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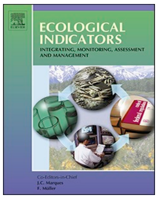

Biological indices to characterize community responses to drying in streams with contrasting flow permanence regimes

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ABSTRACT

Many river networks include temporary reaches that stop flowing and may dry during unpredictable droughts (near-perennial) or more frequently (intermittent). A few biological indices have been developed to assess invertebrate community responses to hydrological variability, including the instream conditions associated with drought, but their performance in temporary streams remains poorly known. We evaluated the ability of two such indices, the *Lotic-invertebrate Index for Flow Evaluation* (LIFE) and the *Drought Effect of Habitat Loss on Invertebrates* (DEHLI), to predict responses to flow cessation and drying in temporary streams with contrasting flow permanence regimes. We used a 26-year dataset comprising spring-season invertebrate community samples and daily discharge measurements from 46 sites in a cool, wet temperate region, to examine relationships between hydrological variables and changes in index scores. We also identified taxon-specific thresholds at which occurrence changed with increasing drying and flowing durations. Both indices effectively characterized responses to increasing no-flow durations. DEHLI also reflected community changes following flow resumptions, identified differences in responses among flow permanence groups, and was particularly able to predict community responses at near-perennial sites. DEHLI scores at near-perennial sites took on average three years after a drying event to return to values typical of perennial sites, whereas responses to increasing flow duration were more erratic at intermittent sites. Lotic specialists declined whereas lentic and semi-aquatic taxa increased in occurrence with no-flow duration after summers with < 50 days without flow, due to changes in the availability of preferred habitat types. Community responses to drying events were less predictable among intermittent than near-perennial sites, likely because differences in habitat conditions and connectivity may lead intermittent communities to harbour contrasting pools of species with strategies that promote persistence during and/or recolonization after drying. We identify DEHLI as an index that can characterize community responses to drying in temporary streams with contrasting flow permanence regimes. We also recommend the development of new indices that include lentic, semi-aquatic and terrestrial as well as lotic taxa, to more comprehensively describe and predict community responses to changing instream conditions.

1. Introduction

Temporary streams are defined by flow cessation, and typically experience partial or complete drying of the streambed sediments (Leigh et al., 2016; Datry et al., 2017). Dominant in dryland river networks, temporary streams are also widespread and common in cool, wet temperate regions (Fritz et al., 2013; Stubbington et al., 2017). Here, flow permanence regimes are diverse, with natural drying forming a predictable, seasonal part of the hydrological cycle in many reaches and also occurring at near-perennial sites during unpredictable droughts (e.g. Larned et al., 2011; Stubbington et al., 2016). In addition, interacting climatic drivers and water resource pressures have increased the spatial and temporal extent of drying in densely populated regions, including shifts to non-natural temporary flow regimes (van Vliet et al., 2013; Chiu et al., 2017). Regardless of cause, drying constitutes a disturbance (sensu Townsend, 1989) and acts as a strong environmental filter that reduces aquatic alpha diversity (Datry et al., 2017; Leigh and Datry, 2017).

Aquatic communities typically differ between perennial and temporary streams and among sites with contrasting temporary flow regimes (Bonada et al., 2007; Katz et al., 2012; Mathers et al., 2019). Communities at sites that often dry may be dominated by resistant and/or resilient taxa (sensu Townsend and Hildrew, 1994). Desiccation-

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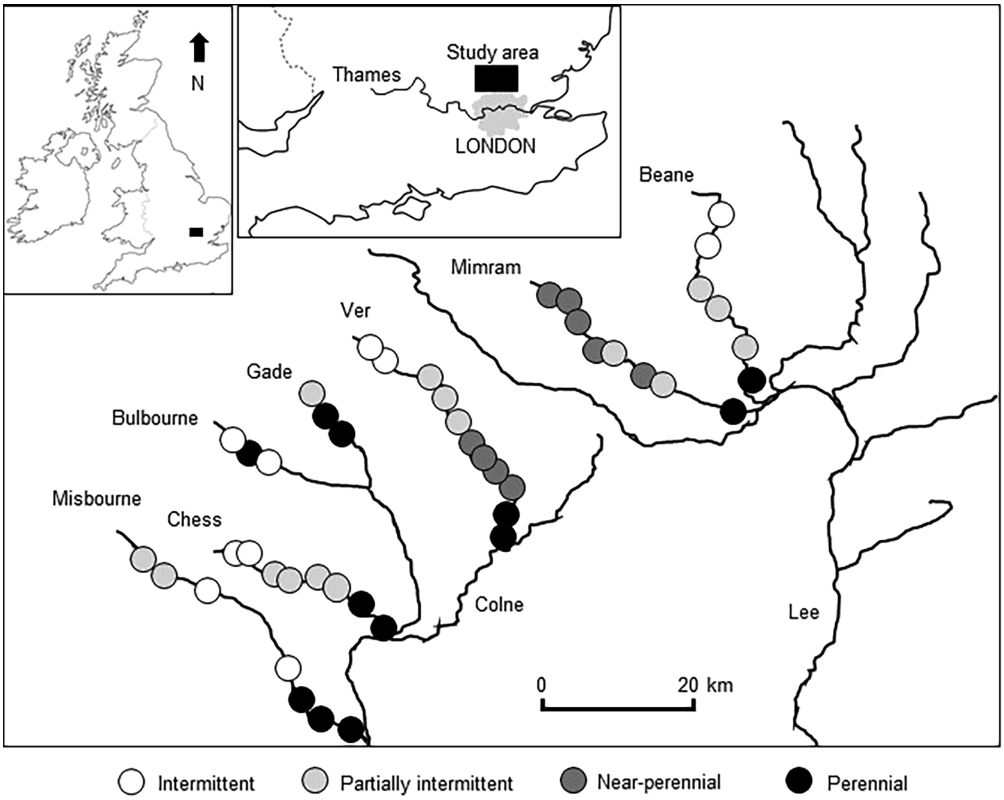

Fig. 1. Location of the study area and study sites. Each site is colour-coded according to its flow permanence regime.

resistant life stages may persist within drying sediments alongside semi-aquatic taxa (Stubbington and Datry, 2013), while lentic taxa may thrive in ponded reaches and isolated pools (Bogan and Lytle, 2007; Hill and Milner, 2018). Resilient lotic taxa recolonize rapidly after flow resumptions, especially where perennial refuges persist nearby, as is common in cool, wet temperate regions (Boulton, 1989; Hill and Milner, 2018; Pařil et al., 2019). In contrast, near-perennial sites may be dominated by lotic taxa that prefer continuous flow, and communities are severely impacted by drying during unpredictable drought disturbance (sensu Resh et al., 1988). Recovery trajectories may extend over multiple years (Resh, 1992; Wood and Petts, 1999), although long-term studies remain limited (Bêche et al., 2009; Chessman, 2015; Mathers et al., 2019). Temporary stream communities also respond to high flows (Fritz and Dodds, 2004; Suren and Jowett, 2006; Bae and Park, 2019) with season-specific responses reflecting changes in the life stages present (Milner et al., 2018).

Natural temporary streams support high biodiversity and perform ecological functions that provide valued ecosystem services (Koundouri et al., 2017; Datry et al., 2018). Biological indices are thus needed to assess how drying affects communities at sites with contrasting flow permanence regimes, including responses to drying and recovery after flow resumes. The *Lotic-invertebrate Index for Flow Evaluation* (LIFE; Extence et al., 1999) characterizes invertebrate community responses to hydrological variability during flowing phases (Dunbar et al., 2010a), but may become less effective at low flows (Monk et al., 2006). Addressing this limitation, the *Drought Effect of Habitat Loss on Invertebrates* (DEHLI) index (Chadd et al., 2017) complements LIFE, describing responses to changes in habitat availability associated with drought development – changes that also occur as temporary streams transition from flowing to ponded then dry states. However, although DEHLI is more sensitive than LIFE to very low flow conditions (Chadd et al., 2017), only the performance of LIFE has been examined in temporary streams (Wilding et al., 2018).

LIFE, DEHLI and other indices summarize community responses to instream habitat conditions, with taxa assigned numeric values that reflect their association with particular environmental states based on expert judgement (Extence et al., 1999; Chadd et al., 2017; Straka et al., 2019). These valuable tools can thus be complemented by characterization of the taxon-specific responses underpinning an observed community-based score (Baker and King, 2010). In particular, identifying the thresholds at which taxon occupancy decreases or increases in response to drying duration could highlight potential 'tipping points' at which biodiversity is reduced by the concurrent loss of multiple taxa (King et al., 2016), creating communities dominated by drying-tolerant specialists (Chase, 2007; Bogan et al., 2013), with consequences for ecosystem functioning. Equally, identifying the temporal change points at which taxa recover after flow resumes could distinguish those that are resistant, resilient, or sensitive to drying. As drying increases in occurrence and intensity due to climate change and water resource pressures (Ledger and Milner, 2015; Spinoni et al., 2018), sensitive taxa may become more vulnerable to extinction if flowing phases remain below the durations needed for recolonization (Bogan et al., 2013; Vanschoenwinkel et al., 2013).

Our aim was to evaluate and compare the ability of two existing indices (DEHLI and LIFE), each developed to summarize invertebrate community responses to hydrological variability, to predict responses to drying events in temperate-zone temporary streams with variable flow permanence regimes. Our specific objectives were: (1) to identify the environmental factors explaining variability in index scores, including among-site differences in flow permanence and the occurrence of no-flow conditions; (2) to evaluate the ability of each index to characterize community responses to these factors; and (3) to characterize taxon-specific responses to flow cessation/drying and to flow resumption, including the thresholds (i.e. the no-flow/drying and flowing durations) at which occupancies increase or decrease.

2. Materials and methods

2.1. Study area

The study area includes seven groundwater-fed rivers (ranging from 10 to 22 km in length), draining the Cretaceous chalk of the River

Thames catchment in southern England, UK (Fig. 1). The river catchments are dominated by arable (mean ± standard deviation [SD] = 53 ± 15%), pasture (27 ± 11%) and urban (12 ± 6%) land uses (Table S1). The climate is temperate with an oceanic influence (i.e. Köppen-Geiger classification Cfb), the mean annual precipitation is 675 mm (National River Flow Archive, 2019) and the mean annual temperature is 9.9 °C (Met Office, 2019). Groundwater inputs influence river discharge, with typical seasonal time lags between precipitation inputs and changes in surface discharge (Grapes et al., 2005). Discharge typically peaks in late winter (February–March), then declines as groundwater levels drop in summer, leading to lowest discharge in late summer/autumn, and potentially to partial or total streambed drying at non-perennial sites. Although dry phases are typically seasonal and predictable, the spatial extent and timing of drying vary considerably among years in relation to groundwater levels and antecedent precipitation, and drying can last for multiple years during drought events (i.e. prolonged periods of below-average precipitation; Tallaksen and Van Lanen, 2004). Further details of the flow regimes and instream states are provided by Sefton et al. (2019). The sites are geomorphologically diverse, including channels that have been modified historically for land drainage, watercress cultivation and mill water provisioning, and more natural reaches with high width:depth ratios (Sear et al., 1999) and well-defined low-flow channels (Berrie, 1992). Sampling sites were located away from direct modifications such as weirs and bank reinforcement, which may have affected local flow conditions. As is typical in groundwater-fed chalk streams, those in the study area are characterized by high alkalinity, conductivity and nutrient levels due to the influence of the underlying bedrock (Berrie, 1992). Sites had good to high water quality based on nitrate concentrations and dissolved oxygen in perennial sections, whereas 33% of sites had moderate or lower phosphate-based quality (Fig. S1, Table S1).

2.2. *Invertebrate samples and biological indices*

We used a dataset comprising 1436 invertebrate samples collected by the Environment Agency (the regulatory authority in England, UK) from 46 river sites in spring (March–May; n = 728; mean ± SD = 16 ± 5 samples site^{-1}) and (September–November; n = 708; 15 ± 7 samples site^{-1}) between 1991 and 2017 (Fig. 1). Not all sites were sampled in all years or both seasons due to drying of sampling sites and changes in regulatory monitoring programmes.

Samples were collected following the standard approach (ISO, 2012) of a 3-min kick/sweep technique using a pond net (0.05 m^2 aperture, 1-mm mesh) with an additional 1-min hand search, including all available habitats in proportion to their occurrence. Aquatic invertebrates were mostly identified to family level, with the exceptions of Oligochaeta, Ostracoda and Hydracarina, which were identified as such. Taxa occurring in on average less than one sample were excluded from all analyses, to minimize biases and noise.

For each sample, we calculated the LIFE (Extence et al., 1999) and DEHLI (Chadd et al., 2017) indices. LIFE is calculated for an invertebrate assemblage by assigning each taxon to both a *flow group* (FG) that reflects its association with fast, moderate, slow-flowing or standing waters or drying/drought-impacted conditions, and to an estimated *abundance class*. Assigned FGs and abundance classes are then combined to give a *flow score* to each taxon, with the mean flow score for all scoring taxa providing the LIFE score for a sample. DEHLI is calculated by assigning each taxon a *drought intolerance* (DI) score based on its association with instream habitats which are typically lost as discharge declines. The DEHLI score for a sample is the mean DI score for all scoring taxa present. Theoretically, LIFE scores range from 0 to 12 and DEHLI scores from 0 to 10, but typically LIFE varies between 5.5 and 8.5 and DEHLI between 2 and 8, with higher and lower scores indicating communities dominated by taxa with affinities with fast-flowing and drying habitats, respectively.

2.3. *Hydrological and other environmental data*

Mean daily discharge was modelled at each invertebrate sampling site (n = 46) based on linear regressions between the spot-gauging records closest to the sampling site and daily discharge data from the nearest gauging station (Fig. S1, Table S2; see Gordon et al., 2004). This type of regression has been demonstrated as suitable for, and is commonly used in, studies examining site-specific ecological responses to hydrological conditions (Gordon et al., 2004; Westwood et al., 2017).

To characterize site-specific flow permanence regimes, we calculated the proportion of years with at least one no-flow event of at least one day (%NFY) and the mean number of no-flow days year^{-1} (MNFY) at each site based on long-term (1995–2017) modelled daily discharge (Table S1). Although 1991–2017 discharge data were available for most sites, we used the period 1995–2017 to calculate %NFY and MNFY because one gauging station started operating in 1994. 'No-flow' days had daily discharges $< 0.001\,\mathrm{m^3\,s^{-1}}$, indicating that water stopped flowing but not necessarily that the site dried; observational data demonstrate that the longer the no-flow period, the more likely a site is to have dried (Sefton et al., 2019). We used %NFY to classify sites into four flow permanence groups: perennial (PR, 0% NFY), near-perennial (N-PR, > 0–20%), partially intermittent (PIR, > 20–60%) and intermittent (IR, > 60%; Fig. 1, Tables S1, S3).

Because our study focused on assessing community responses to no-flow events including drying, we excluded perennial sites from further analyses. We used modelled daily discharge to calculate a set of hydrological variables for each site in each 'winter' (defined here as the 6 months from October to March) and 'summer' (April to September) for the whole study period (Dunbar et al., 2010a). Variables were selected to describe the flowing and no-flow conditions preceding collection of each invertebrate sample. We calculated the sum of no-flow days (SumNoFlow) for each summer and winter, to reflect the combined duration of no-flow events, with longer no-flow periods indicating more intense drying events. We also calculated the standardized Q10 (discharge exceeded 10% of the time) to quantify the magnitude of high flows in each season as: $\mathrm{Q10z} = \frac{\mathrm{Q10 - Qmean}}{\mathrm{QSD}}$, in which Q10 is the observed Q10 value, Qmean is the mean discharge and QSD is the SD calculated for each site in each season. We also determined the number of days since the most recent no-flow event (TimeSinceNFlow) for each sample.

At the time of sampling, visual estimates of the channel substrate composition were made (% boulders, cobbles, pebbles, gravel, sand and silt). Substrate was then summarized as a mean substrate (MSUB) index using the Phi value (Davy-Bowker et al., 2008) calculated for each sample as:

$$\mathrm{MSUB} = \frac{-7.75\,\mathrm{B} - 3.25\,\mathrm{P} + 2.00\,\mathrm{S} + 8.00\mathrm{C}}{100}$$

in which B = % boulders and cobbles, P = % pebbles and gravel, S = % sand and C = % silt. Low MSUB values indicate substrates dominated by coarse-grained particles and high MSUB values describe those dominated by fine-grained particles.

2.4. *Data analysis*

We first visualized temporal trends in hydrological characteristics by plotting the mean SumNoFlow and the mean Q10 (across all sites) for each summer and winter against years.

2.4.1. *Modelling the effects of drying and hydrological variability on DEHLI and LIFE*

We built separate linear mixed-effects models (LMM) to assess the response of DEHLI and LIFE to a set of flow (Q10 [$\mathrm{m^3\,s^{-1}}$]), no-flow (seasonal SumNoFlow [days], TimeSinceNFlow [days]) and other (MSUB [Phi], calendar year) variables and their interactions (Table 1). We selected these explanatory variables and interactions based on variable collinearity and on a priori defined research questions relating

Table 1
Variables used as predictors in each linear mixed-effects model built to assess the response of DEHLI and LIFE indices, their replication level and the question they address.

Variable		Abbreviation	Level	Question addressed
FP	Flow permanence group (IR = intermittent, PIR = partially intermittent and N-PR = near-perennial)	FlowPerm	Site	Do biological indices differ among flow permanence groups?
No-flow conditions	Sum of no-flow days in the preceding summer (Summer-1)	SumNoFlow-Summer-1	Sample	Do biological indices decrease with increasing no-flow duration in each of the two preceding summers?
	Sum of no-flow days in the summer before Summer-1	SumNoFlow-Summer-2	Sample	
	Time since the most recent no-flow event	TimeSinceNFlow	Sample	Do biological indices increase with time since the most recent no-flow event?
High-flow	High-flow magnitude (Q10) in the preceding summer	Q10-Summer-1	Sample	Do biological indices increase with the magnitude of high flows in the preceding winter and summer?
	High-flow magnitude (Q10) in the preceding winter	Q10-Winter	Sample	
Other	Mean substrate index	MSUB	Sample	Do biological indices vary with substrate composition?
	Calendar year (1991–2017)	Year	Sample	Are there long-term temporal changes in biological indices?
	Interactions			
FP vs. no-flow	FlowPerm * TimeSinceNFlow			Does the response to and rate of recovery from no-flow events differ among flow permanence groups?
	FlowPerm * SumNoFlow-Summer-1			
	FlowPerm * SumNoFlow-Summer-2			
No-/high flow	SumNoFlow-Summer-1 * SumNoFlow-Summer-2			Do successive summers with longer no-flow durations have a stronger effect on biological indices?
	Q10-Summer-1 * SumNoFlow-Summer-1			Do high-flow magnitude and no-flow duration interact to influence the responses of biological indices?
Other	TimeSinceNFlow * MSUB			Is the rate of recovery from no-flow events influenced by substrate composition?
	SumNoFlow-Summer-1 * MSUB			Are the responses of biological indices to no-flow events influenced by substrate composition?

to the study aim (Table 1). We used the variance inflation factor (VIF) to assess multicollinearity among predictors and sequentially removed variables with the highest VIF until all variables had a VIF < 3 (Zuur et al., 2010). Based on VIF results, SumNoFlow in the winter preceding sample collection was excluded from models.

We used flow permanence group as a categorical variable, with N-PR as a reference level. We used the sample-specific SumNoFlow in the preceding summer (Summer-1) and the summer before Summer-1 (Summer-2) to assess the effects of summer no-flow conditions, and the Q10 in the preceding winter (Winter) and Summer-1 to assess responses to the high-flow conditions preceding each sample (Table 1). We used TimeSinceNFlow to assess if the duration of the flowing period since the most recent no-flow event influenced index values. Calendar year was used as a predictor to characterize temporal trends. In addition, we used interaction terms to test specific questions; for example, the interaction between SumNoFlow Summer-1 and SumNoFlow Summer-2 assessed the combined effects of successive summers with no-flow conditions (Table 1). To account for the non-independence of samples from individual sites, we used site ($n = 34$) nested within river catchment ($n = 7$) as random factors in each model. Separate LMM were built for spring and autumn samples and yielded comparable results (Tables S4, S5); we therefore present only spring results, with these communities representing more stable states following community assembly after flow resumptions, which typically began in autumn. Each continuous (i.e. non-categorical) explanatory variable was centred around its mean (mean = 0). TimeSinceNflow was log transformed to reduce the effects of highly variable time periods recorded at N-PR sites.

We used a model-averaging approach to calculate parameter estimates and confidence intervals (CI) for each model. We used the Akaike information criterion (AIC) to assess model performance and averaged the model parameter estimates and CI of all models with an $\Delta AIC < 4$ from the model with the lowest AIC (Anderson, 2008). We standardized parameter estimates and CI by their SD for plots, to facilitate comparison of DEHLI and LIFE responses. The number of times a variable or interaction term was selected in the averaged models was used to evaluate its importance.

2.4.2. *Taxon-specific responses to drying*

We performed *Indicator Species Analysis* (IndVal; Dufrêne and Legendre, 1997) to identify taxa (here, primarily families) indicative of each flow permanence group. IndVal calculates an index of association for each taxon based on its occurrence in a priori determined groups (here, flow permanence groups). Because of the unbalanced number of samples per group, we used group-equalized IndVal values (De Cáceres et al., 2010). Values are constrained between 0 and 1, with higher values indicating a stronger association with a given group, the significance of which was tested with 999 random permutations.

We used *Threshold Indicator Taxa ANalysis* (TITAN; Baker and King, 2010) to detect changes in taxa occurrences in response to SumNoFlow-Summer-1 and TimeSinceNFlow. TITAN combines IndVal and change-point analysis (Qian et al., 2003) to identify taxa whose occurrence increases or decreases along an environmental gradient. Only taxa occurring in > 3 samples were included in this analysis (Baker and King, 2010). TITAN analyses were performed with 500 bootstraps on presence-absence matrices. TITAN indicated the SumNoFlow-Summer-1 and the TimeSinceNFlow after which taxon-specific occurrences decreased or increased, thus identifying the taxa that responded most strongly to drying.

We determined the DEHLI DI and LIFE FG scores for each taxon identified by TITAN as increasing or decreasing in occurrence along the SumNoFlow-Summer-1 and/or TimeSinceNFlow gradients. We used linear regressions to assess the relationship between taxon-specific scores and their median change-point value on the SumNoFlow-Summer-1 and TimeSinceNFlow gradients separately. Of the taxa identified by TITAN, 33% lack DI and 22% lack FG scores and were therefore excluded from this analysis. Because too few DI and FG scoring taxa (i.e. $n \leq 4$) increased and decreased with SumNoFlow-Summer-1 and TimeSinceNFlow, respectively, we did not perform linear regressions between these taxa and their average change point.

We used R software version 3.5.0 (R Core Team, 2018) for all analyses, including the *smires* package (Gauster, 2018) to calculate hydrological variables, *nlme* (Pinheiro et al., 2018) and *MuMIn* (Barton, 2012) for model building and averaging, *indicspecies* (De Cáceres and Legendre, 2009) for IndVal, and *TITAN2* (Baker et al., 2015) for TITAN.

3. Results

3.1. Long-term hydrological variability across and within flow permanence groups

Between 1995 and 2017, the mean duration of no-flow days across the study sites exceeded 50 d season^{-1} between winter 1996 and 1997, between summer 2005 and 2006, in winter 2012 and in summer 2017 (Fig. 2a). At the other extreme, particularly high flows from winter 2000 to summer 2001 meant that no site stopped flowing in 2001 (Fig. 2a, b). The 10 IR sites stopped flowing in (mean ± SE) 84 ± 11% of the study years for 156 ± 51 d a^{-1}; 15 PIR sites stopped flowing for 47 ± 9% of years for 65 ± 25 d a^{-1}; flow ceased at nine N-PR sites in 13 ± 5% of years for 9 ± 4 d a^{-1}; and 12 perennial sites never stopped flowing. N-PR sites only occurred in two rivers, where they dominated, whereas PIR and IR sites were distributed across at least five rivers (Fig. 1).

3.2. DEHLI and LIFE index responses to hydrological and other environmental variables

A total of 95 invertebrate families were sampled in spring, with 88 occurring in > 3 samples across IR, PIR and N-PR flow permanence groups. The most frequent taxa were Chironomidae, Oligochaeta, Gammaridae, Sphaeriidae, Limnephilidae and Baetidae, which were present in 99%, 97%, 88%, 88%, 79% and 78% of samples, respectively.

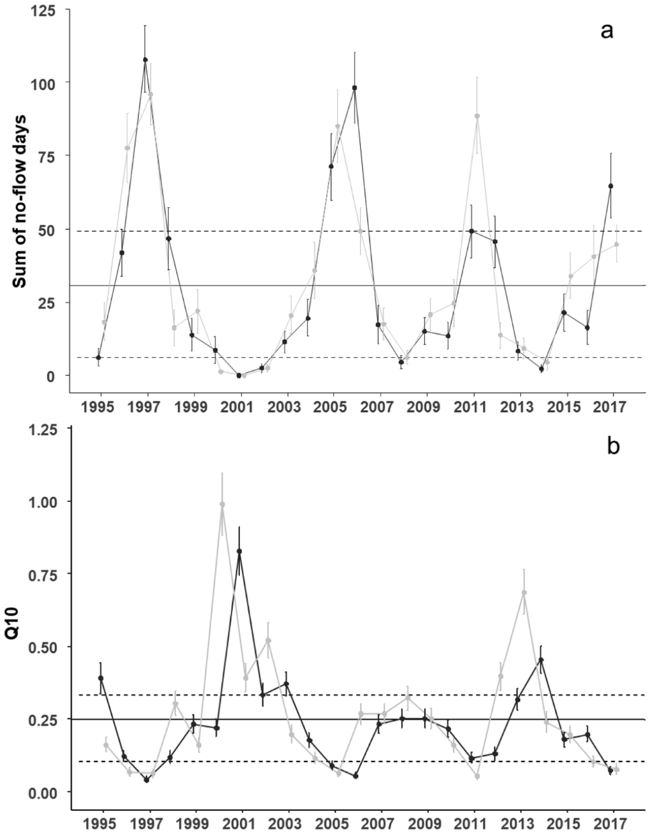

Fig. 2. Mean ± SE of hydrological variables for 46 sites on seven rivers in summer (black; April to September) and winter (grey, October to March) seasons between 1995 and 2017: (a) the mean total number of no-flow days; and (b) the magnitude of high flows, as Q10. Horizontal solid and dotted lines indicate the mean and the 2nd and 8th percentiles calculated over the whole data series, respectively.

Similar predictors were selected in the best (ΔAIC < 4) models for LIFE ($n = 20$) and DEHLI ($n = 15$), often with comparable importance (Fig. 3a). SumNoFlow-Summer-1, Q10-Summer-1, year and MSUB were selected in every best model. FlowPerm and SumNoFlow-Summer-2 were also selected in every best model for DEHLI and in $> 90\%$ of the LIFE models. TimeSinceNFlow was also an important predictor of DEHLI only, being selected in $> 75\%$ of models, whereas it was selected in 38% of the LIFE models. Q10 winter was selected in 64% and 20% of the best models for LIFE and DEHLI, respectively. Interactions between Q10 and SumNoFlow-Summer-1 and between SumNoFlow-Summer-1 and SumNoFlow-Summer-2 were also selected in $> 80\%$ of the best models for both indices (Fig. 3a). The interaction between FlowPerm and TimeSinceNFlow was selected in 86% of the best models for DEHLI only. The interaction between MSUB and SumNoFlow-Summer-1 was an important predictor for LIFE but not DEHLI (Fig. 3a). Other interactions were selected in $< 26\%$ of the models for both indices.

Based on model parameter estimates, IR sites had lower DEHLI and LIFE scores than N-PR sites (Fig. 3b, Table S5), but differences between N-PR and PIR were less pronounced, in particular for LIFE (Figs. 3b and 4, Table S1). DEHLI and LIFE scores both decreased with SumNoFlow-Summer-1 and SumNoFlow-Summer-2 (Fig. 3b, Table S5) but CIs overlapped with 0, suggesting that the effects of a preceding dry summer varied among sites (Fig. S1). The interaction between FlowPerm and SumNoFlow-Summer-1 indicated that the negative response of DEHLI to SumNoFlow-Summer-1 was stronger in N-PR than in PIR and IR, whereas the effect of SumNoFlow-Summer-1 on LIFE scores was less predictable across flow permanence groups (seen as strong overlap of CI with 0; Figs. 3b, S2). The minor, positive interaction between SumNoFlow-Summer-1 and SumNoFlow-Summer-2 for both indices suggested that an increase in no-flow duration in both preceding summers had less of an effect on the indices than expected from a simple additive effect (Fig. 3b, Table S5).

DEHLI scores increased by 0.004 [0.001, 0.008] for every 10% increase in TimeSinceNFlow, i.e. by 0.26 [0.06, 0.46] after one year and 0.31 [0.08, 0.55] after three years (Fig. 3b, Table S5). The interaction between FlowPerm and TimeSinceNFlow for DEHLI indicated weaker responses in IR and PIR than in N-PR. The response of DEHLI to increasing TimeSinceNFlow in N-PR was always positive, increasing rapidly then stabilizing at values comparable to those at perennial sites after approximately three years (Fig. 5a). The response of DEHLI to TimeSinceNFlow in IR and PIR was less consistent; DEHLI scores generally increased (Fig. 5b, c), but decreased with TimeSinceNFlow at some sites (Fig. S3), and never stabilized (Fig. 5b, c). The response of LIFE to increasing TimeSinceNFlow was less predictable (Fig. 3b) and more variable (Fig. S3).

Q10-Summer-1 had a negative effect on both DEHLI and LIFE scores, suggesting community sensitivity to high summer flows (Fig. 3b, Table S5). The negative interaction between Q10-Summer-1 and SumNoFlow-Summer-1 indicated that high Q10 combined with a long no-flow duration in the preceding summer had a stronger negative effect on both indices than expected from a simple additive effect. Q10-Winter had a positive effect on LIFE scores, suggesting that high winter flows may favour communities dominated by taxa with preferences for fast to moderate flows.

Year was a strong predictor of DEHLI and LIFE scores, which increased with time since 1991 by approx. 0.31 and 0.37 every ten years, respectively (Fig. 3b, Table S5). DEHLI and LIFE scores also decreased as MSUB increased, indicating that fine-grained sediments supported lower-scoring communities than coarser sediments. The interaction between MSUB and SumNoFlow-Summer-1 for LIFE indicated a lower-magnitude negative effect of increasing SumNoFlow-Summer-1 at high MSUB values, i.e. in finer sediments.

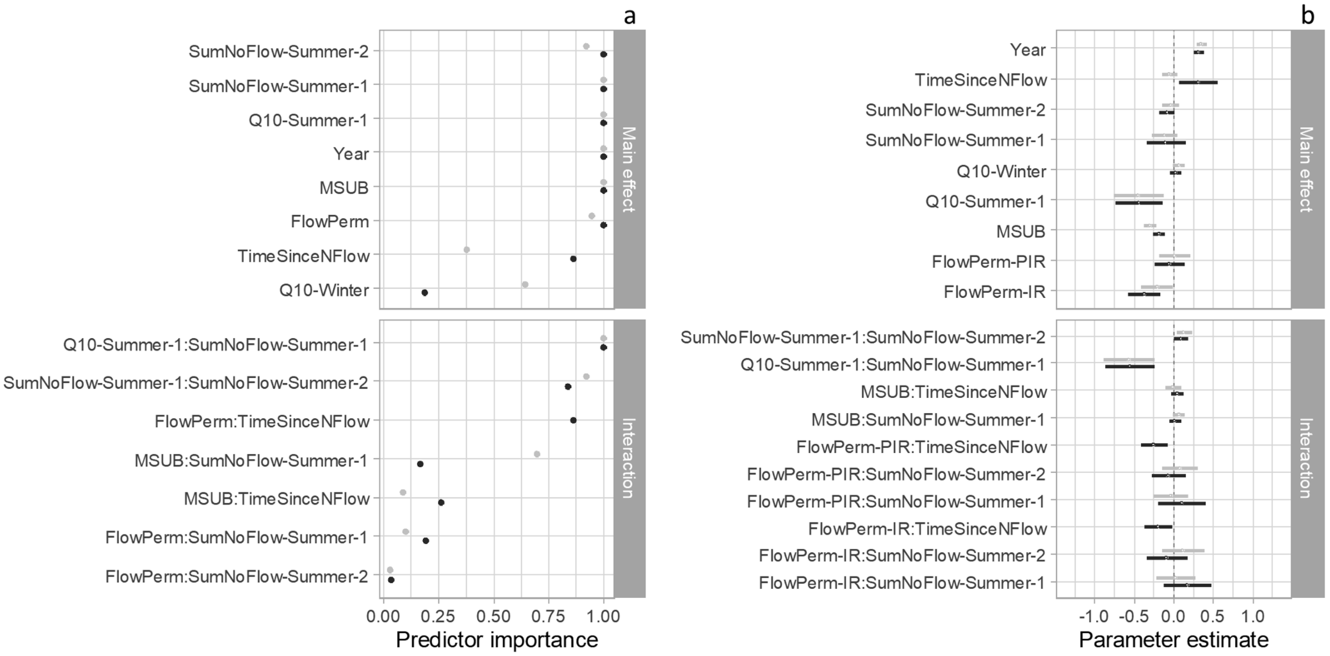

Fig. 3. Results of the model selection for LIFE (grey) and DEHLI (black): (a) the proportion of best models in which each variable (main effect) and each of their interactions was selected; (b) the standardized effect size and confidence interval (parameter estimates) for each variable and their interactions measured by averaging models with an ΔAIC < 4. Effects sizes were standardized to facilitate comparisons between models and predictor variables. For the categorical variable FlowPerm, N-PR (near-perennial) was used as reference level. PIR = partially intermittent and IR = intermittent; see Table 1 for definition and description of other abbreviations.

3.3. Taxon-specific responses to hydrological variables and flow permanence regimes

IndVal identified 35, seven and six taxa as indicators of N-PR, PIR and IR sites, respectively (Table S6). N-PR indicators were mostly lotic taxa (e.g. Baetidae, Goeridae, Hydropsychidae and Simuliidae) whereas families including lentic taxa such as damselflies (Coenagrionidae), aquatic beetles (Dytiscidae) and snails (Lymnaeidae), semi-aquatic beetles (Helophoridae) and terrestrial snails (Hygromiidae) were indicative of PIR and IR (Table S6).

Based on TITAN, nine families increased and 35 families decreased in occurrence as SumNoFlow-Summer-1 increased (Fig. 6a). For taxa which decreased in occurrence, change points were between 0 and 50 no-flow days in the preceding summer, with the highest magnitude changes occurring for Baetidae, Elmidae, Glossosomatidae, Hydropsychidae and Ancylidae (Fig. 6a). Most taxa that increased in occurrence with SumNoFlow-Summer-1 were associated with lentic habitats (Dytiscidae, Lymnaeidae), were semi-aquatic (Curculionidae, Succineidae, Tipulidae) or were meiofauna (Ostracoda; Fig. 6a).

Most of the 42 taxa that increased in occurrence with TimeSinceNFlow increased between 60 days and six years since the most recent no-flow event (Fig. 6b). The highest magnitude increases were for Goeridae, Hydropsychidae and Nemouridae after two, five and ten years, respectively (Fig. 6b). The occurrence of Baetidae and Simuliidae generally increased within one year of the most recent no-flow event, whereas the occurrence of six taxa (most of which also increased with SumNoFlow-Summer-1) decreased within three years (Fig. 6b).

The taxon-specific DEHLI DI (linear regression: $t = -2.77$, $p = 0.01$, adjusted $R^2 = 0.21$) but not the LIFE FG scores ($p = 0.26$) of the taxa which decreased in occurrence with SumNoFlow-Summer-1, decreased with increasing change-point values. Neither DEHLI DI nor LIFE FG scores of the taxa which increased in occurrence with TimeSinceNFlow changed with their change-point values ($p > 0.42$).

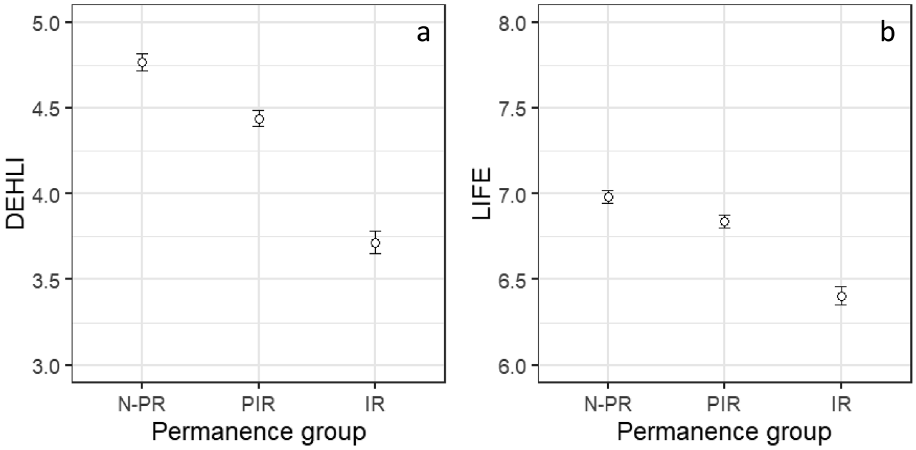

Fig. 4. Mean ± SE (a) DEHLI and (b) LIFE scores for near-perennial (N-PR), partially intermittent (PIR) and intermittent (IR) flow permanence groups. Y axes are on the same scale, spanning two units for each index.

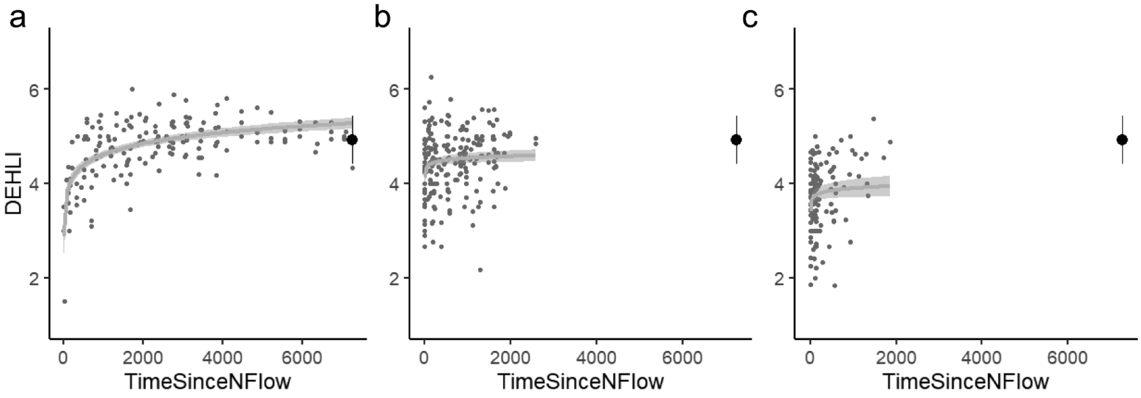

Fig. 5. Logarithmic regression between DEHLI scores and the time since the most recent no-flow event (TimeSinceNFlow) in days for (a) near-perennial (N-PR), (b) partially intermittent (PIR) and (c) intermittent (IR) sites. Larrge black dots and vertical lines represent the mean ± standard deviation of DEHLI scores at perennial sites.

4. Discussion

We evaluated the ability of two existing indices, developed primarily to characterize invertebrate community responses to hydrological variability and changes in instream habitat conditions at perennial sites, to a comparable suite of environmental changes in non-perennial rivers (i.e. temporary streams). Chadd et al. (2017) explored community responses to low and high flows at eight perennial sites and found that DEHLI scores were more sensitive than LIFE scores to changes in instream conditions associated with drought. Wilding et al. (2018) also explored the response of LIFE across sites with different flow permanence regimes, finding that index scores decreased and their variability increased with intermittence. Building on this research, our study encompassed 34 sites with near-perennial (N-PR) to intermittent (IR) flow permanence regimes and compared DEHLI and LIFE responses to no-flow metrics, with longer no-flow periods verified by field observations as increasingly indicative of streambed drying.

We found that both DEHLI and LIFE responded to increasing no-flow durations and high-flow magnitudes, but that DEHLI was more effective at predicting community changes following flow resumptions. DEHLI also identified differences in responses among flow permanence groups, and was particularly able to predict community responses at near-perennial sites, which dry only during unpredictable drought disturbances. LIFE was more able to predict responses to high flows and

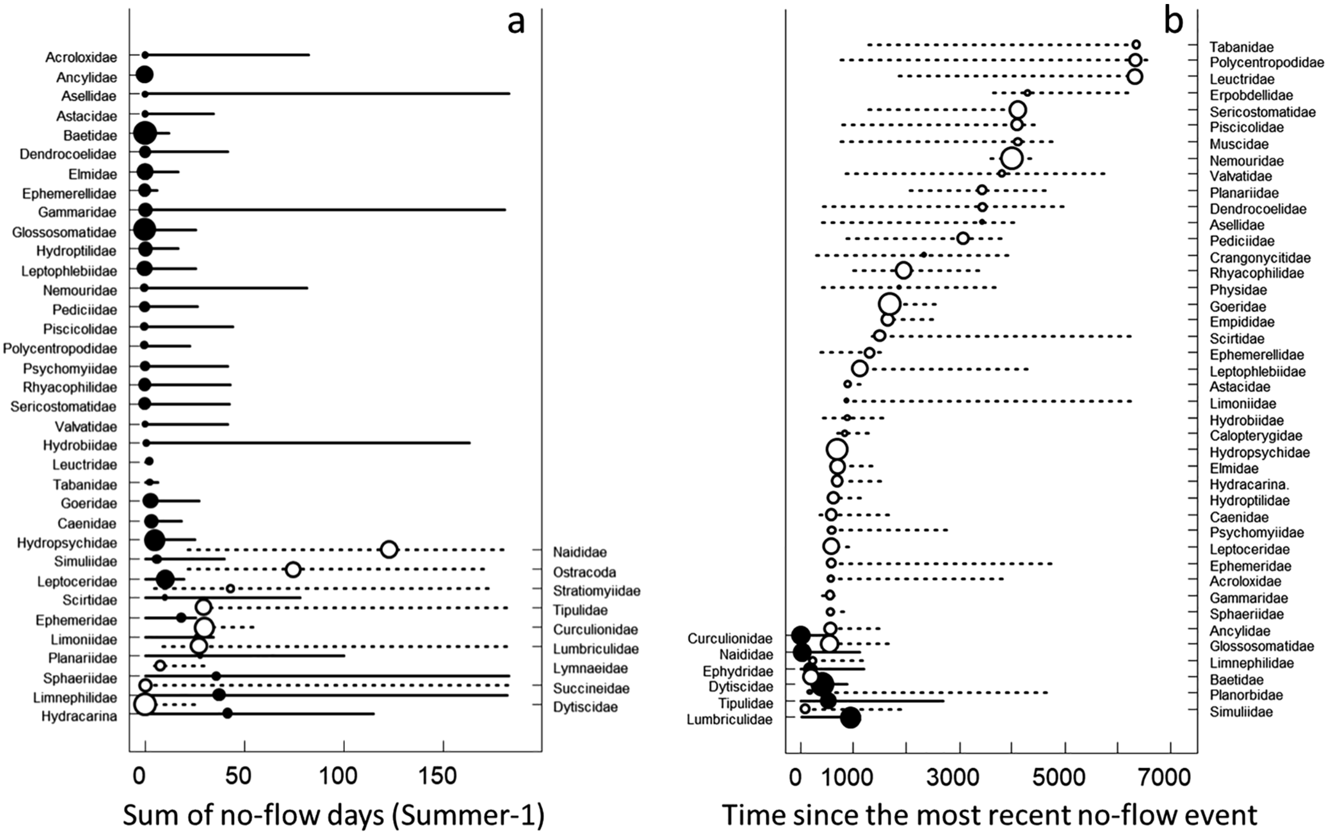

Fig. 6. TITAN results indicating taxa for which occurrence increased (left-hand axes, black circles and solid lines) and decreased (right-hand axes, white-filled circles and dotted lines) with (a) the sum of no-flow days in the preceding summer and (b) the time since the most recent no flow event, in days. Circles indicate mean change points (50th quartile) in the occurrence of each taxon, calculated based on 500 bootstraps. The bigger the circle the more significant the change. Horizontal lines delimitate the 5th and 95th quartiles calculated based on 500 bootstraps.

interactions between flow and sediments. We also identified multiple taxa which responded negatively or positively to changes in drying and flowing durations, confirming drying as a key driver of taxa occurrence across sites with contrasting flow permanence regimes (Leigh and Datry 2017; Soria et al., 2017). As temporary streams increase in extent in global regions including temperate zones, we highlight DEHLI as an index able to characterize community responses to drying and distinguish between streams with contrasting flow permanence regimes.

4.1. DEHLI and LIFE can distinguish among flow permanence regimes

Community composition typically differs among sites with contrasting flow permanence regimes (Bonada et al., 2007; Sarremejane et al., 2017a; Wilding et al., 2018), with the occurrence of lotic-associated and drying-adapted taxa typically decreasing and increasing, respectively, with drying frequency (Arscott et al., 2010; Leigh and Datry, 2017). Accordingly, both DEHLI and LIFE scores declined with increasing intermittence from N-PR to IR sites, indicating a higher proportion of low-flow and drying-resistant taxa at sites with lower flow permanence. DEHLI distinguished between flow permanence regimes more effectively, with mean index scores of 4.8 at N-PR sites and 3.7 at IR sites, i.e. the spatial equivalent of temporal changes in scores associated with changing habitat availability during drought (Chadd et al., 2017). DEHLI may therefore be a suitable index to characterize differences in community composition among flow permanence regimes.

4.2. Responses of biological indices and communities to increasing drying duration

Community responses to increasing drying duration may vary among flow permanence regimes because perennial and near-perennial communities dominated by lotic specialists are more sensitive to drying than those at intermittent sites, which also harbour lentic and semi-aquatic species that persist or thrive under no-flow and dry conditions (Bae and Park, 2019; Bogan et al., 2019; Hill and Milner, 2018). DEHLI responses to increasing no-flow duration in the preceding summer differed among flow permanence regimes: scores for N-PR communities decreased with increasing no-flow duration, whereas partially intermittent (PIR) and IR scores remained relatively stable, or were less predictable, across the same gradient. These results suggest that DEHLI, an aquatic-invertebrate based index, characterizes responses to drying most effectively at N-PR sites, where communities typically included many lotic specialists that experience infrequent drying. DEHLI responses were more erratic at PIR and IR than at N-PR sites, likely because the index excludes some semi-aquatic and lentic specialists typical of these streams, and because many taxa within temporary-stream communities may be drying-adapted and therefore less responsive to drying (Boersma et al., 2014; Sarremejane et al., 2017a). Successive summers with no-flow events generally had a lesser combined effect on DEHLI than expected from their simple additive effect. Elimination of sensitive taxa and selection of relatively drying-resistant taxa during the first summer's no-flow event may have reduced response magnitude in the second dry year.

Taxon-specific responses to increasing drying duration depend on resistance or resilience strategies, for example desiccation tolerance promotes in situ survival during dry phases and high dispersal capacities enable recolonization from perennial refuges (Bonada et al., 2007; Arscott et al., 2010; Sarremejane et al., 2017a). Taxon-specific DEHLI scores fell as TITAN indicator taxa declined in occurrence with increasing no-flow durations, indicating that these scores effectively reflect taxon-specific sensitivities to increasing no-flows and drying. The occurrence of most 'decreaser' taxa fell within 50 days without flow, indicating that a large proportion of typical lotic communities may be lost as no-flow durations exceed this threshold. Taxa that decreased in frequency first were primarily lotic taxa (e.g. Ancylidae, Baetidae, Elmidae, Ephemerellidae, Hydropsychidae and Rhyacophilidae), indicating their sensitivity to drying events as short as a week, as also reported in semi-arid (Chester and Robson, 2011; Vander Vorste et al., 2016) and boreal climates (Sarremejane et al., 2018).

The occurrence of several lentic and semi-aquatic taxa increased with summer no-flow duration. For example, semi-aquatic Curculionidae beetles typically feed on aquatic and semi-aquatic macrophytes (Newman, 1991) and may become more abundant as waters recede and vegetation colonizes the streambed. In addition, some Dytiscidae beetles, Lymnaeidae snails and Tipulidae fly larvae can persist in dry surface sediments (Stubbington et al., 2016), likely explaining their increasing occupancy with increasing drying duration. Although few semi-aquatic taxa are included in DEHLI and LIFE, their evident response to drying duration suggests their potential as informative taxa in future indices developed to characterize ecological responses to drying (England et al., 2019; Stubbington et al., 2018).

4.3. Biological indices and community responses to increasing flowing-phase duration

The capacity of communities to recover from disturbance depends on disturbance characteristics, taxon-specific dispersal capacities and the availability of recolonist sources, with sufficiently low disturbance frequencies allowing taxa to recolonize through dispersal from local refuges (e.g. the hyporheic zone and pools; Pařil et al., 2019; Stubbington, 2012; Vander Vorste et al., 2016) and/or regional refuges (e.g. perennial streams; Bogan and Boersma 2012; Sarremejane et al., 2017a). Frequently disturbed communities, such as in temporary streams in which wet and dry phases repeatedly alternate, may be limited to a subset of species with strong resistance or resilience strategies such as adult flight and rapid juvenile development, accelerating community recovery post-disturbance (Stubbington et al., 2016).

The time since the most recent no-flow event was a major predictor of DEHLI scores, indicating that the occurrence of lotic specialists in the community increases with flow permanence (see TITAN results Section 3.3). This pattern was particularly evident at N-PR sites, where DEHLI scores needed on average three years to return to values similar to perennial sites: typical lotic communities may need this long to recover from drying events. Similarly, Wood and Petts (1999) documented a three-year recovery period for macroinvertebrate communities after a severe drought caused drying of near-perennial chalk stream sites. However, the abundance of some taxa that decreased with no-flow duration recovered only after more than ten years of flow (e.g. Nemouridae and Sericostomatidae). Resh (1992) also found that a sericostomatid caddisfly population took nine years to recover following drying of a near-perennial stream in mediterranean California, suggesting that such taxa need prolonged periods of continuous flow to establish. Similarly, many nemourids are associated with perennial spring and springbrook habitats (Smith and Wood, 2002), suggesting a preference for continuous, stable flows. The weak to moderate dispersal capacity and limited distribution of these taxa may also explain the longer periods needed for populations to re-establish post disturbance (Sarremejane et al., 2018).

The DEHLI index response to time since the most recent no-flow event was more variable in IR and PIR than in N-PR, suggesting erratic community responses to increasing flow permanence; responses also reflected longitudinal connectivity and the spatial extent of drying. IR and PIR are generally located farther from perennial reaches than N-PR and the recolonization of the most isolated sites may therefore be more variable (e.g. Sarremejane et al, 2017b), particularly if dry reaches remain between temporary sites at which flow has resumed. Whereas IR and PIR communities at well-connected sites may be joined by some lotic specialists with rapid recolonization strategies as flow permanence increases, sites frequently exposed to drying and/or isolated from recolonist sources may remain dominated by desiccation-resistant and semi-aquatic taxa (Boersma et al., 2014). The shorter durations between each no-flow event in IR and PIR may limit recolonization by lotic specialists, thus allowing the establishment of distinct communities of taxa with lower DEHLI scores, which may not respond to increasing flow duration. Although sensitive to surface water loss, lotic-specialist taxa such as Baetidae and Simuliidae have relatively short lifecycles and wide distributions, enabling them to track changes in flow conditions and rapidly recolonize after a disturbance ends (Sarremejane et al., 2018), explaining why DEHLI scores increased with flow duration at some IR and PIR sites.

4.4. Biological indices and community responses to high flows and their interaction with no-flow events

High flows may promote the persistence of lotic communities, but also constitute a disturbance if individuals are displaced from the substrate (Death, 2008). Whereas high flow magnitudes had an overall positive effect on LIFE and to a lesser extent DEHLI, summer high flows caused both indices to decline. Communities may be less adapted to summer high flows than winter ones, if flood disturbances are less common in summer and life cycles have evolved adaptions to such patterns (Lytle and Poff, 2004). For example, Milner et al. (2018) showed that a summer flood had a much greater impact on invertebrate communities in a glacial stream than a winter flood, because insect life-stages were more disturbance-tolerant in winter than in summer.

Successive, contrasting disturbances (e.g. drying and flooding) can strongly modify community composition (Stubbington et al., 2009; Woodward et al., 2015). Combined increasing no-flow duration and high-flow magnitude in summer had a negative effect on both DEHLI and LIFE scores. Whereas high flows may select for lotic specialists, no-flow should select for lentic and semi-aquatic taxa, and all may decline in response to the contrasting disturbances, explaining why successive high-flow and no-flow events decreased index scores.

4.5. Response of biological indices to other factors

Biological indices may vary with environmental factors other than those they were designed to assess, because taxa concurrently respond to multiple interacting drivers. DEHLI and LIFE scores increased with increasing substrate particle size, likely due to fundamental relationships between flow and sediment size (Gordon et al., 2004): coarse-grained substrates may result from the erosion of finer particles by higher flow velocities, and thus support fast-flow-adapted taxa. The interaction between mean substrate size and no-flow duration also suggests that the decrease in LIFE scores with increasing duration was less pronounced at fine-grained sites. A sharper decline in coarse-grained habitats may reflect higher LIFE scores at sites dominated by drying-sensitive lotic taxa, whereas finer sediments support communities with lower initial index scores.

Although not the focus of our study, we observed an increase in index scores between 1991 and 2017 (also see Dunbar et al., 2010b). Vaughan and Ormerod (2014) related increases in benthic invertebrate richness in England between 1991 and 2011 to improving water quality. Such improvements should primarily lead to increases in the occurrence of the sensitive mayflies, stoneflies and caddisflies typically associated with lotic habitats, explaining why DEHLI and LIFE scores increased during the study. Also, the spread of the invasive signal crayfish (*Pacifastacus leniusculus*) in the study area (Hayes, 2012) and its selective predation on slow-moving snails and leeches (Mathers et al., 2016; 2018) may have reduced the occurrence of lentic specialists, therefore leading to increases in scores. The natural stressor of drying interacts with multiple anthropogenic pressures to determine ecological responses to environmental variability, and further research is needed to explore index performance across sites with different environmental characteristics and experiencing different impact types and levels.

5. Conclusion

Our results highlight DEHLI as a particularly suitable tool for differentiating among communities at sites with different flow permanence regimes and for assessing lotic community recovery after flow resumes at near-perennial sites. However, further research is needed to determine the extent to which DEHLI can predict community responses in temporary streams, and such research should ideally be informed by detailed descriptions of instream habitat conditions and site-specific hydrological history (Mathers et al., 2019; Sefton et al., 2019). In addition, indices including lentic, semi-aquatic and terrestrial taxa require development, to more accurately predict drying effects across flow permanence regimes (England et al., 2019; Stubbington et al., 2018). The predicted increase in the occurrence of extreme climatic events (e.g. Prudhomme et al., 2014) may permanently alter community composition if the time between events is shorter than the time necessary for a community to recover (Haghkerdar et al., 2019). Indices assessing the impact of natural extreme events across rivers with different flow permanence regimes and environmental characteristics will enable characterization and prediction of community responses to natural variability. An ultimate goal is to integrate such indices with those characterizing responses to anthropogenic activities (Stubbington et al., 2018), to inform the development of biomonitoring tools that disentangle biotic responses to human impacts and flow intermittence in temporary streams, as these dynamic ecosystems increase in extent in a changing world.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2019.105620.

References

Anderson, D.R., 2008. In: Model Based Inference in the Life Sciences. Springer-Verlag, New York. https://doi.org/10.1007/978-0-387-74075-1.

Arscott, D.B., Larned, S., Scarsbrook, M.R., Lambert, P., 2010. Aquatic invertebrate community structure along an intermittence gradient: Selwyn River, New Zealand. J. N. Am. Benthol. Soc. 29, 530–545. https://doi.org/10.1899/08-124.1.

Bae, M.J., Park, Y.S., 2019. Evaluation of precipitation impacts on benthic macroinvertebrate communities at three different stream types. Ecol. Indic. 102, 446–456. https://doi.org/10.1016/j.ecolind.2019.02.060.

Baker, M.E., King, R.S., Kahle, D., 2015. Package 'TITAN2'. R package version 2.2-1. https://CRAN.R-project.org/package=TITAN2.

Baker, M.E., King, R.S., 2010. A new method for detecting and interpreting biodiversity and ecological community thresholds. Methods Ecol. Evol. 1, 25–37. https://doi.org/10.1111/j.2041-210X.2009.00007.x.

Barton, K., 2012. MuMIn: multi-model inference. R package version 1.7.7. https://CRAN.R-project.org/package=MuMIn.

Bêche, L.A., Connors, P.G., Resh, V.H., Merenlender, A.M., 2009. Resilience of fishes and invertebrates to prolonged drought in two California streams. Ecography 32, 778–788. https://doi.org/10.1111/j.1600-0587.2009.05612.x.

Berrie, A.D., 1992. The chalk stream environment. Hydrobiologia 248, 3–9. https://doi.org/10.1007/BF00008881.

Boersma, K.S., Bogan, M.T., Henrichs, B.A., Lytle, D.A., 2014. Invertebrate assemblages of pools in arid-land streams have high functional redundancy and are resistant to severe drying. Freshw. Biol. 59, 491–501. https://doi.org/10.1111/fwb.12280.

Bogan, M.T., Boersma, K.S., 2012. Aerial dispersal of aquatic invertebrates along and away from arid-land streams. Freshw. Sci. 31, 1131–1144. https://doi.org/10.1899/12-066.1.

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. Freshw. Biol. 58, 1016–1028. https://doi.org/10.1111/fwb.12105.

Bogan, M.T., Leidy, R.A., Neuhaus, L., Hernandez, C.J., Carlson, S., 2019. Biodiversity value of remnant pools in an intermittent stream during the great California drought. Aquat. Conserv. 29, 976–989. https://doi.org/10.1002/aqc.3109.

Bogan, M.T., Lytle, D.A., 2007. Seasonal flow variation allows 'time-sharing' by disparate aquatic insect communities in montane desert streams. Freshw. Biol. 52, 290–304. https://doi.org/10.1111/j.1365-2427.2006.01691.x.

Bonada, N., Rieradevall, M., Prat, N., 2007. Macroinvertebrate community structure and biological traits related to flow permanence in a Mediterranean river network. Hydrobiologia 589, 91–106. https://doi.org/10.1007/s10750-007-0723-5.

Boulton, A.J., 1989. Over-summering refuges of aquatic macroinvertebrates in two intermittent streams in central Victoria. Trans. R. Soc. S. Aust. 113, 23–34.

Chadd, R.P., England, J.A., Constable, D., Dunbar, M.J., Extence, C.A., Leeming, D.J., Murray-Bligh, J.A., Wood, P.J., 2017. An index to track the ecological effects of drought development and recovery on riverine invertebrate communities. Ecol. Indic. 82, 344–356. https://doi.org/10.1016/j.ecolind.2017.06.058.

Chase, J.M., 2007. Drought mediates the importance of stochastic community assembly. Proc. Natl. Acad. Sci. 104, 17430–17434. https://doi.org/10.1073/pnas.0704350104.

Chessman, B.C., 2015. Relationships between lotic macroinvertebrate traits and responses to extreme drought. Freshw. Biol. 60, 50–63. https://doi.org/10.1111/fwb.12466.

Chester, E.T., Robson, B.J., 2011. Drought refuges, spatial scale and recolonisation by invertebrates in non-perennial streams. Freshw. Biol. 56, 2094–2104. https://doi.org/10.1111/j.1365-2427.2011.02644.x.

Chiu, M.-C., Leigh, C., Mazor, R., Cid, N., Resh, V., 2017. Anthropogenic threats to intermittent rivers and ephemeral streams. In: Datry, T., Bonada, N., Boulton, A.J. (Eds.), Intermittent Rivers and Ephemeral Streams: Ecology and Management. Academic Press, Elsevier, Netherlands, pp. 433–454. https://doi.org/10.1016/B978-0-12-803835-2.00017-6.

Datry, T., Bonada, N., Boulton, A.J., 2017. General introduction. In: Datry, T., Bonada, N., Boulton, A.J. (Eds.), Intermittent Rivers and Ephemeral Streams: Ecology and Management. Academic Press, Elsevier, Netherlands, pp. 1–20. https://doi.org/10.1016/B978-0-12-803835-2.00001-2.

Datry, T., Boulton, A.J., Bonada, N., Fritz, K., Leigh, C., Sauquet, E., Tockner, K., Hugueny, B., Dahm, C.N., 2018. Flow intermittence and ecosystem services in rivers of the Anthropocene. J. Appl. Ecol. 55, 353–364. https://doi.org/10.1111/1365-2664.12941.

Davy-Bowker, J., Clarke, R., Corbin, T., Vincent, H., Pretty, J., Hawczak, A., Blackburn, J., Murphy, J., Jones, I., 2008. River invertebrate classification tool. Final Report. SNIFFER Project WFD72c. SNIFFER, Edinburgh.

De Cáceres, M., Legendre, P., 2009. Associations between species and groups of sites: indices and statistical inference. Ecology 90, 3566–3574. https://doi.org/10.1890/08-1823.1.

De Cáceres, M., Legendre, P., Moretti, M., 2010. Improving indicator species analysis by combining groups of sites. Oikos 119, 1674–1684. https://doi.org/10.1111/j.1600-0706.2010.18334.x.

Death, R.G., 2008. The effect of floods on aquatic invertebrate communities. In: Lancaster, J., Briers, R. (Eds.), Aquatic Insects: Challenges to Populations. CABI, Oxford, UK, pp. 103–121.

Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. 67, 345–366. https://doi.org/10.1890/0012-9615(1997) 067[0345:SAAIST]2.0.CO;2.

Dunbar, M.J., Pedersen, M.L., Cadman, D., Extence, C., Waddingham, J., Chadd, R., Larsen, S.E., 2010a. River discharge and local-scale physical habitat influence macroinvertebrate LIFE scores. Freshw. Biol. 55, 226–242. https://doi.org/10.1111/j.1365-2427.2009.02306.x.

Dunbar, M.J., Warren, M., Extence, C., Baker, L., Cadman, D., Mould, D.J., Hall, J., Chadd, R., 2010b. Interaction between macroinvertebrates, discharge and physical habitat in upland rivers. Aquatic Conserv. 20, S31–S44. https://doi.org/10.1002/aqc.1089.

England, J., Chadd, R., Dunbar, M.J., Sarremejane, R., Stubbington, R., Westwood, C.G., Leeming, D., 2019. An invertebrate-based index to characterize ecological responses to flow intermittence in rivers. Fundam. Appl. Limnol. 193, 93–117. https://doi.org/10.1127/fal/2019/1206.

Extence, C.A., Balbi, D.M., Chadd, R.P., 1999. River flow indexing using British benthic macroinvertebrates: a framework for setting hydroecological objectives. Regul. Rivers: Res. Manage. 15, 545–574. https://doi.org/10.1002/(SICI)1099-1646(199911/12)15:6 < 545:AID-RRR561 > 3.0.CO;2-W.

Fritz, K.M., Dodds, W.K., 2004. Resistance and resilience of macroinvertebrate assemblages to drying and flood in a tallgrass prairie stream system. Hydrobiologia 527, 99–112. https://doi.org/10.1023/B:HYDR.0000043188.53497.9b.

Fritz, K.M., Hagenbuch, E., D'Amico, E., Reif, M., Wigington Jr., P.J., Leibowitz, S.G., Comeleo, R.L., Ebersole, J.L., Nadeau, T., 2013. Comparing the extent and permanence of headwater streams from two field surveys to values from hydrographic databases and maps. J. Am. Water Resour. Assoc. 49, 867–882. https://doi.org/10.1111/jawr.12040.

Gauster, T., 2018. R-package smires: science and management of intermittent rivers and ephemeral streams. https://github.com/mundl/smires.

Gordon, N.D., McMahon, T.A., Finlayson, B.L., Gippel, C.J., Nathan, R.J., 2004. Stream Hydrology: An Introduction for Ecologists, second ed. Wiley, New York.

Grapes, T.R., Bradley, C., Petts, G.E., 2005. Dynamics of river–aquifer interactions along a chalk stream: the River Lambourn, UK. Hydrol. Proc. 19, 2035–2053. https://doi.org/10.1002/hyp.5665.

Haghkerdar, J.M., McLachlan, J.K., Ireland, A., Greig, H.S., 2019. Repeat disturbances have cumulative impacts on stream communities. Ecol. Evol. 9, 2898–2906. https://doi.org/10.1002/ece3.4968.

Hayes, R.B., 2012. Consequences for Lotic Ecosystems of Invasion by Signal Crayfish. PhD thesis. Queen Mary University, London.

Hill, M.J., Milner, V.S., 2018. Ponding in intermittent streams: a refuge for lotic taxa and a habitat for newly colonising taxa? Sci. Total Environ. 628, 1308–1316. https://doi.org/10.1016/j.scitotenv.2018.02.162.

ISO, 2012. ISO 1087 Water Quality – Guidelines for the Selection of Sampling Methods and Devices for Benthic Macroinvertebrates in Fresh Waters. International Organization for Standardization, Geneva.

Katz, G.L., Denslow, M.W., Stromberg, J.C., 2012. The Goldilocks effect: intermittent streams sustain more plant species than those with perennial or ephemeral flow. Freshw. Biol. 57, 467–480. https://doi.org/10.1111/j.1365-2427.2011.02714.x.

King, R.S., Scoggins, M., Porras, A., 2016. Stream biodiversity is disproportionately lost to urbanization when flow permanence declines: evidence from southwestern North America. Freshw Science 35, 340–352. https://doi.org/10.1086/684943.

Koundouri, P., Boulton, A.J., Datry, T., Souliotis, I., 2017. Ecosystem services, values, and societal perceptions of intermittent rivers and ephemeral streams. In: Datry, T., Bonada, N., Boulton, A.J. (Eds.), Intermittent Rivers and Ephemeral Streams: Ecology and Management. Academic Press, Elsevier, Netherlands, pp. 455–476. https://doi.org/10.1016/B978-0-12-803835-2.00018-8.

Larned, S.T., Schmidt, J., Datry, T., Konrad, C.P., Dumas, J.K., Diettrich, J.C., 2011. Longitudinal river ecohydrology: flow variation down the lengths of alluvial rivers. Ecohydrology 4, 532–548. https://doi.org/10.1002/eco.126.

Ledger, M.E., Milner, A.M., 2015. Extreme events in running waters. Freshw. Biol. 60, 2455–2460. https://doi.org/10.1111/fwb.12673.

Leigh, C., Boulton, A.J., Courtwright, J.L., Fritz, K., May, C.L., Walker, R.H., Datry, T., 2016. Ecological research and management of intermittent rivers: an historical review and future directions. Freshw. Biol. 61, 1181–1199. https://doi.org/10.1111/fwb.12646.

Leigh, C., Datry, T., 2017. Drying as a primary hydrological determinant of biodiversity in river systems: a broad-scale analysis. Ecography 40, 487–499. https://doi.org/10.1111/ecog.02230.

Lytle, D.A., Poff, N.L., 2004. Adaptation to natural flow regimes. Trends Ecol. Evol. 19, 94–100. https://doi.org/10.1016/j.tree.2003.10.002.

Mathers, K.L., Chadd, R.P., Dunbar, M.J., Extence, C.A., Reeds, J., Rice, S.P., Wood, P.J., 2016. The long-term effects of invasive signal cray fish (*Pacifastacus leniusculus*) on instream macroinvertebrate communities. Sci. Total Environ. 556, 207–218. https://doi.org/10.1016/j.scitotenv.2016.01.215.

Mathers, K.L., Rice, S.P., Wood, P.J., 2018. Temporal variability in lotic macroinvertebrate communities associated with invasive signal crayfish (*Pacifastacus leniusculus*) activity levels and substrate character. Biol. Invasions 20, 567–582. https://doi.org/10.1007/s10530-017-1557-3.

Mathers, K.L., Stubbington, R., Leeming, D., Westwood, C., England, J., 2019. Structural and functional responses of macroinvertebrate assemblages to long-term flow variability at perennial and non-perennial sites. Ecohydrology 2112. https://doi.org/10.1002/eco.2112.

Met Office, 2019. Hemel Hempstead climate. https://www.metoffice.gov.uk/public/weather/climate (accessed 20 February 2019).

Milner, A.M., Picken, J.L., Klaar, M.J., Robertson, A.L., Clitherow, L.R., Eagle, L., Brown, L.E., 2018. River ecosystem resilience to extreme flood events. Ecol. Evol. 8, 8354–8363. https://doi.org/10.1002/ece3.4300.

Monk, W.A., Wood, P.J., Hannah, D.M., Wilson, D.A., Extence, C.A., Chadd, R.P., 2006. Flow variability and macroinvertebrate community response within riverine systems. River Res. Appl. 22, 595–615. https://doi.org/10.1002/rra.933.

National River Flow Archive, 2019. https://nrfa.ceh.ac.uk/data/search (accessed 20 February 2019).

Newman, R.M., 1991. Herbivory and detritivory on freshwater macrophytes by invertebrates: a review. J. N. Am. Benthol. Soc. 10, 89–114. https://doi.org/10.2307/1467571.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Core Team., 2018. nlme: Linear and nonlinear mixed effects models. R package version 3.1-137. https://CRAN.R-project.org/package = nlme.

Pařil, P., Leigh, C., Polášek, M., Sarremejane, R., Řezníčková, P., Dostálová, A., Stubbington, R., 2019. Short-term streambed drying events alter amphipod population structure in a central European stream. Fundam. Appl. Limnol. 193, 51–64. https://doi.org/10.1127/fal/2019/1164.

Prudhomme, C., Giuntoli, I., Robinson, E.L., Clark, D.B., Arnell, N.W., Dankers, R., Fekete, B.M., Franssen, W., Gerten, D., Gosling, S.N., Hagemann, S., Hannah, D.M., Kim, H., Masaki, Y., Satoh, Y., Stacke, T., Wada, Y., Wisser, D., 2014. Hydrological droughts in the 21st century, hotspots and uncertainties from a global multimodel ensemble experiment. Proc. Natl. Acad. Sci. 111, 3262–3267. https://doi.org/10.1073/pnas.1222473110.

Qian, S.S., King, R.S., Richardson, C.J., 2003. Two statistical methods for the detection of environmental thresholds. Ecol. Modell. 166, 87–97. https://doi.org/10.1016/S0304-3800(03)00097-8.

R Core Team, 2018. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org/.

Resh, V.H., 1992. Year-to-year changes in the age structure of a caddisfly population following loss and recovery of a springbrook habitat. Ecography 15, 314–317. https://doi.org/10.1111/j.1600-0587.1992.tb00041.x.

Resh, V.H., Brown, A.V., Covich, A.P., Gurtz, M.E., Li, H.W., Minshall, G.W., Reice, S.R., Sheldon, A.L., Wallace, J.B., Wissmar, R.C., 1988. The role of disturbance in stream ecology. J. N. Am. Benthol. Soc. 7, 433–455. https://doi.org/10.2307/1467300.

Sarremejane, R., Cañedo-Argüelles, M., Prat, N., Mykrä, H., Muotka, T., Bonada, N., 2017a. Do metacommunities vary through time? Intermittent rivers as model systems. J. Biogeogr. 44, 2752–2763. https://doi.org/10.1111/jbi.13077.

Sarremejane, R., Mykrä, H., Bonada, N., Aroviita, J., Muotka, T., 2017b. Habitat connectivity and dispersal ability drive the assembly mechanisms of macroinvertebrate communities in river networks. Freshw. Biol. 62, 1073–1082. https://doi.org/10.1111/fwb.12926.

Sarremejane, R., Mykrä, H., Huttunen, K.L., Mustonen, K.R., Marttila, H., Paavola, R., Sippel, K., Veijalainen, N., Muotka, T., 2018. Climate-driven hydrological variability determines inter-annual changes in stream invertebrate community assembly. Oikos 127, 1586–1595. https://doi.org/10.1111/oik.05329.

Sear, D.A., Armitage, P.D., Dawson, F.H., 1999. Groundwater dominated rivers. Hydrol. Proc. 13, 255–276. https://doi.org/10.1002/(SICI)1099-1085(19990228)13:3 < 255::AID-HYP737 > 3.0.CO;2-Y.

Sefton, C., Parry, S., England, J., Angell, G., 2019. Visualising and quantifying the variability of hydrological state in intermittent rivers. Fundam. Appl. Limnol. 193, 21–38. https://doi.org/10.1127/fal/2019/1149.

Smith, H., Wood, P.J., 2002. Flow permanence and macroinvertebrate community variability in limestone spring systems. Hydrobiologia 487, 45–58. https://doi.org/10.1023/A:1022932303652.

Soria, M., Leigh, C., Datry, T., Bini, L.M., Bonada, N., 2017. Biodiversity in perennial and intermittent rivers: a meta-analysis. Oikos 126, 1078–1089. https://doi.org/10.1111/oik.04118.

Spinoni, J., Vogt, J.V., Naumann, G., Barbosa, P., Dosio, A., 2018. Will drought events become more frequent and severe in Europe? Int. J. Climatol. 38, 1718–1736. https://doi.org/10.1002/joc.5291.

Straka, M., Polášek, M., Syrovátka, V., Stubbington, R., Zahrádková, S., Šikulová, L., Řezníčková, P., Němejcová, D., Opatřilová, L., Datry, T., Pařil, P., 2019. Recognition of stream drying based on benthic macroinvertebrates: A new tool in Central Europe. Ecol. Indicat. https://doi.org/10.1016/j.ecolind.2019.105486.

Stubbington, R., 2012. The hyporheic zone as an invertebrate refuge: a review of variability in space, time, taxa and behaviour. Mar. Freshw. Res. 63, 293–311. https://doi.org/10.1071/MF1119.

Stubbington, R., Chadd, R., Cid, N., Csabai, Z., Miliša, M., Morais, M., Munné, A., Pařil, P., Pešić, V., Tziortzis, I., 2018. Biomonitoring of intermittent rivers and ephemeral streams in Europe: current practice and priorities to enhance ecological status assessments. Sci. Total Environ. 618, 1096–1113. https://doi.org/10.1016/j.scitotenv.2017.09.137.

Stubbington, R., Datry, T., 2013. The macroinvertebrate seedbank promotes community persistence in temporary rivers across climate zones. Freshw. Biol. 58, 1202–1220. https://doi.org/10.1111/fwb.12121.

Stubbington, R., Wood, P.J., Boulton, A.J., 2009. Low flow controls on benthic and hyporheic macroinvertebrate assemblages during supra-seasonal drought. Hydrol. Proc. 23, 2252–2263. https://doi.org/10.1002/hyp.7290.

Stubbington, R., Gunn, J., Little, S., Worrall, T.P., Wood, P.J., 2016. Macroinvertebrate seedbank composition in relation to antecedent duration of drying and multiple wet-dry cycles in a temporary stream. Freshw. Biol. 61, 1293–1307. https://doi.org/10.1111/fwb.12770.

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 Rev.: Water 4, e1223. https://doi.org/10.1002/wat2.1223.

Suren, A.M., Jowett, I.G., 2006. Effects of floods versus low flows on invertebrates in a New Zealand gravel-bed river. Freshw. Biol. 51, 2207–2227. https://doi.org/10.1111/j.1365-2427.2006.01646.x.

Tallaksen, L.M., Van Lanen, H.A. (Eds.), 2004. Hydrological Drought: Processes and Estimation Methods for Streamflow and Groundwater. Elsevier, Netherlands.

Townsend, C.R., 1989. The patch dynamics concept of stream community ecology. J. N. Am. Benthol. Soc. 8, 36–50. https://doi.org/10.2307/1467400.

Townsend, C.R., Hildrew, A.G., 1994. Species traits in relation to a habitat templet for river systems. Freshw. Biol. 31, 265–275. https://doi.org/10.1111/j.1365-2427.1994.tb01740.x.

van Vliet, M.T., Franssen, W.H., Yearsley, J.R., Ludwig, F., Haddeland, I., Lettenmaier, D.P., Kabat, P., 2013. Global river discharge and water temperature under climate change. Glob. Environ. Change 23, 450–464. https://doi.org/10.1016/j.gloenvcha.2012.11.002.

Vander Vorste, R., Malard, F., Datry, T., 2016. Is drift the primary process promoting the resilience of river invertebrate communities? A manipulative field experiment in an intermittent alluvial river. Freshw. Biol. 61, 1276–1292. https://doi.org/10.1111/fwb.12658.

Vanschoenwinkel, B., Buschke, F., Brendonck, L., 2013. Disturbance regime alters the impact of dispersal on alpha and beta diversity in a natural metacommunity. Ecology 94, 2547–2557. https://doi.org/10.1890/12-1576.1.

Vaughan, I.P., Ormerod, S.J., 2014. Linking interdecadal changes in British river ecosystems to water quality and climate dynamics. Glob. Change Biol. 20, 2725–2740. https://doi.org/10.1111/gcb.12616.

Westwood, C.G., England, J., Dunbar, M.J., Holmes, N.T., Leeming, D.J., Hammond, D., 2017. An approach to setting ecological flow thresholds for southern English chalk streams. Water Environ. J. 31, 528–536. https://doi.org/10.1111/wej.12275.

Wilding, N.A., White, J.C., Chadd, R.P., House, A., Wood, P.J., 2018. The influence of flow permanence and drying pattern on macroinvertebrate biomonitoring tools used in the assessment of riverine ecosystems. Ecol. Indic. 85, 548–555. https://doi.org/10.1016/j.ecolind.2017.10.059.

Wood, P.J., Petts, G.E., 1999. The influence of drought on chalk stream macroinvertebrates. Hydrol. Proc. 13, 387–399. https://doi.org/10.1002/(SICI)1099-1085(19990228)13:3%3C387::AID-HYP745%3E3.0.CO;2-R.

Woodward, G., Bonada, N., Feeley, H.B., Giller, P.S., 2015. Resilience of a stream community to extreme climatic events and long-term recovery from a catastrophic flood. Freshw. Biol. 60, 2497–2510. https://doi.org/10.1111/fwb.12592.

Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. Methods Ecol. Evol. 1, 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x.