



An invertebrate-based index to characterize ecological responses to flow intermittence in rivers

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With 5 figures and 5 tables

Abstract: Intermittent streams occur across global regions, and are increasingly recognized to support high biodiversity and perform important ecological roles within catchments. New tools are needed to better characterize biotic responses to the full spectrum of environmental conditions that occur in these dynamic systems, because the biological indices developed to assess ecological responses to flow in perennial rivers may be inaccurate in intermittent streams. We present the Monitoring Intermittent Streams index (MIS-index), a new biological index that can be used to assess invertebrate responses to environmental changes spanning flowing, ponded and drying states. As well as fully aquatic taxa, the index includes semi-aquatic and terrestrial invertebrates from marginal habitats, which are collected during the standard surveys used by regulatory agencies to assess ecological quality. We explore how including these taxa within an index informs our understanding of aquatic–terrestrial invertebrate community responses to changing habitat composition, as intermittent streams transition from lotic to lentic then drier conditions. We explain the development of the MIS-index and explore its performance compared with other indices. We suggest index combinations that can be used to detect different aspects of ecological responses to variation in instream conditions, and highlight the advantages of including semi-aquatic and terrestrial taxa. We call for researchers to test the performance of the MIS-index across a wide range of intermittent stream types, to enable its development into an internationally applicable tool for the holistic assessment of ecological responses to changing hydrological conditions including drying.

Keywords: biotic index; flow; intermittence; intermittent rivers and ephemeral streams; temporary rivers; temporary streams

Introduction

Intermittent streams are natural ecosystems that experience profound changes in instream conditions including (by definition) the cessation of flow and, typically, the partial or complete loss of surface water. Anthropogenic drivers including water abstraction and human land use interact to modify natural inter-

mittent flow regimes, thus impacting their capacity to support high biodiversity and perform important ecological roles (Chiu et al. 2017). Ecological responses to altered flow regimes can be particularly pronounced if flow permanence shifts from perennial to intermittent or vice versa, and in intermittent streams, changes in the extent of dry phases also cause profound shifts in community composition (Datry et al. 2017). Whereas

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ecological responses to altered flow regimes have received considerable attention in perennial streams, including the development of hydrological indices (Richter et al. 1996; Monk et al. 2007; Poff et al. 2010), fewer tools have been developed for intermittent streams (Gallart et al. 2012; Prat et al. 2014), and none that incorporate responses of biota across the aquatic–terrestrial spectrum. With climate change increasing the occurrence of drought (i.e. a deficit in water in comparison to the long-term average; Tallaksen & van Lanen 2004; Prudhomme et al. 2014) and drying, and thus extending the spatial and temporal extent of intermittence in many global regions, development of such indices is needed to facilitate effective management of intermittent streams.

Freshwater invertebrate communities, including taxa associated with lotic and lentic waters, can be used as indicators of flow-regime change. Community responses may be effectively summarized by indices that characterize ecological effects and therefore inform setting of hydroecological objectives to mitigate anthropogenic and drought impacts and, where necessary, to restore natural flow regimes (Klaar et al. 2014). For example, the LIFE (Lotic-invertebrate Index for Flow Evaluation) index (Extence et al. 1999), calculated using the flow preferences of aquatic invertebrate taxa, is used to assess ecological responses to changing flow regimes (Gosling 2012; Klaar et al. 2014).

A second index, Drought Effect of Habitat Loss on Invertebrates (DEHLI; Chadd et al. 2017), has been developed to characterize ecological responses to key stages of channel drying associated with drought events, including flow cessation and surface water loss. Based on presence–absence observations of invertebrate families, DEHLI considers only aquatic taxa, not the semi-aquatic and terrestrial taxa that occur in marginal and riparian habitats and that may colonize channels as flow declines. However, such taxa are collected during routine invertebrate sampling, which encompasses all riverine habitats including marginal areas (ISO 2012). Although DEHLI has the potential to track biotic responses as flow recedes in a drying channel, complementary approaches encompassing the taxa present in all stream habitats are needed to facilitate effective management of ecosystems affected by interacting drought and anthropogenic pressures (Chadd et al. 2017).

We present the development of a new invertebrate index, which incorporates lotic, lentic, semi-aquatic and terrestrial taxa to characterize ecological responses to habitat changes associated with flow inter-

mittence: the Monitoring Intermittent Streams index (MIS-index). We use the term *intermittent streams* sensu Leigh et al. (2016), to encompass all rivers and streams that sometimes cease to flow and may dry; as such, it is comparable to the terms *temporary streams* (Acuña et al. 2014; Stubbington et al. 2017a) and *intermittent rivers and ephemeral streams* (IRES; Datry et al. 2017).

Biotic indices have previously been developed based on expert opinion (e.g. Chester 1980; Extence et al. 1999; Chadd et al. 2017), derivation of relationships using statistical approaches (e.g. Murphy et al. 2015), and a combination of both (e.g. Walley & Hawkes 1996; Turley et al. 2015). We outline the development of the MIS-index, which uses a combination approach. We use existing literature and expert opinion to assign taxa to groups based on their association with habitats recorded within intermittent streams. These different ‘mesohabitats’, ‘biotopes’ or ‘functional habitats’ (Armitage et al. 1995; Padmore 1997; Harper et al. 1998) support distinct invertebrate assemblages (Kemp et al. 1999; Kemp et al. 2000; Demars et al. 2012). We then use statistical modelling to derive a set of internally consistent weighting factors, one for each taxon group. These weighting factors facilitate the aggregation of presence/absence data for each taxon group into a single index.

We compare the MIS-index with biotic indices used to assess aquatic invertebrate responses to changes in flow (LIFE; Extence et al. 1999) and to instream habitat changes associated with drought (DEHLI; Chadd et al. 2017), and highlight its potential for future use.

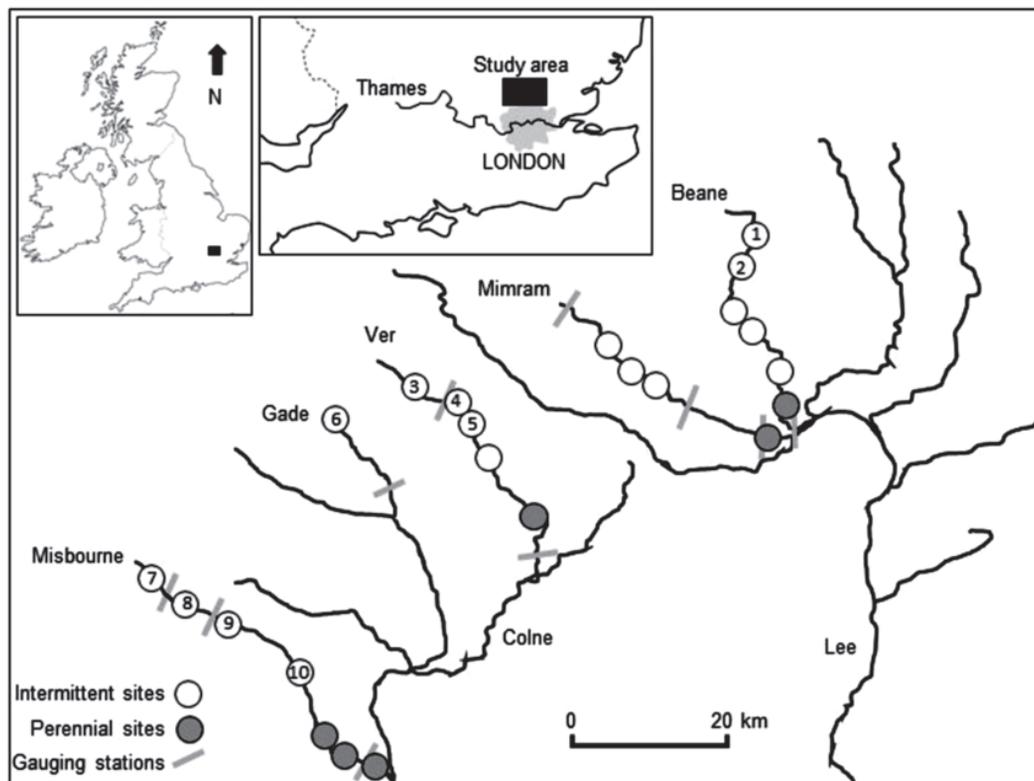
Methods

Assignment of taxa to habitat-association groups

We used published information (see Supplementary Material), a trait database (Schmidt-Kloiber & Hering 2015) and long-term field observations of recognized experts to assign each taxon to one of six groups based on its habitat associations: lotic (fast), lotic, generalist, lentic, semi-aquatic, and terrestrial (Table 1). We assigned most taxa to groups at multiple taxonomic resolutions and, for insects, multiple life stages. For example, we assigned juveniles of the family Limnephilidae as lotic, with genera and species assigned to groups including lotic (fast), lotic and generalist. We assigned taxa with broad habitat associations spanning multiple groups to the generalist group. In total, we assigned 536 taxa to these habitat-associated ‘MIS-groups’, comprising 31 lotic (fast) taxa, 72 lotic taxa, 166 generalist taxa, 115 lentic taxa, 72 semi-aquatic taxa, and 80 terrestrial taxa (Supplementary Material Table S1).

Table 1. Definition of each invertebrate habitat-association group (i.e. MIS-group) used within the MIS-index.

MIS-group	Definition
Lotic (fast)	Taxa primarily associated with riffle and rapid habitats (sensu Newson et al. 1998).
Lotic	Taxa primarily associated with run and glide habitats, but that occur rarely in pool habitats (sensu Newson et al. 1998).
Generalist	Taxa that occur across a wide range of running-water and standing-water habitats.
Lentic	Taxa usually associated with pool and marginal dead-water habitats (sensu Newson et al. 1998).
Semi-aquatic	Taxa associated with seasonally inundated areas, waterlogged soil and marginal marshy habitats. Water-dependent but not fully aquatic.
Terrestrial	Taxa primarily associated with terrestrial habitats.

**Fig. 1.** Location of the 23 invertebrate monitoring sites, spanning six chalk streams in the adjacent Colne and Lee catchments in southern England, UK. Sites 1–10 have invertebrate samples associated with zero-flow conditions in the antecedent six month periods (9 to 27 depending on site; Supplementary Material Table S2).

Index development dataset

The invertebrate dataset we used to develop the MIS-index was collected at 23 sites across five streams (1–7 sites per stream) overlaying limestone (chalk) geology within the River Thames catchment in southern England, UK. The Misbourne, Gade and Ver are within the River Colne sub-catchment, and the Mimram and Beane are in the adjacent River Lee sub-catchment (Fig. 1). The streams are predominantly groundwater-fed, and seasonal and annual fluctuations in the water table (Sear et al. 1999; Sefton et al. 2019) result in intermittent flow at 17 sites; the remaining 6 sites are perennial (Supplementary Material Ta-

ble S2). Catchment land use is primarily agricultural (63–77% arable and pasture; NRFA 2018).

All samples were collected by or for the Environment Agency (the statutory environmental regulator within England) in spring (March–May) and autumn (September–November) between 1993 and 2017. Years and seasons sampled were site-specific and no site was sampled in every year/season, due to operational reasons or when the streambed was completely dry at intermittent sites. Invertebrates were collected following the standard approach used by UK regulatory agencies (ISO 2012): a 3-min kick/sweep technique using a pond-net, supplemented by hand searching. All available habitats were sampled in pro-

Table 2. Percentage occurrence and mean taxa richness of each habitat-association group (MIS-group) within the dataset used for MIS-index development.

MIS-group	Occurrence (%)			Mean richness sample ⁻¹		
	Both seasons	Spring	Autumn	Both seasons	Spring	Autumn
Lotic (fast)	88	86	90	3.73	3.60	3.85
Lotic	97	96	99	6.06	6.62	7.39
Generalist	100	100	100	11.89	13.38	14.06
Lentic	70	71	68	1.39	1.53	1.67
Semi-aquatic	67	71	61	1.05	1.36	1.04
Terrestrial	11	11	10	0.12	0.14	0.14

Table 3. Candidate explanatory variables used to fit a maximal model within the exploratory analysis.

Description	Short description
Percentage of zero-flow (%ZF) days in the six-month season (summer, S; winter, W) prior to sampling.	%ZF-S1au (autumn samples) %ZF-W1sp (spring samples)
Percentage of zero-flow days in the summer of the calendar year prior to sampling.	%ZF-S1sp (spring samples) %ZF-S2au (autumn samples)
Percentage of zero-flow days in the summer two calendar years prior to sampling.	%ZF-S2sp (spring samples)
Standardized Q10 and Q70 discharge in the six-month season prior to sampling.	Q10z, Q70z
Calendar year of the sample, re-centred to the year 2000.	Year.2000
Substrate, expressed as the mean substrate composition (phi).	phi

portion to their occurrence, including sweeps through vegetation patches and between the roots of overhanging trees. As flow decreased, sampling included splashing water onto areas covered by very shallow water and collecting any invertebrates washed out. Visual estimates of channel substrate composition within the sampled area (% boulders, cobbles, pebbles, gravel, sand and silt) were made in association with each invertebrate sample, and the mean substrate size summarized as phi (Donoghue 2016).

The dataset selected for index development comprised collected samples for which aquatic taxa, were identified to species (with the exception of Oligochaeta and Chironomidae) and for which any semi-aquatic and terrestrial species were also identified, totalling; 503 samples. The number of samples per site ranged from 3 to 41 (mean \pm SD = 22 ± 13.21) (Supplementary Material Table S2). The percentage occurrence in each habitat association group within the samples ranged from 100% for generalists to 10% for terrestrial taxa in the autumn and the mean taxa richness among habitat-association groups varied between 0.12 (terrestrial) and 11.89 (generalist; Table 2).

For seven sites, we obtained hydrological (daily mean discharge) time-series data from nearby fixed gauging stations (Supplementary Material Table S2). For the other 17 sites closer spot-gauging discharge measurements were available. We transposed the nearest fixed gauged mean daily discharge to each of the 17 sites using linear regression against spot-gauge discharges (Gordon et al. 2004; Malcolm et al. 2012; Supplementary Material Table S3). Using the site-specific discharges, flow statistics were calculated for each water year (October–September) at each site for two periods: ‘summer’ (April–September) and ‘winter’ (October–March), following Dunbar et al. (2010a; 2010b). For each site, we calculated one low-flow, one

high-flow and one zero-flow statistic for each period in each year. We chose the low-flow metric Q70 (i.e. the discharge exceeded 70% of the time) because lower thresholds resulted in less distinction between intermittent sites, and we used the common Q10 metric to describe high, but not flood flows. We standardized these two discharge magnitude statistics by site as z-scores (Q70z and Q10z respectively), to enable comparison of relative discharge patterns across sites, using the approach outlined in Dunbar et al. (2010a; 2010b). To represent intermittence, we calculated the percentage of zero-flow days (%ZF) in each season-water-year period for each site. As zero-flow records do not distinguish between ponded and dry conditions, each discharge series was calibrated with routine long-term observational data collected by the Environment Agency (Sefton et al. 2019). An improved match was achieved by counting any flows $< 0.01 \text{ m}^3 \text{ s}^{-1}$ as indicative of a dry channel.

We matched spring invertebrate samples with each of the three discharge statistics (Q70z, Q10z and %ZF) in the immediately preceding winter (W1), and also the %ZF statistic for the preceding summer (S1) and the summer before S1 (S2; Table 3). We matched autumn samples with the three discharge statistics (Q70z, Q10z and %ZF) for the immediately preceding summer (S1) and also the %ZF statistic for the summer before S1 (S2) (Table 3); exploratory analysis demonstrated no relationship between autumn samples and preceding winter flows. Invertebrate samples could therefore have been collected either during or after the ‘preceding’ hydrological season, for example either in March or between April and May for spring samples matched with the preceding winter. The ecological relevance of these time periods has previously been demonstrated (Dunbar et al. 2010a; Dunbar et al. 2010b).

Index development

We undertook all analyses in R version 3.4.4 (R Core Team 2018). To assess the relative association of the taxon richness in each MIS-group with each flow statistic (Table 3), plus substrate conditions recorded on the day of sampling, we built generalized linear mixed-effects models (GLMM). We fitted separate models for spring and autumn samples, because invertebrate indices can show season-specific responses to hydrological drivers (Wood et al. 2000; Dunbar et al. 2010b). We fitted six models (one for each MIS-group) with the *glmer* function from the R package the *lme4* (Bates et al. 2015), using a Poisson error term and a log link function.

To fit a maximal model, we used the mean substrate particle size (ϕ), the calendar year of sample collection, plus the four candidate flow predictor variables for autumn samples, and five for spring samples (Table 3). We centred calendar year on the year 2000 to assist model stability, i.e. to avoid the estimation of a meaningless intercept parameter at calendar year 0. We used a random-effects structure of samples within sites.

Model diagnostics showed no substantial overdispersion or underdispersion, indicating the Poisson error term as appropriate. We ranked all possible subsets of the maximal model using the Akaike Information Criterion (AIC). We then simplified the exploratory models by creating a composite average of the models with a Δ AIC of <4 from the top model (Burnham & Anderson 2002; Anderson 2008), using the R package *MuMIn* (Barton 2018). For this subset, we also compared the direction of the partial relationship (positive or negative, with other predictor variables held constant) and relative importance for each model parameter. Relative importance was defined as a weighted measure of the proportion of models which included the parameter, with values of 1 and 0 indicating presence in every model and no model, respectively. Relative importance is a measure of model selection uncertainty, which we quantified to recognize correlations between the partly-interchangeable candidate explanatory variables.

To enable us to summarize taxonomic data from a sample as a single MIS-index value, we determined taxon weighting factors for each MIS-group. We modelled the responses of taxa richness to intermittence (%ZF) in each MIS-group together as a multivariate response in one GLMM, using the function *MCMCglmm* in the package *MCMCglmm* (Hadfield 2010). We chose this approach because it respects the hierarchical data structure, and uses an underlying model appropriate for the zero-bounded, integer response variables (taxa richness), with an implied mean-variance relationship (Warton et al. 2012). For this model form, we used a random-effects structure of observations within samples within sites, with each observation comprising the taxa richness in a single MIS-group, and a Poisson error distribution.

We configured the model with MIS-group as an indicator variable (fixed-effect factor) with six levels, constructed as a set of sum-to-zero contrasts and a single time-varying %ZF predictor variable: antecedent summer %ZF for autumn samples (%ZF-S1au), and %ZF in the summer of the previous year for spring samples (%ZF-S1sp). We also specified an interaction term between the MIS-group indicator variable and the %ZF flow statistics and tabulated their slope parameter estimates. Focusing on the single %ZF variable allowed us to manage model complexity, deriving only one set of taxon weighting factors, while still partially accounting for indirect relationships between antecedent zero-flow and physical habitat characteris-

tics (notably substrate composition). It also implicitly includes some of the effects of zero-flow characteristic over longer time-scales, because they themselves are partially correlated with the chosen %ZF variable, due to the storage of the underlying chalk aquifer. Compared with the exploratory models for the univariate response of each MIS-group, this multivariate model provided consistency in the resultant parameters, respected co-occurrence between taxa richness in the different MIS-groups from the same sample, and avoided potential imprecision arising from fitting separate models for each MIS-group. We multiplied the final parameters by -100 to give interpretable values which form the final MIS-group weighting factors.

We calculated the MIS-index as the weighted average of the weighting factor and the taxa richness for each MIS-group (see Results), with positive values broadly indicating a community more characteristic of flowing conditions, and negative values conversely indicating drier conditions. MIS-index scores were calculated for each of the 503 samples using the formula:

$$MIS_index_j = \frac{\sum_{i=1..6} M_{si} \cdot T_{ij}}{\sum T_j}$$

where s denotes season (spring, autumn)

$i = 1..6$ denotes the six MIS-groups

s = denotes season (separate weighting factors for spring and autumn samples)

M_{si} is the weighting factor for MIS-group i in season s (following Table 5)

T_{ij} is the number of taxa in group M_{si} in sample j

T_j is the total number of taxa in sample j

Temporal and spatial performance of the MIS-index

To demonstrate the application of the MIS-index to temporal data, we excluded the single River Gade site (6, Fig. 1) from the development dataset, to allow its use as a test site. We selected this site because it is the only site on this river, and is therefore relatively independent. We built linear mixed-effects models (LMM) using the function *lme* in the package *nlme* (Pinheiro et al. 2018) with separate models used to assess the relationship between MIS-index scores and antecedent %ZF (S1, S2 and W1) and mean daily discharge (S1, S2 and W1). Season was included as a random factor in every model.

To explore spatial variation we compared MIS-index scores with distance downstream for the River Ver in 2005 (sites I-M; Supplementary Material Fig. S1). This example was selected due to the completeness of data for this river-year combination and the increase in intermittence with distance from the mapped source. We compared the MIS-index with the site-specific flow permanence regime using the mean number of zero-flow days per year for each site based on long-term (1995–2017) modelled daily discharge (Supplementary Material Table S3). We used mean number of zero flow days since this metric was not used in the development of the index.

Comparison of the MIS-index and the DEHLI and LIFE indices

We used Spearman rank to correlate MIS-index scores for each sample with species-level LIFE and DEHLI index scores, to establish the extent of overlap with these two indices. To explore these relationships further, we compared MIS-index scores to

DEHLI and species-LIFE scores at sites with invertebrate samples associated with antecedent %ZF conditions (i.e. sites 1–10; Fig. 1) which varied from 9 to 27 samples per site (Supplementary Material Table S2).

Results

Univariate models: MIS-group responses to flow, intermittence and substrate composition

Exploratory univariate response modelling of each MIS-group provided some support for inclusion of each candidate explanatory variable. Furthermore, there was evidence in maximal and model-averaged models (explanatory variables listed in Table 3) that the response of taxa richness to antecedent %ZF differed among MIS-groups. For example, in autumn, the model-average parameter estimate for the lotic (fast) MIS-group was -0.00874 (\pm SD = 0.0038), this indicates the change in taxa richness per percentage point change in zero flow days in the summer immediately prior to sampling, with the other variables in the model (Table 3) held constant. In contrast, the parameter estimate for terrestrial was $+0.0128$ (\pm SD = 0.0077) (Supplementary Material Table S4a&b).

In autumn, for five of the six MIS-groups (not terrestrial), either %ZF-S1au or %ZF-S2au was selected in 79% of the candidate models with a Δ AIC within 4 of the top model. For terrestrial taxa, relative importance values of 0.58–0.65 provided comparable, moderate levels of support for each of the four flow

variables. In spring, %ZF flow variables were selected in 97% of four of six models. Models for lentic and semi-aquatic groups were less clear, and the relative importance of only one explanatory flow variable (Q10z for lentic taxa) was >0.5 .

In autumn, lotic (fast), lotic and generalist group taxa richness responded negatively to %ZF, whereas lentic, semi-aquatic and terrestrial group richness responded positively (Table 4). The partial response to %ZF was similar in spring and autumn, although there was an inconsistent and relatively weak response for lentic taxa richness in spring (relative importance of 0.39 [negative for %ZF-W1sp], 0.31 [negative for %ZF-S1sp] and 0.29 [negative for %Z-S2sp]). Partial responses to flow magnitude (Q70z and Q10z) were also relatively weak and inconsistent for all MIS-groups.

In both spring and autumn, MIS-groups 1–4 (i.e. aquatic taxa) generally had consistent partial relationships with mean substrate size, with higher richness of lotic (fast) and lotic taxa associated with coarser substrates, and higher richness of generalist and lentic taxa associated with finer substrates. Semi-aquatic and terrestrial taxa showed less consistent partial relationships with mean substrate size (Table 4). Taxa richness in each MIS-group also showed temporal trends in both seasons, with lotic (fast) richness increasing over the 24-year study period, and generalist, lentic, semi-aquatic and terrestrial taxa decreasing; trends for lotic taxa were inconclusive.

Table 4. Relative importance values for six explanatory variables in separate GLMM models for each MIS-group. *Italics* denotes a negative relationship; **bold** text denotes a positive relationship. Dark and light grey backgrounds highlight relative importance above 0.9 and between 0.5–0.9, respectively. All relationships are partial, i.e. to be interpreted with the other variables held constant. Explanatory variables and MIS-groups are described in Tables 3 and 1, respectively.

Season	Explanatory variable	Lotic (fast)	Lotic	Generalist	Lentic	Semi-aquatic	Terrestrial
Autumn	%ZF-S1au	<i>0.97</i>	<i>0.21</i>	<i>0.79</i>	0.51	1.00	0.58
	%ZF-S2au	<i>0.51</i>	1.00	<i>0.62</i>	1.00	<i>0.18</i>	0.61
	Q70z	0.23	0.31	<i>0.50</i>	0.32	0.31	0.60
	Q10z	<i>0.30</i>	0.24	<i>0.47</i>	<i>0.63</i>	<i>0.44</i>	0.65
	Year	0.80	0.27	<i>1.00</i>	<i>1.00</i>	<i>1.00</i>	<i>1.00</i>
	Phi	<i>1.00</i>	<i>0.53</i>	0.79	0.76	<i>0.20</i>	0.30
Spring	%ZF-W1sp	<i>0.98</i>	<i>0.34</i>	<i>0.52</i>	<i>0.39</i>	<i>0.19</i>	0.20
	%ZF-S1sp	<i>0.40</i>	1.00	<i>0.71</i>	<i>0.31</i>	0.27	0.97
	%ZF-S2sp	<i>0.53</i>	<i>0.35</i>	0.97	0.29	<i>0.18</i>	0.28
	Q70z	0.41	0.57	<i>0.27</i>	0.30	<i>0.40</i>	<i>0.62</i>
	Q10z	<i>0.27</i>	<i>0.68</i>	<i>0.90</i>	<i>0.61</i>	0.34	<i>0.27</i>
	Year	1.00	0.34	<i>1.00</i>	<i>1.00</i>	<i>1.00</i>	<i>1.00</i>
	Phi	<i>1.00</i>	<i>0.49</i>	0.23	1.00	<i>0.50</i>	<i>0.17</i>

Table 5. Weighting factors for each MIS-group, calibrated from separate spring and autumn multivariate GLMM using % zero-flow days (%ZF * -100) as a single explanatory variable.

MIS-group	Autumn	Spring
Lotic (fast)	13	13
Lotic	7	11
Generalist	-2	2
Lentic	-10	-3
Semi-aquatic	-10	-7
Terrestrial	-17	-21

GLMM-derived weighting factors increased in affinity for antecedent %ZF conditions across MIS-groups from lotic (fast) to terrestrial. The derived weighting factors were close to zero for generalist taxa (Table 5) and for lentic taxa in spring. Patterns observed in both seasons were broadly comparable, although in spring the monotonic change in weighting factor spanned all MIS-groups; in autumn, lentic and

semi-aquatic groups had similar weighting factors; and the lotic (fast) and lotic group weighting factors were more similar in spring compared to autumn (Table 5).

Temporal MIS-index performance at the River Gade test site

MIS-index scores varied between -3.12 and 2.23 and (mean ± SD = 0.13 ± 1.58) in autumn and between 1.32 and 5.23 (mean ± SD = 3.31 ± 1.01) in spring on the River Gade test site (6, Fig. 1; Fig. 2a). Autumn scores increased from 1999 to 2004, from 2006 to 2009 and from 2010 to 2017 following periods of drought (1995–1997, 2005–2006, 2010–2012; Met Office 2019). Spring scores were consistently higher than the autumn scores. Both seasons showed similar pattern over time with greater divergence after high-flow events (2001–2002 and 2014). Low scores in autumn 2005 and 2011 and a decline in score in spring 2006

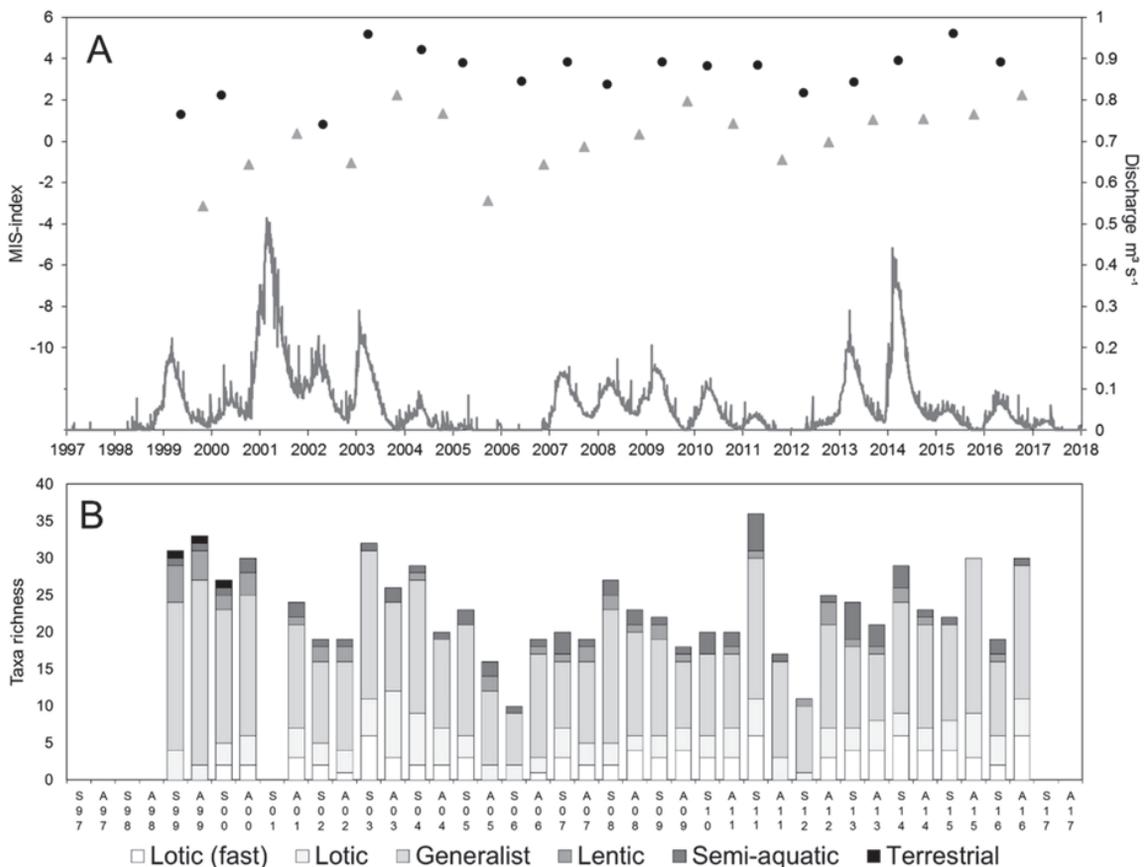


Fig. 2. (A) Discharge and spring (black circles) and autumn (grey triangles) MIS-index scores for the River Gade test site (6; Fig. 1). (B) MIS-group taxa richness by sample in autumn (A) and spring (S) between 1997 (97) and 2017 (17). Blank columns indicate that no sample was taken.

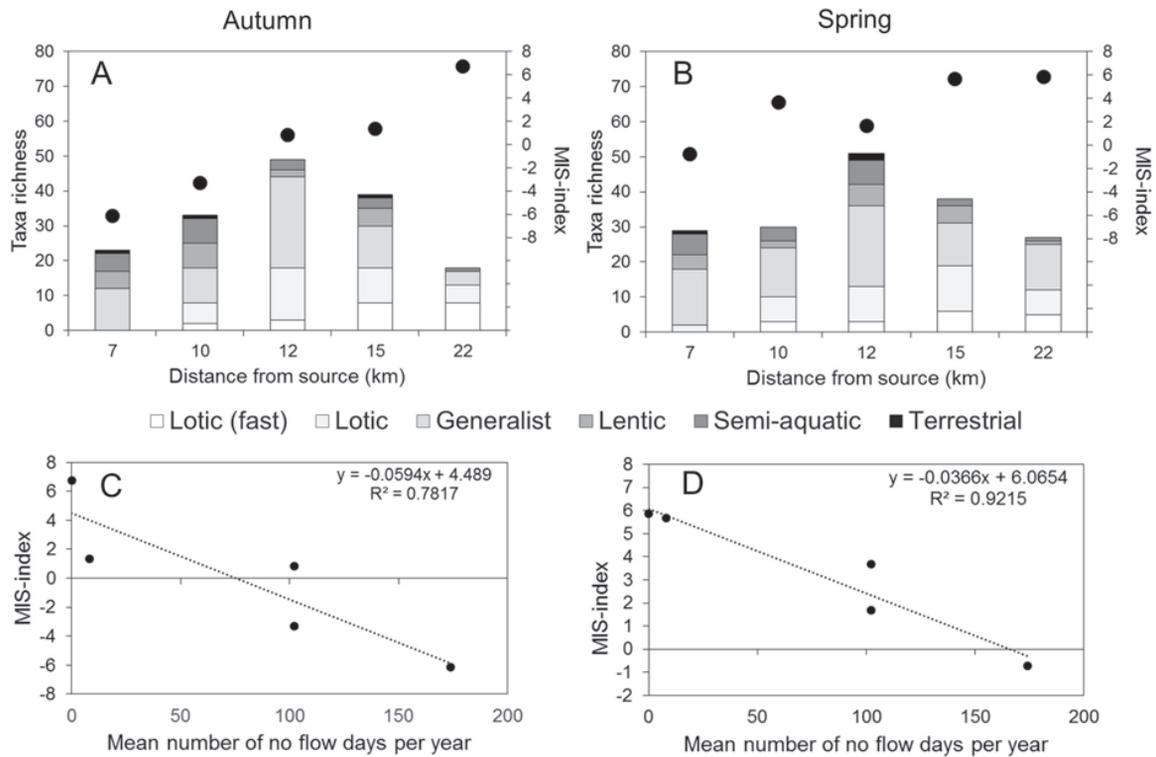


Fig. 3. Spatial variability in MIS-group taxa richness and MIS-Index scores with distance downstream; site location are shown in Supplementary Material Fig. S1; River Ver sites I–M (A & C = autumn, B & D = spring).

and 2012 corresponded with an absence of lotic (fast) taxa (Fig. 2b). The highest scores (e.g. spring 2003, 2015 and autumn 2016) reflected higher richness of lotic (fast) taxa and lotic taxa (e.g. autumn 2003) and a reduction in semi-aquatic taxa (Fig. 2b). There was a lag between the peak flow of 2001/02 and the high spring score of 5.19 with a similar lag following high flows in 2014 and the spring 2015 score of 5.23 (Fig. 2a). MIS-index scores decreased with %ZF-S1 (LMM, Confidence intervals (CI)[−0.033:−0.001]) and %ZF-S2 (CI[−0.033:−0.006]) and increased with mean daily discharge in S2 (CI[2.006:17.935]) but did not change with %ZF-W1 or mean discharge (S1 and W1) with overlapping CI with 0.

Spatial MIS-index performance on the River Ver

MIS-index scores varied between −6.13 and 6.72 along the length of the Ver in autumn 2005, increasing progressively from upstream to downstream despite variation in taxa richness between sites (Fig. 3a). Lower scores were associated with the presence of semi-aquatic and terrestrial taxa and an absence or low occurrence of lotic (fast) and lotic taxa. Spring scores ranged between −0.72 and 5.85 and were consistently

higher than autumn scores (Fig. 3b). Although scores also generally increased from upstream (I; Supplementary Material Fig. S1) to downstream (M; Supplementary Material Fig. S2) in spring, site K (Supplementary Material Fig. S1) scored lower than site upstream (J; Supplementary Material Fig. S1), due to the greater presence of both semi-aquatic and terrestrial taxa (Fig. 3b). The highest score was recorded at the most downstream site (M; Supplementary Material Fig. S1), which had the lowest taxa richness but the greatest proportion of lotic (fast) taxa. MIS-index scores decreased with an increasing mean number of zero-flow days per year for each site in both autumn and spring (Fig. 3c&d).

Comparison of the MIS-index and the DEHLI and LIFE indices

In autumn, there was some correlation between MIS-index and both LIFE (Spearman $r_s = 0.719$) and DEHLI ($r_s = 0.757$) index scores, despite considerable scatter (Fig. 4). In spring, there was virtually no correlation between MIS-index and either LIFE ($r_s = 0.084$) or DEHLI ($r_s = 0.063$). Comparable patterns were observed when considering only samples associated

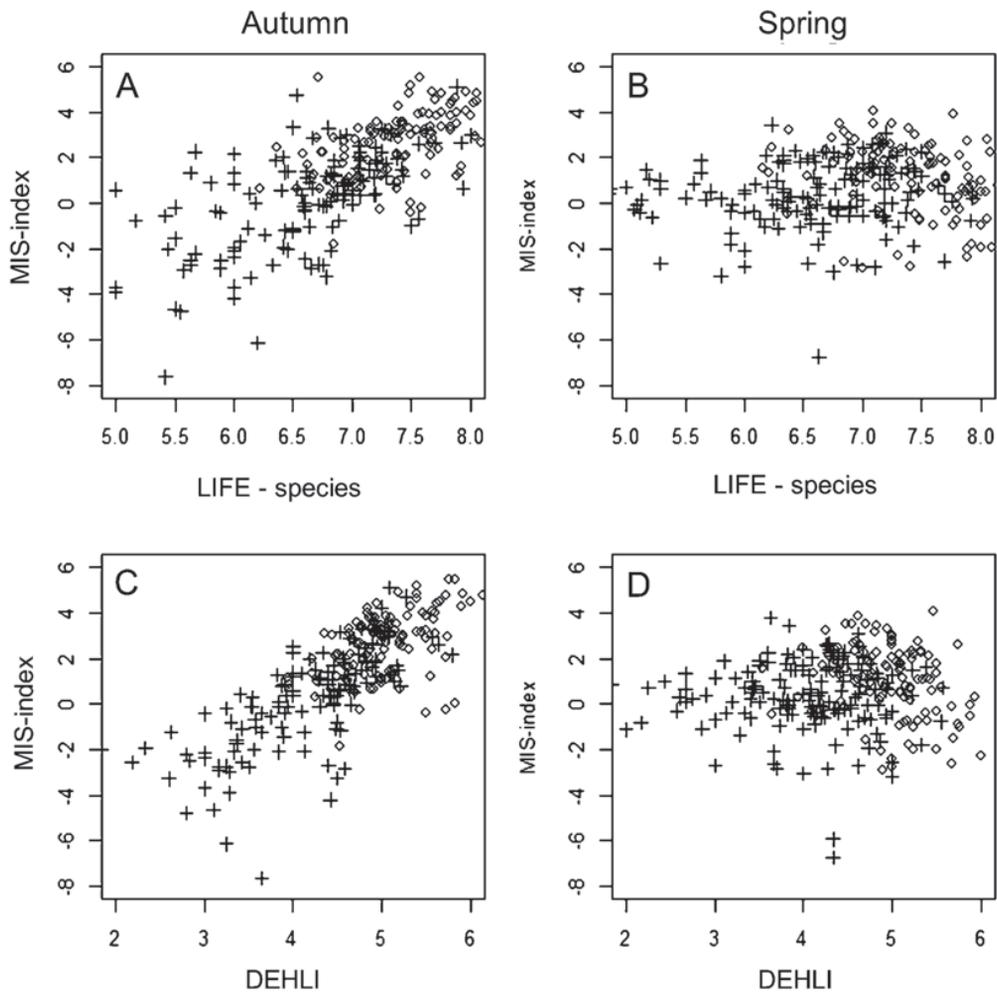


Fig. 4. Associations between MIS-index scores and species LIFE (species) scores (Extence et al. 1999) for autumn (A) and spring (B) and DEHLI scores (Chadd et al. 2017) for autumn (C) and spring (D). Samples associated with zero flow in the antecedent six-month periods are indicated with + and samples with antecedent flowing water conditions with ◇.

with antecedent intermittent flow: in autumn some correlation was observed between the MIS-index and both LIFE and DEHLI ($r_s = 0.613$ and $r_s = 0.775$, respectively), whereas in spring there was no correlation of the MIS-index with either index ($r_s = 0.196$ and $r_s = 0.037$, respectively). In both seasons, samples collected after uninterrupted antecedent flow (i.e. %ZF of 0 for the relative six month period) were associated with higher LIFE and DEHLI scores, but there was no clear trend in MIS-index scores.

MIS-index responses to antecedent %ZF were site specific. In autumn, the MIS-index consistently increased with LIFE scores (Fig. 5a) except at sites 3 and 4 on the River Ver (Fig. 1). In spring (Fig. 5b), negative correlations were observed at one site on the

Ver (3) and three on the River Misbourne (7, 9, 10; Fig. 1). These sites are all located within intermittent upper reaches and experience dry periods of variable duration. In autumn, MIS-index scores consistently increased with DEHLI across all sites (Fig. 5c), whereas in spring, patterns of correlation between indices differed among sites (Fig. 5d). The three sites with negative correlations between MIS-index and DEHLI scores (2, 3 and 6; Fig. 1) are in reaches that regularly experience dry periods exceeding one year. Three sites with a positive correlation between these indices (1, 4 and 8; Fig. 1) also dry, but less regularly and for shorter durations. MIS-index scores changed little as DEHLI increased at the remaining sites, which have variable patterns of intermittence.

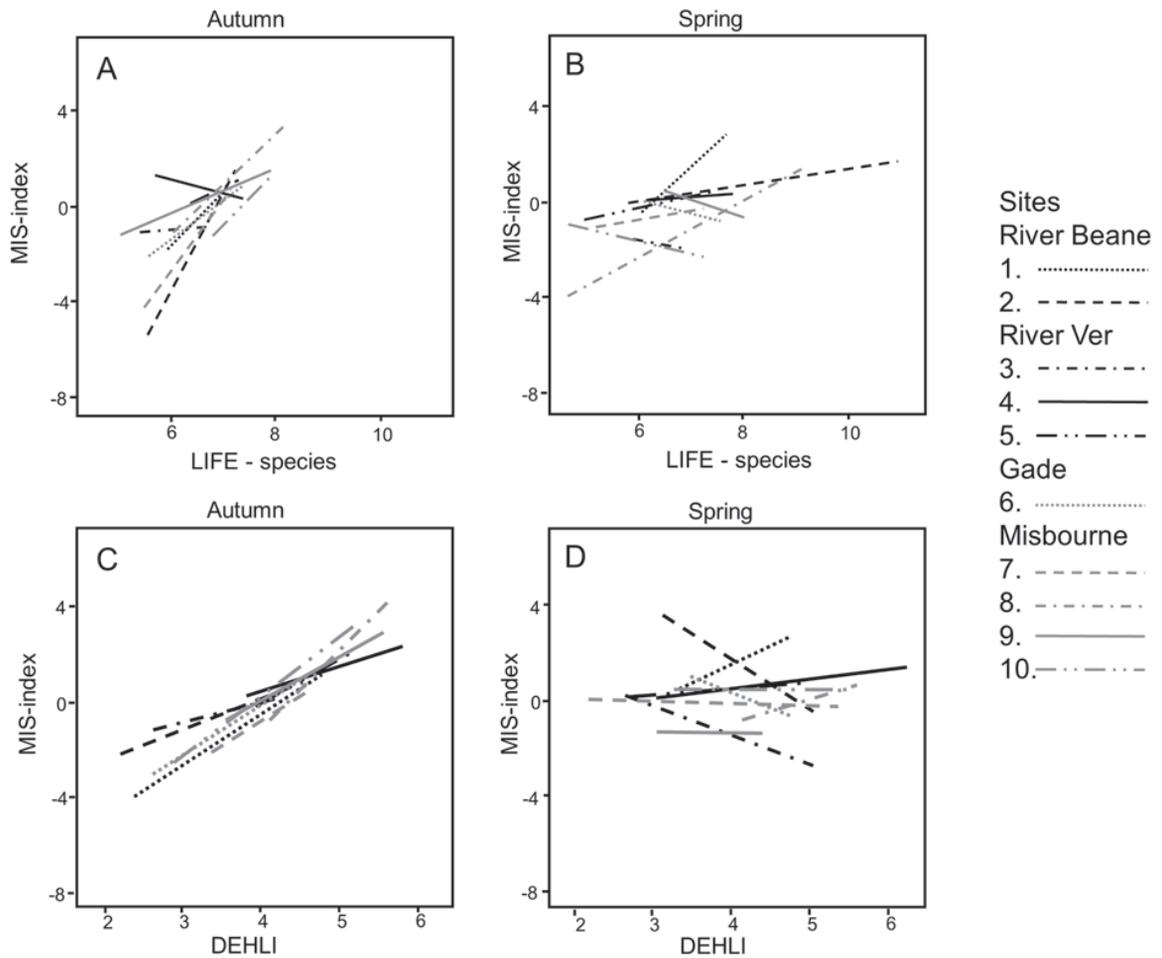


Fig. 5. Associations (fitted as separate linear regression models, $\text{MIS-index} \sim \text{DEHLI}$) between MIS-index scores and species LIFE scores (Extence et al. 1999) for autumn (**A**) and spring (**B**) and DEHLI scores (Chadd et al. 2017) for all samples in autumn (**C**) and spring (**D**) for sites 1–10. Site locations are shown in Fig. 1.

Discussion

Recent research has highlighted the need to improve our understanding of ecological responses to flow intermittence, including recognition that intermittent stream communities comprise dynamic assemblages of taxa spanning the aquatic-terrestrial continuum (Larned et al. 2010; Corti & Datry 2016). The MIS-index is the first attempt to incorporate taxa associated with a full range of habitats, from fast-flowing water to a drying bed, into a single metric indicating community responses to changing instream conditions. By summarizing instream communities in a single score, the MIS-index can inform interpretation of ecological responses to drying in both research and regulatory contexts. Application of our index will enable a more holistic characterization of ecological responses

to surface water loss, thus underpinning international drives towards more effective monitoring of ecological quality in intermittent streams (Mazor et al. 2014; Steward et al. 2018; Stubbington et al. 2018; Stubbington et al. 2019).

Performance of habitat-association groups

The strongest relationships between taxa richness within MIS-groups and environmental metrics were with zero-flow (ZF) days. We observed negative relationships between ZF durations in the two preceding summers and lotic (fast), lotic and generalist taxa during autumn, and negative relationships between ZF periods in the preceding winter (lotic fast) and spring (lotic). These results reflect the higher number of taxa associated with faster velocities during years with longer periods of discharge. In contrast, terrestrial and

semi-aquatic taxa-richness increased with antecedent %ZF metrics, reflecting a greater extent and diversity of damp and dry instream habitats (Datry et al. 2017; Sefton et al. 2019). Our results thus contribute to the emerging recognition of intermittent streambeds as habitats in which high spatial and temporal beta-diversity result from 'time-sharing' by dynamic assemblages of lotic, lentic and terrestrial taxa (Bogan & Lytle 2007; Corti & Datry 2016; Stubbington et al. 2017b).

We noted a positive association between lentic and semi-aquatic taxa in autumn assemblages and %ZF metrics, reflecting the persistence of taxa benefiting from extensive lentic and damp habitats during the preceding summer (Sefton et al. 2019), and supporting the suggestion that colonization of isolated pools by lentic taxa enhances intermittent stream biodiversity (Bogan & Lytle 2007; Hill & Milner 2018). We demonstrated temporal variation in MIS-index scores corresponding to antecedent changes in discharge. Exploration of temporal variability in MIS-index scores in different streams could enable quantification and comparison of biodiversity in streams with contrasting intermittence regimes.

Taxa richness of lotic (fast) and lentic MIS-groups decreased and increased, respectively, with a decrease in mean substrate size. Such relationships likely reflect the scouring effects of increasing flow velocity on substrate composition, as also observed for LIFE index (Dunbar et al. 2010a; Dunbar et al. 2010b). Changes in index scores are underpinned by multiple taxon-specific habitat associations (Buffagni et al. 2009), for example the lotic (fast) MIS-group includes *Hydropsyche* caddisfly and *Simulium* blackfly juveniles, reflecting their flow-dependent feeding habits (Edington & Hildrew 1995; Bass 1998). Our results highlight how intermittence (%ZF) and substrate interact to influence taxa richness in different MIS-groups, with the spatiotemporal variability of physical habitat mosaics promoting high invertebrate biodiversity (Larned et al. 2010; Datry et al. 2016).

After accounting for relationships with substrate characteristics and discharge, the taxa richness of each MIS-index group showed strong temporal trends over the 24-year study period, including an increase in lotic (fast) taxa richness and decreases in generalist, lentic, semi-aquatic and terrestrial taxa richness. These results may indicate that long-term temporal changes in hydrological conditions favoured lotic taxa, which may reflect reductions in groundwater abstraction implemented to increase discharge and changes in intermittence in the Rivers Misbourne and Ver (Perrow

et al. 2007; Clayton et al. 2008). MIS-group richness may also have been responding to uncharacterized variables.

Responses of habitat-association groups to flow statistics

We demonstrated decreases in MIS-index scores in response to the mean number of zero-flow days per year and antecedent intermittence. Although the primary driver of response was intermittence, flow magnitude, as described by Q70z and Q10z, exhibited weaker and more variable relationships with all MIS-index groups than %ZF metrics. These findings suggest that intermittence, and in particular drying, overrides ecological responses to flow magnitude to act as a fundamental driver of community composition (Leigh & Datry 2016; Soria et al. 2017). Our results indicate that this relationship applies to semi-aquatic and terrestrial as well as aquatic invertebrate assemblages, with the magnitude, frequency and duration of inundation events also recognized as key influences on terrestrial community composition in aquatic-terrestrial habitats such as exposed riverine sediments (Sadler et al. 2008) and floodplains (Adis & Junk 2002). Lotic (fast) and lotic MIS-groups were positively associated with greater Q70z low-flow discharges in both seasons, reflecting the increased availability of flowing water habitat at higher discharges. Lotic (fast) in autumn and lotic (fast) and lotic in spring were negatively associated with Q10z, reflecting reduced populations of velocity-dependent taxa at higher peak-flow magnitudes. This may reflect high-flow events scouring sediments and displacing invertebrates during extreme high flows (Palmer et al. 1995).

The positive weak response of the lentic group to Q70z could reflect the extensive still-water marginal habitats available at most sites during higher Q70z in antecedent periods. Such areas can be exploited by associated taxa such as *Cloeon dipterum* mayflies (Buffagni et al. 2009), *Gyraulus laevis* snails (Dillon 2000) and bugs such as *Micronecta* (Savage 1989). Lentic taxa were negatively associated with Q10z, which may reflect the loss of still-water refuges and wash-out of common taxa such as certain Limnephilid caddisflies and *Caenis* mayflies (Gibbins et al. 2009). Higher Q70z in the preceding summer promoted autumn taxa richness in all MIS-groups except generalists, which may reflect the morphology of streams with high width:depth ratios (e.g. Sear et al. 1999) and well-defined low-flow channels (e.g. Berrie 1992), creating both low-flow and high-flow refuges.

Terrestrial taxa responded negatively to Q70z in spring and positively in autumn. In spring, these low flows would be higher throughout the 6 months preceding sampling (i.e. including winter), leaving little or no habitat suitable for terrestrial taxa when Q70z is relatively high. Conversely, in autumn, following higher Q70z in the preceding 6 months (including summer), more terrestrial taxa were present, which may reflect the increased wetting of the marginal areas and increased wash-in of taxa from previously dry areas.

We derived a relatively strong weighting factor for terrestrial taxa despite their relative rarity, highlighting their importance within metrics developed to track the effects of intermittence. Although our sampling approach was not specifically designed to assess semi-aquatic or terrestrial taxa, they are routinely collected, and our results emphasize the advantages of considering these taxa in intermittent stream assessments. Semi-aquatic and terrestrial taxa were restricted to relatively few orders, and comprised mostly beetles (Coleoptera), some true flies (Diptera) and gastropods (Mollusca), and a few true bugs (Heteroptera; Appendix 1). Many such taxa are associated with drying marginal areas and other dynamic aquatic–terrestrial habitats such as temporary ponds (Biggs et al. 2016) and floodplains (Cooper et al. 2009). For example, many carabid beetles of the large *Bembidion* genus inhabit sediments within marginal and riparian zones (Luff 2007); many chrysomelid beetles are strongly associated with river banks (Hubble 2012); and larval stages of terrestrial Diptera such as Stratiomyid soldier flies and Tipulid craneflies are associated with moist sediments in marginal areas (Stubbs & Drake 2014; Boardman 2016).

Comparison with other indices

Our results highlight that the MIS-index complements (and does not replace) the existing indices LIFE (Extence et al. 1999) and DEHLI (Chadd et al. 2017), which concentrate on flow associations and drought-related habitat losses in perennial streams, respectively. In contrast, the MIS-index explores ecological responses to habitat changes including concurrent gain and loss of habitats within a dynamic aquatic–terrestrial mosaic.

We observed some correlation between MIS-index and DEHLI scores in autumn but little within spring, which may reflect the reduced influence of flow or habitat loss on spring communities. The MIS-index responded to %ZF and habitat composition and DE-

HLI to habitat loss, and the correlation between these indices in autumn may reflect the greater influence of habitat availability. In spring, when discharge is generally higher, the variable influences of site-specific conditions, longer antecedent flow intermittence and morphology create more among-site variability in habitat types. These observations suggest that the MIS-index can respond to variation in habitat availability associated with changes in flow independently of the existing indices. We thus highlight its potential to complement such indices by reflecting ecological responses to changing habitat availability for aquatic, semi-aquatic and terrestrial taxa. The MIS-index has particular potential for use in intermittent streams, and ecosystems characterized by temporal changes in the extent of aquatic and terrestrial habitats. The MIS-index could be used alongside other biotic indices to characterize invertebrate community responses to various aspects of hydrological variability, flow intermittence and anthropogenic pressures (e.g. Clews & Ormerod 2009; Extence et al. 2017). However, further research is needed to explore seasonal variation in the MIS-index response to environmental variability.

Future development

MIS-index development was informed by data collected from one river type: the chalk streams of southern England (Mainstone et al. 1999). These globally rare systems include rivers protected by international legislation, making them a UK research and management interest (Chadd et al. 2017; White et al. 2018; Stubbington et al. 2019). Despite our focus, the inclusion of 536 taxa in the index and our documentation of their habitat associations may enable its application, with or without adaptation, to communities in other intermittent stream types across and beyond the UK. Taxon-specific habitat associations are likely to be comparable across regions, as evidenced by the application of indices such as LIFE in hydroecological modelling across and beyond Europe (Dunbar et al. 2010a; Ncube et al. 2018).

The MIS-index requires testing to determine the extent to which the described associations between taxa and habitats and weightings are generally applicable, in particular for semi-aquatic and terrestrial taxa, which are less well explored. Such testing across a wide range of regions and stream types is essential in the development of an index (e.g. Dunbar et al. 2010a; Dunbar et al. 2010b; Armanini et al. 2011; Extence et al. 2017). Notably, our classification of one *terrestrial* group is equivalent to defining a single *aquatic* group,

and its 80 terrestrial members are likely to include ubiquitous taxa (the terrestrial equivalent of our *generalist* group) such as the European crane fly *Tipula paludosa* (CABI 2018), those associated with marginal and riparian habitats (e.g. *Bembidion* spp. and other carabids, Eyre et al. 1996), and potentially intermittent stream specialists (Steward et al. 2011). Wide testing is therefore likely to improve the precision of the defined associations between taxa and different habitats (Supplementary Material Table S1). Any new taxa encountered can be allocated to one or more habitat-association groups, allowing the index to be extended to represent a more diverse range of intermittent stream types across a larger geographical area. We recommend that assessments of intermittent streams also incorporate specific dry-phase assessments (see Steward et al. 2018; Stubbington et al. 2018; Stubbington et al. 2019), to enhance our understanding of the terrestrial taxa that colonize as flow recedes.

Conclusions

We suggest the MIS-index as a tool to complement established indices that demonstrate the ecological effects of changes in habitat availability resulting from hydrological variability, including partial or complete surface water loss. A primary strength of the index is its inclusion of taxa from across the aquatic–terrestrial spectrum, including lentic specialists which exploit slow-flowing and ponded instream habitats and semi-aquatic and terrestrial taxa which colonize as water levels drop below the sediment surface. Recognizing responses to natural intermittence informs our understanding of responses to pressures impacting on ecological quality and biodiversity value of intermittent streams. The MIS-index provides a consistent means of characterizing responses, although testing of the approach is required. We call for scientists and managers to identify the semi-aquatic and terrestrial taxa they collect, to provide the data needed to test this approach. As intermittent streams become increasingly common due to both climatic drivers and water resource pressures (van Vliet et al. 2016), such an approach would enable scientists and managers to consider taxa associated with a full range of instream conditions in holistic ecosystem health assessments.

Acknowledgements

This paper is dedicated to the memory of David Leeming, who developed the concept of the index but sadly died before it could be completed. We thank the numerous experts who

advised regarding the allocation of taxa to habitat-association groups. We thank John Murphy, two anonymous reviewers and the guest editor Paul Wood for their comments, which greatly enhanced this manuscript. The views expressed in this paper are those of the authors and do not necessarily represent the views of their organizations.

Authors' contributions

David Leeming (deceased) developed the original concept of the index, led on the taxa allocations and undertook most of the sampling and invertebrate identification. Chris Westwood collated the hydrological dataset. Mike Dunbar undertook the statistical analysis. Judy England and Richard Chadd contributed to the taxa allocations. Judy England and Rachel Stubbington led the writing of the manuscript (incorporating notes left by David Leeming) with contributions, review and constructive input from the other co-authors.

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Manuscript received: 18 November 2018

Revisions requested: 29 January 2019

Revised version received: 18 June 2019

Manuscript accepted: 24 June 2019

Supplementary Material

Fig. S1. Location of the 23 invertebrate monitoring sites and fixed discharge gauging stations in six chalk streams in the adjacent Colne and Lee catchments in southern England, UK. Site letter codes match those in Table S1.

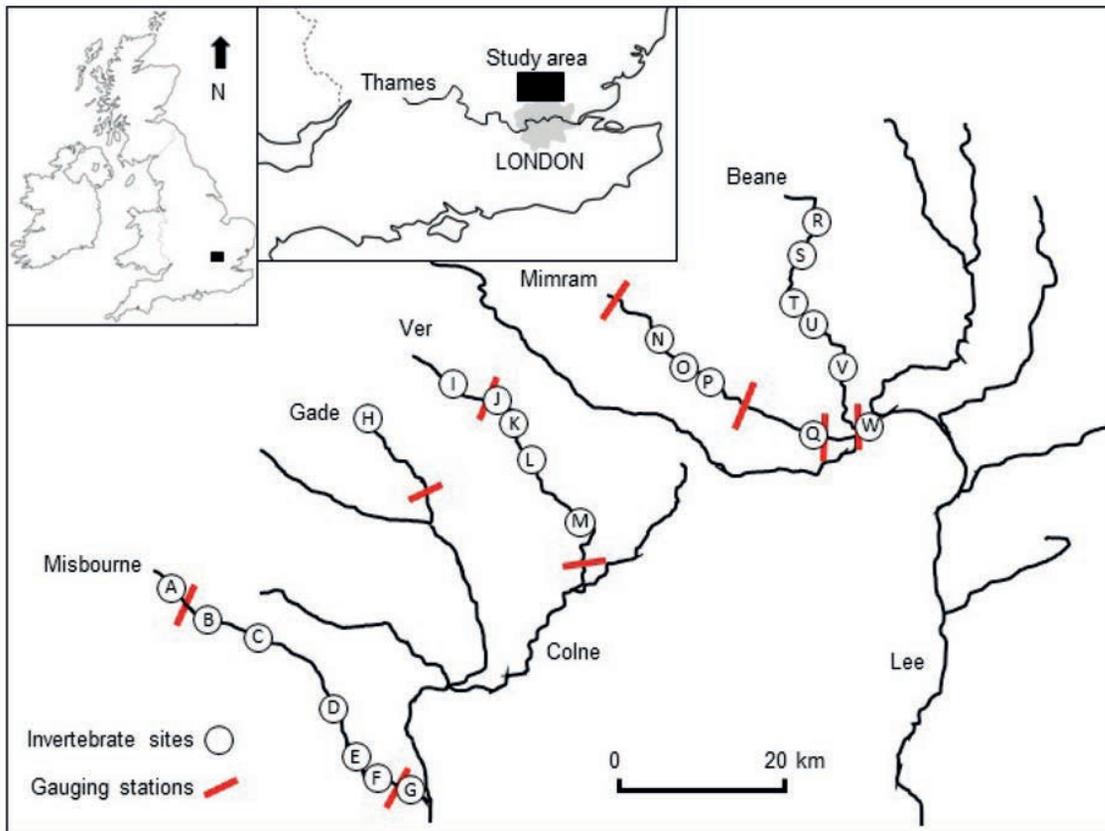


Table S1. Taxa assigned to each habitat preference group.

Lotic (fast)

Agapetus fuscipes Curtis
Agapetus sp.
Brachycentrus subnubilis Curtis
Drusus annulatus (Stephens)
Elmis aenea (Muller)
Heptagenia sulphurea (Muller)
Hydropsyche angustipennis (Curtis)
Hydropsyche instabilis (Curtis)
Hydropsyche pellucidula (Curtis)
Hydropsyche siltalai Dohler
Hydropsyche sp.
Isoptera grammatica (Poda)
Lepidostoma hirtum (Fab.)
Leuctra fusca (Linnaeus)
Limnophora riparia (Fallén)
Leuctra sp.
Micropterna sequax McLachlan
Odontocerum albicorne (Scopoli)
Plectrocnemia conspersa (Curtis)
Rhyacophila dorsalis (Curtis)
Rhyacophila sp.

Rhyacophilidae

Riolus subviolaceus (Muller)
Silo nigricornis (Pictet)
Simulium (Eusimulium) aureum Fries
Simulium (Eusimulium) aureum group
Simulium (Nevermannia) angustitarse (Lundstrom)
Simulium (Nevermannia) angustitarse group
Simulium (Nevermannia) lundstromi (Enderlein)
Simulium (Simulium) ornatum group
Simulium sp.

Lotic.

Adicella reducta (McLachlan)
Agabus biguttatus (Olivier)
Agabus didymus (Olivier)
Agabus paludosus (Fabricius)
Anabolia nervosa (Curtis)
Ancyclus fluviatilis Müller
Athripsodes albifrons (L.)
Athripsodes bilineatus (Linnaeus)
Athripsodes cinereus (Curtis)
Austroptamobius pallipes (Lereboullet)
Baetidae

<i>Baetis rhodani</i> (Pictet)	<i>Tipula (Acutipula) fulvipennis</i> De Geer
<i>Baetis scambus</i> Eaton	<i>Agabus</i> sp.
<i>Baetis vernus</i> Curtis	<i>Agraylea multipunctata</i> Curtis
<i>Brychius elevatus</i> (Panzer)	<i>Agraylea sexmaculata</i> Curtis
<i>Caenis rivulorum</i> Eaton	Ancyliidae (incl. Acroloxidae)
<i>Calopteryx splendens</i> (Harris)	<i>Anisus vortex</i> (L.)
<i>Centroptilum luteolum</i> (Müller)	<i>Antocha vitripennis</i> (Meigen)
<i>Chaetopteryx villosa</i> (Fab.)	<i>Asellus aquaticus</i> (L.)
<i>Chelifera</i> group.	<i>Asellus meridianus</i> Racovitza
<i>Chrysopilus</i> sp.	<i>Athripsodes</i> sp.
<i>Clinocera</i> group.	<i>Bathyomphalus contortus</i> (L.)
<i>Cyrnus trimaculatus</i> (Curtis)	<i>Bithynia leachii</i> (Sheppard)
<i>Dicranota</i> sp.	<i>Bithynia tentaculata</i> (L.)
Elmidae	Caenidae
<i>Ephemera danica</i> Muller	<i>Caenis horaria</i> (L.)
<i>Gammarus pulex</i> (L.)	<i>Caenis luctuosa</i> (Burmeister)
<i>Glossiphonia complanata</i> (L.)	<i>Ceraclea senilis</i> (Burmeister)
<i>Goera pilosa</i> (Fab.)	<i>Ceraclea</i> sp.
Goeridae (pupa)	Ceratopogonidae
<i>Halesus digitatus</i> (Schrank)	Chironomidae
<i>Halesus radiatus</i> (Curtis)	Chordodidae
<i>Halesus</i> sp.	Coenagrionidae
<i>Halipilus (Halipilus) fluviatilis</i> Aube	Colymbetinae (larva)
<i>Halipilus (Liaphlus) laminatus</i> (Schaller)	Copepoda
<i>Hemerodromia</i> group.	<i>Corixa panzeri</i> (Fieber)
<i>Hydroptila</i> sp.	Corixidae (Corixinae) (nymph)
<i>Limnephilus extricatus</i> McLachlan	<i>Dendrocoelum lacteum</i> (Muller)
<i>Limnius volckmari</i> (Panzer)	<i>Dixa nebulosa</i> Meigen
<i>Lype phaeopa</i> (Stephens)	<i>Dixa nubilipennis/maculata</i> agg.
<i>Lype reducta</i> (Hagen)	<i>Dixa submaculata</i> Edwards
<i>Lype</i> sp.	<i>Dixella aestivalis</i> (Meigen)
<i>Nebrioporus elegans</i> (Panzer)	<i>Dugesia polychroa</i> group
<i>Nemurella picteti</i> Klapalek	<i>Dugesia</i> sp.
<i>Niphargus aquilex</i> Schiodte	<i>Dugesia tigrina</i> (Girard)
<i>Notidobia ciliaris</i> (Linnaeus)	Dytiscidae
<i>Orectochilus villosus</i> (Müller)	<i>Elodes</i> sp.
<i>Oulimnius</i> sp.	<i>Eloeophila</i> sp.
<i>Oulimnius tuberculatus</i> (Müller)	Empididae
<i>Oxycera morrisii</i> Curtis	Empididae (gilled pupa)
<i>Oxycera trilineata</i> (L.)	Enchytraeidae
<i>Paraleptophlebia submarginata</i> (Stephens)	<i>Erpobdella octoculata</i> (L.)
<i>Pisidium amnicum</i> (Muller)	Erpobdellidae
<i>Pisidium henslowanum</i> (Sheppard)	<i>Euphyllidorea lineola</i> (Meigen)
<i>Pisidium tenuilineatum</i> Stelfox	Gammaridae (inc. Crangonyctidae)
<i>Platambus maculatus</i> (L.)	<i>Gerris (Gerris) lacustris</i> (L.)
<i>Polycelis felina</i> (Dalyell)	<i>Gerris</i> sp.
<i>Potamophylax latipennis</i> Curtis	<i>Glossiphonia (Alboglossiphonia) heteroclita</i> (L.)
Psychomyiidae	Glossiphoniidae
<i>Seratella ignita</i> (Poda)	<i>Glyphotaelius pellucidus</i> (Retzius)
<i>Sericostoma personatum</i> (Spence)	<i>Gyraulus (Armiger) crista</i> (L.)
<i>Simulium (Simulium) noelleri</i> Friederichs	<i>Gyraulus albus</i> (Müller)
<i>Simulium (Wilhelmia) equinum</i> (L.)	Gyrinidae
<i>Simulium (Wilhelmia)</i> sp.	<i>Gyrinus</i> sp.
<i>Simulium erythrocephalum</i> (De Geer)	<i>Gyrinus substriatus</i> Stephens
<i>Simulium vernum</i> complex	<i>Haemopsis sanguisuga</i> (L.)
<i>Stictotarsus duodecimpustulatus</i> (Fab.)	Halipilidae
<i>Tinodes waeneri</i> (L.)	<i>Halipilus (Halipilus) immaculatus</i> Gerhardt
<i>Valvata piscinalis</i> (Müller)	<i>Halipilus (Halipilus) sibiricus</i> Motschyulsky
<i>Velia caprai</i> Tamanini	<i>Halipilus (Neohalipilus) lineatocollis</i> (Marsham)
<i>Velia</i> sp. (nymph)	<i>Halipilus</i> sp. (larva)
<i>Wiedemannia</i> group	<i>Helius</i> sp.
Generalist.	<i>Helobdella stagnalis</i> (L.)

<i>Helophorus (Helophorus) flavipes</i> Fab.	<i>Pisidium nitidum</i> Jenyns
<i>Helophorus (Helophorus) obscurus</i> Mulsant	<i>Pisidium</i> sp.
<i>Helophorus (Meghelophorus) grandis</i> Illiger	<i>Pisidium subtruncatum</i> Malm
<i>Helophorus (Rhopahelophorus) brevipalpis</i> Bedel	Planariidae (Incl. Dugesiidae)
<i>Helophorus</i> sp.	Planorbidae
<i>Hesperocorixa sahlbergi</i> (Fieber)	<i>Planorbis (Planorbis)</i> sp.
Hydracarina	<i>Planorbis carinatus</i> Müller
<i>Hydraena riparia</i> Kugelann	<i>Planorbis planorbis</i> (L.)
Hydraenidae	<i>Polycelis nigra</i> group
Hydrobiidae (Incl. Bithyniidae)	<i>Polycelis</i> sp.
<i>Hydrometra stagnorum</i> (L.)	Polycentropidae
Hydrophilidae	<i>Polycentropus flavomaculatus</i> (Pictet)
Hydrophilidae (Hydrophilidae) (larva)	<i>Polycentropus irroratus</i> (Curtis)
Hydroporinae	<i>Potamopyrgus antipodarum</i> (Gray)
<i>Hydroporus marginatus</i> (Duftschmidt)	<i>Proclleon pennulatum</i> Eaton
<i>Hydroporus</i> sp. (larva)	<i>Pseudolimnophila</i> sp.
Hydroptilidae	<i>Ptychoptera lacustris</i> Meigen
<i>Ilybius fuliginosus</i> (Fab.)	<i>Ptychoptera minuta</i> Tonnoir
<i>Ischnura elegans</i> (Van der Linden)	<i>Ptychoptera</i> sp.
<i>Laccobius (Macrolaccobius) sinuatus</i> Motschulsky	<i>Radix balthica</i> (L.)
<i>Laccobius (Macrolaccobius) striatulus</i> (Fab.)	<i>Sialis lutaria</i> (L.)
<i>Laccophilus minutus</i> (L.)	<i>Sigara (Sigara) dorsalis</i> (Leach)
Leptoceridae	<i>Sigara (Subsigara) distincta</i> (Fieber)
Limnephilidae	<i>Sigara (Subsigara) falleni</i> (Fieber)
<i>Limnephilus lunatus</i> Curtis	<i>Sigara (Subsigara) fossarum</i> (Leach)
<i>Limnephilus marmoratus</i> Curtis	<i>Sisyra</i> sp.
<i>Limnephilus rhombicus</i> (L.)	Sphaeriidae
<i>Limnephilus</i> sp.	<i>Sphaerium corneum</i> (L.)
<i>Limnephilus vittatus</i> (Fab.)	Spongillidae
<i>Limnophila (Limnophila) punctata</i> group	Stratiomyidae
Limoniidae	<i>Theromyzon tessulatum</i> (Muller)
Lumbriculidae	<i>Tipula (Acutipula) maxima</i> Poda
Lymnaeidae	<i>Tipula (Yamatotipula) montium</i> group
<i>Molanna angustata</i> Curtis	<i>Tipula</i> sp.
<i>Molophilus obscurus</i> group	Tipulidae (Tipulinae)
<i>Molophilus</i> sp.	Tipulidae (Tipuloidea)
Muscidae	<i>Tonnoiriella pulchra</i> (Eaton)
<i>Mystacides azurea</i> (L.)	<i>Trocheta pseudodina</i> Neesemann
<i>Mystacides nigra</i> (L.)	<i>Trocheta subviridis</i> Dutrochet
<i>Mystacides</i> sp.	<i>Ulomyia fuliginosa</i> (Meigen)
Naididae	<i>Valvata cristata</i> Müller
Nematoda	<i>Vanoyia tenuicornis</i> (Macquart)
<i>Neolimnomyia (Neolimnomyia) filata</i> group	Lentic.
<i>Nephrotoma analis</i> Schummel	<i>Episyrphus balteatus</i> (De Geer)
Oligochaeta	<i>Acentria nivea</i> (= <i>ephemerella</i>) (Olivier)
<i>Ormosia (Ormosia)</i> sp.	<i>Acroloxus lacustris</i> (L.)
Ostracoda	<i>Aeshna cyanea</i> (Muller)
<i>Oxycera nigricornis</i> Olivier	<i>Aeshna</i> sp.
<i>Oxycera rara</i> Scopoli	<i>Agabus bipustulatus</i> (L.)
<i>Oxyethira</i> sp.	<i>Agabus nebulosus</i> (Forster)
<i>Pacifastacus leniusculus</i> Dana	<i>Agabus sturmii</i> (Gyllenhal)
<i>Pericoma</i> sp.	<i>Anacaena limbata</i> (Fab.)
<i>Pericoma trivialis</i> group	<i>Anacaena lutescens</i> (Stephens)
<i>Peripsychoda fusca</i> (Macquart)	<i>Anopheles (Anopheles) claviger</i> (Meigen)
<i>Physa fontinalis</i> (L.)	<i>Anopheles (Anopheles)</i> sp.
<i>Physella acuta</i> group	<i>Athripsodes aterrimus</i> (Stephens)
Physidae	<i>Beraea pullata</i> (Curtis)
<i>Pilaria (Pilaria) discicollis</i> group	<i>Beraeodes minutus</i> (L.)
<i>Piscicola geometra</i> (L.)	<i>Berosus</i> sp. (larva)
<i>Pisidium casertanum</i> (Poli)	<i>Caenis robusta</i> Eaton
<i>Pisidium hibernicum</i> Westerlund	<i>Callicorixa praeusta</i> (Fieber)
<i>Pisidium milium</i> Held	<i>Cataclysta lemnata</i> (L.)

- Ceraclea fulva* (Rambur)
Cercyon convexiusculus Stephens
Cercyon sp.
Chaoborus sp.
Chrysogaster (Melanogaster) hirtella group
 Chrysomelidae
 Chydoridae
 Cladocera
Cloeon dipterum (L.)
Coenagrion puella (L.)
Colymbetes fuscus (L.)
Corixa punctata (Illiger)
Corixa sp. (nymph)
Crangonyx pseudogracilis Bousfield
Culex sp.
 Culicidae (pupa)
Culiseta (Culiseta) annulata group
Cymatia coleoptrata (Fab.)
Cyphon sp. (larva)
Dixella autumnalis (Meigen)
Dixella martinii (Peus)
Dryops sp. (larva)
Dytiscus marginalis L.
Dytiscus sp.
Elophila nymphaeata (L.)
Enallagma cyathigerum (Charpentier)
Enochrus melanocephalus (Olivier)
Ephydra sp.
 Ephyridae
Eristalis group
Erpobdella testacea (Savigny)
Gerris (Gerris) odontogaster (Zetterstedt)
Gerris (Gerris) thoracicus Schummel
Guignotus pusillus (F.)
Gyraulus laevis (Alder)
Haliphus (Haliphiidius) confinis Stephens
Haliphus (Liaphlus) flavicollis Sturm
Hecamede albicans (Meigen)
Helochares lividus (Forster)
Helophorus (Helophorus) griseus Herbst
Helophorus (Meghelophorus) aequalis Thomson
Hemiclepsis marginata (Muller)
Hesperocorixa linnaei (Fieber)
Hesperocorixa moesta (Fieber)
Hippeutis complanatus (L.)
Hydrellia sp.
Hydrobius fuscipes L.
Hydroporus palustris (L.)
Hydroporus planus (Fab.)
Hygrobia hermanni (Fab.)
Hygrotus impressopunctatus (Schaller)
Hygrotus inaequalis (Fab.)
Hyphydrus ovatus (L.)
Laccobius (Laccobius) colon (Stephens)
Laccobius (Macrolaccobius) bipunctatus (Fab.)
Laccophilus hyalinus (De Geer)
Laccophilus sp. (larva)
Leptocerus tineiformis Curtis
Limnephilus flavicornis (Fab.)
Limnephilus rhombicus (L.)
Lymnaea stagnalis (L.)
Micronecta (Micronecta) poweri (Douglas & Scott)
Micronecta sp.
Microvelia reticulata (Burmeister)
Musculium lacustre (Muller)
Mystacides longicornis (L.)
Nepa cinerea L.
Notonecta glauca L.
Notonecta maculata Fab.
Notonecta sp.
Notonecta viridis Delcourt
Nymphula stagnata (Donovan)
Oplodontha viridula (Fab.)
Parydra sp.
Phryganea bipunctata Retzius
Phryganea grandis L.
 Phryganeidae
Pisidium obtusale (Lamarck)
Planorbarius corneus (L.)
Plateumaris sericea (L.)
Plea minutissima Leach
Pyrrosoma nymphula (Sulzer)
Rhantus exsoletus (Forster)
Rhantus sp. (larva)
Rhantus suturalis (MacLeay)
 Sciomyzidae
Sigara (Pseudovermicorixa) nigrolineata (Fieber)
Sigara (Vermicorixa) lateralis (Leach)
 Sphaeriidiinae
Stagnicola fusca/palustris (Müller/Pfeiffer)
Stratiomys potamida (Meigen)
Stratiomys sp.
Sympetrum sp.
Sympetrum striolatum (Charpentier)
 Syrphiidae (Syrphiinae)
Tetanocera ferruginea group
Semi-aquatic.
Agonum (Europhilus) fuliginosum (Panzer)
Agonum (Europhilus) thoreyi Dejean
Altica lythri Aube
Anisus leucostoma Millet
Anotylus rugosus (Fab.)
Ashfordia granulata (Alder)
Bembidion (Diplocampa) assimile Gyllenhal
Beris sp.
Bibio sp.
 Calliphoridae
 Cantharidae
 Cecidomyiidae
 Chloropidae
 Chrysomelinae (larva)
Coccidula rufa (Herbst)
 Collembola
 Dolichopodidae
Drupenatus nasturtii (Germar)
Euastethus sp.
Euconulus alderi Gray
Galba truncatula (Müller)
Galerucella lineola (Fab.)
Galerucella nymphaeae (L.)
Ischnodemus sabuleti (Fallén)
 Isotomidae
Lesteva punctata Erichson
Lesteva sp.
Limonia sp.
Lispe sp.

<i>Lonchoptera</i> sp.	<i>Cionus tuberculatus</i> (Scopoli)
Lumbricidae	<i>Cochlicopa lubrica</i> (Müller)
Lycosidae	<i>Cochlicopa lubricella</i> (Porro)
<i>Nephrotoma quadrifaria</i> (Meigen)	<i>Cochlicopa</i> sp.
<i>Oscinella</i> sp.	<i>Contarinia</i> sp.
<i>Oxychilus cellarius</i> (Müller)	<i>Crepidodera</i> (= <i>Chalcoides aurata</i>) (Marshall)
<i>Oxychilus helveticus</i> (Blum)	<i>Curtonotus aulicus</i> (Panzer)
<i>Oxychilus</i> sp.	Delphacidae
<i>Oxyloma pfeifferi</i> (Rossmassler)	Diptera Indet.
<i>Phaedon armoraciae</i> (L.)	<i>Discus rotundatus</i> (Müller)
<i>Phaedon cochleariae</i> (Fab.)	<i>Dohrniphora</i> sp.
<i>Phaedon</i> sp.	<i>Drosophila subobscura</i> group
<i>Pirata</i> sp.	Drosophilidae
<i>Pisidium personatum</i> Malm	Elateridae (larva)
<i>Prasocuris junci</i> (Brahm)	<i>Fannia</i> sp.
<i>Prasocuris phellandrii</i> (L.)	Halticinae
<i>Psammoecus bipunctatus</i> Fab.	<i>Heterogaster urticae</i> (Fab.)
<i>Pteromicra</i> sp.	Indet. Calyptata pupae
<i>Saldula saltatoria</i> (L.)	<i>Lauria cylindracea</i> (da Costa)
<i>Scatopse</i> sp.	<i>Leistus spinibarbis</i> (Fab.)
Scatopsidae	<i>Longitarsus parvulus</i> (Paykull)
Staphylinidae	<i>Longitarsus</i> sp.
Staphylinidae: Aleocharinae	<i>Megasternum concinnum</i> (Marshall)
<i>Stenus (Hypostenus) cicindeloides</i> (Schaller)	<i>Meligethes aeneus</i> (Fab.)
<i>Stenus (Hypostenus) solutus</i> Erichson	<i>Microchrysa polita</i> (L.)
<i>Stenus (Metastenus) bifoveolatus</i> Gyllenhal	<i>Monacha cantiana</i> (Montagu)
<i>Stenus (Metastenus) canescens</i> Rosenhauer	<i>Nephrotoma flavescens/maculata</i>
<i>Stenus (Metastenus) nitidiusculus</i> Stephens	<i>Nephrotoma flavipalpis</i> (Meigen)
<i>Stenus (Metastenus) picipennis</i> Erichson	<i>Nesovitrea (Perpolita) hammonis</i> (Ström)
<i>Stenus (Metastenus) pubescens</i> Stephens	<i>Pachygaster (Praomyia) leachii</i> (Curtis)
<i>Stenus (Stenus) boops</i> Ljungh	<i>Pachygaster atra</i> (Panzer)
<i>Stenus (Stenus) clavicornis</i> (Scopoli)	<i>Paradromius linearis</i> (Olivier)
<i>Stenus (Stenus) juno</i> (Paykull)	Phoridae
<i>Stenus (Stenus) nitens</i> Stephens	<i>Phyllobius pyri</i> (L.)
<i>Stenus</i> sp.	<i>Phyllotreta atra</i> (Fab.)
<i>Succinea putris</i> (L.)	<i>Phyllotreta nigripes</i> (Fab.)
Succineidae	<i>Plagiognathus arbustorum</i> (Fab.)
Tabanidae	<i>Platypeza</i> sp.
<i>Tipula (Lunaticipula) vernalis</i> Meigen	<i>Pogonocherus hispidus</i> (L.)
<i>Tipula (Savtshenkia) staegeri</i> Nielsen	<i>Protapion nigritarse</i> (Kirby)
<i>Tipula (Tipula) oleracea</i> group	Psilidae
<i>Tytthaspis sedecimpunctata</i> (L.)	<i>Psylliodes affinis</i> (Paykull)
<i>Zonitoides nitidus</i> (Müller)	<i>Rhizophagus parallellocollis</i> Gyllenhal
Terrestrial.	<i>Rhizobius litura</i> (Fab.)
<i>Aegopinella nitidula</i> (Draparnaud)	<i>Sargus/Chlorisops</i> Indet.
<i>Amara familiaris</i> (Duftschmid)	Sciaridae
<i>Anthocoris nemorum</i> (L.)	<i>Scolopostethus affinis</i> (Schilling)
<i>Aphodius contaminatus</i> (Herbst)	<i>Sehirus luctuosus</i> Mulsant & Rey
<i>Aphodius prodromus</i> (Brahm)	<i>Silpha laevigata</i> F.
<i>Aphthona euphorbiae</i> (Schrank)	<i>Simplocaria semistriata</i> (Fab.)
<i>Atheta fungi</i> (Gravenhorst)	<i>Sitona humeralis</i> Stephens
<i>Atheta</i> sp.	<i>Sitona lineatus</i> (L.)
<i>Barypeithes pellucidus</i> (Boheman)	Stratiomyidae (Pachygastrinae)
<i>Bembidion (Metallina) lampros</i> (Herbst)	<i>Tachyporus solutus</i> Erichson
<i>Callicerus rigidicornis</i> (Erichson)	Terrestrial Coleoptera
Carabidae	Terrestrial Coleoptera (larva)
Carabidae (larva)	Terrestrial Hemiptera
<i>Cepaea</i> sp.	<i>Tipula (Lunaticipula) lunata</i> L.
Cercopidae	<i>Tipula (Savtshenkia) obsoleta</i> Meigen
<i>Ceutorhynchus pallidactylus</i> (= <i>quadridens</i>) (Marshall)	<i>Tipula (Tipula) paludosa</i> Meigen
<i>Chloromyia formosa</i> (Scopoli)	<i>Trichia (Trochulus) striolatus</i> (Pfeiffer)
<i>Chrysomela populi</i> L.	<i>Trichocera hiemalis</i> (Degeer)

Table S2. Mean number of zero-flow days year⁻¹; total number of samples; and the number of samples for which zero-flow days occurred during the antecedent time periods, i.e. the six-month ‘summer’ or ‘winter’ seasons prior to sampling, for each invertebrate monitoring site. Site codes match locations shown in Fig. S1 for all sites and in Fig 1. for the sites used for more detailed comparisons of the MIS-index and LIFE and DEHLI scores (see Fig. 4).

Site (Fig. S1)	Site (Fig. 1)	Mean number of zero-flow days year ⁻¹	Total number of samples	Number of samples with zero-flow days in the antecedent 6-month season
A	7	80.6	27	9
B	8	44.8	37	14
C	9	111.5	28	12
D	10	201.8	11	9
E		0	41	0
F		0	38	0
G		0	35	0
H	6	72.4	35	16
I	3	249.6	11	10
J	4	102.2	29	14
K	5	102.2	32	15
L		8.1	30	0
M		0	26	0
N		5.6	3	0
O		33.2	3	0
P		5.6	3	0
Q		0	32	0
R	1	161.1	27	27
S	2	87	23	16
T		87	4	0
U		45	5	0
V		45	5	0
W		0	18	0

Table S3. Summary of the linear regression analyses used to derive site-specific discharge (see Gordon et al. 2004) for each invertebrate monitoring site. Site codes match locations shown in Fig. S1.

Site	Distance (m) to spot gauge or gauging station	Regression	R ₂ value	
A	0	Direct gauge data used		Little Missenden gauging station
B	250	$y = 1.199x - 0.040$	0.887	
C	0	$y = 1.229x - 0.583$	0.583	October 1993 – October 2010
		$y = 1.033x - 0.050$	0.901	November 2010 – January 2016
D ¹	82	$y = 0.672x - 0.092$	0.665	October 1993 – May 2010
		$y = 2.455x - 0.247$	0.949	November 2000 – January 2008
		$y = 1.156x - 0.163$	0.789	February 2011 – June 2015
		$y = 1.652x - 0.144$	0.700	December 2000 – June 2016
E ¹	0	$y = 0.740x - 0.026$	0.886	
F	714	Direct gauge data used		Denham Lodge gauging station
G	276	Direct gauge data used		Denham Lodge gauging station
H	0	$y = 0.302x - 0.046$	0.792	
I	0	$y = 0.702x - 0.0485$	0.882	
J	147	Direct gauge data used		Redbourn gauging station
K	600	Direct gauge data used		Redbourn gauging station & River Red
L	17	$y = 0.849x - 0.029$	0.775	
M	26	$y = 0.843x - 0.054$	0.958	
N	0	$y = 2.227x - 0.005$	0.935	
O	468	$y = 2.227x - 0.005$	0.935	
P	0	$y = 2.935x - 0.048$	0.940	
Q	0	Direct gauge data used		Panshanger gauging station
R	1100	$y = 0.076x - 0.044$	0.548	
S	0	$y = 0.091x - 0.021$	0.626	
T	0	$y = 0.164x - 0.045$	0.667	
U	0	$y = 0.184x - 0.039$	0.848	
V	900	$y = 0.369x - 0.024$	0.810	
W	160	Direct gauge data used		Hartham Park gauging station

¹ Sites D and E have multiple regressions, reflecting changes in hydrological relationship during different times and under different discharge conditions.

Discharge data for the gauging stations can be obtained from the National River Flow Archive: <https://nrfa.ceh.ac.uk/>

We thank hydrologists at the Environment Agency and Affinity Water who provided the regression equations.

Table S4a. Model-averaged parameter estimates with standard errors for separate models for taxa richness in each MIS-group – autumn data. The variables substrate, Q10z, Q70z and Year were re-scaled to occupy a 0–100 scale.

MIS-group	Intercept	Substrate (phi)	%ZF ² days antecedent summer	%ZF ² days summer of previous year	Q10z ³	Q70z ⁴	Year
Lotic-fast	1.46 (0.26)	-0.010 (0.003)	-0.009 (0.004)	-0.003 (0.002)	-0.002 (0.003)	0.002 (0.003)	0.003 (0.002)
Lotic	1.97 (0.15)	-0.002 (0.002)	-0.001 (0.002)	-0.006 (0.002)	0.0001 (0.002)	0.001 (0.002)	0.0006 (0.001)
Generalist	2.89 (0.13)	0.002 (0.001)	-0.002 (0.001)	-0.002 (0.001)	-0.001 (0.001)	-0.001 (0.001)	-0.003 (0.0009)
Lentic	1.72 (0.39)	0.005 (0.003)	0.004 (0.002)	0.005 (0.002)	-0.006 (0.004)	0.001 (0.005)	-0.019 (0.003)
Semi-aquatic	0.85 (0.32)	-0.001 (0.003)	0.008 (0.003)	-0.0004 (0.003)	-0.006 (0.006)	0.005 (0.007)	-0.012 (0.003)
Terrestrial	-0.795 (0.81)	0.006 (0.007)	0.0128 (0.008)	0.011 (0.005)	-0.034 (0.023)	0.029 (0.021)	-0.022 (0.007)

² % zero flow³ standardized discharge exceeded 10% of the time⁴ standardized discharge exceeded 70% of the time**Table S4b.** Model-averaged parameter estimates with standard errors for separate models for taxa richness in each MIS-group – spring data. The variables substrate, Q10z, Q70z and Year were re-scaled to occupy a 0–100 scale.

MIS-group	Intercept	Substrate (phi)	%ZF ² days antecedent summer	%ZF ² days summer of previous year	Q10z ³	Q70z ⁴	Year
Lotic-fast	0.801 (0.26)	-0.008 (0.003)	-0.007 (0.003)	-0.002 (0.002)	-0.001 (0.002)	0.003 (0.002)	0.008 (0.002)
Lotic	1.97 (0.17)	-0.003 (0.002)	-0.009 (0.002)	-0.001 (0.002)	-0.003 (0.002)	0.003 (0.002)	0.001 (0.001)
Generalist	3.09 (0.10)	0.001 (0.001)	-0.004 (0.001)	-0.002 (0.001)	-0.002 (0.001)	-0.0004 (0.001)	-0.004 (8e-04)
Lentic	0.85 (0.28)	0.0096 (0.003)	-0.003 (0.002)	0.002 (0.002)	-0.005 (0.003)	0.002 (0.004)	-0.009 (0.002)
Semi-aquatic	0.91 (0.30)	-0.004 (0.003)	0.0014 (0.002)	-0.002 (0.002)	0.003 (0.004)	-0.004 (0.004)	-0.007 (0.003)
Terrestrial	-0.23 (0.44)	-0.001 (0.004)	0.0138 (0.003)	0.002 (0.004)	-0.006 (0.008)	-0.012 (0.004)	-0.022 (0.003)

² % zero flow³ standardized discharge exceeded 10% of the time⁴ standardized discharge exceeded 70% of the time

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