natural England, 2007) in consultation with Environment Agency managers, as their preferred and maximum acceptable durations for use in regulatory biomonitoring, respectively. Based on their similar composition to 24-hour traps but greater richness and abundance (see summer sampling *Results*), only 7-day pitfall trapping was used to survey the same sites in autumn.

Ground searches were conducted along a 10 m channel length, with the search area extending laterally to encompass channel margins to the bank base. One sample per site was collected during a 1-hour search, with the time divided proportionately between each habitat. Vegetation and soft sediments were disturbed, substrate grains and woody material turned, and leaf litter searched, and all active invertebrates collected using an aspirator. The time spent moving between habitat types and transferring specimens to sample pots was included within the 1-hour search time. Samples were preserved in 50% ethylene glycol.

Eight pitfall traps were installed at each site, representing all habitats in proportion to their occurrence and with each trap separated from others by ≥1 m. Each trap consisted of two plastic cups (70 mm diameter, 90 mm height) placed one inside the other, which were dug into the sediment so that their rims were flush with the bed. A 25 mL solution of 50% ethylene glycol and 0.5% detergent was added to each trap. A wooden roof was positioned approximately 1 cm above the rim to prevent entry of rain and falling debris while allowing access to all invertebrates but no mammals or birds. After the 24-hour or 7-day period had elapsed, trap contents were emptied and preserved in 50% ethylene glycol.

Invertebrate identification

Aquatic invertebrates were identified to the lowest taxonomic resolution possible, typically species or genus. Most Diptera, early instar and/or damaged Insecta, some adult and larval Coleoptera, Niphargidae (Amphipoda), Planorbidae (Gastropoda) and Bivalvia were identified to family; some Chironomidae (Diptera) were identified to subfamily or tribe; and Collembola, Hydrachnidia, Oligochaeta and Ostracoda were not identified further. Most terrestrial Coleoptera and Isopoda were identified to genus or species, with some small or ambiguous specimens left at family. Terrestrial Oribatida, Orthoptera and some Trombidiformes were identified to family, and Araneae, Chilopoda, Collembola, Diplopoda, Diptera, Gastropoda, Hemiptera, Hymenoptera, Oligochaeta and some Trombidiformes were identified as such.

Data analysis

Environmental data

Fourteen summary indices were calculated for each MoRPh survey via the MoRPh website (Gurnell *et al*., 2016). Nine indices describe river channel characteristics (number of flow types, highest energy flow type, number of bed materials, coarsest extensive bed material particle size, average bed material particle size [phi units, class], extent of bed siltation, channel physical habitat complexity and the number of aquatic vegetation morphotypes), two detail riparian characteristics (physical habitat complexity and vegetation complexity), and three indicate human pressures and impacts (degree of human pressure imposed by bank top land cover, channel reinforcement and extent of non-native invasive species; Shuker *et al*., 2017). Index values range from 0 (extremely low) to a theoretical maximum of 10 (extremely high), with some lower expected maximums.

Invertebrate community data

Prior to analysis, we pooled invertebrates from the eight pseudo-replicated pitfall traps to create one terrestrial invertebrate community sample per site (Luff, 1996; Natural England, 2007). For each aquatic and terrestrial sample, we assigned taxa identified to multiple resolutions (e.g. genus and family) to the single most likely taxon (e.g. genus), to avoid overestimating taxa richness while conserving the greatest degree of taxonomic resolution.

We calculated two univariate metrics to describe each assemblage: mean abundance and taxa richness, as the mean number of individuals and taxa per sample, respectively. We also calculated the total richness of aquatic taxa in each flow permanence group and terrestrial taxa in each dry period duration group. We calculated four indices to summarise the aquatic invertebrate community: the Community Conservation Index (CCI), the abundance-weighted Whalley Hawkes Paisley Trigg (WHPT) index and its average score per taxon (ASPT) and the Monitoring Intermittent Streams index (MIS-index). CCI is an indicator of conservation value that incorporates the richness and relative rarity of species in an assemblage (Chadd and Extence, 2004). The WHPT index (Paisley *et al*., 2014), provides a measure of general environmental degradation, in particular water quality; its ASPT is independent of sample size. The MIS-index describes community responses to environmental changes spanning flowing, ponded and dry states in temporary streams (England *et al*., 2019). We assigned recorded taxa not included within the MIS-index to 'MIS-groups' based on their habitat preferences. We used the online tool *Pantheon* (Webb *et al*., 2018a) to obtain information about the conservation status, habitat and resource preferences, and feeding guilds of terrestrial invertebrates, and to assign each native species a Species Quality Score (SQS) of between 1 (not rare or scarce) and 32 (species of the highest conservation concern according to national and international classifications; Webb *et al*., 2018b). SQS were summed, divided by the number of species and multiplied by 100 to calculate the Species Quality Index (SQI), which summarises the rarity and richness of species in each assemblage.

Low replication necessitated the pooling of hyporheic samples from intermittent and long flowing sites in a *temporary* group, and the pooling of terrestrial samples from both seasons in the test for differences between dry period durations. We used Shapiro–Wilk tests to assess the normality of univariate metrics and $\log(x+1)$ transformed variables with non-normal distributions prior to further analysis. Differences in univariate metrics between flow permanence regimes (benthic: intermittent, long flowing, perennial; hyporheic: perennial, temporary), dry period durations (terrestrial: long, medium, short-dry), sampling methods (terrestrial: ground search, pitfall trap) and seasons (terrestrial: autumn, summer) were tested using one-way ANOVA, supplemented by post hoc Tukey tests where differences were identified.

Variability in invertebrate community composition between flow permanence regimes, dry period durations and sampling methods was examined using permutational multivariate ANOVA (PERMANOVA; Anderson, 2001) on Bray-Curtis dissimilarity matrices of raw abundance data. Where PERMANOVA identified differences among categories, pairwise tests were performed. Non-metric multidimensional scaling (NMDS) ordinations were generated to visualise variability in community composition.

Analyses were done in R version 3.6.1 (R Core Team, 2019) using the packages biomonitoR (Laini *et al*., 2019) to calculate taxa richness, WHPT and WHPT-ASPT, and vegan (Oksanen *et al*., 2018) to run ANOVA, NMDS and PERMANOVA.

Results

Environmental characteristics of sampling sites

Site characteristics

The physical habitat characteristics of aquatic and terrestrial sites, as summarised using MoRPh indices, are presented in Figs. S1–S2 and Table S1. Many sites were typical of chalk streams in south England: wide, shallow channels with substrates dominated by gravel to cobble-sized clasts, although superficial bed siltation affected three aquatic sampling sites (Fig. S1c–e). The most notable among-site variation was in the number of aquatic vegetation morphotypes, which ranged from 4 at an aquatic site surveyed during a flowing phase (Fig. S1a) to 0 in a terrestrial long-dry channel dominated by terrestrial vegetation (Fig. S2a). Although not recorded by the MoRPh method, we also observed several terrestrial vegetation morphotypes within dry channels, including mosses, grasses, broad-leaved herbs and trees (Fig. S2). Channel physical habitat complexity was consistently low (1.3–2.1) except for two aquatic sites at which higher values were recorded (3.8, 3.3; Fig. S1d–e). Riparian physical habitat complexity was generally low, ranging between 1.7 and 2.1 at terrestrial sites and 1.8–4.3 at aquatic sites, with higher values associated with in-channel depositional features such as bars and berms (Fig. S1d–e). Riparian vegetation structural complexity was also low (2–4.5), reflecting the nature of the surrounding ground cover of pasture and recreational grassland; higher scores were associated with marginal shrubs and trees. Bank tops were affected by few human pressures, but notably higher (4, 6) at two roadside terrestrial sites (Fig. S2a–b). Channel reinforcement only affected one site (Fig. S2c).

Surface water dissolved oxygen concentrations varied between 9.4 and 11.4 mg/L, water temperature ranged from 10.0 to 11.6°C, and pH varied between 7.5 and 7.9 (Table S2). Mean discharge increased from upstream to downstream, from 0.061 m^3/s at the upstream intermittent site to 0.585 m^3/s at the downstream perennial site. Depth was lower at intermittent (0.13 ± 0.04 m) and long flowing sites (0.15 ± 0.01 m) compared to perennial sites (0.40 ± 0.01 m), whereas flow velocity was relatively high (0.53 ± 0.03 m/s) at all sites except the upstream intermittent site (0.17 m/s; Table S2).

Invertebrate community responses to flow permanence and drying

Benthic invertebrate communities

In total, 10 115 individuals from 80 taxa were collected in kick samples from six sites, including a total of 62, 43 and 30 taxa at perennial, long flowing and intermittent sites, respectively (Table S3). *Gammarus pulex* (Gammaridae: Amphipoda), Limnephilidae (Trichoptera), Oligochaeta, *Serratella ignita* (Ephemerellidae: Ephemeroptera) and *Hydroptila* (Hydroptilidae: Trichoptera) dominated, accounting for 27, 13, 9, 9 and 7% of all individuals, respectively. Most dominant taxa were widespread, but *S. ignita* was absent from the upstream intermittent site and *Hydroptila* only occurred at long flowing sites and the upstream perennial site. Community composition was comparable among all flow permanence regimes (PERMANOVA, P = 0.067; Fig. 2).

Taxa richness was higher at perennial (mean 46.0 ± 2.0 taxa/sample) compared to intermittent sites (24.5 ± 1.5 taxa/sample; Tukey test, P = 0.023), whereas long flowing sites had statistically comparable richness (34.0 ± 4 taxa/sample) to both perennial (46.0 ± 2 taxa/sample, P = 0.103) and intermittent sites (24.5 ± 1.5 taxa/sample, P = 0.173; Fig. 3a). Abundance did not differ significantly among flow permanence regimes, but varied between 1000 ± 124 individuals/sample at long flowing sites and 3016 ± 1050 individuals/sample at perennial sites (one-way ANOVA, $F_{2, 3}$ = 3.51, P = 0.164; Fig. 3b).

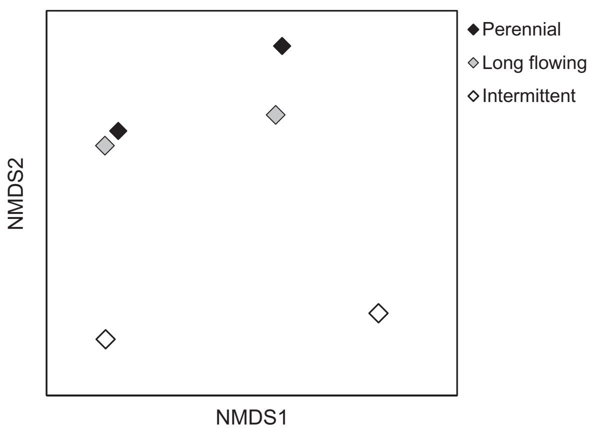

Fig. 2. Non-metric multidimensional scaling (NMDS) of benthic invertebrate community composition in relation to flow permanence regimes.

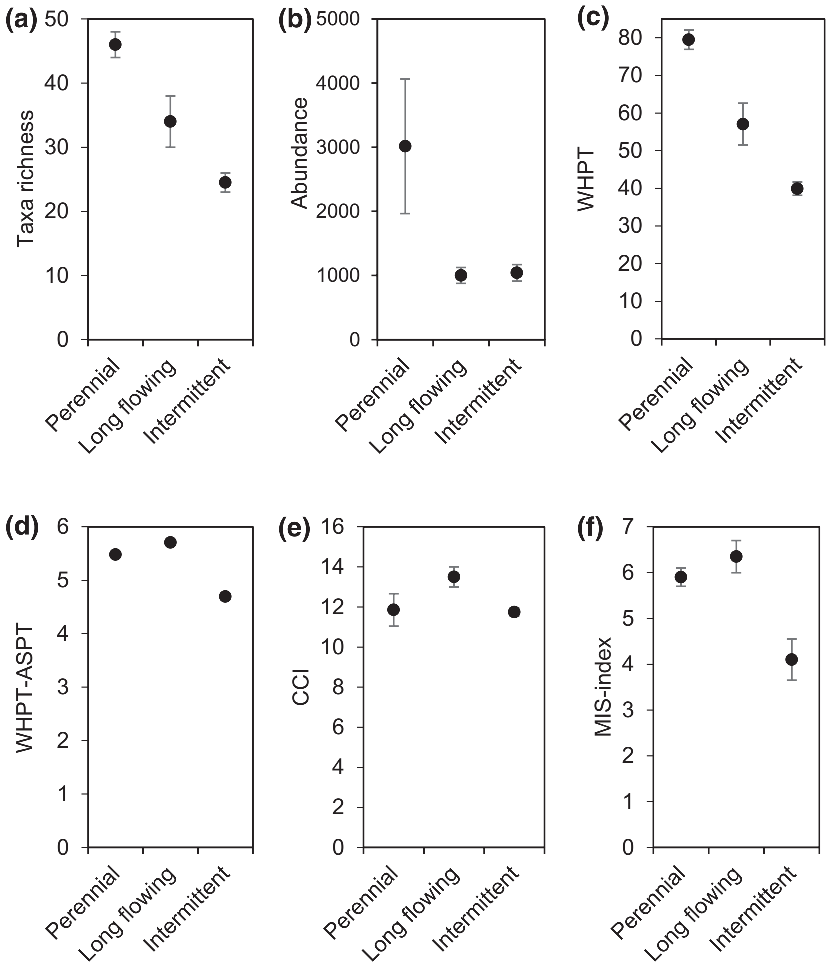

Fig. 3. Mean ± 1 SE benthic invertebrate community metrics at sites with perennial, long flowing and intermittent flow permanence regimes: (a) taxa richness, (b) abundance, (c) WHPT, (d) WHPT-ASPT, (e) CCI, (f) MIS-index. Abbreviations are defined in the text.

WHPT declined with flow permanence, from perennial (79.5 ± 2.6), to long flowing (57.1 ± 5.6), to intermittent sites (39.9 ± 1.8); differences between perennial and both long flowing (Tukey test, P = 0.046) and intermittent (P = 0.010) sites were significant, whereas the two temporary regimes were comparable (P = 0.091; Fig. 3c). WHPT-ASPT scores were comparable at perennial and long flowing sites (Tukey test, P = 0.053; Fig. 3d), but values were lower at intermittent (4.70 ± 0.07) than at long flowing (5.71 ± 0.02) and perennial (5.48 ± 0.01) sites (P = 0.001 and P = 0.002, respectively). CCI scores were comparable at perennial (11.9 ± 0.8), long flowing (13.5 ± 0.5) and intermittent sites (11.7 ± 0.2; one-way ANOVA, $F_{2, 3}$ = 3.051, P = 0.189; Fig. 3e). The MIS-index was also comparable among flow permanence regimes, ranging between 6.4 ± 0.35 at long flowing sites and 4.1 ± 0.45 at intermittent sites (one-way ANOVA, $F_{2, 3}$ = 8.635, P = 0.057; Fig. 3f).

Hyporheic invertebrate communities

In total, 143 invertebrates from 21 taxa were collected in five hyporheic samples, each comprising four replicates (Table S4); clogging by fine sediments prevented sample collection at the upstream long flowing site. A total of 17, 6 and 9 taxa were recorded at perennial, long flowing and intermittent sites, respectively. Oligochaeta, *G. pulex*, Chironomidae and Ceratopogonidae (Diptera), Limnephilidae, *S. ignita* and *Caenis luctuosa/macrura* accounted for 37, 16, 8, 7, 6, 5 and 4% of all individuals, respectively. These dominant taxa occurred in all samples, except for *C. luctuosa/macrura* which was recorded only at the downstream perennial site.

Despite separation on the NMDS ordination (Fig. 4), community composition was statistically comparable between perennial and temporary (long flowing and intermittent) flow permanence regimes (PERMANOVA, P = 0.100). Taxa richness was also comparable among regimes, but varied between 6.7 ± 1.2 taxa/sample at temporary sites up to 11.5 ± 0.5 taxa/sample at perennial sites (one-way ANOVA, $F_{2,3}$ = 9.18, P = 0.056; Fig. 5a). Abundance was lower at temporary sites (18.0 ± 4.4 individuals/sample) than at perennial sites (44.5 ± 4.5 individuals/sample; $F_{2,3}$ = 16.36, P = 0.027; Fig. 5b).

Terrestrial invertebrate communities

In summer, taxa richness in ground searches (11.4 ± 2.5 taxa/site; Table S5) and 24-hour pitfall traps (17.7 ± 3.7; Table S6) was lower than in 7-day pitfall traps (39.2 ± 1.1; Table S7; Tukey tests, both P < 0.001). Forty taxa were sampled by at least two methods, and 4, 7 and 49 taxa occurred only in 24-hour traps, ground searches and 7-day traps, respectively. Abundance was also higher in 7-day pitfall traps (815 ± 134 individuals/site) than in 24-hour traps (203 ± 128) and ground searches (30 ± 9; both P < 0.005). Community composition was comparable between sampling methods (PERMANOVA, P = 0.078). We therefore used only 7-day pitfall traps for autumn sampling (Table S8), and present results from both seasons below.

In total, 7209 invertebrates from 120 taxa were collected in 10 7-day samples (each comprising eight pitfall traps) collected from five sites in two seasons. A total of 48, 54 and 36 taxa were recorded from short-dry, medium-dry and long-dry sites in summer, with 29, 53 and 20 taxa sampled in these categories in autumn, and 63, 84 and 42 taxa per category in total. The dominant taxon was Collembola, accounting for 33% of all invertebrates, followed by Coleoptera (17%), Hymenoptera (14%), Diptera (13%), Araneae (9%) and Trombidiformes (5%). These major taxa occurred in all samples, except Hymenoptera and Diplopoda, which were absent from short-dry sites in autumn.

Taxa richness was statistically comparable between dry period durations (Fig. 6a,d; one-way ANOVA, $F_{2,3}$ = 1.30, P = 0.330), although values were moderately higher at medium-dry sites (39.0 ± 1.0 taxa/sample) compared to other sites (31.3 ± 6.5 taxa/sample). Abundance was also comparable among durations (Fig. 6b,e; $F_{2,3}$ = 3.98, P = 0.070), being moderately lower at short-dry sites (459 ± 39 individuals/sample) and most variable at medium-dry sites (982 ± 156 individuals/sample). Community composition differed between summer and autumn (Fig. 7; PERMANOVA, P = 0.027) and among dry period durations (PERMANOVA, P = 0.013).

Taxonomic differences among dry period durations were observed. For example, isopods were not recorded at short-dry sites, whereas 127 individuals from at least 6 species occurred at the long-dry site, and the carabid genus *Bembidion* was absent from the long-dry site, whereas 22 individuals from 5 species occurred across short-dry sites in summer (Tables S6–7). SQI scores were comparable among dry period durations (one-way ANOVA, $F_{2,3}$ = 0.15,

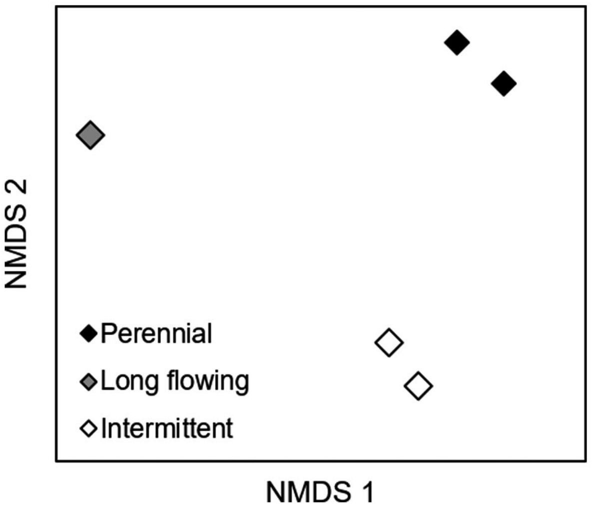

Fig. 4. Non-metric multidimensional scaling (NMDS) of hyporheic invertebrate community composition in relation to flow permanence regimes.

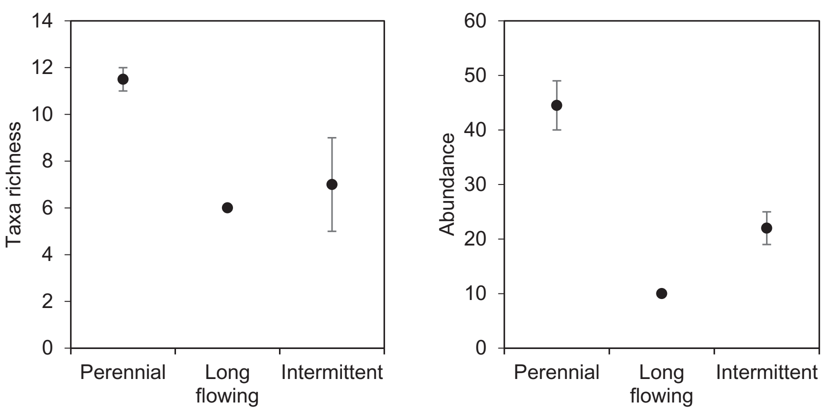

Fig. 5. Mean ± 1 SE hyporheic invertebrate community metrics at sites with perennial, long flowing and intermittent flow permanence regimes: (a) taxa richness, (b) abundance.

P = 0.861; Fig. 6c,f). Site-specific scores ranged between 100 and 153, with the higher value representing a medium-dry site in summer, at which *Badister unipustulatus* (nationally scarce) and *B. peltatus* (nationally rare) were recorded alongside 19 common species (Table S7).

Discussion

Our characterisation of invertebrates on a single temporary stream demonstrates the contribution that both aquatic and terrestrial communities make to total biodiversity in dynamic ecosystems. These biodiversity contributions were enhanced by both aquatic and terrestrial species of conservation concern.

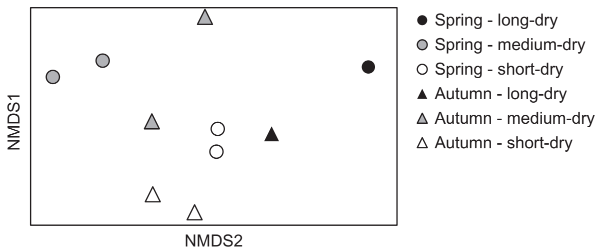

Fig. 6. Mean ± 1 SE (a, d) taxa richness, (b, e) abundance, (c, f) Species Quality Index (SQI) of terrestrial invertebrate communities at sites with different dry period durations in summer (a–c) and autumn (d–f).

Aquatic invertebrate community responses to flow permanence

Despite comparable composition across sites (which likely reflected our limited replication), the taxonomic richness of benthic communities was higher at perennial sites compared to intermittent sites, whereas richness was comparable between samples from long flowing and both other permanence categories. Taxa restricted to perennial sites included the limnephilid caddisflies *Anabolia nervosa*, *Glyphotaelius pellucidus* and *Halesus*, and the mayflies *C. luctuosa/macrura* and Heptageniidae, all of which are associated with flowing waters (Extence *et al*., 1999). Similarly, the taxonomic richness of hyporheic communities was moderately higher at perennial compared to temporary sites, and included *C. luctuosa/macrura* and the caddisflies *Agapetus fuscipes* (Glossosomatidae) and *Odontocerum*

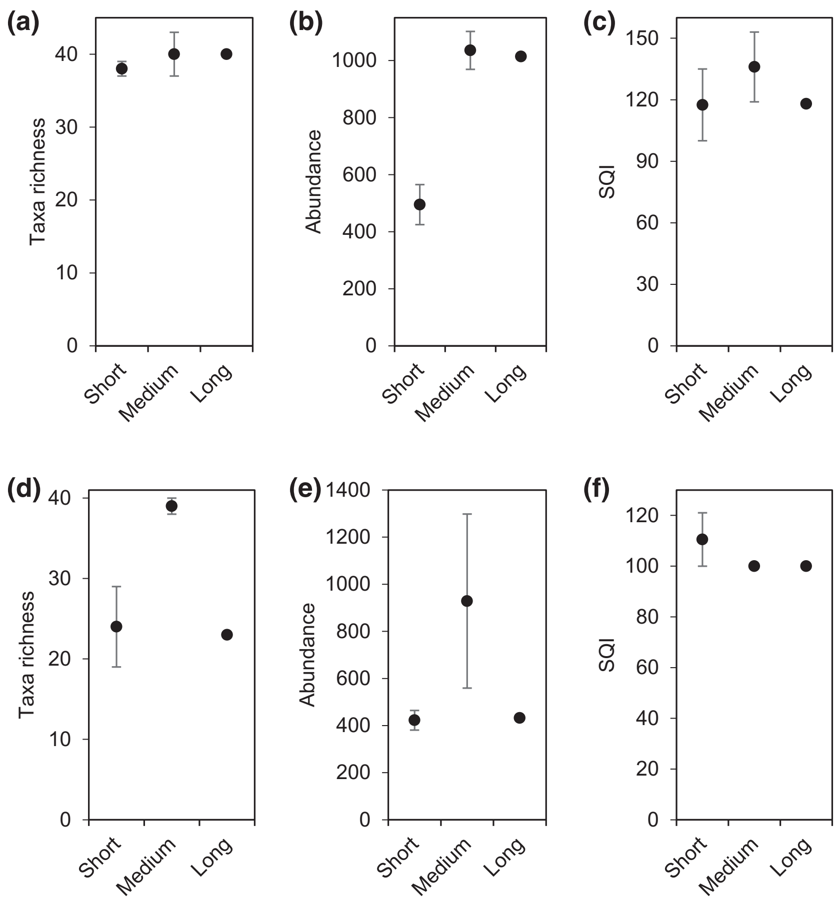

Fig. 7. Non-metric multidimensional scaling (NMDS) of terrestrial invertebrate community composition in relation to season and dry period duration.

albicorne (Odontoceridae). Such results agree with previous research indicating that the absence of sensitive lotic species reduces aquatic invertebrate richness in non-perennial streams (Datry *et al*., 2014) including chalk streams (White *et al*., 2018).

Despite lower total richness, winterbourne sites supported rare taxa that were absent from perennial sites. We recorded 22 juveniles of the stonefly *Nemoura lacustris* (Nemouridae), adding to recent reports from south England (Hammett, 2012; Armitage and Bass, 2013; Tapia *et al*., 2018). We recorded *N. lacustris* across all four winterbourne sites and none at perennial sites, supporting description of this species as a temporary stream specialist. 'Seedbanks' of desiccation-tolerant invertebrate life stages can support a high proportion of flowing-phase taxa in cool, humid regions (Stubbington and Datry, 2013; Stubbington *et al*., 2016b) and *N. lacustris* deposits eggs that remain dormant in 'dry' sediments then hatch in water after exposure to low temperatures in winter (Tapia *et al*., 2018). We recorded active *N. lacustris* in riffle/run habitats with gravel-dominated substrates and abundant vegetation including the emergent grass *Phalaris arundinacea,* from which they can graze biofilms (Tapia *et al*., 2018). Similarly, Armitage and Bass (2013) recorded the taxon at gravel-dominated sites with dense vegetation, indicating its habitat preferences beyond the temporary flow regime that enables egg dormancy and thus, lifecycle completion.

Other species restricted to temporary sites included 15 Leptophlebiidae (Ephemeroptera) juveniles across both long flowing sites. We identified several as *Paraleptophlebia* but specimens lacked the species-level identification features that distinguish the widespread *P. submarginata* from *P. werneri,* a nationally scarce specialist associated with temporary streams including winterbournes (Macadam, 2016); further surveys are needed to fully document its UK distribution. We also recorded 275 Simuliidae (Diptera) larvae across three temporary sites. Species-level simuliid identification is again needed to determine the group's diversity and the distribution of *Metacnephia amphora*, which is known from few UK sites and is associated with winterbournes (Ladle and Bass, 1975; Armitage and Bass, 2013). Such specialists contribute to the conservation status of temporary stream communities, and our few replicates and coarse identification level likely contributed to comparable CCI (Chadd and Extence, 2004) values across sites with contrasting flow permanence regimes.

Despite moderately lower taxa richness, significantly lower abundance, restriction of 10 taxa to either temporary or perennial sites, and clear separation on the NMDS ordination, hyporheic communities were statistically comparable among flow permanence regimes, likely due to low replication. All hyporheic taxa were also present in benthic samples, and no taxa of conservation interest were recorded in subsurface sediments. We thus found no evidence that the relative stability of the subsurface sediments promotes inhabitation by more diverse, abundant invertebrate assemblages across perennial and temporary sites compared to those in benthic sediments. Vertical migrations into deeper sediments may be triggered by surface water loss, and differences between benthic and hyporheic assemblages may therefore be more pronounced after drying (Stubbington, 2012). However, dry phases may present logistic challenges that impede hyporheic sampling, as discussed below.

Terrestrial invertebrate community responses to flow permanence

We recorded 120 terrestrial invertebrate taxa in 10 aggregated samples taken from five sites on one stream, which had dried between 2 weeks and over 3 years earlier. Ours is a considerable underestimate of taxonomic richness, because we focused on beetles (in particular the Carabidae) due to their known diversity, and thus, potential as indicators of ecological quality (Boscaini *et al*., 2000; Stubbington *et al*., 2019b). For example, Corti and Datry (2016) recorded 44 species in 13 spider families (which we identified as Araneae) and 18 genera/species in the ant family Formicidae (which we identified as Hymenoptera), in the dry channel of an alluvial gravel-bed river in temperate France. We are not aware of published research exploring terrestrial invertebrates in UK dry channels, except for the qualitative observations of Moon (1956), also from one chalk stream. More surveys are needed to better characterise the terrestrial biodiversity of these habitats.

We recorded 97 beetle taxa, including 47 Carabidae, 24 Staphylinidae and 7 Dytiscidae. The numeric dominance of carabids and staphylinids in dry channels is typical across regions (e.g. McCluney and Sabo, 2012; Corti *et al*., 2013; Rosado *et al*., 2015; see Stubbington *et al*., 2019a). Such highly mobile taxa may colonise channels as waters recede, extending their range from marginal and riparian habitats to exploit newly available resources, including stranded aquatic organisms (Stehr and Branson, 1938). Accordingly, of 53 adult beetles assigned to feeding guilds, 49 were predators. We also recorded *Drilus flavescens* (Drilidae), which is associated with calcareous substrates, and four saprophagous species including *Heterocerus fenestratus* (Heteroceridae), which Moon (1956) also recorded in a dry chalk stream. These mobile, adaptable opportunists may also colonise dry channels to exploit resources including dead aquatic invertebrates (Mascagni, 2014). However, among-site taxonomic variability including the absence of the species-rich carabid genus *Bembidion* from the long-dry site, a grass-dominated roadside channel, indicates that this opportunism is tempered by habitat characteristics.

Of the 47 recorded carabids, 14 are associated with drawdown zones (Table S9), and two (*Badister unipustulatus, Pterostichus anthracinus*) – along with two staphylinids (*Lathrobium fovulum, L. impressum*) – are indicative of the 'undisturbed fluctuating marsh' assemblage type associated with UK floodplains and drawdown zones (Webb *et al*., 2018a). Collectively, these four species indicate favourable condition of protected habitats, highlighting the potential conservation interest of dry channel habitats. We also identified four nationally rare or scarce species: *Amara montivaga, B. unipustulatus*, *B. peltatus* and *P. anthracinus* (Carabidae), and one recently downgraded from nationally scarce, *D. flavescens* (Drilidae; Telfer, 2016). Like *B. unipustulatus* and *P. anthracinus*, *B. peltatus* is associated with drawdown zones. In contrast, *A. montivaga* occurs in chalk-substrate terrestrial habitats (Davis and Jones, 1978), and is characteristic of a 'bare sand and chalk' assemblage associated with early successional habitats, and thus, supported by natural disturbances such as stream drying (Webb *et al*., 2018a). We also recorded *Bembidion decorum* and *B. dentellum*, both specialists of exposed riverine sediments (Eyre and Luff, 2002). Our observations indicate that these species also colonise other habitats in riverine networks by adult flight (Niemelä and Spence, 1999; Ulyshen *et al*., 2005). Their persistence in fluctuating wet-dry habitats may be enabled by submersion tolerance (Adis and Junk, 2002).

Aquatic invertebrate community characterisation

Total WHPT scores increased with flow permanence in association with increasing taxa richness, whereas WHPT-ASPT scores were comparable at perennial and long flowing sites and lower at intermittent sites. The relative stability of ASPT scores indicates this index as potentially appropriate to assess the ecological quality of winterbourne reaches (Wilding *et al*., 2018). Adaptations to enhance index performance could include the exclusion of lotic specialists that are absent from temporary sites regardless of their ecological quality, and timing of surveys to allow enough time for recolonisation after flow resumes (Stubbington *et al*., 2018). Our temporary sites had been flowing for >7 weeks; further research is needed to characterise how communities, and thus, index values change over time following flow onset and to determine the minimum period before aquatic communities become effective biomonitors (Prat *et al*., 2014). The period may differ depending on the spatial arrangement of temporary and perennial reaches, and communities in winterbourne headwaters may need longer to recover due to an absence of upstream waters that enable rapid colonisation by drift (Wilding *et al*., 2018; Crabot *et al*., 2019). Indices designed specifically for temporary streams may complement standard metrics to enable assessment of instream habitat variability (England *et al*., 2019). For example, the statistical comparability of MIS-index values at temporary and perennial sites likely reflects our few replicates, and we recommend further testing to establish the utility of this new index across temporary stream types.

Despite their suggested potential as biomonitors of ecological health that persist after benthic communities are lost (Leigh *et al*., 2013), we were unable to sample hyporheic assemblages during dry phases. Where drying clogged the bed sediments, standpipe insertion was hampered; where standpipes *were* installed, the water table was below the sampling depth and suction forces could not be generated despite priming the apparatus with water. Hyporheic sample collection following surface water loss may thus be limited to saturated, permeable sediments.

Terrestrial invertebrate community characterisation

Fewer taxa were collected during summer ground searches compared to 7-day pitfall traps, for example, 13 compared to 38 carabid species, 2 compared to 14 staphylinid species and one compared to seven woodlouse species. Equally, a few taxa were only sampled by ground searches, notably soldier beetles (Cantharidae: Coleoptera) and *Chrysolina* (Chrysomelidae: Coleoptera). These taxa occurred at low abundance (≤5 individuals) and their absence from pitfall traps may reflect their tendency to fly rather than crawl (Alexander, 2014). Although ground searches favour capture of such taxa and also have logistic advantages over pitfall traps, low overall taxa richness may limit their effective characterisation of assemblage responses to environmental drivers. Biodiversity estimates are likely to be maximised by sampling strategies that encompass both methods.

Taxa richness and abundance were moderately higher in early summer than autumn, and although abundance was relatively low at short-dry sites in both seasons, the smallest sample contained 381 individuals. Terrestrial invertebrates thus colonise channels quickly enough to enable surveys within 2 weeks of drying. Comparable major taxa were captured in both seasons, but there were considerable seasonal differences within groups. For example, of 47 carabids, 22 species were recorded only in summer, 8 only in autumn, and 17 occurred in both seasons. For other taxa, seasonal subsets were recorded; for example, all three isopods recorded in autumn were among seven sampled in summer. Equally, several infrequent taxa occurred only in autumn, including *D. flavescens* and *H. fenestratus*. The coincident seasonal activity of families across most major taxa may make spring/summer an appropriate survey season for dry channels, as for other habitats (Natural England, 2007).

However, sampling across multiple seasons enables the capture of rare taxa, and thus, more comprehensive assemblage characterisation. In addition, adapting habitat survey methods (e.g. MoRPh) to better represent dry channel features (including terrestrial plant morphotypes) could inform future research into the environmental drivers of terrestrial community composition.

Conclusions

(1) Both wet and dry channels supported invertebrate communities that contributed to temporary stream biodiversity, with 54 aquatic and 120 terrestrial taxa recorded, some of which were identified only to order.

(2) Species of conservation interest occurred in both wet and dry channels, including two nationally rare specialists: aquatic juveniles of the stonefly *Nemoura lacustris* and terrestrial *Badister peltatus* ground beetles.

(3) Of the methods tested, kick sampling and 7-day pitfall trapping in summer were most effective in characterising aquatic and terrestrial invertebrate assemblages, respectively.

(4) The wide range of environmental preferences of invertebrate taxa in both aquatic and terrestrial assemblages indicates their potential as biomonitors of ecological quality, warranting further research to characterise assemblage responses to specific environmental drivers.

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Data availability statement

The data that support the findings of this study are openly available as Supporting Information.

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