The Plant Flow Index: a new method to assess the hydroecological condition of temporary rivers and streams.

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Highlights

- We assigned weighted scores to 34 common plant taxa based on their response to river drying.

- We combined the scores to create the Plant Flow Index.

- PFI was more responsive to recent river drying than existing plant community indices.

- PFI is unique as an index to characterize plant community responses to river drying.

Abstract

Temporary streams are widespread in global river networks, and hydroecological tools are needed to assess biotic responses to changes in environmental conditions between wet and dry states. Plant communities can be abundant and diverse in temporary streams, and vary in their tolerance of changing water availability and associated habitat conditions, but globally, no indices have been developed to document community-level responses to intermittence. We present the first index developed to assess plant assemblage responses to changing habitat conditions in temporary stream channels: the Plant Flow Index (PFI). Using a regional 22-year dataset from lowland groundwater-fed headwater streams in the UK, we establish relationships between the occurrence and abundance of 34 common aquatic, semi-aquatic and terrestrial taxa and the proportion of time the channel was dry within the antecedent 12 months. Species/taxon-specific responses to channel drying were weighted and used to calculate a single score representing each community. We compare the PFI to three other plant assessment methods, which demonstrates its greater ability to

reflect the effects of intermittent flow and specifically drying events. The PFI represents a flexible index that can be modified to include additional and/or different taxa and their responses to intermittence, allowing its application across regions and river types with contrasting environmental characteristics and intermittence regimes. As temporary streams increase in both space and time, this index represents a valuable tool to track ecological responses to intermittence at both broad and fine spatial and temporal scales.

Keywords: intermittency, ephemeral streams, plants, bioassessment, biomonitoring, vegetation

1. Introduction

Temporary streams are defined as those which periodically cease to flow, and may dry completely (Leigh et al., 2016). These ecosystems are widespread and diverse in both dryland and temperate regions (Sheldon, 2005; Stubbington et al., 2017), due in large part to their prevalence in headwaters (Acuña et al., 2014). Flow cessation and streambed drying are increasing in both space and time in many global regions, due to the effects of climate change (Döll and Schmied, 2012; IPCC, 2018) and increasing water usage by an expanding population (Shiklomanov and Rodda, 2003; Gerten et al., 2013).

Intermittence makes temporary streams dynamic habitats with in-channel states ranging from flowing to dry and encompassing transitional periods in which isolated or connected pools persist (Leigh et al., 2016; Stubbington, et al., 2017). These alternations between states can create mosaics of flowing, ponded and dry habitats which vary in space and time (Larned et al., 2010). Each state supports a different biological community, with the contributions of both aquatic and terrestrial taxa increasing total biodiversity in temporary streams (Corti and Datry, 2016; Bunting et al., 2020).

Despite recent advances, our understanding of community structure and thus ecosystem functioning in temporary streams remains limited (e.g. Datry et al., 2016; Leigh et al., 2016), partly due to a lack of effective tools to assess biological responses to intermittence and environmental quality (Stubbington et al., 2018). However, there are tools to examine the responses of aquatic macroinvertebrate communities to changes in habitat availability during unpredictable drought events in near-perennial streams (Drought Effect of Habitat Loss on Invertebrates – DEHLI; Chadd et al., 2017), and to changes in in-channel state (Monitoring Intermittent Streams index – MIS-index; England et al., 2019) and antecedent drying events (Biodrought index; Straka et al., 2019) in temporary streams. In contrast, comparable tools to assess plant communities remain in the early stages of development (Westwood et al., 2017, 2020). Specifically, vegetational responses to drying have been assessed within temperate lowland groundwater-fed streams (Holmes, 1999), demonstrating that plant communities change over timespans of months to decades, with losses of obligate aquatic species being balanced by increases in terrestrial taxa as flow declines and water is lost (Westwood et al., 2006a, 2017, 2020). Such responses indicate that plant communities are potential indicators of antecedent in-channel conditions in temporary streams.

The duration of the dry phase is an important influence on community response to drying (Katz et al., 2012; Leigh and Datry, 2017; Colls et al., 2019). In streams with predictable drying for shorter durations (e.g. <3 months), plant communities adapted to these conditions can include a high diversity of aquatic and wetland macrophytes (Westwood et al., 2006a; Franklin et al., 2008). By contrast, in systems experiencing longer dry periods, semi-aquatic and terrestrial taxa often encroach into the channel from the margins and riparian zone as the dominance of aquatic macrophytes declines (Holmes, 1999; Franklin et al., 2008; Stromberg and Merritt, 2016). Under prolonged dry conditions, in-channel communities can be entirely composed of terrestrial species growing in soil (Holmes, 1999; Westwood et al., 2020).

Plants influence their riverine environment, acting as ecosystem engineers by facilitating sediment accumulation, altering flow patterns and influencing nutrient concentrations (Clarke, 2002; Gurnell et al., 2010; Gurnell, 2014). This close interaction between river plants and their environment makes them useful indicators of differing habitat conditions, including those resulting from intermittence (Westwood et al., 2020). However, studies remain largely qualitative (e.g. Franklin et al., 2008; Katz et al., 2011; Stromberg and Merritt, 2016) and, to the best of our knowledge, no indices have been developed to document plant community responses to changing habitat conditions in temporary streams.

We developed a new *Plant Flow Index* (PFI), to characterize plant community responses to habitat characteristics as a result of hydrological variability and intermittence. Using observations of the responses of individual taxa to intermittence in headwater streams in the Thames Basin, UK, we assigned each taxon a code to reflect its response to intermittence, plus a weighting factor based on the percentage area covered. We used these values to calculate the PFI score for a community. Using two datasets from lowland UK groundwater-fed headwater streams, we compared the ability of the PFI and three other plant assemblage assessment methods to describe responses to intermittence during the antecedent 12 months. Of these other assessment methods, two respond to intermittence: the abundance-weighted Ellenberg moisture preference values for plants (AWE; based on Hill et al., 1999) and the Winterbourne Classification (WC), which describes 10 plant community types characteristic of flow regimes ranging from highly intermittent to perennial (see Westwood et al., 2020). The third method is the Mean Trophic Rank index (MTR; Holmes et al., 1999), which responds to nutrient enrichment and has shown promise in responding to environmental quality in dry channels (Stubbington et al., 2019).

Our aims were: (1) to develop the PFI, evaluate correlations between the PFI and existing assessment methods (AWE and MTR), and establish whether particular PFI scores are associated with the different WC community types; (2) to evaluate the responses of the PFI, AWE and MTR indices to antecedent intermittence and specifically drying; (3) to explore associations between PFI scores and site-specific environmental characteristics (mesohabitat types, water width, channel slope and substrate); and (4) to illustrate the dynamical application of the PFI for the analysis of inter-annual and long term changes in vegetation at four contrasting sites.

2. Materials and Methods

2.1 Study area

We used data collected during plant community field surveys in the headwaters of groundwater-fed rivers within the Thames catchment: a 22-year (1992-2013) dataset spanning 57 sites across 11 rivers, which we divided to create a development (I) dataset (846 surveys), a test (II) dataset (718 surveys) and a 5-year (2015-2019) (III) dataset from 39 sites across five rivers (220 surveys) (Fig. 1). The area has a temperate climate with an oceanic influence (i.e. Köppen-Geiger classification Cfb) with mean annual air temperatures that typically range from 9.5°C to 11.5°C and average annual precipitation of 550 mm to 950 mm (Met Office, 2019a). Land use is predominantly agricultural with a mix of arable, permanent and rough pasture, and some woodland (NRFA, 2020). The area is predominantly underlain by Cretaceous chalk, resulting in seasonal, predictable channel drying in response to changes in groundwater levels; although the spatial extent and timing of drying varies among years in relation to antecedent rainfall. Stream discharge typically peaks in January-March, then declines as groundwater levels drop, leading to minimum discharge in August-October and potentially to complete loss of surface water in parts of the river where flow is temporary. The peak flows generally correspond with the start of the plant growth season, which has a mean of 273 days (Department of Energy and Climate Change, 2013). The area experienced droughts (i.e. deficits in water in comparison to the long-term average; Tallaksen and van Lanen 2004,) in 1992, 1996-1998, 2006 and 2012, with a period of high aquifer recharge occurring in 2001-2003 (Marsh et al., 2007, 2013; Met

Office 2019b). During periods of drought some sites remain dry for more than a year and during periods of high groundwater some sites remain wet for more than a year.

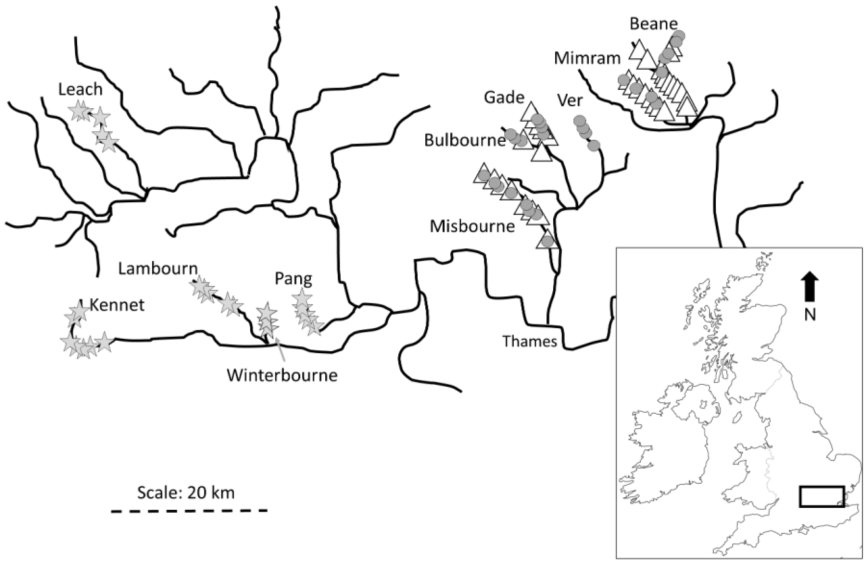

Fig. 1 The location of sites at which plant communities were surveyed from 1992-2013 (dataset I, circles; dataset II, stars) and from 2015-2019 (dataset III, triangles).

2.2 Contrasting case study locations

Four sites were selected to illustrate the application of PFI, one on each of the Rivers Bulbourne and Misboune and two on the River Ver (Fig. 1; Supplementary Material), which differ in their morphology and channel characteristics. All sites were surveyed annually from 1993-2013 and experienced flowing, ponded and dry conditions during the study period in response to changing groundwater levels partly in response to abstraction. Groundwater abstraction affects all three catchments. Water company data showed that during the study period, the abstraction regime remained consistent in the Bulbourne catchment but had a declining temporal pattern in the Ver and Misbourne catchments, increasing the Ver's baseflow from 1993 onwards (Clayton et al., 2008), and the Misbourne's from 1998 onwards (Perrow et al., 2007).

2.3 Field methods

Plant surveys for the period 1992-2013 were undertaken within a defined area of the channel bed, including in-channel and marginal areas to the base of the bank. Site lengths ranged between 10 m and 50 m depending on channel width, with wider channels needing shorter lengths to characterize their plant communities (Holmes, 1999). As a result, survey areas were in the range 50-70 m^2.

Surveys conducted over 2015-2019 followed the LEAFPACS2 method (UK-TAG 2014), with a standard 100 m site length. Visual assessments were made of substrate composition (% cobbles, gravel/pebbles, sand, silt and soil) and mesohabitat type (% riffle, run, pool, slack [areas of slow-flowing water] and dry bed). We assigned scores to the five substrate categories (5-1 respectively, with cobbles 5 and soil 1); resulting values were summed and divided by 100 to produce a single score for each survey, ranging from 1-5, with higher values indicating coarser substrates. A comparable approach was applied to the mesohabitat data (5 for riffle, 4 for run etc.) with resultant higher values indicating dominance of faster flowing habitats. For each survey, we measured the width of the water at four equidistant points along the site length, then averaged the results. Using a Light Detection and Ranging (LIDAR) map layer within Arc GIS, we calculated the channel slope as the change in elevation between points 500 m upstream and downstream of each site's midpoint, with the results expressed as m km^{-1}.

Aquatic and semi-aquatic taxa were identified to species level, except for *Callitriche* spp., *Vaucheria* spp. and *Verrucaria* spp., which were recorded at genus level; terrestrial grasses and herbs were recorded as such (Table 1). Surveys were undertaken across flowing, ponded and dry in-channel states. Percentage cover within the survey area was visually assessed for each plant taxon allowing comparability between the surveys despite the different sized areas.

2.4 Hydrological data

2.4 Hydrological data

For 52 of the sites, we used close (<1 km) spot-gauging measurements and regressed these against fixed-gauge records to construct time series of site-specific discharge (Gordon, et al., 2004; Malcolm, et al., 2012; Supplementary Material). For the other 5 sites, we obtained hydrological time-series data (daily mean discharge) from fixed gauging stations <5 km away (NFRA, 2020). Since these sites are perennial and not affected by intermittent flow, main gauge values were considered reliable indicators of local conditions. We calculated the proportion of zero-flow days (%ZF) for each site-specific time series for the 12 months prior to each survey, this being the time period during which plants are most responsive to hydrological variability (Holmes, 1999; Westwood, et al., 2020). To distinguish between zero-flow readings representing a dry channel and ponded water, we calibrated the discharge records with visual assessments of in-channel conditions made at monthly intervals between 1997 and 2013 (Sefton et al., 2019), using a lower cut-off value of <0.01 $m^3 s^{-1}$ to define a dry channel (Supplementary Material).

2.5 Development of the Plant Flow Index (PFI)

We developed the PFI using dataset I (Fig. 1). To explore taxon-specific responses to site-specific intermittence regimes, we matched records of individual plant taxa with the locally modelled %ZF during the antecedent 12 months. We categorized the resulting site-specific discharge time series and associated taxa records into twelve 10% intermittence bands from 0-100% ZF, where 0% ZF denotes continuous flow and 100% ZF indicates a channel that was dry throughout the antecedent 12 months. We allocated PFI codes to each taxon based on its modal value reflecting its association with %ZF of 0 or 0.1-10% (10), >10-20% (9), >20-30% (8), >30-40% (7), >40-50% (6), >50-60% (5), >60-70% (4), >70-80% (3), >80-90% (2), >90-99.9% (1) and 100% (0). The size of the standard error of the mean within each category was used to evaluate the reliability of the allocated score. PFI codes were allocated to all 34 taxa within dataset I (see *Results* 3.1). To calculate the weighting factor, reflecting each species/taxon's percentage cover, we followed the cover weighting codes (CWC) of Holmes et al. (1999): <0.1% (1), 0.1-1% (2), >1-2.5% (3), >2.5-5% (4), >5-10% (5), >10-25% (6), >25-50% (7), >50-75% (8) and >75% (9). For each survey, we then multiplied the PFI taxon scores by CWC, to give weighted PFI taxon scores. Finally, we multiplied the result by 10 to give scores on a scale comparable with %ZF assessments and the MTR metric. To calculate the PFI for each community, we used the equation:

$$PFI = \frac{\sum(PFI\ taxon\ code \times CWC)}{\sum CWC} \times 10$$

2.6 Comparison between plant assessment methods

We used dataset II (Fig. 1) to identify any correlation of PFI scores with AWE and MTR scores using Pearson product-moment correlation analysis. We then regressed the index scores against %ZF to determine responses to channel drying and the strength and significance of site-specific linear regression coefficients. AWE scores were derived by identifying the

Ellenberg F number (a measure of moisture preference) for each taxon using Hill et al. (1999) and establishing abundance-weighted scores using percentage cover (Table S2, Supplementary Material). The Ellenberg F scores for six species of *Callitriche* were averaged to F11. The numbers assigned to obligate aquatic species that have higher F numbers (10-12) increase with percentage cover, those assigned to wetland and terrestrial species (8-5) decrease as cover increases, and species with F number 9 remain constant, as the original mid-point between F numbers 12 and 6. Terrestrial taxa were added to the protocol and weighted as F 5, which indicates a preference for moist soil/sediment. Individual weighted taxon scores were then averaged to give an AWE score for the community. MTR scores were calculated using Holmes et al., (1999, see Supplementary Material for details).

Associations between WC and the PFI, AWE and MTR indices were explored using Pearson product-moment correlation analysis. WC community types were assigned following Westwood et al., (2020) and allocated the numbers 1 to 10, with higher scores reflecting communities associated with drying (Table S2, Supplementary Material). Using dataset III (2015-2019; Fig. 1), we compared the range of PFI scores with each WC community type.

2.7 Comparison of the PFI and environmental characteristics

We used dataset III (Fig. 1) to examine relationships between PFI scores and site-specific environmental characteristics. We regressed the PFI scores against four environmental variables recorded during the 2015-2019 plant surveys: mesohabitat types, water width, channel slope and substrate. We calculated the PFI scores and taxon richness for our four case study sites (section 2.2) to explore the dynamical application of the PFI by assessing change over time using long term (22 years) hydrological records of %ZF and the environmental characteristics of the channel.

3. RESULTS

3.1 Development of the Plant Flow Index (PFI): assignment of PFI taxon codes

Of the 34 taxa, 15 were allocated a code of 10, associated with the lowest %ZF, with 1-3 taxa assigned to each of the codes 2-9 and 0, and with no taxa allocated a code of 1 (Table 1; Fig. S4, Supplementary Material). For many taxa, allocation of PFI taxon codes was straightforward, such as assignment of code 10 to *Ranunculus penicillatus* subsp. *pseudofluitans* (Fig. 2), for which the modal value was 0%ZF and the second highest occurrence was for 0.1-10%ZF. Equally, for terrestrial grasses (code 0), the modal value was 100%ZF and the second highest occurrence was for 90.1-99.9%ZF. The grass *Alopecurus geniculatus* was also allocated code 0. Species that responded to moderate intermittence levels included the grass *Glyceria notata* and the herb *Apium nodiflorum*, which had highest values associated with 60.1-70%ZF and 50.1-60%ZF, generating the codes 4 and 5 respectively.

Table 1. Plant Flow Index (PFI) codes and related percentage zero-flow category allocated to each taxon using dataset I.

PFI codes	Percentage zero flow	Taxon
10	0-10	*Amblystegium fluviatile*
		Berula erecta
		Callitriche spp.
		Carex acutiformis
		Carex riparia
		Catabrosa aquatica
		Lemna minor
		Oenanthe crocata
		Ranunculus pseudofluitans
		Rorripa nasturtium aquaticum
		Sparganium erectum
		Typha latifolia
		Vaucheria spp.

		Veronica anagalis/catenata
		Verrucaria spp.
9	>10-20	*Ranunculus peltatus*
		Stachys palustris
8	>20-30	*Epilobium hirsutum*
		Mentha aquatica
7	>30-40	*Fontinalis antipyretica*
		Iris pseudocorus
6	>40-50	*Glyceria maxima*
		Ranunculus trichophyllus
5	>50-60	Filamentous algae
		Apium nodiflorum
4	>60-70	*Glyceria notata*
		Myosotis scorpioides
		Veronica beccabunga
3	>70-80	*Phalaris arundinacea*
		Solanum dulcamara
2	>80-90	*Myosoton aquaticum*
0	100	*Alopecurus geniculatus*
		Terrestrial grasses
		Terrestrial herbs

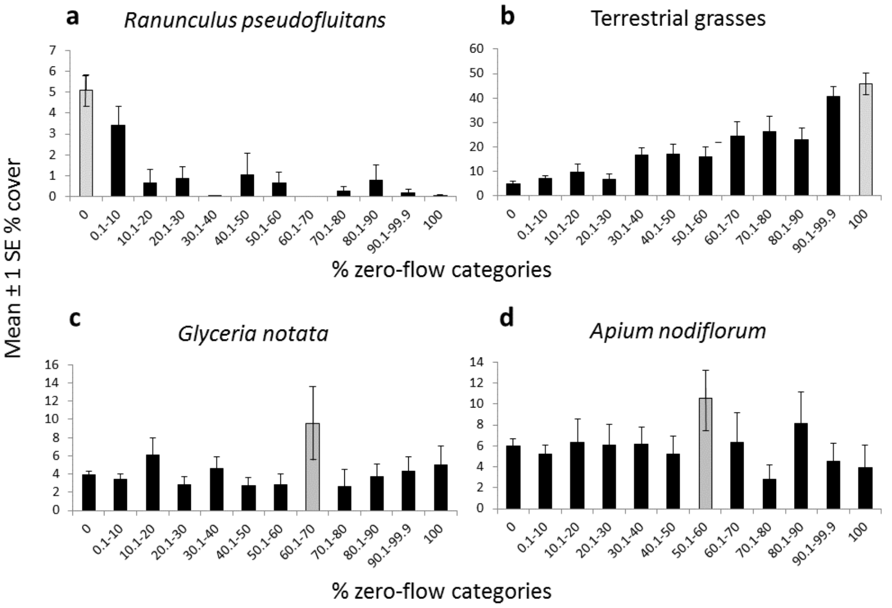

Fig. 2. Mean ± 1 SE % cover of selected plant taxa in each of the % zero-flow categories, as used to assign Plant Flow Index codes using dataset I to: (a) *Ranunculus pseudofluitans*, (b) terrestrial grasses, (c) *Glyceria notata* and (d) *Apium nodiflorum*.

3.2 Comparison between plant assessment methods

The PFI had the strongest correlation with AWE (Pearson correlation coefficient r = 0.90; Fig. 3a) but was only weakly associated with MTR (r = 0.44; Fig. 3b). When comparing the scores with WC, PFI showed the strongest correlation with WC (r = -0.82; Fig. 4a) then AWE (r = -

0.70; Fig. 4b) with MTR showing a weaker association (r = -0.52; Fig. 4c). Correlations between PFI scores and WC community types showed that higher PFI scores were associated with the perennial community types and lower scores with drier communities (Table S3; Fig. S5, Supplementary Material).

Site-level regressions between the PFI, AWE and MTR scores and %ZF in the antecedent 12 months (Table S4, Supplementary Material) identified 14, seven and three instances where the PFI, AWE and MTR showed the strongest relationship, respectively. PFI scores tended to decrease with increasing %ZF, but became increasingly variable at >70%ZF (Fig. S6, Supplementary Material).

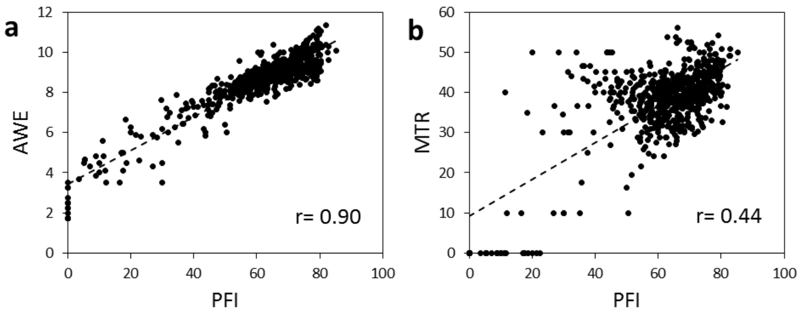

Fig. 3. Correlations between the Plant Flow Index (PFI) and (a) abundance-weighted Ellenberg F score (AWE; based on Hill et al., 1999) and (b) Mean Trophic Rank (MTR; Holmes et al., 1999) scores.

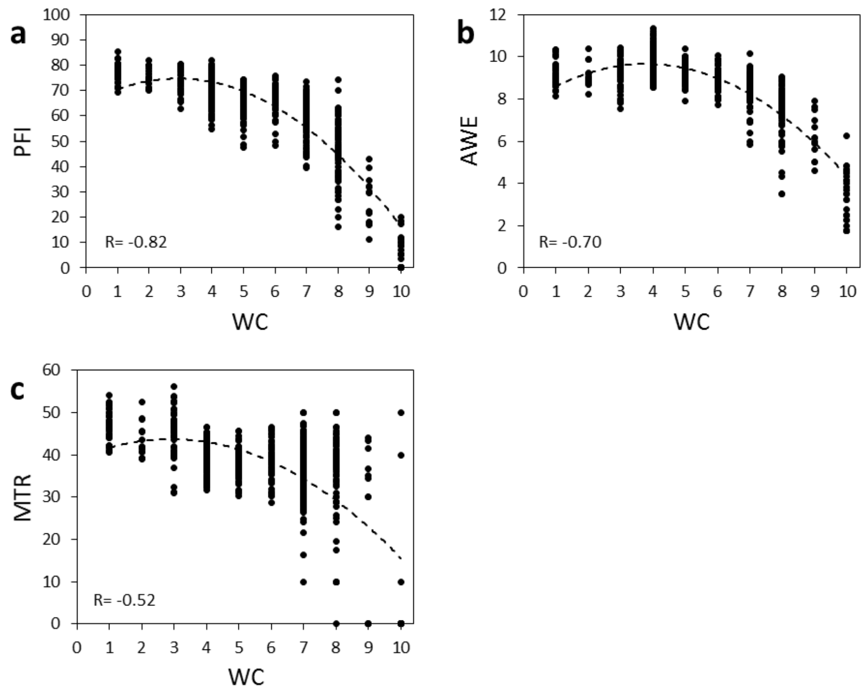

Fig. 4. Correlations between the Winterbourne Classification (WC; Westwood et al., 2020) and: (a) the Plant Flow Index (PFI), (b) abundance-weighted Ellenberg F score (AWE; based on Hill et al., 1999) and (c) Mean Trophic Rank (MTR) scores (Holmes et al., 1999).

3.3 Comparison of PFI and environmental characteristics.

PFI exhibited moderate, positive relationships with mesohabitat, water width and substrate and a weak negative relationship with channel slope (linear regression; P<0.001; Fig. 5). In all cases, PFI produced higher and more significant coefficients than either AWE or MTR (see Table S5, Supplementary Material).

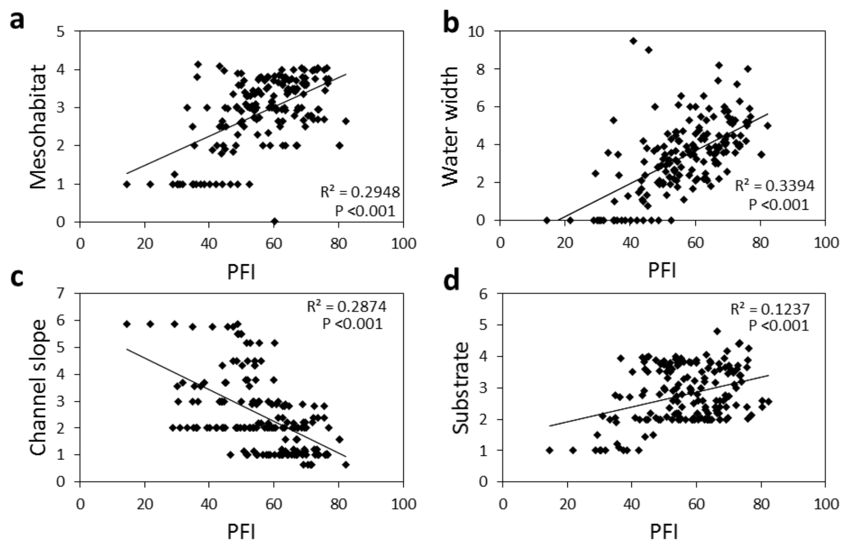

Fig. 5. Linear regressions between the Plant Flow Index (PFI) and the four environmental variables (a) mesohabitat type, (b) water width, (c) channel slope and (d) substrate.

3.4 Case study: a comparison of PFI temporal patterns at four contrasting sites

The Bulbourne site supported a mean taxa richness of 10.5 ± 0.95 taxa per annual survey between 1992 and 2013. The %ZF varied considerably during the study period, peaking at 84% in 1997 during the 1996-1998 drought (Fig. 6a). Similar peaks (72% in 2006; 69% in 2012) occurred during subsequent droughts whereas the %ZF fell to zero in the intervening years (1995, 2000-2002 and 2009). PFI scores ranged from 17-80 with a high proportion of terrestrial taxa (PFI taxon code 0) and other lower scoring groups (2-5) recorded during drier periods (Fig. 6b). In wetter periods, more aquatic taxa (PFI taxon code 10) became abundant, most notably *Callitriche* spp. and *R. nasturtium aquaticum*. Lower PFI scores were associated with higher %ZF (Fig. 6a). The PFI score changed from 73 to 24 within only 2 years (1995-1997) with a corresponding increase in %ZF from 0% to 84%. The PFI subsequently increased from 22 to 60 (1998-1999) as %ZF decreased from 63% to 1%. Similar decreases in PFI scores were associated with subsequent increases in %ZF and reflected increased cover of terrestrial taxa (0) and the wetland grass *A. geniculatus* (0) (Fig. 6b).

The mean richness of the Misbourne site was 5.9 ± 0.6 taxa per annual survey (1992 and 2013). The most abundant taxa were terrestrial grasses (PFI taxon code 0) and terrestrial herbs (PFI taxon code 0). Lower PFI scores were associated with changes in %ZF with a marked time-lag between channel recharge and vegetation response. The lowest value of PFI (0) was recorded in 1999 following a peak of %ZF in 1997 and 1998 (100 and 91% respectively; Fig. 5c). A second record of PFI 0 was recorded in 2007 following a peak of 94%ZF in 2006. A prolonged period of flowing conditions (2000-2004) corresponded with an increase in PFI reaching a peak of 55 in 2004 and 2005. The gradual increase in score reflected the growth of 2-5 group taxa in 2000 and 6+ taxa in 2001 (Fig. 5d). The same score (PFI 55) was also reached in 2011 following a shorter dry period (2006) when taxa from the higher scoring groups were recorded as %ZF decreased.

At the lower Ver site, mean taxa richness was 19.6 ± 0.57 taxa per annual survey between 1992 and 2013. *R. pseudofluitans* (mean abundance 20 ± 3.96%) and *R. nasturtium aquaticum* (mean abundance 22 ± 3.8%) were the most abundant taxa. The %ZF varied considerably among years, reaching 100% ZF during each drought (1992, 1996-1998, 2006 and 2012) and falling to zero in the intervening years (Fig. 6e). PFI scores ranged from 52 to 78, increasing from 52 in 1993 to 72 in 1994 following the 1992 drought, as %ZF changed from 98% to 0%. Despite increases in %ZF in 1997 and 2012-2013, there were only minor dips in PFI during these drought years. At these times, the percentage cover of *R. pseudofluitans* (PFI taxon code 10) was temporarily reduced and the cover of terrestrial taxa (0) increased (Fig. 6f). But increases in *R. nasturtium aquaticum* (PFI taxon code 10) and *Catabrosa aquatica* (PFI taxon code 10) meant that relatively high PFI scores were maintained. Throughout the 1993-2013 study period, there was a gradual decrease in %ZF and a corresponding increase in PFI scores (Fig. 6e). The upper Ver site had a mean taxa richness of 9.0 ± 0.66 taxa per annual survey. The most abundant taxa were terrestrial grasses (PFI taxon code 0) and *R. nasturtium aquaticum* (PFI taxon code 10). Decreases in PFI score were associated with increased %ZF (Fig. 6g). The increase in %ZF from 1996-1998

(0-100%) was associated with a drop in PFI from 52 to 13. A similar pattern was observed over 2004-2008 and 2012-2013. Lower PFI scores were associated with the loss of PFI code 10 taxa though lower scoring taxa were recorded (Fig. 6h). Only in 1993 at the start of the survey period were scoring taxa not recorded. Throughout the 1993-2013 study period, there was a gradual decrease in %ZF and a corresponding increase in PFI scores (Fig. 6g).

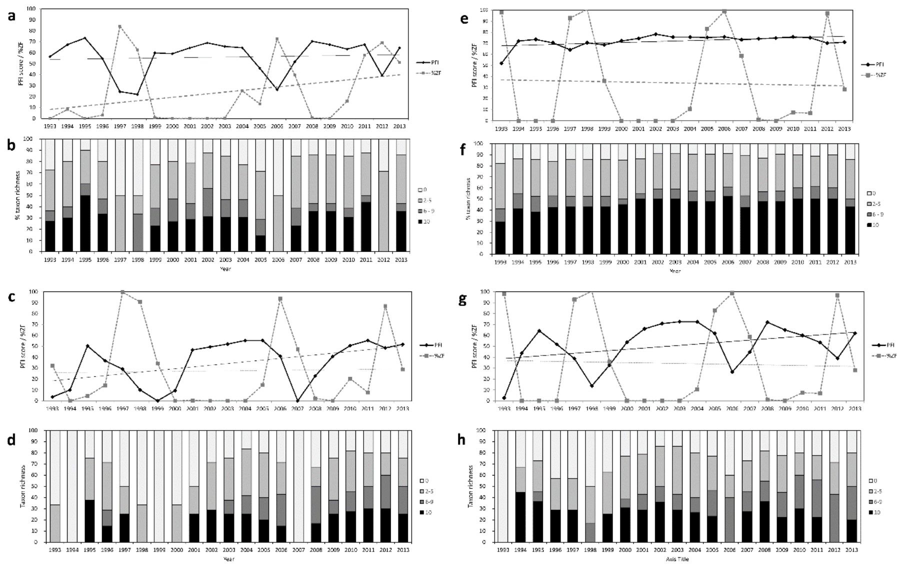

Fig. 6. Plant Flow Index (PFI) scores (solid black lines) and % zero flow (%ZF; hashed grey lines) for the Bulbourne (a), Misbourne (c) and Ver lower (e) and upper (g) case study sites between 1993 and 2013. Thick and thin lines indicate score changes and trends,

respectively. Plant taxa richness grouped according to PFI taxon codes 0, 2-5, 6-9 and 10 for the Bulbourne (b) Misbourne (d) and Ver lower (f) and upper (h).

4. DISCUSSION

Temporary streams are recognized as dynamic aquatic–terrestrial ecosystems that change in space and time to support high biodiversity (Larned et al., 2010; Stubbington et al., 2017). However, characterization of ecological responses to flow intermittence – and in particular, drying – have focused on aquatic macroinvertebrate communities, whereas plant communities remain poorly known. We present the Plant Flow Index (PFI): the first index to summarize vegetational changes in response to flow intermittence, particularly drying, in temporary streams. PFI incorporates all taxa, from obligate aquatic to fully terrestrial, into a single metric. The index therefore gives a holistic view of how assemblages respond as in-channel conditions shift between wet and dry states, thus supporting international drives towards more effective monitoring of ecological quality in temporary streams (Mazor et al., 2014, Steward et al., 2018; Stubbington et al., 2018; Stubbington et al., 2019).

4.1 Development of the PFI

By representing the occurrence and abundance of different plant species across different levels of drying, the PFI effectively reflects community change in response to antecedent hydrological conditions. The allocation of taxa to different intermittence bands, and representation of their abundance, provides an approach that is simple to understand and easy to apply. The allocation of individual taxa to categories reflected their known ecological preferences. For example, *Callitriche* spp. (PFI taxon code 10) had a modal category of 0%ZF and 0.1-10%ZF indicating a strong response to wet conditions. This association with wet conditions is also reflected by the high Ellenberg F scores for *Callitriche stagnalis* and *C. obtusangula*, the commonest *Callitriche* species in chalk streams; (Hill et al., 1999). However, the occurrence of *Callitriche* spp. over a range of %ZF categories reflects its ability to grow both in flowing water (Haslam 2006), and in ponded sections (Grime et al., 1988, Stace 1997 Haslam 2006). *Sparganium erectum* (PFI taxon code 10), responded to continuous flow, but was also common at 80.1-90%ZF, reflecting its ability both to create and colonize deep deposits of silt (Asaeda et al., 2010), enabling it to persist during the loss of surface flow as long as the channel remained wet. As more data are collected in ponded conditions, greater resolution distinguishing between flowing and ponded conditions could be incorporated and may make the PFI even more responsive.

4.2 Comparison of plant assessment approaches to intermittence

The PFI enables assessment of entire in-channel plant assemblages, enabling its application across a wide range of hydrological conditions from dry channels to continuous flow. The index can track community changes more readily than classifications undertaken periodically on these river systems (Westwood et al., 2006a, 2017, 2020), with further testing and refinement being made possible by the addition of new data. PFI exhibited more associations (14) with %ZF than other indices, and also a stronger relationship with the WC than either AWE or MTR. The association of PFI scores with the WC enables inference of classified community types from given ranges of PFI scores. Notably, the point at which flow-dependent taxa disappear from the WC and are replaced with marginal, wetland and terrestrial taxa (between community types Wi6 and Wi7) corresponds with a sharp decrease in PFI scores (from 50-60%ZF to 60-70%ZF; Fig. S2; Supplementary Material). This may indicate an important shift in the plant communities in relation to progressive drying, which is characterized by a sharp decrease in the grass *Glyceria maxima* and increases in both filamentous algae and the herb *Apium nodiflorum* (Fig. S1, Supplementary Material). This suggests a stepped biotic response to the progressive (ramp) disturbance of drying, which Boulton (2003) hypothesized, but for which evidence is scant.

The AWE had some association with %ZF but was less responsive than PFI. The AWE of the taxa in our datasets had a limited range of numbers, with velocity-dependent taxa such as *Ranunculus* spp. scoring 12 and terrestrial taxa scoring 5, out of a total range of 1-12 (Ellenberg 1979, 1988, Ellenberg et al., 1991, Hill et al.,, 1999). Although Ellenberg F has the merit of being an internationally recognized approach for allocating species to classes based on their moisture requirements, only seven of its 12 classes were assigned to the taxa in our datasets from the headwater streams of chalk catchments in southern England. This limitation may extend across other regions and highlights the utility of the PFI, which performed better, and can be updated with additional taxa as new data become available.

Stubbington et al., (2019) reported that MTR required further evaluation to establish its potential for use in dry-phase biomonitoring. The weak response of MTR to intermittence observed here suggests that the MTR may be suitable to track quality changes in temporary streams, despite intermittence. Our study confirms that further work is needed to assess the applicability of MTR as a means of assessing nutrient levels in temporary streams during both wet and dry phases.

4.3 Associations between PFI and environmental variables

The PFI exhibited moderate positive relationships with mesohabitat type, water width and substrate, and a negative relationship with channel slope: higher scores were associated with faster flows, coarser substrates, greater water widths and relatively low topographic gradients. Well-documented interactions between different plant species and river morphology (Gurnell et al., 2010; Gurnell 2014; Gurnell and Grabowski, 2015) are likely to explain the influence of channel characteristics on PFI. Similarly, invertebrate-based indices developed to document responses to hydrological variability also respond to morphological drivers including channel shape (e.g. Dunbar et al., 2010a, 2010b).

4.4 Application of PFI

Three of our 4 case studies illustrated that the PFI can track plant community response to intermittence. By contrast, the plant community at the lower Ver site appeared more resistant to intermittence, as reflected by fairly stable PFI scores despite %ZF twice reaching 100%. This may reflect the different morphological site characteristics as river biota experience flow indirectly via local-scale physical habitat changing river velocities (Dunbar et al., 2010a, 2010b, Gurnell, 2014).

Further research is needed to understand how morphological characteristics interact with hydrological state to influence plant communities. The PFI may enable such research by providing a single metric summarising community characteristics in relation to hydrological conditions. We therefore recommend that future plant surveys of temporary streams include a thorough assessment of physical habitat to identify the full range of conditions that influence plant assemblages.

The diverging trends of increasing PFI and decreasing %ZF at both Ver sites suggest an increased proportion of aquatic plants within the assemblage over time, perhaps reflecting higher flows after the reduction in abstraction (Clayton et al., 2008). Such trends highlight the capacity of the PFI to track both intra-annual and inter-annual responses to intermittence. The ability of PFI to summarize each community as a single number that reflects hydrological conditions, could help identify naturally functioning habitats that can be protected, and aid the selection of sites for river restoration (Addy et al., 2016).

5. CONCLUSION

Our results highlight PFI as a suitable tool for summarizing vegetation community changes in response to drying. The PFI approach is flexible and can be easily updated. To date, characterization of plant communities in temporary streams has concentrated on aquatic and wetland species, with terrestrial taxa aggregated as grasses and herbs, or left undocumented (Dieterich and Anderson, 1998; Holmes, 1999; Sabater et al., 2017; Westwood et al., 2020). The identification of these terrestrial taxa could add considerable further detail to the PFI's ability to represent biotic responses to changing in-channel conditions in temporary streams, as it has done for invertebrate-based metrics (England et al., 2019). Also, PFI is based on responses to intermittence within the 12 months before sample collection, reflecting the controlling influence that antecedent flow has on riverine plant communities (Bornette and Puijalon, 2011). However, further research is needed to explore plant responses to longer antecedent drying periods, to better represent taxa that can withstand longer dry periods and thus have longer response times.

The PFI provides an approach that can be widely adapted and applied for different temporary stream types, but it first needs type-specific testing and evaluation. Adaptation of PFI for arid regions, in which hydrological gradients are much sharper than in the UK, may provide community characterization associated with greater extremes of intermittence if they have sufficiently developed in-channel plant communities. The PFI provides a means for researchers, regulators and managers to assess ecological changes in response to stream drying, and represents an initial step towards disentangling the effects of multiple interacting natural and anthropogenic stressors on riverine plants.

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Chris Westwood: Conceptualization, methodology, data curation, writing – original draft preparation. **Judy England**: visualization, **all authors:** Writing – reviewing and editing.

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