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A revised classification of temperate lowland groundwater-fed headwater streams based on their flora.

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Abstract

Prolonged drought conditions affect the ecological functioning of freshwater ecosystems, leading to the temporary simplification or loss of aquatic biological communities, as surface water is progressively reduced or dry phases are extended in intermittent streams. We classify the plant communities within 24 groundwater-fed headwater streams in southern England and examine changes over a 21-year period following a severe three-year drought. In comparison with a previous study, our revised classification reveals a simplification in plant communities driven by a decline in the abundance of obligate aquatic species and an increase in the abundance of semi-aquatic species. We demonstrate plant community structure as a strong indicator of a site's flow history, including intermittence. We recommend that future surveys also encompass terrestrial plants as well as semi-aquatic and aquatic plants and habitat assessments to further enhance understanding of how instream communities change between flowing, ponded and dry phases in intermittent systems.

Key words: macrophyte, biomonitoring, supra-seasonal drought, headwaters, streambed drying, aquatic–terrestrial ecosystems, temporary streams

Introduction

As a result of climate change (IPCC 2018) and increasing human demand for water (Franklin et al. 2008), intermittent flow and streambed drying , which already characterize many global river systems, are increasing in both space and time (Acuna *et al.* 2014; Prudhomme *et al.* 2014). Research examining these intermittent rivers has increased in recent years (e.g. Datry *et al.* 2016; Leigh *et al.* 2016; Datry *et al.* 2017), most of which focuses on macroinvertebrates, yet vegetation can also facilitate the assessment of how instream communities respond to drying (Sabater *et al.* 2017; Stubbington *et al.* 2019).

During supra-seasonal droughts (*sensu* Lake 2003), drying in naturally intermittent streams is more extensive, and can occur in near-perennial sections (Wood and Petts 1999, Stubbington et al. 2016). Southern England, a cool, wet temperate (i.e. oceanic climate) region experienced a prolonged groundwater drought extending from 1989 to 1992 (Met Office 2019). The winter recharge of the aquifers which underlie this region was much reduced during the drought period. Consequently, baseflow to the streams and rivers diminished during this time, resulting in a temporary shrinkage of the active river network (NRA 1993).

Following the 1989-1992 drought Holmes (1999) undertook a biomonitoring survey (1992-1995) to track post-drought changes in plant communities. Holmes (1999) used a classification approach to identify distinct plant communities (which he called Perennial [permanently flowing], Winterbourne [limited annual drying], Ditch [morphologically degraded channels with regular drying] and Intermittent [extensive and prolonged drying]) and to characterize the flow regimes which support them. This approach, which takes into account both aquatic and terrestrial taxa, can be used to identify characteristic communities and set ecological flow thresholds and desired intermittence patterns (Westwood *et al*. 2017).

The aim of the current study is to update and refine the classification produced by Holmes (1999) using the original sample data from 24 rivers together with data from additional surveys conducted in 12 of the original rivers up to 2013, plus a further set of surveys from 38 sites on four of these rivers between 2015 and 2018 (see *The study area* for details). We compare this updated classification to the original classification. We examine the classified results in relation to hydrological data including estimates of the percentage of zero-flow days in the 12, 24 and 36 months prior to surveying. We also examine plant communities in relation to channel substrate data recorded as part of more recent surveys, to enhance understanding of how the physical environment mediates the vegetation/hydrology relationship. We explore the use of plants as indicators of long and short-term flow intermittence and whether the communities they form can indicate a site's flow history and/or other local environmental characteristics.

Methods

The study area

The study area extends across southern England and comprises 118 sites on the upper reaches of 24 groundwater-fed rivers (Fig. 1). The area is predominantly underlain by Cretaceous chalk geology, except for sites on the Bristol Avon, Churn and Leach in the north west of the study area, which are on Jurassic limestone. The area experienced periods of drought resulting in a broad range of site-specific conditions (from low flows to complete and prolonged surface water loss) in 1992, 1996-1998, 2006 and 2012, with a period of high aquifer recharge occurring in 2001-2003 (Met Office 2019).

Survey sites are heterogeneous in physical character and range from roadside urban ditches, to channels with high hydromorphological complexity within more natural settings. Surrounding land use for most sites is agricultural with a mix of arable, permanent and rough pasture and some woodland. Groundwater is the main public water supply resource in the region and is heavily abstracted due to high demand (Arnell *et al*. 2015).

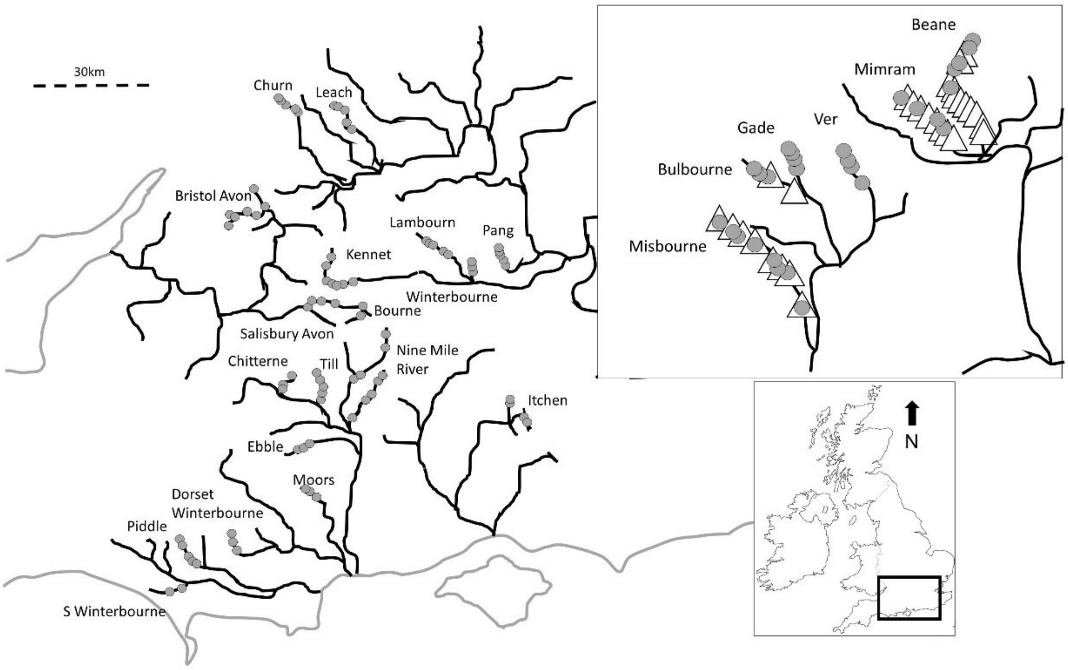


Fig 1. Location of the plant survey sites in south England. The original Holmes (1999) sites are indicated by grey circles and the 2015-2018 sites by white triangles.

Field methods

From 1992-2013 plants were surveyed within a defined area of the channel bed to the base of the bank including instream and marginal areas. Aquatic and semi-aquatic taxa were mainly identified to species, some to genus e.g. *Callitriche* spp., and non-aquatic grasses and herbs were recorded as such. Percentage cover was recorded for each taxon. Surveys were undertaken irrespective of instream state (standing water, isolated pools, or a completely dry bed). Site length ranged between 10 m and 50 m depending on channel width, with wider channels needing shorter lengths to effectively characterize the plant communities (see Holmes 1999). As a result, site areas were in the range 50-70 m^2. Surveys conducted in 2015-2018 followed the standard LEAFPACS2 method, with a 100 m site length and including visual assessment of substrate composition (% boulders, cobbles, pebbles, gravel, sand, silt and soil; UK-TAG 2014).

Discharge data

Daily mean river discharge data were extracted (https://nrfa.ceh.ac.uk/) for the downstream gauging stations closest to survey sites in the north east of the study area (Rivers Beane, Bulbourne, Gade, Mimram, Misbourne and Ver) . We transposed the nearest fixed gauged mean daily discharge to each site using linear regression against spot-gauge discharges (Gordon *et al.* 2004, Malcolm *et al*. 2012). From the site specific data we estimated the percentage of time with zero flows within the 12, 24 and 36 months prior to the surveys. As a record of zero flow does not distinguish between ponded water and a dry channel, the discharge series was calibrated with routine long-term visual assessments (Sefton *et al.* 2019). An improved match was achieved by counting any flows < 0.01 m^3/s as indicative of a dry channel.

Data analysis

The full list of 120 plant taxa observed was reduced to the 37 most frequently occurring (i.e. with a mean abundance thoughout the whole dataset of >1), to avoid the 'noise' generated by very rare taxa or taxa recorded infrequently (Table S1). The data were square-root transformed to normalise their distribution then classified using two-way indicator species analysis (TWINSPAN), a divisive, hierarchical clustering method devised by Hill (1979), with adjustments made by Oksanen and Minchin (1997). TWINSPAN was used in preference to more contemporary approaches, to ensure that the original (Holmes 1999) and new classifications were directly comparable. As with Holmes' (1999) classification, data analysis was taken to four levels of division and generated 32 candidate clusters based on community structure and composition. Analysis of similarities (ANOSIM) was used to identify distinct clusters at the level $r^2 \geq 0.2$, $p = \leq 0.001$. Group membership was explored using Similarity Percentages (SIMPER), which measure the contribution of individual taxa to the observed within and between-group similarity. For each group species/taxa richness and Simpson's diversity index (SI = 1-D) (Simpson, 1949) were calculated.

The plant data (37 taxa) were square-root transformed and ordinated using non-metric multi-dimensional scaling (nMDS), using a Bray Curtis dissimilarity matrix with 200 iterations of the data, within the package PRIMER v.7. The dimension 1 scores were used in linear regression against the site-specific discharge data available for six rivers (29 sites - Beane, Bulbourne, Gade, Mimram, Misbourne and Ver). The strength of regression coefficients between the dimension 1 scores and the site-specific discharges were used to determine which of the antecedent discharge periods (12, 24 or 36 months) best represented changes to the vegetation. The relative coverages of individual taxa were compared with the percentage of zero-flow (%ZF) days in the preceding 12 months (the time period producing the strongest coefficients) to identify how different taxa responded to differing degrees of flow intermittence.

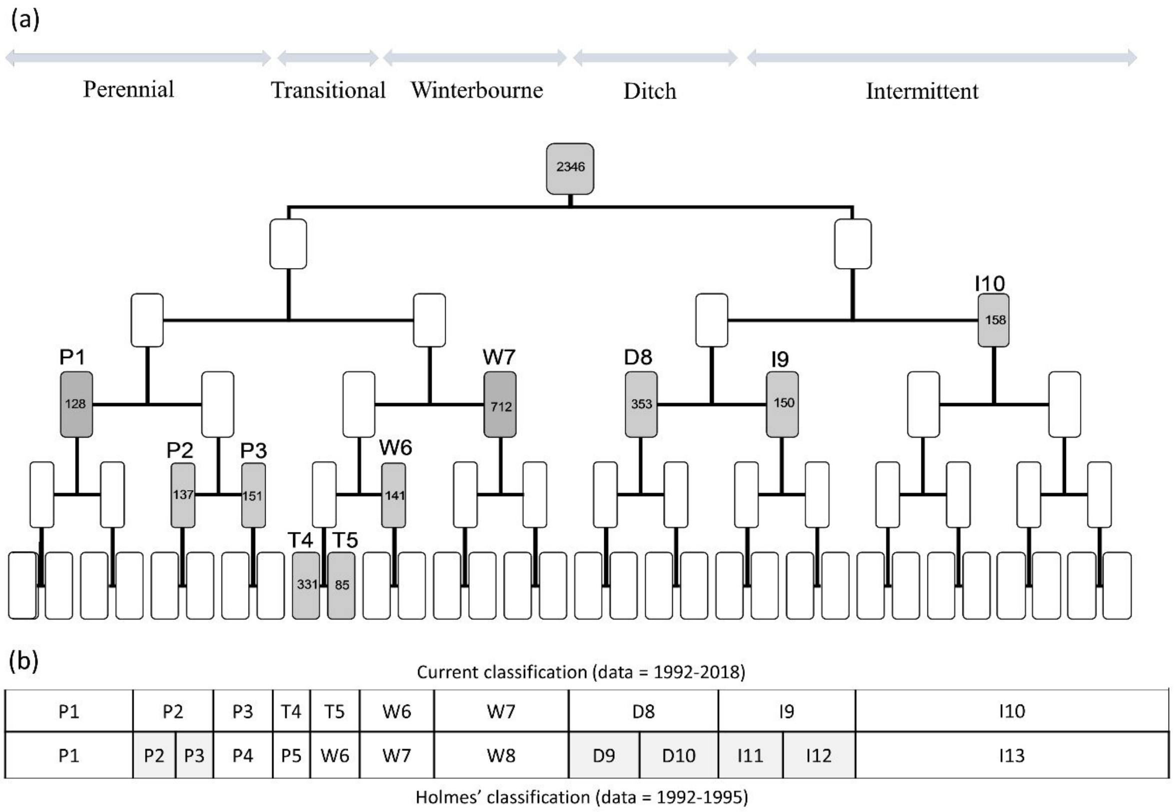
For the 2015-2018 surveys undertaken using the LEAFPACS2 method, the channel substrate observations were averaged for each community type as a way of characterising the physical habitat of the different communities.

Results

Identification of community types

Ten distinct plant community types were identified (TWINSPAN clusters; ANOSIM r^2 = 0.47, p = <0.001, range: r^2 = 0.21-0.98). These were broadly similar in composition to those found by Holmes (1999) but fewer than the 13 groups he recorded (Fig. 2). The average within-group similarity was 45.1% (range: 33% - 65%) and the average between-group dissimilarity was 73.7% (range: 53% - 93%). The groups were named in line with Holmes' (1999) original convention (Perennial, Winterbourne, Ditch and Intermittent), with the addition of an extra category for 'Transitional' communities, which occurred between Perennial and Winterbourne communities and experience very low flows and drying only under extreme drought conditions.

The 10 community types were arranged along a gradient of flow intermittence (Fig. 2; no intermittence to the left, high intermittence to the right). Communities representing the most intermittent sites (i.e. Ditch and Intermittent sites [types: D8-I10 in Fig. 2]) were separated from others at level 1, and accounted for 28% of the total dataset. Subsequent levels of division defined the other main community groups (Perennial, Transitional, Winterbourne), with subdivisions of these made at levels 3 and 4. The Winterbourne community type W7 is by far the biggest group comprising 30% of all samples, but attempts to subdivide it resulted in weak coefficients (ANOSIM $r^2 = 0.09$, $p = 0.001$; within-group similarity: 24.7% and 24.9%; between-group dissimilarity: 32%). Six of the original Holmes (1999) community types are aggregated into three larger groups within the new classification (Fig. 2b), (minimum statistical test of ANOSIM: $r^2 \geq 0.2$, $p = \leq 0.001$).



P1	P2		P3	T4	T5	W6	W7	D8		I9		I10
P1	P2	P3	P4	P5	W6	W7	W8	D9	D10	I11	I12	I13

Fig. 2. (a) Dendrogram showing the relative position of the plant community types along a gradient of flow intermittence, indicating (b) previous (Holmes 1999) and current classifications (P=Perennial, T=Transitional, W=Winterbourne, D=Ditch and I=Intermittent).

Plant community characteristics

The average contribution of different plant species/taxa varied by community types with obligate aquatics associated with the Perennial groups and terrestrial/wetland plants associated with the more intermittent community types (i.e. Intermittent and Ditch; Fig. 3; Table S2). Several species, including *Berula erecta, Ranunculus pseudofluitans, Verrucaria* spp. and *Sparganium erectum* are restricted to or mostly associated with the Perennial communities. Non-aquatic taxa occur in every community type, whereas *Apium nodiflorum*, *Glyceria* spp., *Rorripa nasturtium aquaticum* and *Phalaris arundinacea* occur in all communities except I10.

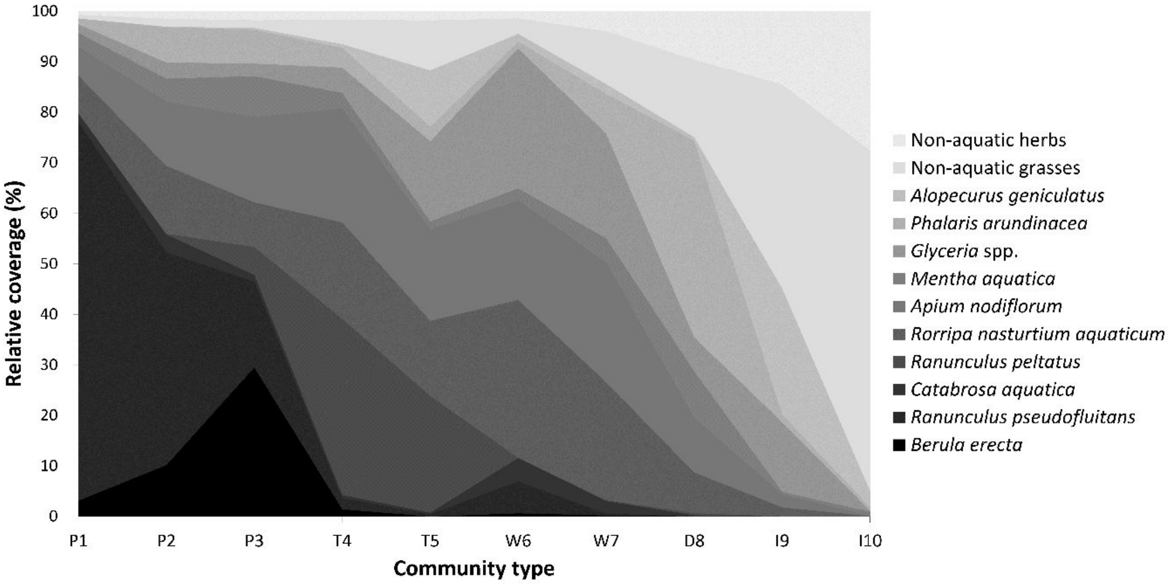


Fig. 3 Relative coverage of the 12 most frequently occurring species/taxa within each of the community types (P=Perennial, T=Transitional, W=Winterbourne, D=Ditch and I=Intermittent).

At group level, the Perennial group (P1-P3) is defined by the presence of the obligate rheophile *Ranunculus pseudofluitans* and <2% non-aquatic taxa (Table S1). The Transitional group (T4, T5) features *Ranunculus peltatus*, although some *R. pseudofluitans* is still present and a small component (0 - 7%) of non-aquatic taxa is common (Table S1). The Winterbourne group (W6, W7) is the most characteristic community type for sites which dry for 0-30% of each year (Table 1). The Ditch (D8) and Intermittent (I9, I10) groups, reflecting >30% intermittence, have increasing amounts of non-aquatic taxa and/or wetland grasses, with 100% plant coverage being common in the Intermittent group (Table 1).

Table 1 Descriptions of plant community types, with average Simpson's Diversity, typical annual periodicity of intermittence and net change in frequency over the survey period (1992-2013 for 24 rivers). The average distribution of species/taxa across the 10 community types for those with an average abundance within the total dataset of > 1 are provided in Table S2.

Plant community type	Description	Typical annual dry period	Mean Simpson's diversity (± standard error)	Net % change in frequency 1992-2013
P1	Dominated by *Ranunculus pseudofluitans* and typical of fast-flowing stretches with predominantly gravel/pebble substrates. Minor accumulations of silt at the channel margins support limited abundances of emergent herbs.	0% (always flowing)	0.56 (± 0.014)	-17%
P2	Dominated by *R. pseudofluitans* and typical of fast to moderate flow with predominantly gravel/pebble substrates and silty margins. Emergent herbs, sedges and tall grasses are more common at the margins than P1	0% (always flowing)	0.74 (± 0.011)	+12%
P3	Typical of moderate flow, with *Berula erecta* common and sometimes dominant. *R. pseudofluitans* is common at lower abundances than in P1 and P2. *Apium nodiflorum* and *Mentha aquatica* are both often higher in abundance than P1 or P2.	0-5% (only dry in very severe droughts)	0.75 (± 0.012)	+20%
T4	Often contains a high proportion of *Ranunculus peltatus* and *Callitriche* spp. *R. pseudofluitans* may occur at low abundance at greater discharges. Plant coverage is higher than for the Perennial group and often includes non-aquatic grasses.	0-5% (low flows but only dry in severe droughts)	0.68 (± 0.009)	+9%
T5	Typically contains a high proportion of *R. peltatus,* with a greater presence of non-aquatic	0-10% (very low	0.67 (± 0.015)	-48%

	taxa and abundance of *Glyceria* spp. than T4, reflecting fluctuating flows and occasional drying. Plant coverage is higher than for the Perennial group.	flows and may dry in moderate droughts)		
W6	Characterized by high proportions of *Rorippa nasturtium aquaticum, A. nodiflorum* and *Glyceria* spp. The community is characteristic of lower flows in late summer and autumn, when marginal herbs encroach upon the channel, concentrating the flow that supports obligate aquatic taxa. *Veronica beccabunga* is characteristic of this community.	0-20% (very low flows and dry in moderate droughts)	0.60 (± 0.016)	+21%
W7	The most common community type, and representing the point at which rheophilic taxa cease to occur and marginal herbs and grasses dominate. Generally lower plant coverage than Perennial and Transitional groups. Sites are often impounded with deeper ponded conditions promoting the growth of filamentous algae (predominantly *Cladophoera* spp.) and restricting the growth of *R. pseudofluitans*. *Veronica beccabunga* is characteristic of this community.	10-30% (regular intermittence, limited drying in most years)	0.68 (± 0.006)	-17%
D8	Characteristic of ponding and regular drying, dominated by *Phalaris arundinacea*. Declining proportions of water-demanding taxa such as *R. nasturtium aquaticum*, *A. nodiflorum* and *Glyceria notata* are balanced by increases in the more drought-tolerant *Mentha aquatica* and *Epilobium hirsutum*; there is a regular component of non-aquatic taxa.	30-90% (regular intermittence, some drying)	0.58 (± 0.011)	+33%
I9	Characterized by the occurrence of the wetland grass *Alopecurus geniculatus*, reflecting either the loss of surface water or its recent return. A high coverage of non-aquatic taxa is typical.	50-90% (regular intermittence, some drying)	0.55 (± 0.012)	-10%
I10	With low aquatic richness this community denotes the final stage of channel drying, with only the wetland grass *A. geniculatus* indicating a river channel. Non-aquatic taxa, and particularly grasses, often account for 100% of the assemblage, growing in soil.	50-100% (regular intermittence, dry channels)	0.42 (± 0.014)	-35%

Plant community and flow relationships

The plant community response to drying varied between sites, with 15 of the 29 sites responding most strongly to the %ZF within the antecedent 12-month periods. Eight sites responded most strongly to the antecedent 24-month period and 4 sites (Beane 5, Gade 1, Misbourne 6 and 7) had a longer ‘lag phase’ responding most strongly to the %ZF in the previous 36 months (Table S3).

Comparison of the relative coverages of individual species/taxa against the %ZF in the preceding 12 months indicated the limited tolerance to drying of the obligate aquatics *R. pseudofluitans* and *Berula erecta* (Fig. 4.), whereas the species/taxa that are the most associated with intermittence were *A. nodiflorum, R. nasturtium aquaticum, Glyceria* spp. and non-aquatic taxa. Certain species were characteristic of a particular level of intermittence, for instance, *Veronica beccabunga* favoured 50-70%, *R. nasturtium aquaticum* 20-30% and *R. peltatus* 0-10%, whereas *R. pseudofluitans* was characteristic of perennial flow. The total plant coverage increased steadily with increasing intermittence, from an average of 52% (SE±3.1) at perennial sites to an average of 90% (SE±2.3) at sites experiencing dry phases of 12 months or more, at which point the community consisted almost entirely of non-aquatic taxa.

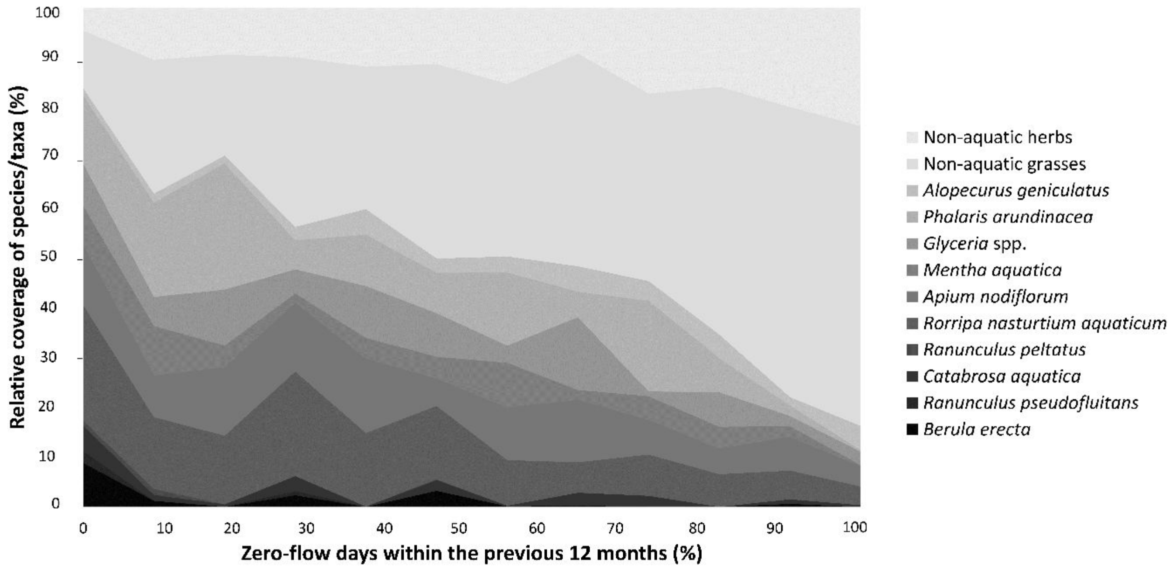


Fig. 4. The responses of 12 most frequently occurring species/taxa to increasing flow intermittence.

The annual frequency of community types over the 22-year study period (Fig. S1) shows how the contribution of the different community types varies over time. Throughout the period, the most frequent community is W7, except in 2006 and 2012 when D8 is most frequent and 1992 when I9 was most frequent. There was a high frequency of Intermittent and Ditch types in the dry years of 1992, 1996-1998, 2006 and 2012, whereas Winterbourne, Transitional and Perennial communities dominated between 2001 and 2003, following high aquifer recharge.

Plant community/site characteristics.

The Perennial community P1 occurred almost exclusively on gravel and pebble substrates, whilst the Perennial communities (P2 and P3) occurred on a range of substrates, including gravel, pebbles and sand, and with greater amounts of silt present (Fig. 5). The Transitional communities were associated with pebble and gravel dominated substrates and Winterbourne communities with higher proportions of silt. Lower proportions of silt and higher proportions of soil were observed for the Ditch communities and soil dominated where Intermittent communities were found (Fig. 5.).

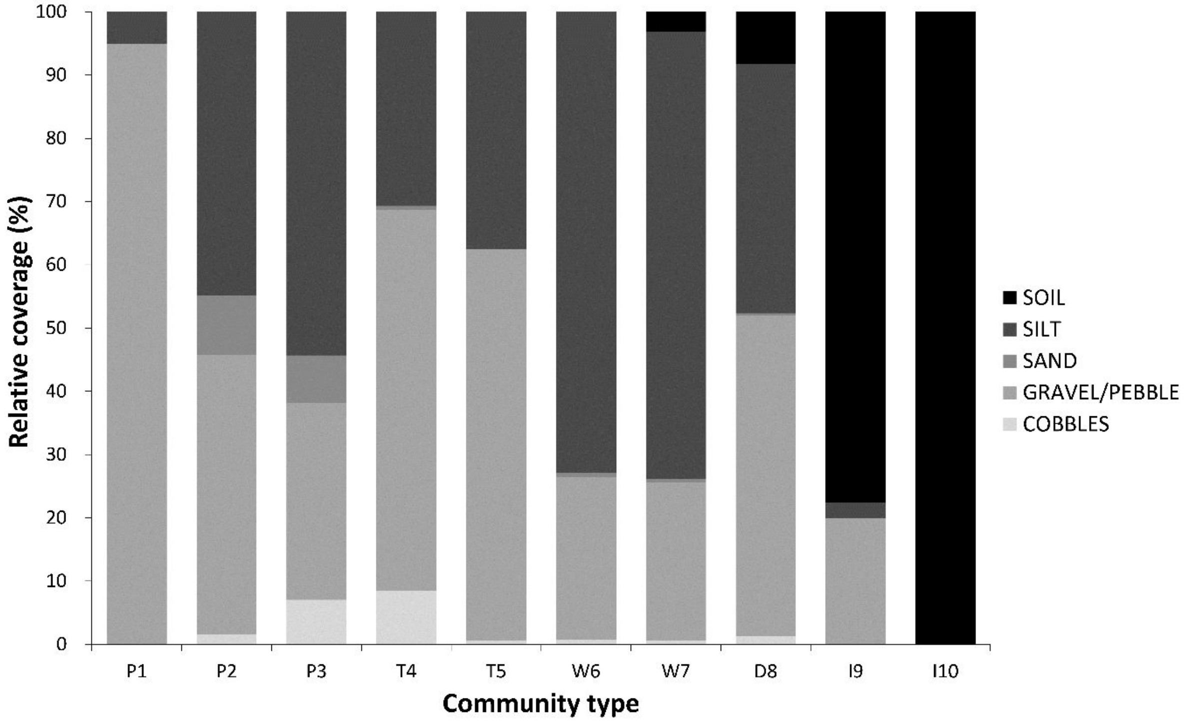


Fig. 5. Substrate composition at sites within each community type, calculated as the mean value of each variable per community type (P=Perennial, T=Transitional, W=Winterbourne, D=Ditch and I=Intermittent).

Discussion

The communities identified and described through our classification demonstrate that plants can be biomonitors that effectively characterize responses to flow intermittence, specifically ponded and dry instream conditions. From a temporal perspective, these communities represent various stages of succession in relation to variation in discharge both within and between years (Baattrup-Pedersen and Riis 1999). From a spatial perspective, communities denoted varying degrees of intermittence (Katz *et al.* 2011).

Changes in community composition in response to flow and intermittence

The general historic trend observed within the classified communities suggests an overall simplification of the plant assemblages from 13 community types within the original classification (Holmes 1999) to 10 within our updated classification. Variation in frequency of the different communities allows examination of changes at a regional scale and reveals a rapid biotic response to the 1989-1992 supra-seasonal drought, followed by a period of longer-term community adjustment and retrenchment. Changes in the frequency of particular communities reflects variation in the presence of particular taxa. For example, the reduction of P1 community observations reflects a net loss of -32% of *R. pseudofluitans* across the study area, a plant within priority habitats protected under the EC Habitats Directive (92/43/EEC). Its decline may reflect 'chalk stream malaise', a local description of biotic responses to various combinations of decreases in discharge and velocities, channel modification, increased fine sediment loading, and increased nutrient inputs (Environment Agency 2000; Heywood and Walling 2003; Jarvie *et al*. 2004). The decline in *R. pseudofluitans* was mirrored by an increase in *R. peltatus*, which can withstand low flows and drying channels and can grow across damp substrates (Grime *et al*. 1992; Volder *et al*. 1997). This increase in *R. peltatus* explains the increase in T4 communities.

At the 'drier' end of the continuum, the decrease in the occurrence of the I9 community can be linked to the reduced occurrence of wetland grass *Alopecurus geniculatus*. Observations of this grass increased in response to flow resumption following prolonged droughts, such as in the three years after the 1989-1992 event (Holmes, 1999) but were less common in our more recent surveys. A wider decline in *A. geniculatus* has previously been noted in the UK (Carey *et al.* 2008), possibly due to the drainage and cultivation of riparian damp meadows. However, the low recorded diversity of both Intermittent communities (Table 1) reflects a lack of aquatic and semi-aquatic taxa and not the diversity of the communities as a whole, which were observed to often contain a wide variety of terrestrial plants.

The aquatic plant community recovery following the extended drought promoted a greater diversity of species able to exploit the various physical niches provided (Holmes 1999; Sabater *et al.* 2017). We observed that in the absence of this drought 'disturbance', there was a simplification of the community with an increase in tall wetland grasses such as *P. arundinacea* and *Glyceria maxima*. This highlights the importance of drying events in resetting the coloniztion clock (Perrow *et al.* 2007) and promoting temporal and spatial beta diversity (i.e. variation in community composition in time and space) within intermittent rivers (Datry *et al*. 2016, Tonkin *et al.* 2017).

Substrate composition associated with different community types

We found that perennial communities were associated with gravel and pebble-dominated substrates and the more intermittent communities (Intermittent and Ditch types) with silt and soil-dominated substrates. Different plant species are associated with different substrate types (e.g. Barko and Smart 1986; Clarke and Wharton 2001) and different substrates also interact with drying to influence plant growth and survival as water retention capacity declines with increasing sediment size (Walczak *et al.* 2002) and affects nutrient availability (Song *et al.* 2007). Consequently, for a given drying duration, the intensity of water stress differs according to sediment composition, in turn influencing the resistance and resilience of plants (De Wilde *et al.*, 2017). However, how substrate, channel morphology, as well as variables including shading interact to affect water content within drying channels remains unclear (Westwood *et al.* 2006; Stubbington *et al.* 2019). To address this knowledge gap, we recommend that future plant surveys should be accompanied by systematic recording of the physical environment including characterization of the riparian zone. An improved understanding of the effects of the physical environment will indicate conditions governing the resistance and resilience of different species and communities to intermittence, improving our ability to maintain their requirements for flowing, ponded and/or dry instream conditions while managing demands for water resources (Franklin *et al.* 2008).

Assessment of communities across the continuum of intermittence

Analysis in relation to antecedent flow intermittence showed the relative abundance of species/taxa as indicative of flow history. The observed link between flow intermittence and the response of differing plant communities to 12, 24 or 36-month antecedent percentage of zero flow (%ZF) mirrors previous analyses demonstrating varying lag phases in community response to hydrological variation (Klijn and Witte 1999; Westwood *et al*. 2017). The collection of plant data from intermittent streams thus far has concentrated on aquatic and wetland species, with little attention paid to the terrestrial taxa encountered, these instead being aggregated as 'non-aquatic' grasses and herbs or left undocumented (Dieterich and Anderson 1998, Holmes 1999, Westwood *et al.* 2006, 2017, Sabater *et al*. 2017). To expand our understanding of how plant communities transition across the flowing, ponded and dry phases of intermittent systems, a more comprehensive community characterisation that encompasses plants from obligate aquatic to terrestrial across the full range of intermittence is needed (Steward *et al.* 2018; Stubbington *et al.* 2019).

Towards a new set of management tools

Large-scale plant surveys such as the one analysed here demonstrate their usefulness in understanding temporal and spatial patterns in response to environmental variability (Holmes 2006). Although Holmes (1999) created a uniquely valuable dataset which will guide future developments in plant biomonitoring, the community types we identified, based on 37 taxa, should facilitate more rapid assessments to establish plant community responses to changing flow regimes in lowland groundwater-fed streams. Our survey and classification approach could be adapted to explore plant community responses across a range of intermittent stream types, by determining the extent to which the described associations of individual taxa and communities are generally applicable.

Our results confirm the controlling influence that the flow regime has on plant communities of intermittent rivers (Bornette and Puijalon 2011). Understanding these controls could inform how to characterize EU Water Framework Directive ecological status, identify the reference conditions we need to achieve and the flow regime required to support them (Stubbington et al. 2017). This understanding can inform local and regional resource management by providing a reliable gauge of the flow requirements needed to support contrasting site-specific and temporally variable communities, leading to the development of specific flow targets (e.g. Holmes 1999, Westwood *et al*. 2017). In addition, plant communities can be used to characterize flow permanence regimes in the absence of hydrological data, which is often lacking for temporary streams (Costigan *et al.* 2017; Beaufort *et al.* 2018). Management strategies which allocate flows for instream ecological needs are well established (Franklin *et al.* 2008; Acreman *et al.* 2014). However, defining environmental flows is more complicated for intermittent streams, because target regimes must simultaneously consider both the discharge and the patterns of intermittence that promote plant diversity and abundance (Sabater *et al.* 2017). Incorporating a more comprehensive characterisation of plant communities across the continuum of intermittence will help advance our understanding of wider biotic responses to hydrological and other environmental changes (Stubbington *et al*. 2018, 2019; England *et al.* 2019) and inform the derivation of novel assessment methods that are specifically designed for intermittent streams.

Conclusions

1. Plant community structure provides a reliable guide to a site's flow history, especially in terms of its flow intermittence, which is particularly useful at ungauged sites.
2. A prolonged drought promoted a greater diversity of plant communities as flows resumed and species exploited the various physical niches provided. In the absence of prolonged drought, communities became increasingly simplified, featuring fewer obligate aquatic taxa but greater growths of tall wetland grasses.
3. Flow is the master variable controlling riverine plant community composition, but its interactions with channel morphology remains poorly explored. Future surveys should therefore include more detailed physical site assessments.
4. To advance our understanding of how biological communities change as intermittent systems transition between flowing, ponded and dry phases, future surveys should encompass identification of terrestrial plants.
5. As intermittent streams become increasingly common due to both climatic drivers and water resource pressures, tools are needed to effectively predict, monitor and manage the effects of flow variability on biotic communities. Developing such tools should encompass taxa associated with a full range of instream conditions, to enable scientists and managers to conduct holistic ecosystem health assessment

Acknowledgements

This paper is dedicated to the memory of Dr Nigel Holmes (Alconbury Consultants), whose tireless efforts created this unique regional dataset, as well as so much else in river science. It was while preparing for a full reclassification of the data in 2014 that he sadly died without warning. We hope he would have approved of our efforts and agreed with our findings. Data available on request from the authors.

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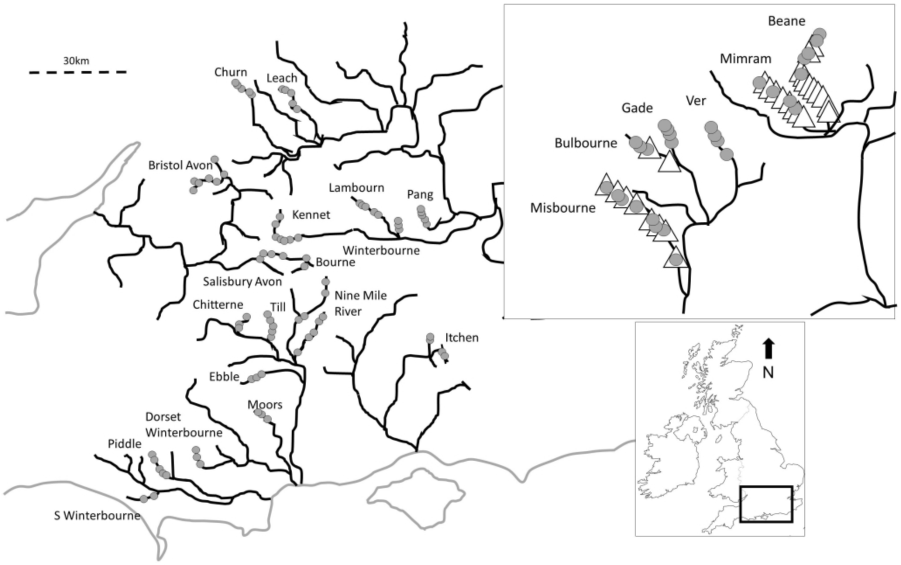

Fig 1. Location of the plant survey sites in south England. The original Holmes (1999) sites are indicated by grey circles and the 2015-2018 sites by white triangles.

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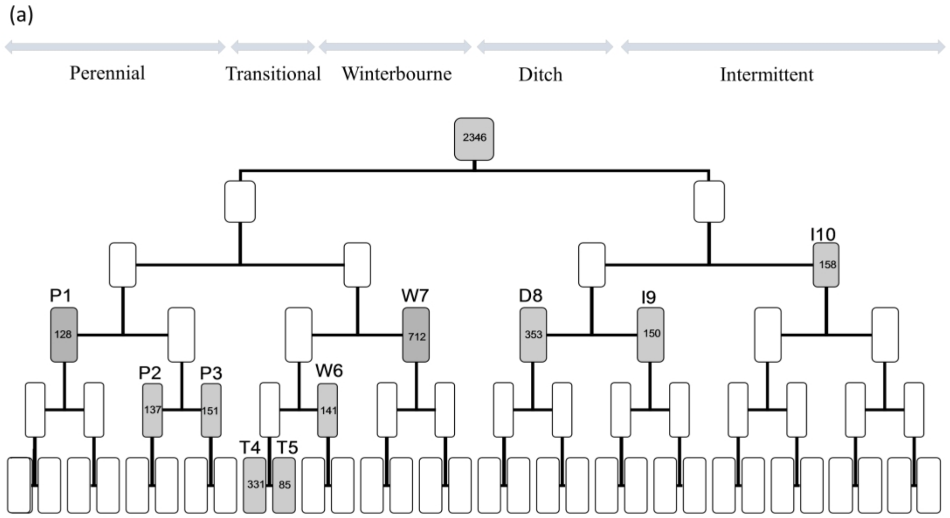
(a)



(b)

Current classification (data = 1992-2018)

<table>
<tr><td>P1</td><td colspan="2">P2</td><td>P3</td><td>T4</td><td>T5</td><td>W6</td><td>W7</td><td colspan="2">D8</td><td colspan="2">I9</td><td>I10</td></tr>
<tr><td>P1</td><td>P2</td><td>P3</td><td>P4</td><td>P5</td><td>W6</td><td>W7</td><td>W8</td><td>D9</td><td>D10</td><td>I11</td><td>I12</td><td>I13</td></tr>
</table>

Holmes' classification (data = 1992-1995)

Fig. 2. (a) Dendrogram showing the relative position of the plant community types along a gradient of flow intermittence, indicating (b) previous (Holmes 1999) and current classifications (P=Perennial, T=Transitional, W=Winterbourne, D=Ditch and I=Intermittent).

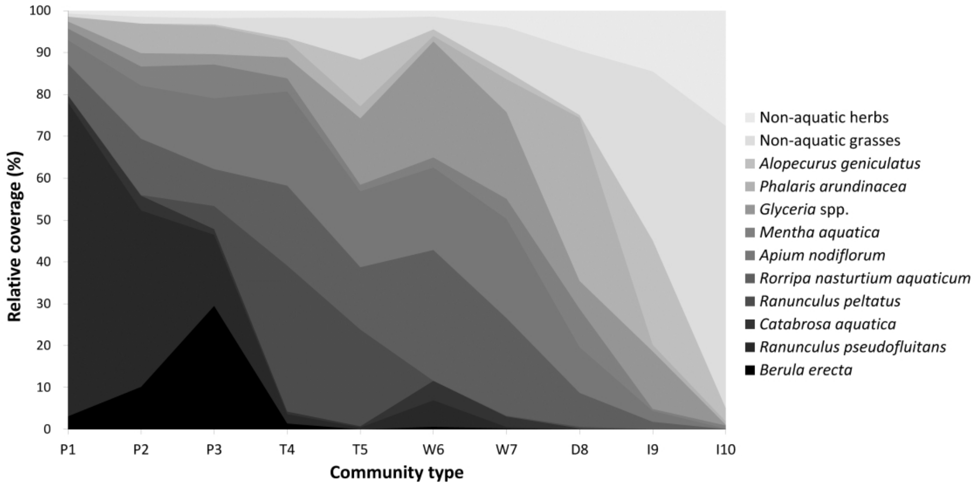


Fig. 3 Relative coverage of the 12 most frequently occurring species/taxa within each of the community types (P=Perennial, T=Transitional, W=Winterbourne, D=Ditch and I=Intermittent).

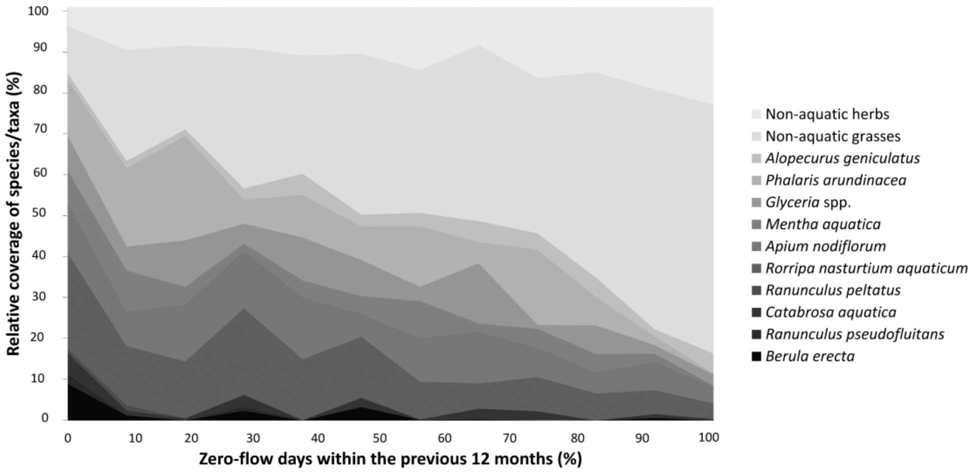


Fig. 4. The responses of 12 most frequently occurring species/taxa to increasing flow intermittence.

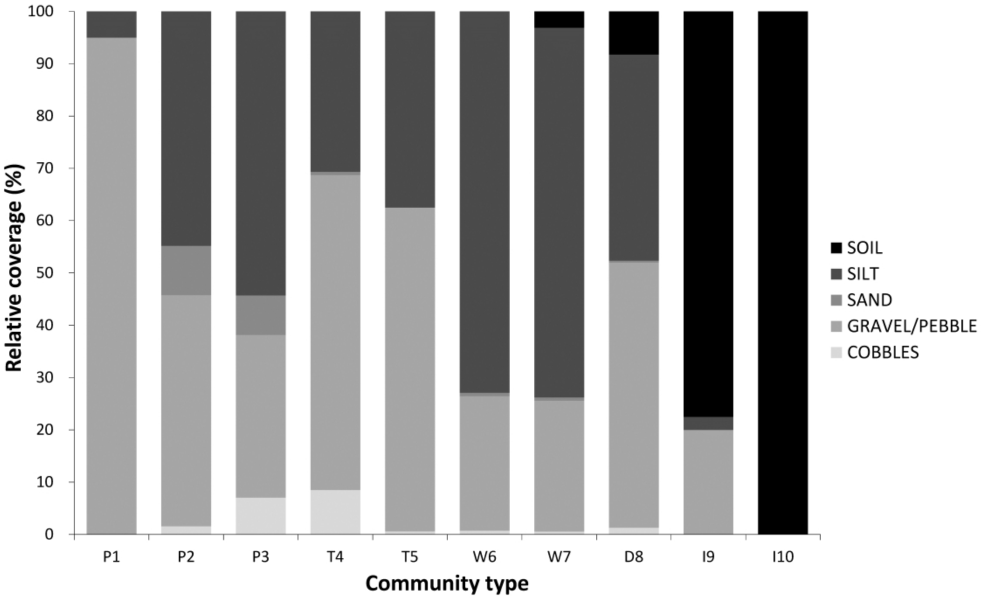


Fig. 5. Substrate composition at sites within each community type, calculated as the mean value of each variable per community type (P=Perennial, T=Transitional, W=Winterbourne, D=Ditch and I=Intermittent).