

RESEARCH ARTICLE

WILEY

Spring forth diversity: Specialist species contribute to the conservation value of headwater springs and streams at the landscape scale

Jamal Kabir^{1,2}  | Giulio Biondi^{1,3}  | Kieran J. Gething¹  | Thomas Aspin⁴  |
Tim Sykes⁴  | Rachel Stubbington¹ 

¹School of Science and Technology,
Nottingham Trent University, Nottingham, UK

²School of Biosciences, University of
Nottingham, Nottingham, UK

³Centre for Conservation and Restoration
Science (CCRS), Edinburgh Napier University,
Edinburgh, UK

⁴Environment Agency, Bristol, UK

Correspondence

Rachel Stubbington, School of Science and
Technology, Nottingham Trent University,
Nottingham, UK.

Email: rachel.stubbington@ntu.ac.uk

Abstract

Headwater springs and streams often occur in relatively remote areas, reducing their exposure to human influences and thus increasing their collective capacity to support high biodiversity. Their aquatic macroinvertebrate communities can include species of conservation interest, some of which are specialists associated with groundwater inputs, low water temperature or temporary flow. However, the inaccessibility of some spring and stream networks has left their communities poorly characterized, limiting our capacity to implement effective conservation strategies. We characterized the biodiversity and conservation value of macroinvertebrate communities in a network of 51 relatively inaccessible and unimpacted headwater spring and stream sites spanning multiple catchments in a single landscape type: the chalk downland of south England. At each site, we kick sampled macroinvertebrate communities and recorded environmental variables, including flow permanence. To represent each community, we calculated taxa richness, coverage-adjusted Hill-Shannon diversity, the local contribution to beta diversity, and an index of richness and species rarity. We used the latter three metrics to rank sites based on their biodiversity and conservation value and analyzed relationships between metrics and environmental variables. We found specialists of springs, cold waters, groundwaters and temporary flow regimes, including rare species of conservation value. Some metrics responded to environmental variables, but top-ranking sites had highly variable environmental characteristics. We highlight the value of individual headwater streams with contrasting characteristics as contributors to ecologically heterogeneous site networks. Our results can inform landscape-scale management strategies that protect headwaters as refuges that support biodiverse communities, including rare species, as they adapt to global change.

KEYWORDS

flow permanence, freshwater spring, headwater spring, headwater stream, landscape-scale conservation, macroinvertebrate, winterbourne

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2024 The Authors. *River Research and Applications* published by John Wiley & Sons Ltd.

1 | INTRODUCTION

Headwater springs and streams are widespread, abundant freshwater ecosystems that are often hidden in the most remote and inaccessible parts of river networks (Meyer et al., 2007). Groundwater-dominated headwaters are thermally stable but can be hydrologically variable, and include perennial and temporary streams, the latter encompassing a range of non-perennial flow permanence regimes, including seasonally intermittent streams with summer dry phases (Stubbington et al., 2017). In addition to their hydrological heterogeneity, the relative isolation of individual headwater sites promotes variability in environmental parameters including shade, flow velocity, sediment composition and instream woody material (Sponseller et al., 2008; Wallace et al., 1996; Wood et al., 2005). Human influences including land-use pressures introduce further variability among sites. However, their relative inaccessibility and scattered locations have limited cross-catchment and landscape-scale characterization of headwaters.

Although the local-scale biodiversity (i.e., alpha diversity) of headwater springs and streams can be lower than in larger rivers of equivalent condition for groups, including aquatic macroinvertebrates (Clarke et al., 2008; Minshall et al., 1985), their isolation and environmental variability allow headwaters to collectively support high landscape-scale biodiversity (i.e., beta diversity; Finn et al., 2011). In groundwater-fed headwater springs, biodiversity is enhanced by specialist invertebrate species, including crenobionts, stygobionts and cold stenotherms (i.e., spring, groundwater and cold-water specialists, respectively; Durance & Ormerod, 2010; Maurice et al., 2016). In addition, headwaters with contrasting flow permanence regimes are inhabited by different macroinvertebrate communities: perennial reaches typically have higher alpha diversity and support drying-sensitive rheophilic species, whereas reaches with temporary flow often have higher beta diversity and support drying-tolerant specialists (Stubbington et al., 2017). Many crenobionts, stygobionts, cold stenotherms and temporary-stream specialists are rare and/or threatened and thus of conservation interest (Chadd & Extence, 2004; Deharvent et al., 2009; Macadam et al., 2021), enhancing the biodiversity of groundwater-fed springs and streams. However, the biodiversity and conservation value of small waterbodies, including temporary headwaters, has only recently been recognized (Biggs et al., 2017; Stubbington et al., 2017), and the contributions of perennial and temporary sites to landscape-scale biodiversity remain unclear.

Biodiversity is routinely quantified using metrics that describe taxonomic diversity and/or species rarity (Humphries et al., 1995). Alpha diversity is typically measured as taxonomic richness, but metrics that are less influenced by rare species occurrence and sample completeness, such as coverage-adjusted Hill–Shannon (HS) diversity, provide a more robust measure where many species occur at low abundance (as in some headwaters) or when semi-quantitative sampling methods (such as kick sampling) are used (Aspin & House, 2022; Roswell et al., 2021). Complementing such richness-based metrics, indices including the macroinvertebrate-based Community Conservation Index (CCI) (Chadd & Extence, 2004) combine richness and

species rarity information to describe a community's conservation value. Such indices can recognize sites of high conservation value due to the occurrence of rare and threatened species, regardless of their taxonomic richness (Meyer et al., 2007). Establishing local contributions to beta diversity can also identify sites of conservation interest by quantifying a community's compositional uniqueness relative to regional biodiversity (Legendre & De Cáceres, 2013; Ruhí et al., 2017). Collectively, such metrics can identify site-specific management priorities for headwaters within a landscape context.

In densely populated countries such as those spanning western Europe, landscapes relatively undisturbed by humans typically have correspondingly high conservation value. In the UK, the 'downland' overlying the chalk aquifer of southern England is a distinctive landscape recognized for its ecological value (SDNPA, 2023). Watercourses emerging from the chalk aquifer in this landscape include both perennial and 'winterbourne' headwater streams, the latter shifting between wet and dry in-channel conditions in response to seasonal fluctuations in groundwater levels (Berrie, 1992). Although the macroinvertebrate communities of low-gradient, winterbourne headwaters of major chalk rivers have been characterized (e.g., Sarremejane et al., 2020; White et al., 2018; Wood & Petts, 1999; Wright, 1992), the biodiversity within the extensive, but relatively inaccessible springs and streams emerging from the steep slope of the chalk escarpment remains unknown. Such landscape-scale site networks represent an opportunity to investigate how site-specific environmental characteristics, including flow permanence, influence headwater biodiversity.

Our aim was to characterize the biodiversity and conservation value of a network of relatively inaccessible and unimpacted headwater springs and streams spanning multiple catchments in a single landscape type: the chalk downland of south England. We quantified the biodiversity and conservation value of each site based on metrics describing aquatic macroinvertebrate communities. We related variability in community metrics to physical habitat characteristics, including comparison of sites with perennial and temporary flow. We ranked each site's biodiversity and conservation value and examined environmental characteristics in relation to site ranking. Our ultimate aim is to inform landscape-scale management strategies and conservation actions that support biodiversity within ecologically diverse networks of headwater springs and streams.

2 | METHODS

2.1 | Study area

Our study included areas characterized by surface exposure of chalk (CaCO_3 , a finely powdered limestone) bedrock in and near the South Downs National Park, in south England (UK). The South Downs are designated and managed for multiple uses including recreation and nature conservation, although arable and pastoral agriculture are the dominant land uses. The underlying chalk bedrock forms a steep, north-facing escarpment that spans 75 km from east to west

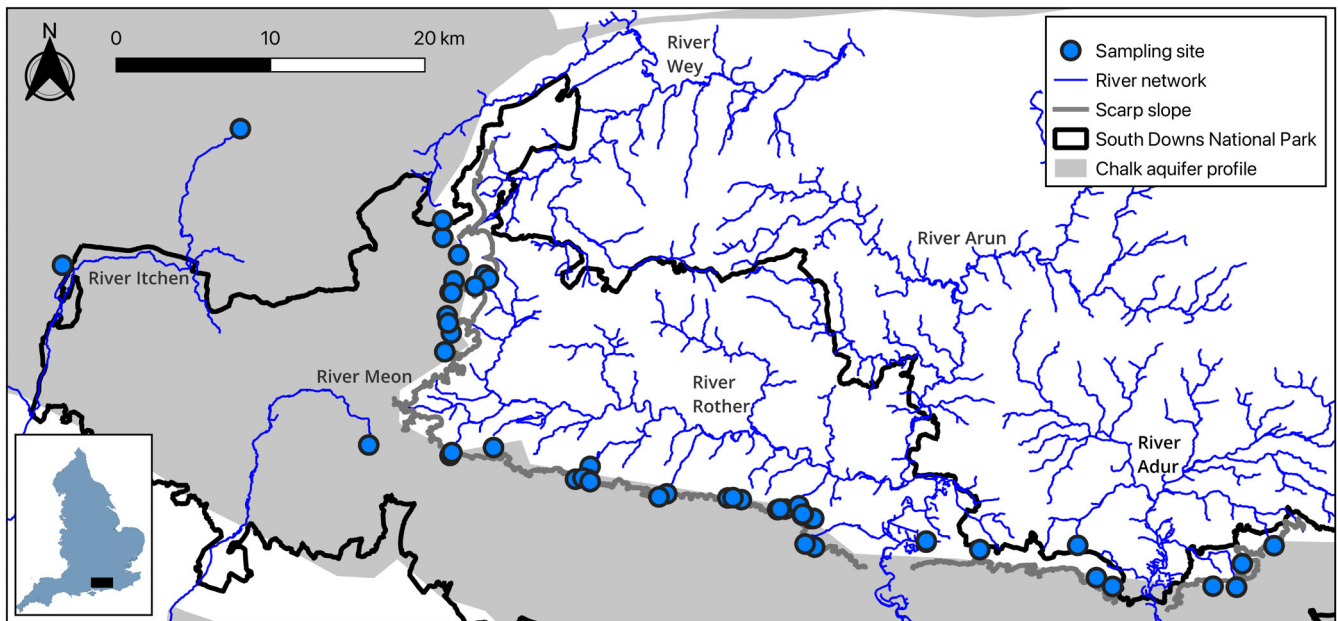


FIGURE 1 Map showing the 51 sites in the study area and its location within England. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/rpa.4275)]

(Figure 1). Here, the relatively impermeable rock beneath the chalk causes groundwater to emerge at the escarpment's base, creating a series of springs that flow into headwater streams. Along this 'spring line', we collected 54 samples from the Adur (6 samples), Arun (7), Itchen (3), Meon (1), Rother (34) and Wey (3) catchments (Figure 1). The highly variable number of samples per catchment prevented analysis of among-catchment variability but did not compromise our landscape-scale characterization of headwater biodiversity.

We sampled one site per stream as close to the source as possible, except on two streams where we sampled 2–4 springs per stream. For logistic reasons, we collected samples in two seasons in 2021: 12 samples in spring (March–June) and 42 in autumn (October–November). Forty-eight sites were sampled once, two sites were sampled in both seasons and one site was sampled in early and late spring; these temporal replicates were retained because preliminary analyses of spring-only, autumn-only or all samples consistently produced comparable results. We collected 38 samples <5 m from the stream source and 10 samples 5 to 200 m (mean \pm SD 7.02 ± 19.87 m) from the source, with these distances reflecting restrictions imposed by land ownership or terrain; distance from the source was unknown for the remaining six samples.

2.2 | Field sampling and macroinvertebrate identification

At each site on each date, we collected a 1-min kick sample of benthic macroinvertebrates (500- μ m-mesh net), with each habitat type sampled in proportion to its occurrence. Each kick sample was supplemented with a 1-min hand search of large grains within the sampling area (Murray-Bligh & Griffiths, 2022). Although 1 min is a shorter duration

than used in regulatory biomonitoring, it is sufficient to characterize macroinvertebrate community responses to environmental variability in small streams (e.g., Lytle & Peckarsky, 2001). Surface water was present at all sites, enabling sample collection. Samples were preserved and transported to the laboratory, where all organisms were identified to the lowest practical taxonomic resolution and the abundance of each taxon was estimated. We identified most organisms to species or species aggregate (e.g., *Gammarus pulex/fossarum*) level, but all Bivalvia, most Diptera (excluding Simuliidae, which were speciated), some Coleoptera, a few Gastropoda and Hirudinea, and early instar insects and damaged specimens were identified to family or genus; and Hydrachnidia and Oligochaeta were recorded as such.

In association with each autumn sample, we took a single measurement of channel width, wetted width, water depth and (due to probe malfunction in spring) water temperature. At all sites, we qualitatively assessed flow permanence, land use, flow velocity, sediment composition, overlying silt, woody material and shade. We classified flow permanence as perennial or temporary using information from landowners and land managers. We categorized the primary (i.e., directly adjacent to the channel) and secondary (further from the channel) land use as broadleaf deciduous woodland, parkland (including gardens), suburban, tilled land, improved pasture, rough pasture or tall herbs/rank vegetation. We combined the latter four land uses as *agriculture* in subsequent analyses, except for one tall herb/rank vegetation site that was analyzed as *woodland*. We recorded the dominant flow velocity as zero (i.e., non-flowing water), low, moderate or fast, with faster flow categories typically reflecting greater hydrological variability, including some slower-velocity habitats. We visually estimated the % of overlying silt and sediment composition, the latter as the % of each major grain size category (i.e., boulders, cobbles, gravel, sand, silt and clay). Sediment composition data were used to calculate

the mean sediment size, where scores range from –8 (equivalent to boulders) to 8 (very fine silt) (Appendix S1; WFD-UKTAG, 2008). We classified the extent of instream woody material as widespread, localized or absent, and recorded shade as heavy, moderate, light or absent.

2.3 | Data analysis

2.3.1 | Macroinvertebrate community composition

All analyses were conducted in R version 4.3.0 (R Core Team, 2023). Before conducting analyses, we assigned taxa identified to multiple levels (e.g., to *Nemoura lacustris*, *Nemoura* and *Nemouridae*) to the single most likely taxon (sensu Cuffney et al., 2007), with 38%, 14% and 48% of taxa assigned to species, genus and family, respectively. This enabled us to maintain the finest taxonomic resolution while avoiding overestimation of richness (Stubbington et al., 2019). Variability in community composition was visualized in relation to flow permanence, primary land use, woody material, flow velocity and shade categories using two-dimensional non-metric multidimensional scaling (NMDS) ordinations, produced in the ‘vegan’ (version 2.6-4, Oksanen et al., 2022) and ‘ggplot2’ (version 3.4.2, Wickham 2016) packages. We calculated ellipses representing the 95% confidence intervals for each category of the NMDS environmental variables using the ‘ordiellipse’ function in ‘vegan’. The influence of environmental variables on community composition was quantified using individual permutational multivariate ANOVA (PERMANOVA; Anderson, 2001) models for each environmental variable, performed on log+1 transformed abundance data based on Bray–Curtis dissimilarity matrices with 999 permutations, using the ‘adonis2’ function in ‘vegan’. To validate the PERMANOVA assumption of comparable compositional variability among levels of the environmental variables, we analyzed the multivariate homogeneity of group dispersions (PERMDISP2; Anderson, 2006) using the ‘betadisper’ function in ‘vegan’.

2.3.2 | Metrics for ranking site conservation value

We quantified alpha diversity using two metrics, taxa richness (the number of taxa per sample, as a widely used and thus easily interpretable metric) and coverage-adjusted HS diversity. HS diversity was calculated using the ‘iNext’ package (version 3.0.0, Hsieh et al., 2016), in which rarefaction and extrapolation were used to standardize all samples to 95% coverage, accounting for differences in taxon detection between samples (Aspin & House, 2022; Roswell et al., 2021).

The conservation value of each community was assessed using the CCI (Chadd & Extence, 2004). We allocated CCI conservation scores from 1 (Very Common) to 10 (Endangered, sensu the British Red Data Books) to species first identified in Great Britain after the publication of Chadd & Extence (2004; i.e., *N. lacustris* [score 7] and *Synagapetus dubitans* [5]) using expert judgment (R. Chadd, pers.

comm.). We used the online database *Pantheon* (Webb et al., 2018) to determine each species' Great Britain Rarity Status.

Local contributions to beta diversity were calculated using the ‘adespatial’ package (version 0.3-16, Dray et al., 2018); scores range from 0 to 1, with higher values indicating higher site-specific contributions to spatial beta diversity (Legendre & De Cáceres, 2013). We used HS diversity (but not taxa richness), CCI and local contribution to beta diversity (LCBD) to rank samples from highest (1) to lowest (54), then calculated the mean rank of the three equally weighted metrics to determine the final ranking representing each sample's relative biodiversity and conservation value.

2.3.3 | Metric responses to environmental characteristics

We used the ‘lme4’ package (version 1.1-33, Bates et al., 2015) to run negative binomial generalized linear mixed-effect models (for richness) and simple linear mixed-effect models (for log+1 transformed HS diversity, CCI and LCBD) to characterize relationships between each metric (response variables) and each predictor: flow permanence, primary land use, secondary land use, flow velocity, mean sediment size, individual sediment %, overlying silt %, woody material and shade. Sites at which flow permanence was unknown were excluded from the relevant models. Sample month was included as a random factor to account for both among-season and within-season variability. We also modeled interactions between primary and secondary land use categories as predictor variables to determine whether secondary land use moderated the effect of primary land use on the metrics (response variables), then characterized the effects of these interactions on mean sediment size (as a response variable).

3 | RESULTS

3.1 | Environmental characteristics of sampling sites

Of our 51 sites, the flow was perennial, temporary and unknown at 26, 21 and 4 sites, respectively. Channel widths ranged from 0.20 to 10 m (mean \pm SD 1.61 \pm 1.65 m). Autumn water temperatures ranged from 8.59 to 14.83°C (11.24 \pm 1.23°C). The dominant primary land use was woodland, agriculture, parkland and suburban at 33, seven, seven and four sites, respectively. The dominant secondary land use was agriculture, woodland, parkland and suburban at 30, nine, eight and four sites, respectively. Overlying silt ranged from 0% at 18 sites to 100% at two sites (32.60 \pm 34.60%). Mean sediment size ranged from –3.25 to 8 Phi (3.35 \pm 3.55, where –3.25 and 8 indicate very coarse gravel and very fine silt, respectively). Flow velocity was high, moderate, low and zero in association with 12, 27, nine and six samples, respectively. Shade was heavy, moderate and light in association with 22, 20 and five samples, respectively, while seven were

unshaded. Woody material was widespread, localized, absent or not recorded in association with 32, 20, one and one sample, respectively.

3.2 | Macroinvertebrate community composition

We identified 17,210 macroinvertebrates from 110 taxa, including 67 identified to species, 11 species aggregates, seven genera, 24 families and two higher taxa, and some taxa identified to multiple levels, for example, species and family. Samples contained 14–1427 (mean \pm SD 319 ± 309) individuals and 2–35 (12.2 ± 6.90) taxa, including 44 taxa represented by 1–3 individuals. The most dominant taxa were the amphipod *G. pulex/fossarum*, the caddisfly *Agapetus fuscipes* and the non-biting midge family Chironomidae, representing 56%, 6% and 6% of all sampled individuals, respectively. These taxa were also the most widespread, occurring in 49, 23 and 37 samples, respectively. Most taxa were insects (75%) and the richest orders were Trichoptera, Diptera and Coleoptera, comprising 24%, 22% and 14% of taxa, respectively. Thirty-three taxa occurred exclusively at perennial sites, including the snails *Gyraulus albus* and *Anisus vortex* and the caddisfly *Drusus annulatus*, while 21 were found only at temporary sites, including the amphipod *Crangonyx pseudogracilis*, the caddisfly *Plectrocnemia geniculata* and the isopod *Proasellus meridianus*.

We identified two species designated as Nationally Rare: the stonefly *N. lacustris* and the caddisfly *S. dubitans*. Seven species had CCI scores of 6 (Regionally Notable: the mayfly *Procloeon bifidum*, the blackfly *Simulium angustitarse* and the amphipod *Niphargus aquilex*) or 7 (Notable: *N. lacustris*, and the amphipods *Niphargus kochianus*, *Niphargus fontanus* and *Crangonyx subterraneus*). *Nemoura lacustris* occurred at four sites, all of which were in woodland and had widespread woody material, and three of which had temporary flow and moderate flow velocity. *Synagapetus dubitans* was recorded at 11 sites, seven of which were perennial and 10 in woodland. *Procloeon bifidum* and *S. angustitarse* were found together at one wooded site with temporary flow. *Niphargus aquilex* was found at three sites with varied environmental characteristics. *Niphargus kochianus* was recorded at one perennial, suburban site with no shade and zero flow. *Niphargus fontanus* occurred at two perennial, woodland sites, one with moderate shade and fast flows and one with heavy shade and moderate velocities. All stygobiont amphipods (i.e., *C. subterraneus* and all *Niphargus* species) were collected at different sites (i.e., no two species co-occurred). *Crangonyx subterraneus* occurred at one temporary, parkland site with heavy shade and zero flow.

We found two cold stenothermic crenobionts: *Crenobia alpina* (Tricladida) and *Crunoecia irrorata* (Trichoptera) occurred in samples with varied environmental characteristics and ranging from 0.2 to 10 m and 0.5 to 12 m from the source, respectively. We also recorded *Simulium costatum* (Diptera; CCI 5, 'Local' i.e., 'of some interest'; Chadd & Extence, 2004) at four sites, two temporary and two perennial, with woodland and suburban land uses, and all with at least moderate flow velocity, moderate shade and some woody material.

Despite NMDS stress values >0.2 (Clarke, 1993), we found no evidence to suggest that macroinvertebrate community composition differed among sites with different flow regimes, primary land uses, flow velocities, shade levels and woody material (Table 1; Figure 2).

3.3 | Metric relationships with environmental variables

Taxa richness ranged from 2 to 35 (mean \pm SD 12.4 ± 6.9) taxa per sample (Figure 3a,b; Figure S1A–C); HS diversity from 1.0 to 12.1 (3.8 ± 2.2 ; Figure 3c,d, Figure S1D–F); and the CCI from 1.0 (at 12 sites, containing only common species) to 25.7 (at one site containing three species which scored CCI 7, 3 and 1, respectively; 7.8 ± 6.4 ; Figure 3e,f; Figure S1G–I). The LCBD ranged from 0.006 to 0.508 (0.02 ± 0.01 ; Figure 3g,h; Figure S1J–L).

Taxa richness, HS diversity, CCI and LCBD were comparable at sites with temporary and perennial flow (Figure 3; Table S1A). LCBD was lower at sites at which the primary land use was woodland compared to agricultural, which may reflect the greater number of woodland sites, while other metrics were comparable at sites with different primary land uses (Table S1B). At sites at which the primary land use was either suburban or woodland and the secondary land use was parkland, taxa richness was higher than at agricultural sites (Table S1B).

Taxa richness increased with mean sediment size, increasing as gravel cover increased and decreasing as silt and clay cover increased (Table S1C,D). HS diversity and LCBD decreased as sand cover increased, while CCI was comparable across sites with varying mean sediment sizes and the % cover of each sediment grain size category (Table S1C,D). Mean sediment size was comparable across all combinations of primary and secondary land use (Table S2).

Taxa richness was higher at sites with fast flow velocities compared to non-flowing sites (Table S1E). In contrast, non-flowing sites had higher LCBD scores than sites with low, moderate or fast velocities (Table S1E). All metrics were comparable at sites with localized and widespread instream woody material (Table S1F). Shading

TABLE 1 Macroinvertebrate community composition responses to site-specific environmental variables, based on permutational multivariate ANOVA.

Environmental variable	Degrees of freedom	F-value	R ²	p
Flow permanence	1, 48	1.26	0.026	0.27
Primary land use	3, 50	1.08	0.026	0.15
Flow velocity	3, 50	0.91	0.071	0.59
Shade	3, 50	0.87	0.050	0.66
Woody material	3, 50	1.03	0.020	0.40

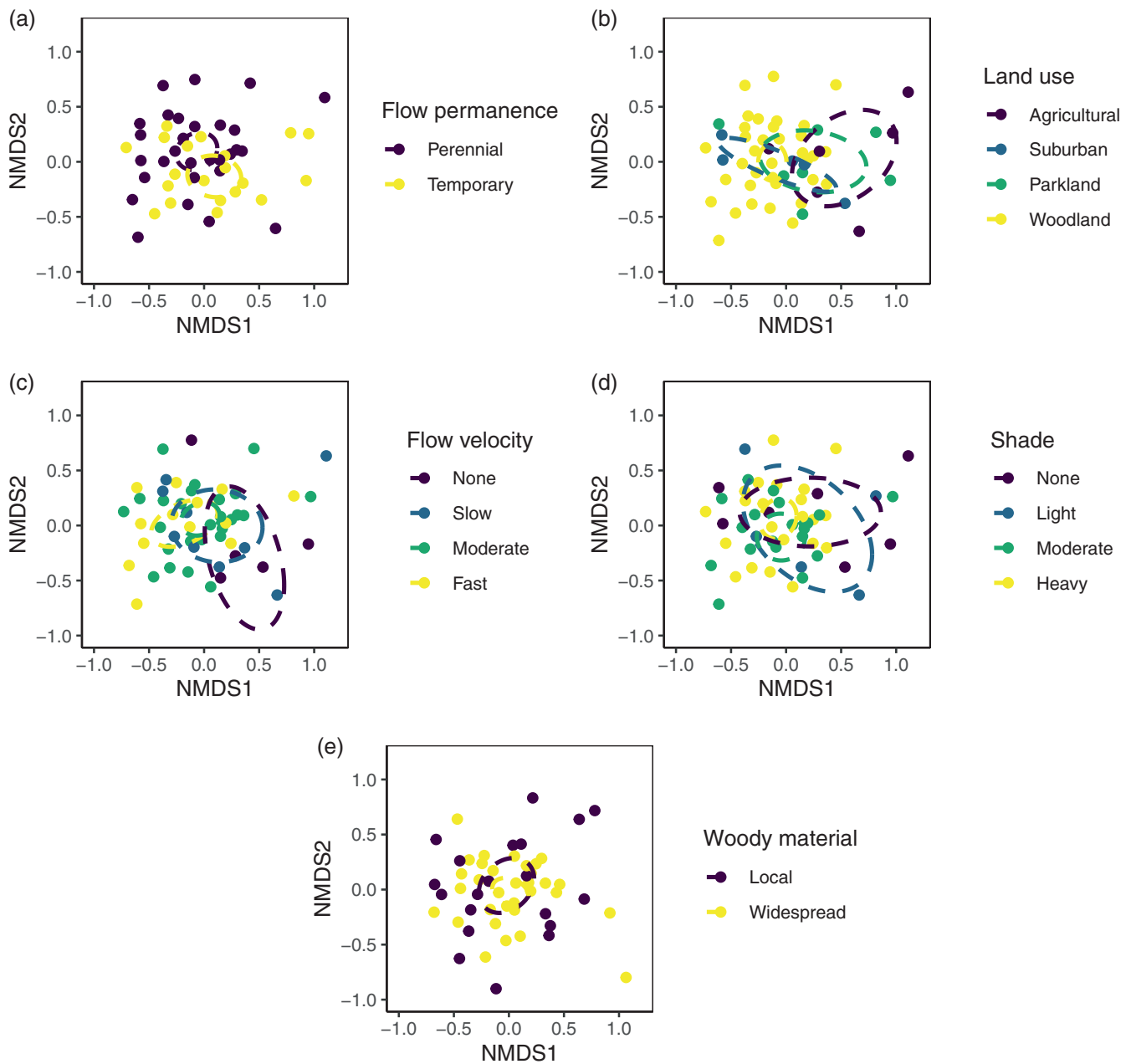


FIGURE 2 Non-metric multidimensional scaling (NMDS) ordination of macroinvertebrate community composition at each site in relation to (a) flow permanence, (b) primary land use, (c) flow velocity, (d) shade and (e) woody material. Dashed ellipses, 95% confidence intervals for each grouping variable. The different positioning of site points in (e) reflects the removal of a site containing no woody material and a site at which this variable was not recorded. [Color figure can be viewed at wileyonlinelibrary.com]

influenced three metrics: LCBD was lower at moderately and heavily shaded sites than at unshaded sites, whereas richness and HS diversity were near-significantly higher at lightly and moderately shaded sites, respectively, than at unshaded sites (Table S1G).

The highest-ranking site (Figure S2; Table S3) ranked 1st in HS diversity, 6th in CCI and 10th in LCBD and contained four of the eight high (6–7) CCI and/or Nationally Rare species (*N. lacustris*, *P. bifidum*, *S. dubitans* and *S. angustitarse*), the highest number in any sample. This site had temporary flow, the primary and secondary land uses were woodland and agriculture, respectively, flow velocity was moderate, shade

levels were heavy and instream woody material was widespread. Samples ranked 2–5 (Figure S2; Table S3) had either temporary or perennial flow (two samples each), primary land use of woodland or agriculture (two and two samples, respectively), secondary land use of agriculture or parkland (three and one samples, respectively), moderate shade levels, flow velocity from moderate to fast and woody material localized or widespread (three and one samples, respectively). The two sites visited in both seasons ranked 6th and 11th in spring and 5th and 47th in autumn, respectively, and the site visited twice in spring ranked 3rd and 19th at the beginning and end of the season.

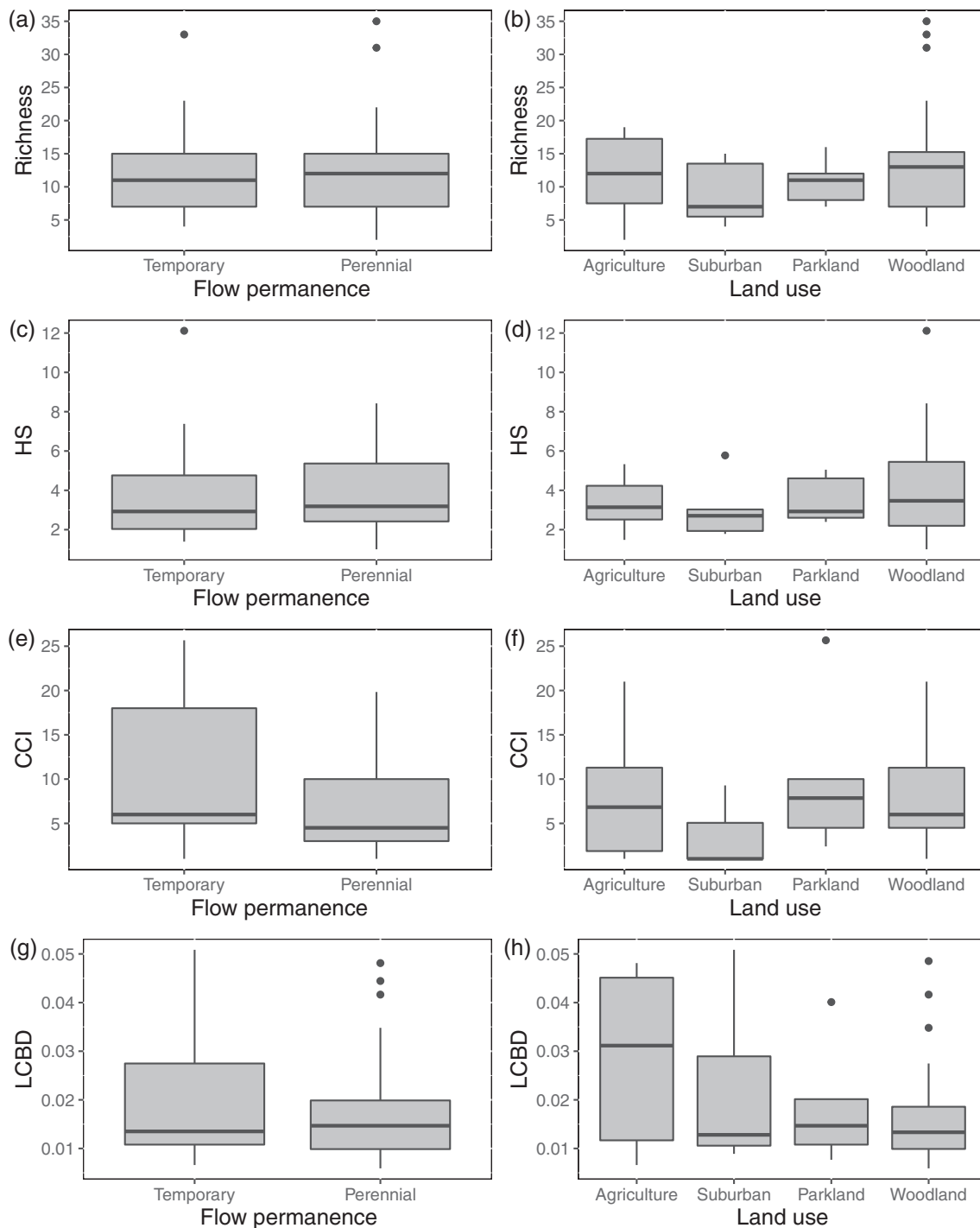


FIGURE 3 Responses of metrics representing macroinvertebrate communities to flow permanence (left column) and land use (right column): (a,b) taxa richness, (c,d) Hill–Shannon diversity (HS), (e,f) the Community Conservation Index (CCI) and (g,h) local contribution to beta diversity (LCBD). Boxes represent the median and interquartile range, and whiskers range from the first and third quartiles to the minimum and maximum values.

4 | DISCUSSION

Our results demonstrate that environmental heterogeneity among headwater springs and streams supports a diverse invertebrate biota including species of conservation interest. Headwater macroinvertebrate communities encompassed a wide range of specialist species

including temporary and perennial-stream specialists, crenobionts, cold stenotherms and stygofauna, reflecting species-specific habitat requirements and thus among-site environmental variability. In contrast to previous research – including that comparing larger, downstream perennial and temporary, winterbourne chalk streams (e.g., Aspin & House, 2022; White et al., 2018) – neither community

composition nor metrics such as taxa richness responded to flow permanence. We attribute this lack of response to the considerable compositional variability both within and among communities at sites with perennial and temporary flow. In turn, this variability was likely driven by the infrequent occurrence of many taxa (Aspin & House, 2022); the geographical isolation of headwaters, which promotes the establishment and maintenance of distinct communities (Finn et al., 2011; Sarremejane et al., 2017); and the recorded habitat heterogeneity. Accordingly, the sites ranked highest for biodiversity and conservation value were environmentally diverse, indicating that networks of sites with contrasting habitat characteristics collectively support species and communities of conservation interest.

4.1 | Environmental heterogeneity supports rare and specialist macroinvertebrates

Rare and specialist species, including eight species classified as Nationally Rare, Notable or Regionally Notable occurred sporadically across our sites. One Nationally Rare species, the temporary-stream specialist stonefly *N. lacustris*, survives dry phases as desiccation-tolerant eggs (Tapia et al., 2018). As is typical, *N. lacustris* was largely confined to sites with temporary flow. Such sites can lack predatory fish and typically support lower densities of generalist, desiccation-sensitive invertebrate predators and competitors (Bogan et al., 2013), enabling desiccation-tolerant specialists to sustain populations (Aspin & House, 2022). In particular, the persistence of *N. lacustris* may depend on long temporary stream sections that exclude the competitive generalist amphipod *G. pulex/fossarum* (Aspin & House, 2022; Kelly et al., 2002). Although these species co-occurred at our sites, *N. lacustris* abundance was only high (i.e., 43 cf. 1–3 individuals per sample) in one community in which *Gammarus* abundance was low (i.e., 46 cf. ≤ 1194 individuals per sample). *Nemoura lacustris* occurred exclusively at sites at which woodland was the primary land use (i.e., sites exposed to relatively low anthropogenic impact levels), but the species also occurs in ditches in agricultural landscapes, indicating its broad habitat preferences beyond the core requirement of intermittence (Gething et al., 2021).

Two blackflies, *S. angustitarse* and *S. costatum* (CCI 6 and 5, respectively), were recorded at five sites. *Simulium angustitarse* is associated with clean, cold waters near river sources (Lechthaler & Car, 2005), and we found the species at one wooded, gravel-dominated site 4.2 m from the groundwater-fed spring source. *Simulium costatum* is typically restricted to perennial calcareous springs and spring-fed streams (J. Bass, pers. comm; Rubtsov, 1990). We recorded the species at three temporary sites, which may reflect its dispersal from nearby perennial reaches. Our identification of at least five species within the genus *Simulium* also highlights the additional insight brought by species-level identification of challenging taxa such as Diptera families.

We recorded four stygofaunal amphipods of conservation interest: the Notable species *N. fontanus*, *N. kochianus* and *C. subterraneus*, and the Regionally Notable *N. aquilex*, which largely occurred at

temporary sites, as reported previously (Miliša et al., 2022; White et al., 2018). These groundwater specialists may persist in temporary reaches due to reduced competition and predation, and because they can survive within low-resource saturated subsurface sediments during dry phases (Fišer et al., 2007). Groundwater invertebrates have been suggested as indicators of water pollution (Becher et al., 2022; Notenboom et al., 1994), and our results provide tentative evidence of species-specific responses to land use (and thus pollution loads), with the widespread species *N. aquilex* occurring in fine-sediment-dominated agricultural streams whereas the rarer *N. fontanus* was found only at woodland (i.e., relatively unimpacted) sites. However, these observations are based on too few specimens to draw conclusions regarding the species-specific potential of stygofauna as bioindicators.

We recorded two crenobiont, cold stenotherm species, which are typical of cold-water springs: *C. alpina* and *C. irrorata*. Both were relatively abundant and widespread at distances <15 m from spring sources, reflecting the favorable thermal environment throughout this stream length: near-surface water temperatures were <15°C at all sites, with benthic temperatures thus likely meeting these species' thermal requirements (Durance & Ormerod, 2010). *Crenobia alpina* was particularly abundant at two temporary sites, where its tolerance of dry phases may be enabled by its capacity to move deeper into subsurface sediments in response to stressful conditions (such as temperature increases or drying) in the surface stream (Durance & Ormerod, 2010; Smith et al., 2003).

We contribute new records of the Nationally Rare caddisfly *S. dubitans*, which was first recorded in the UK in 2010 (in part due to its previous misidentification; Crofts, 2011; Wallace, 2016), in calcareous springs. The species was recorded at 11 sites, 10 of which had woodland as the primary land use, concurring with Crofts' (2011) observations in woodland springs in northern England. Of these 11 sites, five and six had temporary and perennial flow, respectively, aligning with our observations from other temporary headwaters (Roque et al., 2021) and contrasting with the suggestion that *S. dubitans* is absent from temporary streams (Legier & Talin, 1973). Further research is needed to determine whether *S. dubitans* tolerates dry phases in situ or recolonizes after flow resumes, thus advancing our limited understanding of its habitat preferences, in particular for newly discovered UK populations (Crofts, 2011, 2021).

4.2 | Site rankings and metric responses to environmental variability

Our site rankings show that spatial variability in environmental conditions supports landscape-scale biodiversity in headwater networks. Our five top-ranked sites had contrasting environmental characteristics (discussed below) and collectively contained six of eight Nationally Rare, Notable or Regionally Notable species, with the top-ranking site containing four such species – more than any other site. This site supported 33 taxa (compared to the maximum of 35 per site), including four species found at no other site, explaining its high LCBD. In

contrast, unshaded and slow-flowing sites were absent from our top five sites. These characteristics can be associated with human impacts, with a lack of shade evidencing clearance of riparian vegetation, and slow flows potentially indicative of abstraction, land drainage practices and/or impoundment (Allan, 2004). These impacts may reduce resource (e.g., leaf litter) availability and hydrological habitat heterogeneity, thus limiting aquatic biodiversity.

Macroinvertebrate taxonomic richness and diversity can be particularly high in freshwaters surrounded by riparian woodland (Broadmeadow & Nisbet, 2004), then often declines as anthropogenic modification increases (Suurkuukka et al., 2014). However, in our study, no metric (i.e., taxa richness, HS, the CCI or LCBD) responded directly to primary land use, potentially reflecting differences in the local spatial scale at which organisms respond to their environment and the larger scale at which land use is recorded (Sponseller et al., 2008). Accordingly, biodiversity metrics did respond to shading, a local environmental variable influenced by riparian canopy cover and overhanging vegetation and thus land use: richness and HS diversity were near-significantly higher at lightly and moderately shaded sites. Such partially shaded sites may represent a 'Goldilocks' zone for macroinvertebrate biodiversity, in which there is enough light to support macrophytes and biofilms that provide habitat and food for species including grazers (Wright & Symes, 1999), and also enough riparian vegetation to produce inputs of leaf litter that support shredders as well as woody material that promotes habitat complexity (Riley et al., 2009).

Taxa richness increased as mean sediment size increased, and richness as well as LCBD and HS diversity decreased as individual fine sediment types (i.e., sand, silt and/or clay) increased. Biological responses to these individual sediment categories were significant but weak, implying minor, consistent effects. Anthropogenic land uses including intensive agriculture introduce fine sediments into streams, homogenizing benthic sediments and thus reducing macroinvertebrate diversity (Brooks et al., 2021; Wood & Armitage, 1997). Fine sediment also reduces access to subsurface sediments that can act as refuges for macroinvertebrates during dry phases and may thus exacerbate drying-driven taxonomic losses in temporary streams (Vadher et al., 2015). In contrast, coarser sediments have bigger interstitial spaces, providing invertebrates with both habitat and refuge. Collectively, the availability of different sediment types can support taxa with different morphologies, habitat preferences and modes of locomotion (Holomuzki & Biggs, 2003).

Taxa richness was higher at sites with fast flows than at non-flowing sites, whereas LCBD was lower at all flowing sites compared to non-flowing sites. Sites dominated by faster flows may include both faster-flowing coarse-grained and slower-flowing depositional habitats, equating to higher habitat quality and heterogeneity – particularly in low-energy systems such as chalk streams (Acornley & Sear, 1999) – thus supporting more macroinvertebrate taxa (Bickerton, 1995; Degani et al., 1993). Differences in richness may also reflect velocity-mediated predator–prey interactions, whereby reduced velocities may remove the availability of fast-flowing predation refuges. For example, *Simulium* blackfly

larvae select high-velocity microhabitats to limit predation, despite a reduction in feeding efficiency (Malmqvist & Sackmann, 1996). The higher LCBD of non-flowing sites may reflect the temporary flow at five of the six non-flowing sites, which contained numerous infrequently recorded taxa. The stochastic recolonization of temporary headwaters after flow resumes can lead to priority effects that promote spatial beta diversity during flowing phases (Sarremejane et al., 2020).

Of two sites sampled in both spring and the following autumn, one was ranked similarly highly in both seasons (5th and 6th) and one was ranked highly in spring but low in autumn (11th and 47th); the site sampled in early and late spring was ranked higher (3rd compared to 19th) earlier in the season. Taking the latter site as an example, of 48 taxa, 18 were recorded in both samples, and 13 and 17 were recorded only in early and late spring, respectively. Of these 30 single-season taxa, 21 were represented by 1–2 individuals, potentially indicating a low detection rate (Aspin & House, 2022). Even standard 3-min kick samples detect a limited proportion of the taxa present (e.g., 50% of species; Furse et al., 1981) and in habitats such as headwaters – which often support relatively high proportions of uncommon taxa (Aspin & House, 2022) – detection rates may be particularly low. Nonetheless, our detection of 30 of 48 taxa (including 18 insects, many of which experience considerable seasonal variation in occurrence and abundance) in only one month highlights potentially considerable temporal variability in community composition. Multi-season sampling may thus generate a more comprehensive understanding of site-specific biodiversity.

4.3 | Implications for restoration and conservation

Our findings demonstrate that environmental heterogeneity within networks of headwater springs and streams – which encompass a range of natural flow permanence regimes and other site characteristics – collectively support high aquatic macroinvertebrate diversity. In particular, the importance of landscape-scale headwater networks for biodiversity is highlighted by the sporadic occurrence of species of conservation interest, including Nationally Rare species, and specialist species including crenobionts, cold stenotherms, temporary-stream specialists and stygofauna. To protect this biodiversity, effective conservation and restoration of headwaters require a landscape-scale approach. Restoration of impacted sites should seek to enhance biodiversity by regenerating woodland and increasing hydrological habitat heterogeneity. Such restoration could also promote ecological resilience to climate change – a pressure to which species in headwater springs and streams are particularly vulnerable (Macadam et al., 2022).

ACKNOWLEDGMENTS

We thank the Nottingham Trent University Sustainable Futures Research Theme and the Environment Agency for funding this research. We thank Sam Davies, Magdalena Chaborska, Jess Goldring and Avreen Roque for their assistance in the lab and field; and Jon

Bass, Stuart Crofts, Garth Foster, Chloe Hayes, Tim Johns, Lee Knight, Craig Macadam, Gloria Tapia-Ortega, Ian Wallace and Martin Winter for help with identifying invertebrates. We thank two reviewers for feedback that improved our manuscript.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data analysed in this study are available in the Supporting Information.

ORCID

Jamal Kabir  <https://orcid.org/0000-0001-5861-9904>

Giulio Biondi  <https://orcid.org/0009-0007-0288-2034>

Kieran J. Gething  <https://orcid.org/0000-0002-4997-0249>

Thomas Aspin  <https://orcid.org/0000-0003-1599-1532>

Tim Sykes  <https://orcid.org/0000-0002-0665-0368>

Rachel Stubbington  <https://orcid.org/0000-0001-8475-5109>

REFERENCES

- Acornley, R. M., & Sear, D. A. (1999). Sediment transport and siltation of brown trout (*Salmo trutta* L.) spawning gravels in chalk streams. *Hydrological Processes*, 13, 447–458. [https://doi.org/10.1002/\(SICI\)1099-1085\(19990228\)13:3%3C447::AID-HYP749%3E3.0.CO;2-G](https://doi.org/10.1002/(SICI)1099-1085(19990228)13:3%3C447::AID-HYP749%3E3.0.CO;2-G)
- Allan, J. D. (2004). Landscapes and riverscapes: The influence of land use on stream ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, 35, 257–284. <https://doi.org/10.1146/annurev.ecolsys.35.120202.110122>
- Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, 26, 32–46. <https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x>
- Anderson, M. J. (2006). Distance-based tests for homogeneity of multivariate dispersions. *Biometrics*, 62, 245–253. <https://doi.org/10.1111/j.1541-0420.2005.00440.x>
- Aspin, T., & House, A. (2022). Alpha and beta diversity and species co-occurrence patterns in headwaters supporting rare intermittent-stream specialists. *Freshwater Biology*, 67, 1188–1202. <https://doi.org/10.1111/fwb.13910>
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Becher, J., Englisch, C., Griebler, C., & Bayer, P. (2022). Groundwater fauna downtown – Drivers, impacts and implications for subsurface ecosystems in urban areas. *Journal of Contaminant Hydrology*, 248, 104021. <https://doi.org/10.1016/j.jconhyd.2022.104021>
- Berrie, A. D. (1992). The chalk-stream environment. *Hydrobiologia*, 248, 3–9. <https://doi.org/10.1007/BF00008881>
- Bickerton, M. A. (1995). Long-term changes of macroinvertebrate communities in relation to flow variations: The river Glen, Lincolnshire, England. *Regulated Rivers: Research & Management*, 10, 81–92. <https://doi.org/10.1002/rrr.3450100204>
- Biggs, J., von Fumetti, S., & Kelly-Quinn, M. (2017). The importance of small waterbodies for biodiversity and ecosystem services: implications for policy makers. *Hydrobiologia*, 793, 3–39. <https://doi.org/10.1007/s10750-016-3007-0>
- Bogan, M. T., Boersma, K. S., & Lytle, D. A. (2013). Flow intermittency alters longitudinal patterns of invertebrate diversity and assemblage composition in an arid-land stream network. *Freshwater Biology*, 58, 1016–1028. <https://doi.org/10.1111/fwb.12105>
- Broadmeadow, S., & Nisbet, T. R. (2004). The effects of riparian forest management on the freshwater environment: a literature review of best management practice. *Hydrology and Earth System Sciences*, 8, 286–305. <https://doi.org/10.5194/hess-8-286-2004>
- Brooks, A. J., Bray, J., Nichols, S. J., Shenton, M., Kaserzon, S., Mac Nally, R., & Kefford, B. J. (2021). Sensitivity and specificity of macroinvertebrate responses to gradients of multiple agricultural stressors. *Environmental Pollution*, 291, 118092. <https://doi.org/10.1016/j.envpol.2021.118092>
- Chadd, R., & Extence, C. (2004). The conservation of freshwater macroinvertebrate populations: a community-based classification scheme. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 14, 597–624. <https://doi.org/10.1002/aqc.630>
- Clarke, A., Mac Nally, R., Bond, N., & Lake, P. S. (2008). Macroinvertebrate diversity in headwater streams: a review. *Freshwater Biology*, 53, 1707–1721. <https://doi.org/10.1111/j.1365-2427.2008.02041.x>
- Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, 18, 117–143. <https://doi.org/10.1111/j.1442-9993.1993.tb00438.x>
- Crofts, S. M. (2011). *Synagapetus dubitans*, a caddisfly new to Britain [online]. <https://core.ac.uk/download/pdf/11025136.pdf>
- Crofts, S. M. (2021). The caddisfly (Trichoptera) *Synagapetus dubitans* McLachlan, 1879 [online]. <https://cressbrookandlittonflyfishers.co.uk/wp-content/uploads/2021/02/Synagapetus-dubitans-2010-to-2019-report-by-S-M-Crofts.pdf>
- Cuffney, T. F., Bilger, M. D., & Haigler, A. M. (2007). Ambiguous taxa: effects on the characterization and interpretation of invertebrate assemblages. *Journal of the North American Benthological Society*, 26, 286–307. [https://doi.org/10.1899/0887-3593\(2007\)26\[286:ATEOTC\]2.0.CO;2](https://doi.org/10.1899/0887-3593(2007)26[286:ATEOTC]2.0.CO;2)
- Degani, G., Herbst, G. N., Ortal, R., Bromley, H. J., Levanon, D., Netzer, Y., Harari, N., & Glazman, H. (1993). Relationship between current velocity, depth and the invertebrate community in a stable river system. *Hydrobiologia*, 263, 163–172. <https://doi.org/10.1007/BF00006267>
- Deharvent, L., Stoch, F., Gibert, J., Bedos, A., Galassi, D., Zagmajster, M., Brancelj, A., Camacho, A., Fiers, F., Martin, P., Giani, N., Magniez, G., & Marmonier, P. (2009). Groundwater biodiversity in Europe. *Freshwater Biology*, 54, 709–726. <https://doi.org/10.1111/j.1365-2427.2008.01972.x>
- Dray, S., BaumBlanchet, G., Borcard, D., Guenard, G., Jombart, T., Larocque, G., Legendre, P., Madi, N., ... Wagner, H. H. (2018). Adespatial: Multivariate Multiscale Spatial Analysis. R package version 0.3-16. <https://cran.r-project.org/web/packages/adespatial/index.html>
- Durance, I., & Ormerod, S. J. (2010). Evidence for the role of climate in the local extinction of a cool-water trichopteran. *Journal of the North American Benthological Society*, 29, 1367–1378. <https://doi.org/10.1899/09-159.1>
- Finn, D. S., Bonada, N., Múrria, C., & Hughes, J. M. (2011). Small but mighty: headwaters are vital to stream network biodiversity at two levels of organization. *Journal of the North American Benthological Society*, 30, 963–980. <https://doi.org/10.1899/11-012.1>
- Fišer, C., Keber, R., Kereži, V., Moškrič, A., Palandančič, A., Petkovska, V., Potočnik, H., & Sket, B. (2007). Coexistence of species of two amphipod genera: *Niphargus timavi* (Niphargidae) and *Gammarus fossarum* (Gammaridae). *Journal of Natural History*, 41, 2641–2651. <https://doi.org/10.1080/00222930701661225>
- Furse, M. T., Wright, J. F., Armitage, P. D., & Moss, D. (1981). An appraisal of pond-net samples for biological monitoring of lotic macro-invertebrates. *Water Research*, 15, 679–689. [https://doi.org/10.1016/0043-1354\(81\)90160-3](https://doi.org/10.1016/0043-1354(81)90160-3)
- Gething, K. J., Sykes, T., Biondi, G., Macadam, C., & Stubbington, R. (2021). Ditching misconceptions: Rare temporary stream specialists in artificial habitats. *FBA News: The Freshwater Biological Association Newsletter*, 83, 14–18. <https://irep.ntu.ac.uk/id/eprint/44941>
- Holomuzki, J. R., & Biggs, B. J. (2003). Sediment texture mediates high-flow effects on lotic macroinvertebrates. *Journal of the North American Benthological Society*, 22, 542–553. <https://doi.org/10.2307/1468351>

- Hsieh, T. C., Ma, K. H., & Chao, A. (2016). iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution*, 7, 1451–1456. <https://doi.org/10.1111/2041-210X.12613>
- Humphries, C. J., Williams, P. H., & Vane-Wright, R. I. (1995). Measuring biodiversity value for conservation. *Annual Review of Ecology and Systematics*, 26, 93–111. <https://doi.org/10.1146/annurev.es.26.110195.000521>
- Kelly, D. W., Dick, J. T., & Montgomery, W. I. (2002). The functional role of *Gammarus* (Crustacea, Amphipoda): shredders, predators, or both? *Hydrobiologia*, 485, 199–203. <https://doi.org/10.1023/A:1021370405349>
- Lechthaler, W., & Car, M. (2005). *Simuliidae: Key to larvae and pupae from central and western Europe*. Eutaxa—Technisches Büro für Biologie.
- Legendre, P., & De Cáceres, M. (2013). Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. *Ecology Letters*, 16, 951–963. <https://doi.org/10.1111/ele.12141>
- Légier, P., & Talin, J. (1973). Comparaison de ruisseaux permanents et temporaires de la Provence calcaire. *Annales de Limnologie-International Journal of Limnology*, 9, 273–292. <http://hdl.handle.net/1834/22450>
- Lytle, D. A., & Peckarsky, B. L. (2001). Spatial and temporal impacts of a diesel fuel spill on stream invertebrates. *Freshwater Biology*, 46, 693–704. <https://doi.org/10.1046/j.1365-2427.2001.00695.x>
- Macadam, C., Stubbington, R., & Wallace, I. (2021). The specialist insects that rely on the wet-dry habitats of temporary streams. *FBA News: The Freshwater Biological Association Newsletter*, 81, 28–33. https://irep.ntu.ac.uk/id/eprint/44944/1/1498769_Stubbington.pdf
- Macadam, C. R., England, J., & Chadd, R. (2022). The vulnerability of British aquatic insects to climate change. *Knowledge & Management of Aquatic Ecosystems*, 423, 3. <https://doi.org/10.1051/kmae/2022003>
- Malmqvist, B., & Sackmann, G. (1996). Changing risk of predation for a filter-feeding insect along a current velocity gradient. *Oecologia*, 108, 450–458. <https://doi.org/10.1007/BF00333721>
- Maurice, L., Robertson, A. R., White, D., Knight, L., Johns, T., Edwards, F., Arietti, M., Sorensen, J. P. R., Weitowitz, D., Marchant, B. P., & Bloomfield, J. P. (2016). The invertebrate ecology of the chalk aquifer in England (UK). *Hydrogeology Journal*, 24, 459–474. <https://doi.org/10.1007/s10040-015-1334-2>
- Meyer, J. L., Strayer, D. L., Wallace, J. B., Eggert, S. L., Helfman, G. S., & Leonard, N. E. (2007). The contribution of headwater streams to biodiversity in river networks. *Journal of the American Water Resources Association*, 43, 86–103. <https://doi.org/10.1111/j.1752-1688.2007.00008.x>
- Miliša, M., Stubbington, R., Datry, T., Cid, N., Bonada, N., Šumanović, M., & Milošević, D. (2022). Taxon-specific sensitivities to flow intermittence reveal macroinvertebrates as potential bioindicators of intermittent rivers and streams. *Science of the Total Environment*, 804, 150022. <https://doi.org/10.1016/j.scitotenv.2021.150022>
- Minshall, G. W., Petersen, R. C., Jr., & Nimz, C. F. (1985). Species richness in streams of different size from the same drainage basin. *The American Naturalist*, 125, 16–38. <https://doi.org/10.1086/284326>
- Murray-Bligh, J., & Griffiths, M. (2022). *Freshwater biology and ecology handbook: Practitioners' guide to improving and protecting river health*. Foundation for Water Research. <https://fwrinformationcentre.co.uk/biology-and-ecology-handbook/index.html>
- Notenboom, J., Plénet, S., & Turquin, M. J. (1994). Groundwater contamination and its impact on groundwater animals and ecosystems. In J. Gibert, D. L. Danielopol, & J. A. Stanford (Eds.), *Groundwater ecology* (pp. 477–504). Academic Press.
- Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Cáceres, M., Durand, S., ... Weedon, J. (2022). *Vegan: community ecology package*. R package version 2, 6–4. <http://CRAN.R-project.org/package=vegan>
- R Core Team. (2023). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Riley, W. D., Pawson, M. G., Quayle, V., & Ives, M. J. (2009). The effects of stream canopy management on macroinvertebrate communities and juvenile salmonid production in a chalk stream. *Fisheries Management and Ecology*, 16, 100–111. <https://doi.org/10.1111/j.1365-2400.2008.00649.x>
- Roque, A., Gething, K. J., & Stubbington, R. (2021). *The effects of drying on aquatic macroinvertebrate communities in the temporary headwaters of the River Thames*. Nottingham Trent University. https://irep.ntu.ac.uk/id/eprint/48527/1/1740733_Gething.pdf
- Roswell, M., Dushoff, J., & Winfree, R. (2021). A conceptual guide to measuring species diversity. *Oikos*, 130, 321–338. <https://doi.org/10.1111/oik.07202>
- Rubtsov, I. A. (1990). *Blackflies (Simuliidae). Fauna of the USSR. Diptera*. Volume 6, part 6. Brill Academic Publishers.
- Ruhí, A., Datry, T., & Sabo, J. L. (2017). Interpreting beta-diversity components over time to conserve metacommunities in highly dynamic ecosystems. *Conservation Biology*, 31, 1459–1468. <https://doi.org/10.1111/cobi.12906>
- Sarremejane, R., England, J., Sefton, C. E., Parry, S., Eastman, M., & Stubbington, R. (2020). Local and regional drivers influence how aquatic community diversity, resistance and resilience vary in response to drying. *Oikos*, 129, 1877–1890. <https://doi.org/10.1111/oik.07645>
- Sarremejane, R., Mykrä, H., Bonada, N., Aroviita, J., & Muotka, T. (2017). Habitat connectivity and dispersal ability drive the assembly mechanisms of macroinvertebrate communities in river networks. *Freshwater Biology*, 62, 1073–1082. <https://doi.org/10.1111/fwb.12926>
- Smith, H., Wood, P. J., & Gunn, J. (2003). The influence of habitat structure and flow permanence on invertebrate communities in karst spring systems. *Hydrobiologia*, 510, 53–66. <https://doi.org/10.1023/B:HYDR.0000008501.55798.20>
- South Downs National Park Authority (SDNPA). (2023). *Wildlife & Habitats*. SDNPA. <https://www.southdowns.gov.uk/wildlife-habitats/>
- Sponseller, R. A., Benfield, E. F., & Valett, H. M. (2008). Relationships between land use, spatial scale and stream macroinvertebrate communities. *Freshwater Biology*, 46, 1409–1424. <https://doi.org/10.1046/j.1365-2427.2001.00758.x>
- Stubbington, R., England, J., Wood, P. J., & Sefton, C. E. (2017). Temporary streams in temperate zones: recognizing, monitoring and restoring transitional aquatic-terrestrial ecosystems. *Wiley Interdisciplinary Reviews: Water*, 4, e1223. <https://doi.org/10.1002/wat2.1223>
- Stubbington, R., Sarremejane, R., & Datry, T. (2019). Alpha and beta diversity of connected benthic-subsurface invertebrate communities respond to drying in dynamic river ecosystems. *Ecography*, 42, 2060–2073. <https://doi.org/10.1111/ecog.04592>
- Suurkuukka, H., Virtanen, R., Suorsa, V., Soininen, J., Paasivirta, L., & Muotka, T. (2014). Woodland key habitats and stream biodiversity: Does small-scale terrestrial conservation enhance the protection of stream biota? *Biological Conservation*, 170, 10–19. <https://doi.org/10.1016/j.biocon.2013.10.009>
- Tapia, G., Bass, J. A. B., & House, A. (2018). Further occurrence records for the winterbourne stonefly *Nemoura lacustris* Pictet, 1865, (Plecoptera: Nemouridae). *Entomologist's Monthly Magazine*, 154, 60–64. <https://doi.org/10.31184/M00138908.1541.3915>
- Vadher, A. N., Stubbington, R., & Wood, P. J. (2015). Fine sediment reduces vertical migrations of *Gammarus pulex* (Crustacea: Amphipoda) in response to surface water loss. *Hydrobiologia*, 753, 61–71. <https://doi.org/10.1007/s10750-015-2193-5>
- Wallace, I. D. (2016). A review of the status of the caddis flies (Trichoptera) of Great Britain: Species Status No.27. Natural England Commissioned Reports Number 191. Natural England. <https://publications.naturalengland.org.uk/file/5229520159244288>
- Wallace, J. B., Grubaugh, J. W., & Whites, M. R. (1996). Influences of coarse woody debris on stream habitats and invertebrate biodiversity. In J. W. McMin (Ed.), *Proceedings of the workshop on coarse woody debris in southern forests: Effects on biodiversity* (pp. 119–129). United States Department of Agriculture.

- Webb, J., Heaver, D., Lott, D., Dean, H. J., van Breda, J., Curson, J., Harvey, M. C., Gurney, M., Roy, D. B., van Breda, A., Drake, M., Alexander, K. N. A., & Foster, G. (2018). Pantheon – database version 3.7.6. <https://pantheon.brc.ac.uk/>
- WFD-UKTAG (2008). UKTAG river assessment methods: Benthic invertebrate fauna: River Invertebrate Classification Tool (RICT). Edinburgh: Water Framework Directive – United Kingdom Technical Advisory Group (WFD-UKTAG). Retrieved from <https://www.wfduk.org/sites/default/files/Media/Characterisation%20of%20the%20water%20environment/Biological%20Method%20Statements/river%20invertebrates.pdf>
- White, J. C., House, A., Punched, N., Hannah, D. M., Wilding, N. A., & Wood, P. J. (2018). Macroinvertebrate community responses to hydrological controls and groundwater abstraction effects across intermittent and perennial headwater streams. *Science of the Total Environment*, 610, 1514–1526. <https://doi.org/10.1016/j.scitotenv.2017.06.081>
- Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. Springer-Verlag.
- Wood, P. J., & Armitage, P. D. (1997). Biological effects of fine sediment in the lotic environment. *Environmental Management*, 21, 203–217. <https://doi.org/10.1016/j.scitotenv.2017.06.081>
- Wood, P. J., Gunn, J., Smith, H., & Abas-Kutty, A. (2005). Flow permanence and macroinvertebrate community diversity within groundwater dominated headwater streams and springs. *Hydrobiologia*, 545, 55–64. <https://doi.org/10.1007/s10750-005-2213-y>
- Wood, P. J., & Petts, G. E. (1999). The influence of drought on chalk stream macroinvertebrates. *Hydrological Processes*, 13, 387–399. [https://doi.org/10.1002/\(SICI\)1099-1085\(19990228\)13:3%3C387::AID-HYP745%3E3.0.CO;2-R](https://doi.org/10.1002/(SICI)1099-1085(19990228)13:3%3C387::AID-HYP745%3E3.0.CO;2-R)
- Wright, J. F. (1992). Spatial and temporal occurrence of invertebrates in a chalk stream, Berkshire, England. *Hydrobiologia*, 248, 11–30. <https://doi.org/10.1007/BF00008882>
- Wright, J. F., & Symes, K. L. (1999). A nine-year study of the macroinvertebrate fauna of a chalk stream. *Hydrological Processes*, 13, 371–385. [https://doi.org/10.1002/\(SICI\)1099-1085\(19990228\)13:3%3C371::AID-HYP744%3E3.0.CO;2-C](https://doi.org/10.1002/(SICI)1099-1085(19990228)13:3%3C371::AID-HYP744%3E3.0.CO;2-C)

SUPPORTING INFORMATION

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

How to cite this article: Kabir, J., Biondi, G., Gething, K. J., Aspin, T., Sykes, T., & Stubbington, R. (2024). Spring forth diversity: Specialist species contribute to the conservation value of headwater springs and streams at the landscape scale. *River Research and Applications*, 1–12. <https://doi.org/10.1002/rra.4275>