

RESEARCH ARTICLE

Colonisation of terrestrial vegetation in an intermittent river: Diversity responses to seasonal drying

Victoria S. Milner¹  | John S. Dutton² | Chloe Hayes³

¹School of Applied Sciences, University of Huddersfield, Huddersfield, UK

²Sustainable Environments Research Group, School of Science and the Environment, University of Worcester, Worcester, UK

³School of Science and Technology, Nottingham Trent University, Nottingham, UK

Correspondence

Victoria S. Milner, School of Applied Sciences, University of Huddersfield, Queensgate, Huddersfield, HD1 3DH, UK.
Email: v.milner@hud.ac.uk

Funding information

Royal Geographical Society

Abstract

Intermittent rivers are dynamic ecosystems that experience a predictable or unpredictable loss of surface water and are characterised by changing lotic, lentic (ponding) and dry habitats. Plant communities colonising dry channels during the desiccation stage can be diverse, abundant and differ in their tolerances to water availability and habitat conditions. This study examines the colonisation of terrestrial vegetation in two intermittent rivers in the United Kingdom, and whether terrestrial plant taxonomic richness and functional diversity increase during the dry phase. Six reaches were surveyed for terrestrial plants during the dry phase over a standard 100 m length every month from April to October 2021. We found the channel and bank taxonomic richness increased with drying duration. Functional traits of vegetation height, clonality, clonality richness and Ellenberg's value of light moisture also increased with stream desiccation. Bed sediment conditions (the proportion of sand and gravel) and the 12-month antecedent percentage of zero flow days were the key drivers of plant community composition. We believe plant propagules from the riparian zone and channel vegetation on topographic high points in the channel aided plant colonisation of the riverbed once flow ceased. Past research may have underestimated the biodiversity value of intermittent rivers by failing to include the ecological importance of plants during the dry phase. Information on plant diversity of the dry phase is important to determine the overall biodiversity of intermittent rivers for their long-term conservation and management.

KEYWORDS

beta diversity, biodiversity conservation, desiccation, functional traits, plants, taxonomic richness

1 | INTRODUCTION

Intermittent rivers are dynamic ecosystems that experience predictable or unpredictable flow cessations (Datry, Larned, & Tockner, 2014). Globally, intermittent rivers comprise >50% of river networks and occur across all continents (Skoulikidis et al., 2017).

Intermittent rivers are expected to increase in regions characterised by severe climatic drying or with water abstractions (Döll & Schmied, 2012; Garcia, Gibbins, Pardo, & Batalla, 2017). The effect of high hydrological variability leads to spatial and temporal changes in lotic (flowing water), lentic (standing water) and terrestrial (dry riverbed) habitats within intermittent river networks (e.g., Godsey &

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial-NoDerivs](https://creativecommons.org/licenses/by-nc-nd/4.0/) License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2022 The Authors. *River Research and Applications* published by John Wiley & Sons Ltd.

Kirchner, 2014; Lake, 2003; Larned, Datry, Arscott, & Tockner, 2010; Stanley, Fisher, & Grimm, 1997). These three habitat phases contract and expand due to wetting and drying cycles. Drying phases can be disrupted by individual or multiple flow resumptions linked to sporadic rainfall events, which can temporarily change habitat mosaics and strongly influence biodiversity and biogeochemical processes in intermittent rivers (Datry, Pella, Leigh, Bonada, & Hugueny, 2016).

Flow intermittence typically causes marked reductions in the abundance and spatial coverage of aquatic plants (i.e., macrophytes; Sand-Jensen & Frost-Christensen, 1998; de Wilde, Sebei, Puijalon, & Bornette, 2014), and provides temporary habitats for the colonisation of terrestrial plants in dry channels. Surface drying and decreases in interstitial water lead to marked environmental changes in bed sediment characteristics, including water availability, intensification of solar radiation with increased temperatures, and alterations to carbon and oxygen availability (Baldwin & Mitchell, 2000; Rascio, 2002). The duration and intensity of the drying period together with the frequency, duration and magnitude of rewetting events drive plant survival and influence macrophyte resilience (Brock & Casnova, 1997).

The duration of the dry phase strongly governs the recovery of macrophytes and the establishment of terrestrial plant communities (Colls, Timoner, Font, Sabater, & Acuna, 2019; Katz, Denslow, & Stromberg, 2012; Leigh & Datry, 2017). Intermittent rivers typically contain a high diversity of macrophytes and riparian plants when drying occurs for short durations (e.g., <3 months; Westwood, Teeuw, Wade, & Holmes, 2006; Franklin, Dunbar, & Whitehead, 2008). In river systems experiencing longer dry phases, semi-aquatic and terrestrial taxa can colonise a riverbed from channel margins and the riparian zone (Franklin et al., 2008; Holmes, 1999; Stromberg & Merritt, 2016). Where drying is prolonged, plant communities can consist exclusively of terrestrial vegetation rooted in dry riverbeds (Holmes, 1999; Westwood, England, Johns, & Stubbington, 2020). However, little information exists regarding the diversity and composition of terrestrial vegetation inhabiting dry riverbeds, especially in cool, wet temperate (i.e., oceanic climate) regions with previous studies grouping terrestrial plants as 'terrestrial herbs' and 'terrestrial grasses' (Holmes, 1999; Westwood et al., 2020).

The colonisation and spatial coverage of terrestrial vegetation in dry riverbeds are influenced by the size of the regional species pool, and rates of dispersal and immigration (Mouquet, Moore, & Loreau, 2002; Xiao, Zobel, Szava-Kovats, & Partel, 2010). Seed arrival (propagule supply) increases species richness, especially at sites with high environmental heterogeneity (Myers & Harms, 2009), and when the species pool is functionally diverse (Questad & Foster, 2008). Flow resumptions aid the dispersal of seeds and other propagules and help mobilise seed banks. In addition, dry riverbeds can receive seeds from wind-dispersed species. Riparian vegetation, including soil seed banks, is an important source of propagules for vegetation establishment in dry riverbeds (Katz et al., 2012). Soil seed banks comprise the viable seeds in banks, leaf litter, and bed sediments, and are an important adaptation of many herbaceous plants that grow in and along intermittent channels (O'Donnell, Fryirs, & Leishman, 2014).

The colonisation of a dry riverbed by terrestrial vegetation greatly contributes to river channel health. Plant communities support

ecosystem functions by providing shade, allochthonous inputs (Sabater et al., 2017), re-cycling nutrients, stabilizing the substratum, providing a refuge and a habitat for terrestrial invertebrates and small mammals, and enhancing the taxonomic, functional, and structural diversity to watercourses (Gurnell, 2014; Gurnell, O'Hare, O'Hare, Dunbar, & Scarlett, 2010; Holmes, 1999; Westwood, Teeuw, Wade, & Holmes, 2006). In intermittent rivers, aquatic invertebrate density and diversity are typically lower than in perennial reaches (Bogan, Boersma, & Lytle, 2013; Datry et al., 2014). However, the terrestrial communities in dry riverbeds, such as terrestrial invertebrates and plants may counteract the loss of aquatic invertebrates and increase diversity and support ecosystem functions in intermittent rivers. Despite the many ecosystem functions provided by plant communities, there are no studies considering their colonisation and succession in dry riverbeds of good morphological condition (i.e., no water abstractions and low anthropogenic pressures), and underlain by carboniferous limestone deposits. Past research has focussed on predominantly aquatic plant colonisation in intermittent rivers on chalk and of different ecological statuses (e.g., Westwood et al., 2020; Westwood, Teeuw, Wade, & Holmes, 2006; Westwood, Teeuw, Wade, Holmes, & Guyard, 2006). Exploring the spatial and temporal pattern of terrestrial plant colonisation in dry rivers may aid our understanding of the effects of intermittency in cool, wet temperate regions.

The aim of this study is to examine the colonisation of terrestrial vegetation in an intermittent river throughout a dry phase. Most previous studies have examined macroinvertebrates or fish, with limited research attention on other biological communities. This is the first study to examine how terrestrial plants pioneer dry riverbeds in a temperate climate flowing through carboniferous limestone deposits and how the plant's taxonomic and functional diversity varies with increasing dry duration. The following hypotheses were addressed:

1. Plant taxonomic richness will increase, and beta plant diversity will differ with dry phase duration in the channel.
2. Plant taxonomic richness and beta diversity will be higher on the bank than in the dry channel.
3. Functional trait plant diversity (e.g., vegetation height, clonality, clonality richness) will increase in the channel with dry phase duration.

2 | MATERIALS AND METHODS

2.1 | Study area

The fieldwork was carried out on the rivers Manifold and Hamps in the English Peak District, in the UK (Figure 1). Both the Manifold and the Hamps are lowland meandering rivers (210.2–131 m above sea level) with pool-riffle-glide morphology and extensive riparian vegetation (National River Flow Archive [NFRA], 2022). Both rivers are in good morphological condition with longitudinal and lateral connectivity, an unmodified hydrological and sedimentological regime, no water abstractions and low anthropogenic pressures. The catchment

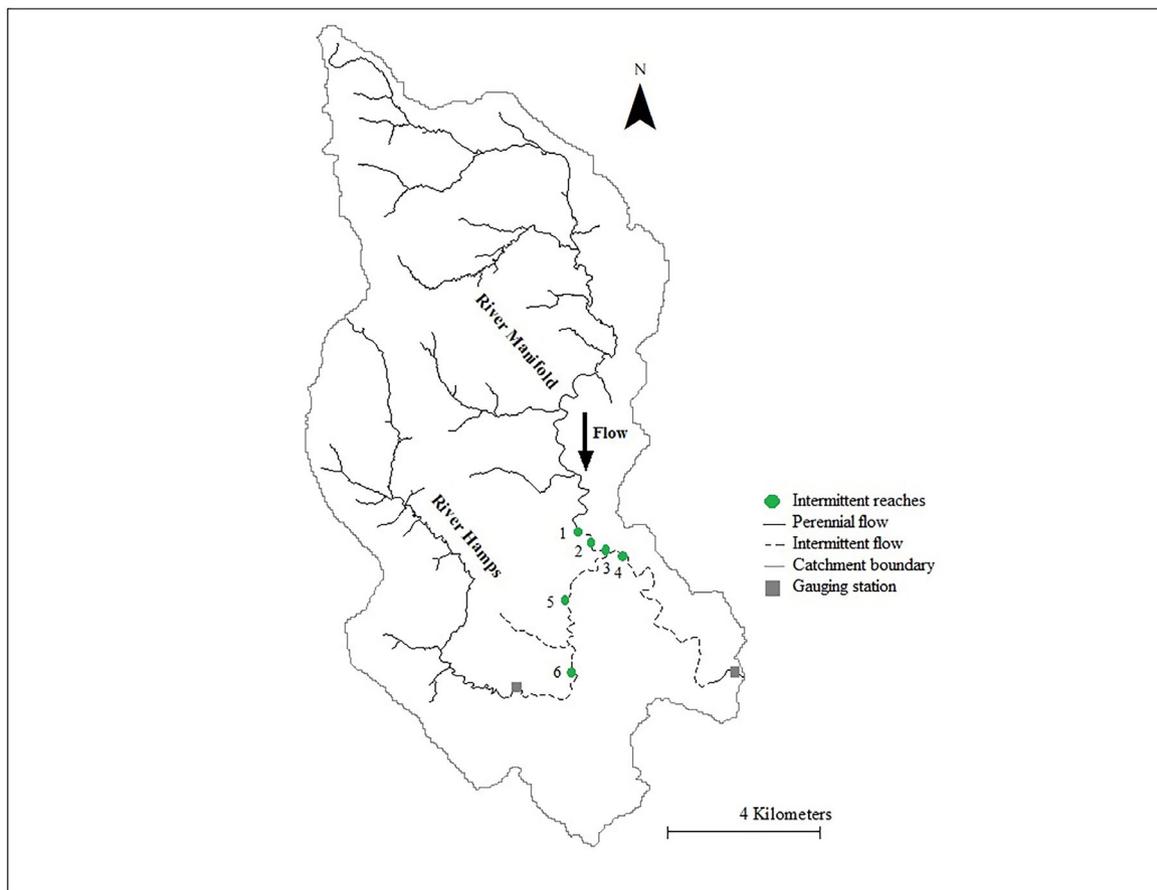


FIGURE 1 Location of the perennial and intermittent sections within the R. Manifold and Hamps, and the position of the study reach and gauging stations (modified from Hill & Milner, 2018) [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/tra.4085)]

area is approximately 148.5 km² and the land use is dominated by grassland (82.2%) with smaller occurrences of broadleaf woodland (5.7%) and moorland (3.4%; NRFA, 2022). The R. Hamps is the main tributary of the R. Manifold and both catchments possess similar meteorological conditions with a mean annual precipitation of 974.74 mm and a mean minimum and maximum temperature of 5.6 and 11.9°C respectively (1991–2020, UK Meteorological Office, 2022).

The mid-reaches of the R. Manifold and Hamps are naturally intermittent for approximately 10 km. The flow regime is perennial upstream and downstream of the intermittent section (Figure 1). Drying normally takes place from April to September due to low precipitation and water flowing underground through carboniferous limestone deposits and resurfacing downstream (Figure 1; Hill & Milner, 2018). During our study in 2021, the R. Hamps and Manifold dried in mid and late March respectively and flow resumed in mid-October. Throughout the study, the intermittent section flowed on 3 and 4 occasions on the R. Manifold and Hamps of between <1 to 27 days due to sporadic rainfall events in May, August and October respectively (please see the supplementary information for details regarding the frequency and duration of all flow resumptions). During drying, the streambed transitions from containing macrophytes to providing a habitat for terrestrial plants.

2.2 | Field procedure

A total of four reaches on the R. Manifold and two reaches on the R. Hamps were sampled for aquatic-terrestrial plant communities during stream desiccation (Figure 1). The location of the study reaches was based on accessibility to the channel with a minimum distance of 500 m between study reaches. We used a modified LEAFPACS2 method (UK-TAG, 2014) to record the percentage cover of each plant taxon over a standard 100 m reach length. Plant taxon was recorded within the dry riverbed, and the banks (including the bank face and within 1 m of the bank-top [in addition to the LEAFPACS2 method]). The LEAFPACS2 method records macrophytes and phytobenthos but we also recorded terrestrial plants (please see the supplementary information for a list of macrophytes and terrestrial plants in our survey). Plants surveys were undertaken each month from mid-April to mid-October 2021, apart from the four reaches on the Manifold in May due to a short flow resumption. The plant surveys in mid-April occurred 16 and 27 days after drying of the R. Hamps and Manifold respectively. All plant species were identified in the field; any unknown species were collected and identified in a laboratory. Plant species, including any macrophytes in the dry riverbed, were identified to the lowest taxonomic resolution possible, with all species recorded at genus or species levels (except mosses and ferns).

Shading of the dry riverbed by overhanging vegetation was recorded for each monthly plant survey as a percentage coverage of the 100 m reach length. Conductivity of bed sediments was measured by a soil conductivity meter in the field at 0, 50 and 100 m intervals for every survey, and conductivity values were subsequently averaged per reach. A ~1 kg bed sediment sample was also collected at 50 m intervals along each reach every month for moisture, organic matter and nitrate analysis at a laboratory (i.e., 3-bed sediment samples per reach per month). An additional bed sediment sample was also collected at 0, 50 and 100 m at each reach once in June 2021 to characterise bed sediment composition. All bed sediment samples were cold stored at ~5°C before analysis.

2.3 | Sample processing

In a laboratory, 500 g of bed sediment was dried at 105°C in an oven for 12 h. Next, the dried bed sediment was sieved using a Fritsch vibratory sieve shaker to determine the percentage contribution of the following grain size fractions: 64–256 mm (cobble), 4–64 mm (pebbles), 2–4 mm (gravel), and < 2 mm (sand). A mean of the bed sediment composition from the three samples was determined per reach (Table 1). In addition, sediment moisture, organic matter and nitrate were determined for every reach at 0, 50 and 100 m intervals each month, and subsequently averaged (Table 1). Please see the supplementary information for detailed information regarding the laboratory procedures.

2.4 | Hydrological data

For each monthly plant survey, we calculated the number of days since the most recent flow event of any duration, which included any flow resumptions (TimeSinceFlow), the number of days since the last major flow event for >3 days (TimeSinceMFlow), and the percentage of zero-flow days for the 12 months prior to each monthly plant survey (Table 2). To calculate these flow indices, we used mean daily discharge from the gauging stations at Ilam for the R. Manifold (station

ID 28038) and at Waterhouses for the R. Hamps (station ID 28041; please see Figure 1 for the location of the gauging station relative to the study reaches). Based on a previous study in the catchment (e.g., Hill & Milner, 2018), reconnaissance surveys at different daily discharges, and discussions with local landowners, we determined the R. Manifold and Hamps dried below mean daily discharges at the gauging stations of 0.20 and 0.31 m³/s respectively. We subsequently calculated the percentage of zero-flow days for the 12 months prior to each monthly plant survey for all reaches based on when the mean daily discharge was less than 0.20 and 0.31 m³/s for the R. Manifold and Hamps.

2.5 | Statistical analyses

For the plant data, taxonomic richness was defined as the number of species present within an individual reach, and beta diversity was defined as the variation in community composition between reaches (Koleff, Gaston, & Lennon, 2003). Taxonomic richness and beta diversity were determined for the dry channel and the banks for each monthly survey. Differences in taxonomic richness in the dry channel and bank habitats between monthly surveys were determined using generalised linear mixed effects models (GLMMs) with a Poisson distribution and a log link structure. As categorical data was used, April (i.e., the first month when sampling was undertaken) was chosen as the intercept within the GLMM. This analysis tested whether plant taxonomic richness differed significantly in the dry channel and bank habitats with the duration of the dry phase. We used one month as a surrogate for the dry-phase duration. A further GLMM was also used to identify any differences in taxonomic diversity between the dry channel and bank habitats with increasing desiccation. For all GLMMs, post hoc comparisons using Tukey post-hoc tests were undertaken to identify where significant differences among monthly plant surveys occurred. The 'lme4' package in R Studio using the 'glmer' function was used for all the GLMM analyses (R Development Core Team, 2021).

Linear mixed models (LMMs) were employed to identify whether channel and bank plant dominance (i.e., Berger-Parker dominance)

TABLE 1 Summary of environmental characteristics for the six reaches. Mean values are shown and values in parentheses indicate the minimum and maximum values.

Reach	Shading (%)	Moisture (%)	Conductivity (m S/m)	Organic matter (%)	Nitrate (mg/INO ₃)	Sediment size (mm)			
						Cobbles (64–256)	Pebbles (4–64)	Gravel (2–4)	Sand (<2)
1	3.9 (2–5)	1.14 (1–1.33)	0.02 (0.01–0.03)	5.6 (2.4–15.2)	2.3 (1–5)	10.1	81.4	2.0	6.6
2	13.9 (3–18)	1.11 (1–1.33)	0.02 (0.01–0.04)	3.4 (1.7–6.2)	3.2 (1–6)	14.6	70.8	2.9	11.7
3	32.7 (7–42)	1.22 (1–1.58)	0.02 (0–0.05)	4.1 (2.1–7.8)	4.5 (1–9)	57.3	32.7	2.2	7.9
4	6.6 (2–10)	1.2 (1–1.3)	0.03 (0–0.08)	3.1 (1.7–5.3)	5.2 (1–7)	13.9	72.2	2.9	11.1
5	12.4 (3–20)	1.32 (1–2)	0.17 (1.12)	3 (2.3–4.4)	3.7 (1–6)	8.6	84.3	2.0	5.1
6	4.1 (2–6)	1.45 (1–3.58)	0.52 (0–3.58)	3.5 (2.5–5.4)	4.7 (1–7)	0	92.7	2.3	5.0

TABLE 2 Overview of hydrological data during the study of the rivers Manifold and Hamps

River	Timing of plant survey	Number of days since the most recent no-flow event (of any duration)	Number of days since the last major flow event for >3 days	Percentage of zero-flow days for the 12 months prior to a plant survey
Manifold	Mid-April	16	16	42.7
Hamps	Mid-April	27	27	62.7
Manifold	Mid-may	-	44	41.9
Hamps	Mid-may	1	55	62.5
Manifold	Mid-June	7	75	35.3
Hamps	Mid-June	15	86	60.3
Manifold	Mid-July	41	99	37.6
Hamps	Mid-July	48	119	60.8
Manifold	Mid-august	1	126	37.3
Hamps	Mid-august	76	147	61.1
Manifold	Mid-September	35	160	44.7
Hamps	Mid-September	110	181	62.2
Manifold	Mid-October	3	190	44.4
Hamps	Mid-October	140	211	64.9

varied with dry phase duration. Raw data was arc-square root transformed to reduce any effects of skewed distributions. All LMMs were fitted using the 'nlme' package and the 'lme' function. The LMMs were fitted by employing the restricted maximum likelihood estimation function and a Gaussian distribution was used. Similar to the GLMM analyses, Tukey's post-hoc tests were carried out to determine any significant variations in plant dominance between months.

The functional characteristics of the channel and bank plant communities were identified by allocating taxa into four plant metrics from multiple biological and ecological traits from Hill, Preston, and Roy (2004; Table 3). The categories included vegetation height (mm), clonality, and an Ellenberg indicator value of light (L; based on Ellenberg et al., 1991, and reproduced from Hill, Mountford, Roy, & Bunce, 1999). The clonality trait was split into two different metrics: the number of clonality traits at a site (clonality) and the number of taxa with a clonality trait (clonality richness). For the Ellenberg L value, plant taxa were assigned a code between 1 and 9 representing plants located in deep shade to full sunlight (Table 3). Next, a reach average was determined for Ellenberg L values and vegetation height. LMMs were used to determine whether height, clonality, clonality richness, and Ellenberg L values differed with increasing dry phase duration. LMMs were employed to identify any variations in functional characteristics and Ellenberg values with desiccation. Subsequently, Tukey's post-hoc tests were undertaken to find any significant differences in functional characteristics throughout the dry phase. For all GLMMs and LMMs analyses, taxonomic richness, plant dominance and functional characteristics were included as fixed factors, whilst reach and month were specified as random factors.

Differences in beta diversity between monthly plant surveys for the (a) dry channel, (b) bank habitats, and (c) the dry channel versus bank habitats were examined using a permutational analysis of

variance (PerMANOVA). Pairwise comparisons (with Bonferroni correction) were used to identify where differences between monthly plant surveys occurred. In all PERMANOVA models, month and reach were fitted as random factors. Similarity percentage analysis (SIMPER) was undertaken to identify which plant species were driving differences in assemblages between months or between the dry channel and bank habitats. Non-metric Multidimensional Scaling (NMDS) ordination plots were used to visualise plant compositional variations between months and habitats. Bray-Curtis similarity coefficients were included in all multivariate analyses (i.e., all PERMANOVA models, SIMPER analyses and NMDS ordinations) on the plant compositional data set.

A PERMANOVA (incorporating hydrological and environmental data) was undertaken to determine the underlying processes driving plant community response. Like previous PERMANOVA models, month and reach were included as random factors. All environmental factors and hydrological metrics were entered into the PERMANOVA models, but only significant drivers of plant community composition were plotted on an NMDS ordination. Envfit (Zelený & Schaffers, 2012) vectors were calculated and applied to the NMDS ordination to visualise the direction and magnitude of each environmental factor and hydrological metric. All analyses were conducted using R version 4.1.1 (R Development Core Team, 2021).

3 | RESULTS

3.1 | Description of plant communities

In total, 73 and 88 plant taxa were recorded within the dry channel and the bank habitats (please see Table SI for a full list of species

TABLE 3 Plant functional traits and Ellenberg codes used within this study (information adapted from Hill et al., 2004)

Category	Trait/ Ellenberg value	Explanation
Height (cm)	1+	Height of the vegetation.
Clonality	0 g	Tussock-forming graminoid may slowly spread.
	0tb	Tuberous or bulbous, slowing cloning by offsets.
	Dra	Detaching ramets above ground (often axillary).
	DRg	Detaching ramets at or below ground.
	DRp	Detaching ramets on prothallus (<i>Trichomanes</i>).
	Frag	Fragmenting is part of normal growth.
	Irreg	Irregularly fragmenting (mainly water plants).
	Node 1	Shortly creeping and rooting at nodes.
	Node 2	Extensively creeping and rooting at nodes.
	Rhiz 1	Rhizome shortly creeping.
	Rhiz 2	Rhizome far creeping.
	Root	Clones formed by suckering from roots.
	Stol 1	Shortly creeping, stolen in illuminated medium.
	Stol 2	Far-creeping by stolen in illuminated medium.
	Tip	Tip rooting (the stems often turn downwards).
Ellenberg codes		1 = plant in deep shade.
For light (L)		9 = plant in full light, mostly found in full sun.

recorded in the study). Plant communities were composed mostly of terrestrial species, some with strong linkages to water, such as *Phalaris arundinacea* (reed canary grass). However, three macrophytes were found during the study and remained in-channel for the duration of surveying: *Veronica beccabunga* (brooklime), *Scrophularia umbrosa* (water figwort) and *Myosotis scorpiodes* (water forget-me-not). Plant taxonomic richness within the dry channel differed between 12 and 42 taxa (mean \pm SE: 26 ± 1.18) per reach and between 19 and 42 taxa (mean \pm SE taxon richness: 32.7 ± 0.9) within the bank habitats per reach. In the channel, the most commonly occurring plant taxa were *Petasites hybridus* (butterbur), *P. arundinacea*, *Equisetum arvense* (horsetail), *Aegopodium podagraria* (ground elder), and *Lolium perenne* (perennial ryegrass). Similarly, *P. hybridus* was the most abundant taxon on the banks. In addition, bank habitats were also dominated by *Allium ursinum* (wild garlic), *Poa trivialis* (rough meadow-grass), *Acer*

pseudoplatanus (sycamore), and *Corylus avellana* (hazel). Twenty-six plant taxa were recorded that occupied less than 1% of a reach (channel and bank habitats), such as *Narcissus poeticus* (daffodils) and *Arum maculatum* (lords-and-ladies), which are spring flowering plants and only occurred in April and May. Other less common plant taxa included *Helminthotheca echioides* (bristly oxtongue) and *Veronica filiformis* (creeping speedwell).

3.2 | Plant taxonomic richness

Plant taxonomic richness in the channel varied significantly with month (Z_1 17.46, $p < .001$; GLMM), which was used as a surrogate for the duration of the dry phase. Plant taxonomic richness differed between April and June (Z_1 1.96, $p < .05$; GLMM), April and July ($Z_1 = 3$, $p < .01$; GLMM), April and August (Z_1 3.21, $p < .001$; GLMM), and April and September ($Z_1 = 3.01$, $p < .01$; GLMM). Channel taxonomic richness was lowest in April (mean \pm SE alpha diversity: 20.8 ± 2.4) and highest in August (mean \pm SE alpha diversity: 30.2 ± 2.7). Significant differences were also observed in bank taxonomic richness within the dry phase (Z_1 49.06, $p < .001$; GLMM). In contrast to the channel communities, bank taxonomic richness only varied between April and October (Z_1 -3.27, $p < .001$; GLMM). Overall, plant taxonomic richness was significantly higher in bank habitats than in the dry channel (Z_1 58.21, $p < .001$; GLMM). Figure 2 visually indicates differences in plant taxonomic richness in the channel and the bank over the duration of the study.

3.3 | Plant dominance

In the channel, Berger-Parker dominance varied significantly with increasing dry phase duration ($t = 10.16$, $p < .001$; linear mixed effect (LME); Figure 3a). In-channel plant dominance differed significantly between April and June ($t = 2.75$, $p < .05$; LME), April and July ($t = 2.10$, $p < .05$; LME), April and August ($t = 2.39$, $p < .05$; LME), April and September $t = 2.87$, $p < .01$; LME) and April and October ($t = 2.39$, $p < .05$; LME). In-channel dominance increased from April to June, declined in July and remained comparable to October (Figure 3a). *P. hybridus* (range of 0%–70%) and *P. arundinacea* (range of 0%–60%) dominated in-channel communities. Both taxa possessed the lowest spatial coverage in April (mean monthly coverage of 7.9% and 12.8% for *P. hybridus* and *P. arundinacea*, the highest in spatial extent in July (mean monthly coverage of 40.8% and 25.5%) with declines in dominance in October (mean monthly coverage of 18.9% and 22.7%).

The dominance of bank vegetation differed significantly with stream drying ($t = 12.35$, $p < .001$; LME; Figure 3b). However, Tukey's post hoc tests revealed no differences in plant coverage between months (all p values $> .05$). *P. hybridus* (range of 8.5%–76%) was the most dominant bank taxon, followed by *Urtica dioica* (stinging nettles; range of 2%–27.5%) and *A. ursinum* (range of 0%–55%). *P. hybridus* increased in spatial coverage from April to August (mean monthly

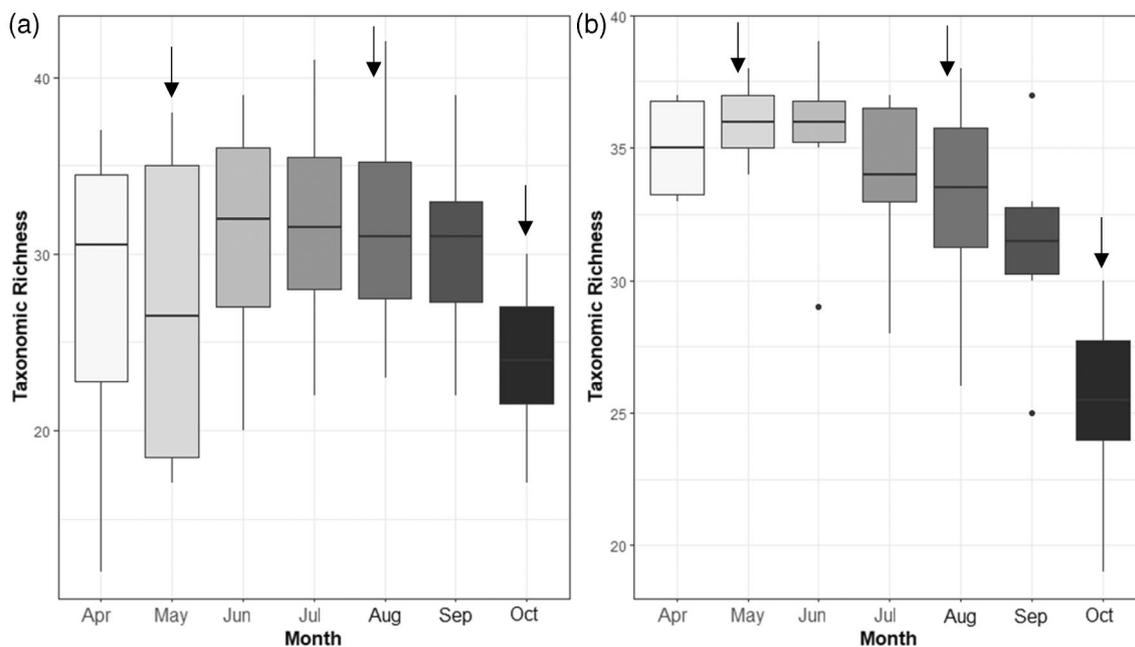


FIGURE 2 Boxplots of plant taxonomic richness for (a) the channel and (b) bank communities during the dry phase. The arrows indicate flow resumptions during the study.

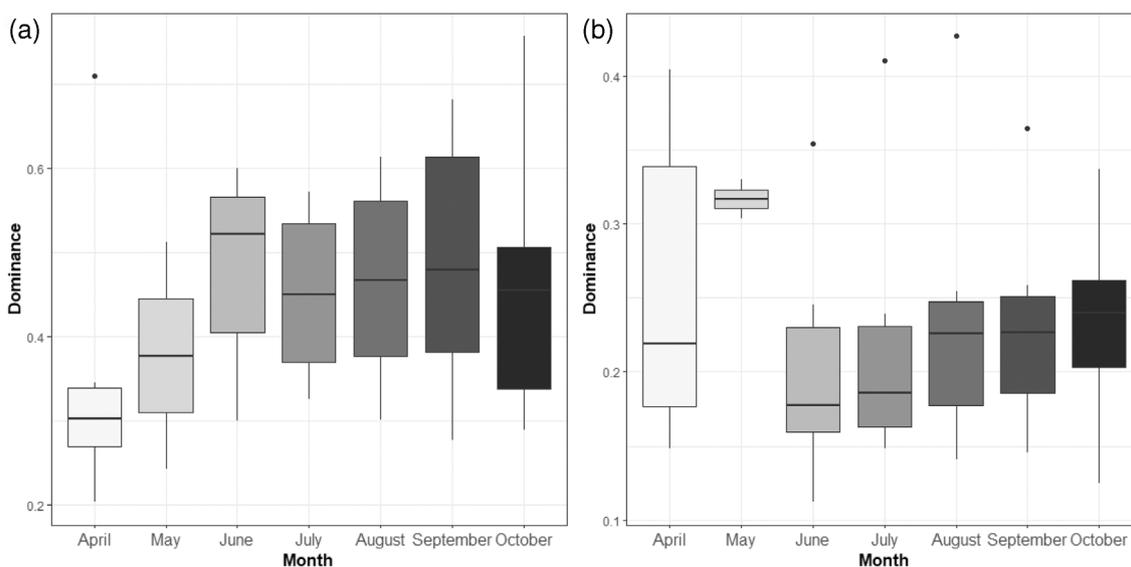


FIGURE 3 Boxplots of plant dominance for (a) the channel and (b) bank communities during the dry phase

coverage of 12% and 46.4%), whereas *U. dioica* increased in dominance from April to June and remained uniformly dominant until October (mean monthly coverage of 3.1%, 14% and 11.7%). *A. ursinum* reached maximum spatial coverage in May (mean monthly coverage of 47.5%) and declined from June (mean monthly coverage of 9.5%) onwards.

3.4 | Plant beta diversity

In-channel plant community composition (PERMANOVA; $F = 1.07$, $p < .001$) varied significantly with month (Figure 4a and Table 4).

Planned contrasts in PERMANOVA identified community composition within the channel differed significantly between April and July, April and August, and April and September (all p values $< .05$). Plant community composition was widely dispersed and overlapping (Figure 4a), which denotes high community heterogeneity within and between months. However, in-channel community composition was still significantly different throughout the study.

The top four plant taxa (identified by a SIMPER analysis) driving compositional differences between April and July were *Allaria petiolata* (garlic mustard), *U. dioica*, *P. hybridus*, and *A. ursinum* (Table 4). *A. ursinum* was dominant in April and the other three taxa were more abundant in July. *U. dioica*, *A. podagraria*, *A. ursinum*, and *E. arvense*

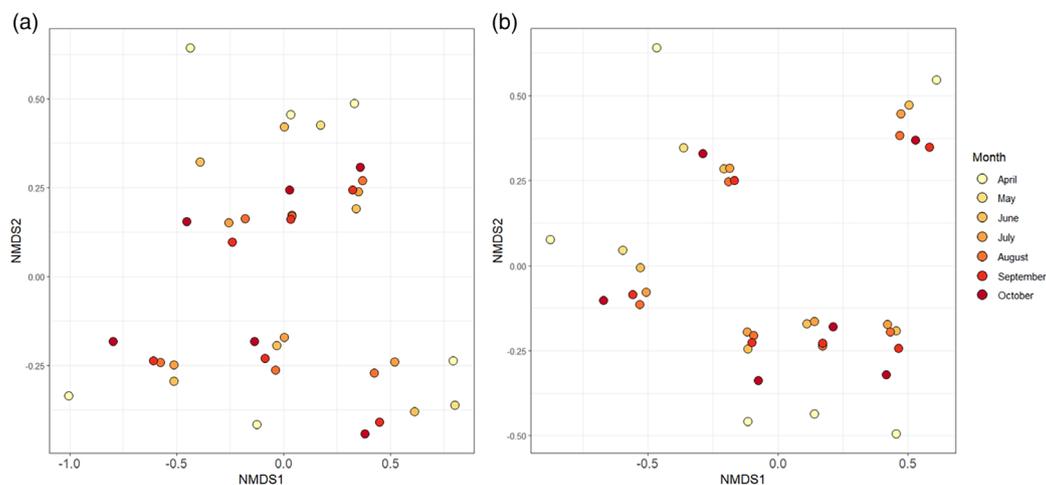


FIGURE 4 Non-metric multi-dimensional scaling (NMDS) ordinations of plant community composition for the (a) channel and (b) banks of the rivers Manifold and Hamps [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 4 Channel and bank plant community composition differences between months

Channel	Average	Standard deviation	Ratio	Month	Dissimilarity (%)	Cumulative dissimilarity (%)	
April vs. July				April	July		
<i>A. petiolata</i>	0.02	0.02	1.43	0.08	0.85	4.99	8.1
<i>U. dioca</i>	0.02	0.02	1.38	0.14	0.91	4.61	12.7
<i>A. ursinum</i>	0.04	0.02	2.38	1.72	0.41	2.21	14.9
<i>P. hybridus</i>	0.05	0.03	1.47	1.87	3.64	0.86	15.8
April vs. August				April	August		
<i>U. dioca</i>	0.02	0.016	1.39	0.14	0.96	4.69	7.81
<i>A. podagraria</i>	0.03	0.021	1.48	0.57	1.69	3.45	11.26
<i>A. ursinum</i>	0.04	0.019	2.22	1.72	0.18	2.3	13.56
<i>E. arvense</i>	0.04	0.026	1.6	0.56	1.78	1.57	15.13
April vs. September				April	September		
<i>A. ursinum</i>	0.05	0.022	2.08	1.72	0	1.65	1.65
<i>A. podagraria</i>	0.04	0.024	1.5	0.57	1.79	2.95	4.6
<i>E. hirsutum</i>	0.01	0.006	0.99	0	0.23	8.86	13.76
<i>G. hederacea</i>	0	0.007	0.52	0	0.13	9.54	23.3
Bank habitat							
April vs. August				April	August		
<i>C. pratensis</i>	0	0	1.37	0.01	0	9.99	9.99
<i>L. galeobdolon</i>	0	0	0.63	0.01	0	9.99	19.98
<i>F. verna</i>	0.01	0	1.78	0.42	0	8.16	28.14
<i>U. dioca</i>	0.02	0.02	1.52	0.72	1.85	1.56	29.7
April vs. September				April	September		
<i>C. pratensis</i>	0	0	1.37	0.01	0	9.99	9.99
<i>L. galeobdolon</i>	0	0	0.63	0.01	0	9.99	19.98
<i>F. verna</i>	0.01	0	1.79	0.42	0	8.22	28.2
<i>U. dioca</i>	0.02	0.02	1.5	0.72	1.84	2.05	30.25

(1.6% dissimilarity) drove compositional differences between April and August. Lastly, *Glechoma hederacea* (ground ivy), *Epilobium hirsutum* (great willowherb), *A. podagraria* and *A. ursinum* (1.7%

dissimilarity) drove plant community composition differences between April and September in the dry channel. Significant differences in bank plant community composition (PERMANOVA; $F = 1.14$, $p < .001$) also

occurred with month (Figure 4b). Planned contrasts highlighted differences in plant community composition between April and August (PERMANOVA; $F = 2.55$, $p < .01$), and April and September (PERMANOVA; $F = 2.74$, $p < .01$). April was characterised by low plant coverage compared to August and September when the bank vegetation had reached high coverage and height. The top four taxa identified by SIMPER in driving the plant community composition between April and August and between April and September were *Lamium galeobdolon* (yellow archangel), *Cardamine pratensis* (cuckoo flower), *Ficaria verna* (lesser celandine), and *U. dioica*.

3.5 | Environmental drivers of plant diversity

PERMANOVA indicated that bed sediments and the percentage of zero-flow days for the 12 months prior to each monthly plant survey affected in-channel plant community composition (Table 5 and Figure 5). Based on the R^2 values, the percentage of sand and fine gravels were the most influential environmental variables driving plant community composition. Figure 5 shows the clustering of reaches 1–4 on the R. Manifold positioned in the centre and left side whilst

reaches 5 and 6 on the R. Hamps are located on the right side of the NMDS ordination. Reaches on the R. Manifold are dominated by the proportion of sand, and medium and fine gravels in the bed sediments, whereas the percentage of zero flow days for the 12 months prior to each monthly plant survey is more important in influencing plant community composition on the R. Hamps.

3.6 | Functional traits associated with drying

All four traits of vegetation height ($t = 7.28$, $p < .001$), clonality ($t = 7.25$, $p < .001$), clonality richness ($t = 19.14$, $p < .01$), and Ellenberg L (e.g., light; $t = 9.35$, $p < .001$), differed significantly with month (Figure 6). Vegetation height varied significantly between April and July ($t = -4.40$, $p < .01$), April and August ($t = -4.57$, $p < .01$), and April and September ($t = -4.28$, $p < .01$). Excluding May, in-channel vegetation height was lowest in April, increased to August and declined in October (Figure 6a). Clonality varied significantly from mid-April to mid-October ($t = 7.25$, $p < .001$), but Tukey's post hoc tests revealed no significant differences between months. In contrast, clonality richness was significantly lower in April than in August

TABLE 5 Influential environmental variables driving in-channel plant community composition

Environmental variable	Df	Sum of squares	R^2	F	Pr (>F)
Percentage of fine and very fine gravels	1	0.732	0.153	12.691	0.001
Percentage of sand	1	1.04	0.217	18.033	0.001
Percentage of ZF days	1	0.462	0.096	8.003	0.001
Percentage of coarse gravel	1	0.256	0.053	4.433	0.001
Percentage of medium gravel	1	0.449	0.094	7.774	0.001

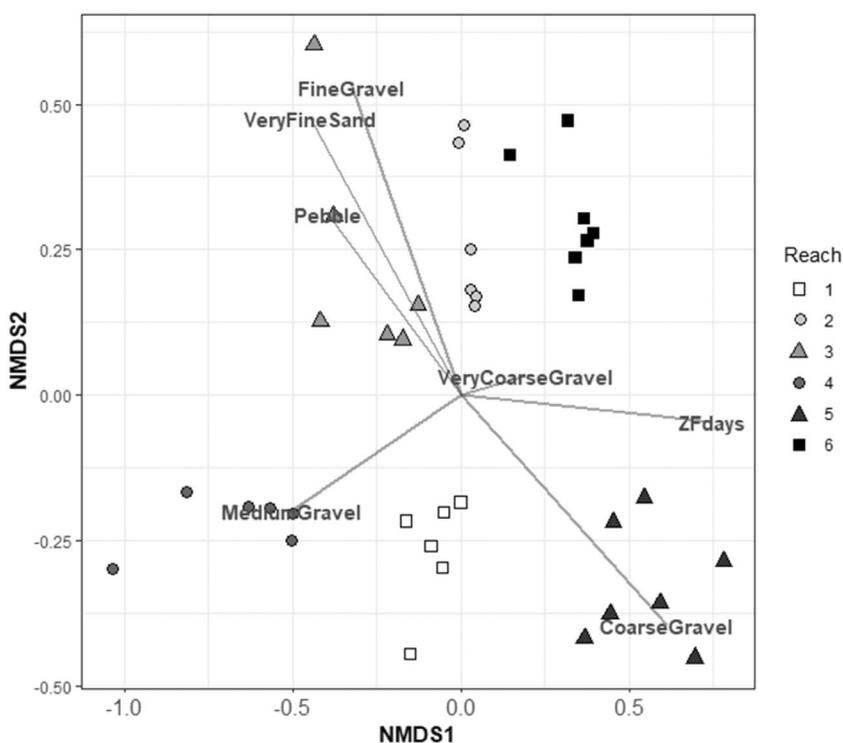


FIGURE 5 Non-metric multi-dimensional scaling (NMDS) ordination depicting the significant environmental variables influencing plant community composition. Please see Figure 1 for the location of the reaches. Abbreviation of ZF days refers to the percentage of zero flow days for the 12 months prior to each monthly plant survey.

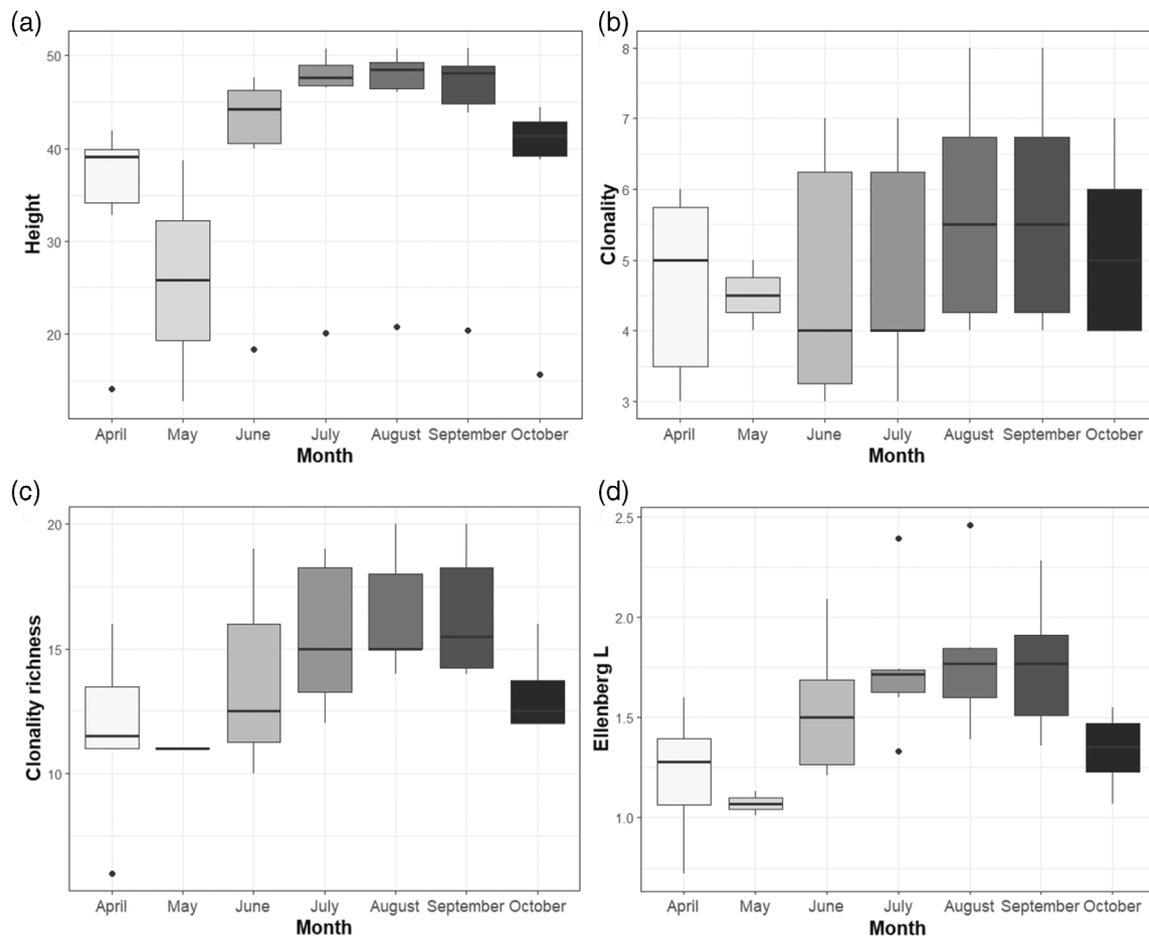


FIGURE 6 Changes in plant functional traits with month. Clonality refers to the number of clonality traits per reach and clonality richness describes the number of taxa with a clonality trait. Ellenberg L is a surrogate for light.

($t = 2.15$, $p < .05$) and September ($t = 2.15$, $p < .05$; Figure 6c). Values of Ellenberg L increased from April to September, excluding May (Figure 6d), with significantly lower Ellenberg L values occurring in April compared to June ($t = -3.36$, $p < .05$), July ($t = -5.52$, $p < .001$), August ($t = -6.06$, $p < .001$) and September ($t = -5.64$, $p < .001$).

4 | DISCUSSION

4.1 | Temporal diversity and variability in community composition

This study illustrates how plants can colonise a dry riverbed and how taxonomic and functional diversity differ during the dry phase (represented by month). Our first hypothesis that taxonomic richness will increase, and beta in-channel diversity will vary with month was supported. Plant taxonomic richness varied significantly during the study. In-channel taxonomic richness was lowest in April, increased through to September (excluding May) and declined in October (Figure 2). A flow resumption occurred in May on the river Manifold. Hence, plant surveys only took place on the two reaches in the R. Hamps, which may account for the low taxonomic richness in May. In-channel beta

community composition also differed significantly during the dry phase (i.e., from late March to mid-October 2021). Plant community composition varied between April and July, April and August, and April and September. In April, in-channel plant communities were characterised by *N. poeticus*, *A. maculatum*, and *A. ursinum*, which are spring flowering plants and typically occur in April and May (Royal Horticultural Society, 2022). All three taxa prefer moist conditions, with *A. ursinum* common in damp shady environments (Rose & O'Reilly, 2006). During our study, the rivers Hamps and Manifold dried in mid and late March respectively, and we believe the damp bed sediments in mid-April provided favourable conditions for the establishment of early colonisers. Community composition in later months was dominated by *P. hybridus*, *P. arundinacea* and *L. perenne* (Figure 7).

We found that plant taxonomic richness was higher in bank habitats than in the dry channel and that in-channel and bank community composition significantly varied during the dry phase, which led us to accept our second hypothesis. Changes in the spatial coverage of *P. hybridus*, *P. arundinacea*, *E. arvense*, *A. podagraria*, and *L. perenne* from April to September contributed to the significant compositional differences between April and July, August, and September for the channel communities and between April and August, and April and



FIGURE 7 Pioneer terrestrial vegetation colonising the dry riverbed on (a) the R. Hamps in June 2021 (after ~86 days of drying; reach 5) and (b) the R. Manifold in July 2021 (after ~99 days of drying; reach 1). *P. hybridus* dominates both reaches with smaller occurrences of *Rumex obtusifolius* (e.g., broad-leaved dock). © Dr Tory Milner [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/tra.4085)]

September for bank communities. *P. hybridus*, *P. arundinacea* and *L. perenne* are all perennial plants with thick rhizomes that develop from axillary buds and grow horizontally (Stace, 2010; Waggy, 2010). In our study reaches, we observed a dense network of *P. hybridus* and *L. perenne* rootstalks on the riverbed. We propose that these taxa predominantly colonised the Manifold and the Hamps by rhizomes that are dormant during the flowing phase, and that grow new shoots vertically upwards through the bed sediments when drying commences. We believe the establishment of a rhizome network in intermittent rivers experiencing predictable wetting and drying is a key resistance and resilience trait of plant colonisation within dry channels.

4.2 | Plant functional traits

Plant functional traits have strong associations with many habitat conditions and have been widely used in terrestrial and aquatic ecosystems at a range of spatial and temporal scales (Delatorre, da Cunha, Rodrigues, Damasceno-Júnior, & Ferreira, 2019; Hong et al., 2021; Shipley et al., 2016). However, this is the first study to our knowledge to use plant functional traits to identify relationships between environmental factors and plant communities in an intermittent river in a cool, wet temperate region. Our findings reveal the traits of vegetation height, clonality, clonality richness and Ellenberg value of light increased in the dry channel with drying, which led us to accept our third hypothesis.

In our study, plant height increased gradually over the growing season towards maturity. Vegetation height traits were measured at the same regrowth stage (i.e., 16 and 27 days after the commencement of streambed drying on the R. Manifold and Hamps respectively, and at monthly intervals afterwards). However, vegetation height at maturity depended on the phenology of each species. Vegetation height can influence the competitive ability of plant species by allowing taller species to dominate by overshadowing smaller species

(Cleland & Harpole, 2010). In our study, Ellenberg L values increased significantly with month. *P. hybridus* (possessing an Ellenberg L value of 6) dominated reaches and produced large leaves which blocked sunlight from reaching the riverbed. As a result, shade-tolerant species, such as *A. podagraria* characterised the second canopy and were less abundant.

Common species in our study included *P. hybridus*, *P. arundinacea*, *E. hirsutum* with lesser occurrences of *M. scorpioides*; all these plants can survive both dry and flowing conditions due to adaptations involving root allocation (Lavergne & Molofsky, 2004), leaf morphology and mass (Sabater et al., 2017) and rhizomes (Nilsson & D'Hertefeldt, 2008; van Groenendael, Klimeš, Klimešová, & Hendriks, 1996), which was the most dominant clonal trait within the communities. The latter adaptation was associated with dominant species, such as *P. hybridus*, *A. podagraria* and *P. arundinacea* and could help explain the increase in clonality, with rhizomes increasing the survival, and thus plant competitive ability and growth, in stressful environmental conditions (Grime, 2001; Nilsson & D'Hertefeldt, 2008; van Groenendael et al., 1996).

Our study found using a taxonomic and functional approach useful to characterise the colonisation of plant communities in an intermittent river network. We found using plant functional traits can help understand biotic responses to changing flow and habitat conditions and advocate future studies to adopt both approaches to determine plant community responses to different periods of intermittency and environmental conditions.

4.3 | Plant propagule dispersal within dry riverbeds

Plant propagules disperse and colonise dry riverbeds through direct deposition from the parent plant and transport by water (hydrochory), wind and animals (Fenner & Thompson, 2005; Goodson, Gurnell, Angold, & Morrissey, 2001; Pollux, Santamaria, & Ouborg, 2005).

Plants in the riparian zone are a major source of plant propagules to intermittent rivers. The presence and spatial extent of the riparian zone (i.e., sporadic or continuous) influences the availability of seeds to dry channels. In our study, we observed numerous vegetated mid-channel bars and sidebars containing *P. arundinacea* and *L. perenne* in dense clumps. These topographic high points in the channel contain vegetation throughout the year and represent a key seed bank in intermittent rivers. We believe plant propagules from the riparian and in-channel vegetation on topographic high points in the channel aided colonisation of the riverbed once flow ceased.

The influence of hydrochory on propagule release and the number of propagules in transport fluctuates throughout the year (Andersson & Nilsson, 2002; Boedeltje, Bakker, Ten Brinke, Van Groenendael, & Soesbergen, 2004; Kubitzki & Ziburski, 1994). Small, low pulses are vital for near-continuous hydrochorous dispersal within river ecosystems (Tockner, Pennetzdorfer, Reiner, Schiemer, & Ward, 1999). During the study period, the rivers Manifold and Hamps experienced three and four short flow pulses, which were typically ~48–36 h. We hypothesise these short-flow pulses transported and deposited freshly produced seeds along the river corridor, and remobilised seeds after their deposition (Andersson, Nilsson, & Johansson, 2000; Goodson, Gurnell, Angold, & Morrissey, 2002). We also believe the timing of the first flow resumption in early May was important in redistributing seeds along the intermittent section shortly following stream desiccation (at the beginning of the growing season).

4.4 | Drivers of plant colonisation

Our study found that heterogeneous bed sediments comprising a mixture of sand, fine and very fine gravels strongly influenced plant community response. The proportion of coarse particles and the content of organic matter within fine sediments (typically defined as inorganic and organic particles <2 mm in size; Jones et al., 2012; Wood & Armitage, 1997) affect sediment water retention (Rawls, Pachepsky, Ritchie, Sobecki, & Bloodworth, 2003; Walczak, Rovdan, & Witkowska-Walczak, 2002). Bed sediments containing a high content of organic matter retain water during desiccation due to organic matter acting as a sponge (De Wilde, Puijalon, & Bornette, 2017). Due to a higher bulk density, silt and clay sediments also possess a high-water retention capacity in contrast to coarse sediments, such as cobbles and pebbles (Saxton & Rawls, 2006; Walczak et al., 2002). Substrate composition through influencing water retention capacity also impacts nutrient availability (Song, Zoh, & Kan, 2007). Hence, the intensity of water stress within bed sediments and the duration of drying interact to influence the resistance and resilience of plants (de Wilde et al., 2017).

The hydrological regime is a key driver of species composition and the successional dynamics of plants (De Wilde et al., 2017). The hydroperiod strongly influences species recruitment, growth and survival (van der Valk, 2005; Van Geest et al., 2005; van Geest, Coops, Roijackers, Buijse, & Scheffer, 2005). Previous studies have stressed

the importance of plant community response to 12, 24 or 36-month antecedent percentage of zero flow (Klijn & Witte, 1999; Westwood et al., 2017; Westwood et al., 2020). In our study, the 12-month antecedent percentage of zero flow days was a major determinant of species composition. During our fieldwork campaign, the rivers Manifold and Hamps experienced three and four rewetting events respectively. We hypothesise the short flow pulses in May and August benefitted in-channel vegetation colonisation and succession by increasing water availability within bed sediments. This short recharge of water availability was very advantageous for plant communities in August when high air temperatures were causing plants to wilt. We speculate that short flow pulses of 2–3 days during a dry phase can positively impact in-channel plant communities by increasing water availability in bed sediments, aiding species recruitment, growth and survival. However, longer flow pulses are likely to inundate terrestrial plant communities in dry channels and cause the end of successional sequences, although some terrestrial species are known to adapt morphologically to survive some levels of inundation (Ayi et al., 2016; Mommer & Visser, 2005). To increase our understanding of the colonisation of plant communities in intermittent systems, future works need to examine how flow pulses of differing durations impact plant colonisation and succession.

4.5 | Conservation and management implications

Our study has indicated the overriding effects of bed sediment characteristics and the flow regime on plant communities in intermittent rivers (Bornette & Puijalon, 2011). High bed sediment heterogeneity (i.e., sand, silt and gravels) supports high taxonomic richness and beta plant diversity and encourages colonisation of dry riverbeds. Fine sediment may further accumulate under patches of vegetation (Cotton, Wharton, Bass, Heppell, & Wotton, 2006; Sand-Jensen, 1998) and around stems (Gurnell, van Oosterhout, de Vlieger, & Goodson, 2006). Our findings indicate the importance of high bed sediment heterogeneity in promoting a diverse in-channel plant community. We carried out our study on an intermittent river network experiencing no water abstractions and low anthropogenic pressures. Our results show the responses of plant communities in two intermittent rivers of good morphological condition. Future work is needed to examine plant community responses in intermittent networks of differing morphological conditions. Such work would support the characterisation of the EU Water Framework Directive ecological status in intermittent rivers and help set reference conditions and the hydrological and environmental conditions required to support these habitats (Stubbington et al., 2018).

In our study, we followed a modified LEAFACS2 method (UK-TAG-, 2014) to record the presence, height and percentage cover of each plant taxon across a 100 m length of dry channel. This method is currently used by the Environment Agency of England across a range of perennial stream types and is a potential repeatable approach to record terrestrial vegetation in an intermittent river network. This fieldwork procedure could be used by other regulatory and

conservation bodies to assess natural capital and ecological status (as mentioned above). Natural capital consists of assets including all physical and biological components of the natural environment (Stubbington et al., 2018). In river ecosystems, natural assets consist of freshwater, sediments, landforms, living material, such as plants and animals and non-living material. For instance, the colonisation of grasses and herbs during desiccation may provide a habitat for pollinating insects, and thus, increase the productivity of adjacent arable land (Bullock et al., 2011). The encroachment and establishment of tree samplings in dry channels can decrease erosion by stabilising sediments (Stubbington, England, et al., 2018), and increase physical habitat heterogeneity by creating depositional features. The methodology used in this study could capture some natural assets provided by terrestrial vegetation in dry riverbeds. Surveys conducted pre- and post-management interventions could also identify the progress of restoration initiatives.

This modified LEAFACS2 method (UK-TAG, 2014) is beneficial for regulatory bodies (in addition to the Environment Agency) by keeping monitoring comparable between perennial and intermittent streams and improving data collection. In addition, the modified LEAFACS2 methodology (as used here to include terrestrial species) has been used successfully on several temporary streams in a chalk catchment to assess the influence of human impact on dry-phase plant communities (Hayes, 2022), providing further support that the methodology is transferrable to other intermittent river networks.

5 | CONCLUSION

Our findings highlight in-channel plant taxonomic richness significantly differed with month. In-channel taxonomic richness typically increased from April to August, plateaued in September and declined in October. In bank habitats, plant taxonomic richness was higher than in-channel communities throughout the dry stage. Functional traits of vegetation height, clonality, clonality richness and Ellenberg L values significantly increased with the duration of the dry phase. The main factors driving compositional differences were bed sediment conditions (i.e., proportions of sand and fine/very fine gravels) and the percentage of zero flow days for the 12 months prior to a plant survey. We hypothesise that the three short flow resumptions increased the water table and prompted mobilisation of seeds and supported germination, which aided further colonisation of the dry channel. We acknowledge our study was conducted on two rivers across one season. Future work should undertake surveys on a multi-year timescale and on geologies of differing permeabilities. As intermittent rivers are predicted to increase in spatial and temporal extent due to climatic drivers and water resource pressures, understanding biotic patterns to environmental variability will be of growing importance for conservation and management plans (Holmes, 2006).

ACKNOWLEDGEMENTS

The authors would like to thank the RGS-IBG for a small research grant (R01096), which was awarded in March 2020 and financially

supported this research. Huge thanks to Dr Julian Martin, the Grants Officer at the RGS-IBG, who was very supportive and encouraging of this work. Thanks also to the RGS-IBG for their flexible approach during the COVID-19 pandemic and for allowing to carry out fieldwork a year later than planned. Finally, thank you to three anonymous reviewers for their time and constructive feedback.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

ORCID

Victoria S. Milner  <https://orcid.org/0000-0001-8027-3647>

REFERENCES

- Andersson, E., & Nilsson, C. (2002). Temporal variation in the drift of plant litter and propagules in a small boreal river. *Freshwater Biology*, 47, 1674–1684.
- Andersson, E., Nilsson, C., & Johansson, M. E. (2000). Plant dispersal in boreal rivers and its relation to the diversity of riparian flora. *Journal of Biogeography*, 27, 1095–1106.
- Ayi, Q., Zeng, B., Liu, J., Li, S., van Bodegom, P. M., & Cornelissen, J. H. (2016). Oxygen absorption by adventitious roots promotes the survival of completely submerged terrestrial plants. *Annals of Botany*, 118, 675–683.
- Baldwin, D. S., & Mitchell, A. M. (2000). The effects of drying and re-flooding on the sediment and soil nutrient dynamics of lowland river-floodplain systems: A synthesis. *Regulated Rivers: Research and Management*, 16, 457–481.
- Boedeltje, G., Bakker, J. P., ten Brinke, A., van Groenendaal, J. M., & Soesbergen, M. (2004). Dispersal phenology of hydrochorous plants in relation to discharge, seed release time and buoyancy of seeds: The flood pulse concept supported. *Journal of Ecology*, 92, 786–796.
- Bogan, M. T., Boersma, K., & Lytle, D. A. (2013). Flow intermittency alters longitudinal patterns of invertebrate diversity and assemblage composition in an arid-land stream network. *Freshwater Biology*, 58, 1016–1028.
- Bornette, G., & Puijalón, S. (2011). Response of aquatic plants to abiotic factors: A review. *Aquatic Sciences*, 73, 1–14. <https://doi.org/10.1007/s00027-010-0162-7>
- Brock, M. A., & Casnova, M. T. (1997). Plant life at the edge of wetlands: Ecological responses to wetting and drying patterns. In N. Klomp & I. Lunt (Eds.), *Frontiers in ecology: Building the links* (pp. 181–192). Oxford: Elsevier, Oxford.
- Bullock, J. M., Jefferson, R. G., Blackstock, T. H., Pakeman, R. J., Emmett, B. A., Pywell, R. J., ... Cooper, N. (2011). *The UK National Ecosystem Technical Report*. Cambridge: UNEP-WCMC.
- Cleland, E. E., & Harpole, W. S. (2010). Nitrogen enrichment and plant communities. *Annals of the New York Academy of Sciences*, 1195, 46–61.
- Colls, M., Timoner, X., Font, C., Sabater, S., & Acuna, V. (2019). Effects of duration, frequency, and severity of the non-flow period on stream biofilm metabolism. *Ecosystems*, 22, 1393–1405. <https://doi.org/10.1007/s10021-019-00345-1>
- Cotton, J. A., Wharton, G., Bass, J. A. B., Heppell, C. M., & Wotton, R. S. (2006). The effects of seasonal changes to in-stream vegetation cover on patterns of flow and accumulation of sediment. *Geomorphology*, 77, 320–334.
- Datry, T., Larned, S. T., Fritz, K. M., Bogan, M. T., Wood, P. J., Meyer, E. I., & Santos, A. N. (2014). Broad-scale patterns of

- invertebrate richness and community composition in temporary rivers: Effects of flow intermittence. *Ecography*, 37, 94–104.
- Datry, T., Larned, S. T., & Tockner, K. (2014). Intermittent Rivers: A challenge for freshwater ecology. *Bioscience*, 64, 229–235.
- Datry, T., Pella, H., Leigh, C., Bonada, N., & Hugueny, B. (2016). A landscape approach to advance intermittent river ecology. *Freshwater Biology*, 61, 1200–1213.
- de Wilde, M., Puijalon, S., & Bornette, G. (2017). Sediment type rules the response of aquatic plant communities to dewatering in wetland. *Journal of Vegetation Science*, 28, 172–183.
- de Wilde, M., Sebei, N., Puijalon, S., & Bornette, G. (2014). Responses of macrophytes to dewatering: Effects of phylogeny and phenotypic plasticity on species performance. *Evolutionary Ecology*, 28, 1155–1167.
- Delatorre, M., da Cunha, N. L., Rodrigues, R. B., Damasceno-Júnior, G. A., & Ferreira, V. L. (2019). Trait-environment relationship of aquatic vegetation in a tropical pond complex system. *Wetlands*, 40, 299–310. <https://doi.org/10.1007/s13157-019-01189-0>
- Döll, P., & Schmied, H. M. (2012). How is the impact of climate change on river flow regimes related to the impact on mean annual runoff? A global-scale analysis. *Environmental Research Letters*, 7, 014037. <https://doi.org/10.1088/1748-9326/7/1/014037>
- Ellenberg, H., Weber, H. E., Düll, R., Wirth, V., Werner, W., & Paulissen, D. (1991). Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobotanica*, 18, 1–248.
- Fenner, M., & Thompson, K. (2005). *The ecology of seeds*. Cambridge: Cambridge University Press.
- Franklin, P., Dunbar, M. J., & Whitehead, P. (2008). Flow controls on lowland river macrophytes: A review. *Science of the Total Environment*, 400, 369–378. <https://doi.org/10.1016/j.scitotenv.2008.06.018>
- García, C., Gibbins, C. N., Pardo, I., & Batalla, R. J. (2017). Long term flow change threatens invertebrate diversity in temporary streams: Evidence from an Island. *Science of the Total Environment*, 580, 1453–1459.
- Godsey, S. E., & Kirchner, J. W. (2014). Dynamic, discontinuous stream networks: Hydrologically driven variations in active drainage density, flowing channels and stream order. *Hydrological Processes*, 28(23), 5791–5803. <https://doi.org/10.1002/hyp.10310>
- Goodson, J. M., Gurnell, A. M., Angold, P. G., & Morrissey, I. P. (2001). Riparian seed banks: Structure, process and implications for riparian management. *Progress in Physical Geography*, 25, 301–325.
- Goodson, J. M., Gurnell, A. M., Angold, P. G., & Morrissey, I. P. (2002). Riparian seed banks along the lower river dove, UK: Their structure and ecological implications. *Geomorphology*, 47, 45–60.
- Grime, J. P. (2001). *Plant strategies, vegetation processes, and ecosystem properties*. New York: John Wiley & Sons.
- Gurnell, A. (2014). Plants as river system engineers. *Earth Surface Processes and Landforms*, 39, 4–25. <https://doi.org/10.1002/esp.3397>
- Gurnell, A. M., O'Hare, J. M., O'Hare, M. T., Dunbar, M. J., & Scarlett, P. M. (2010). An exploration of associations between assemblages of aquatic plant morphotypes and channel geomorphological properties within British rivers. *Geomorphology*, 116, 135–144.
- Gurnell, A. M., van Oosterhout, M. P., de Vlieger, B., & Goodson, J. M. (2006). Reach-scale interactions between aquatic plants and physical habitat: River Frome, Dorset. *River Research and Applications*, 22, 667–680.
- Hayes, C. (2022). *Ecological responses to environmental variability in wet and dry chalk streams*. Unpublished PhD thesis. Nottingham, UK: Nottingham Trent University.
- Hill, M. J., & Milner, V. S. (2018). Ponding in intermittent streams: A refuge for lotic taxa and a habitat for newly colonising taxa? *Science of the Total Environment*, 628–629, 1308–1316.
- Hill, M. O., Mountford, J. O., Roy, D. B., & Bunce, R. G. H. (1999). *Ellenberg's indicator values for British plants*. ECOFACT volume 2 technical annex. Huntingdon: Institute of Terrestrial Ecology.
- Hill, M. O., Preston, C. D., & Roy, D. B. (2004). *PLANTATT attributes of British and Irish plants: Status, size, life history, geography and habitats for use in connection with the new atlas for the British and Irish flora*. Abbots Ripton: Centre for Ecology and Hydrology.
- Holmes, N. T. (1999). Recovery of headwater stream flora following the 1989–1992 groundwater drought. *Hydrological Processes*, 13, 341–354. [https://doi.org/10.1002/\(SICI\)1099-1085\(19990228\)13:3%3C341::AID-HYP742%3E3.0.CO;2-L](https://doi.org/10.1002/(SICI)1099-1085(19990228)13:3%3C341::AID-HYP742%3E3.0.CO;2-L)
- Holmes, N. T. H. (2006). The importance of long-term data sets in science and river management. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 16(4), 329–333. <https://doi.org/10.1002/aqc.785>
- Hong, Z., Ding, S., Zhao, Q., Qui, P., Change, J., Peng, L., ... Gang-Jun, L. (2021). Plant trait-environment trends and their conservation implications for riparian wetlands in the Yellow River. *Science of the Total Environment*, 767, 144867.
- Jones, J. I., Murphy, J. F., Collins, A. L., Sear, D. A., Naden, P. S., & Armitage, P. D. (2012). The impact of fine sediment on macroinvertebrates. *River Research and Applications*, 28, 1055–1071. <https://doi.org/10.1002/rra.1516>
- 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. *Freshwater Biology*, 57, 467–480.
- Klijn, F., & Witte, J. M. (1999). Eco-hydrology: Groundwater flow and site factors in plant ecology. *Hydrogeology Journal*, 7, 65–77.
- Koleff, P., Gaston, K. J., & Lennon, J. J. (2003). Measuring beta diversity for presence-absence data. *Journal of Animal Ecology*, 72, 367–382.
- Kubitzki, K., & Ziburski, A. (1994). Seed dispersal in flood-plain forests of Amazonia. *Biotropica*, 26, 30–43.
- Lake, P. S. (2003). Ecological effects of perturbation by drought in flowing waters. *Freshwater Biology*, 48, 1161–1172.
- Larned, S. T., Datry, T., Arscott, D. B., & Tockner, K. (2010). Emerging concepts in temporary-river ecology. *Freshwater Biology*, 55, 717–738.
- Lavergne, S., & Molofsky, J. (2004). Reed canary grass (*Phalaris arundinacea*) as a biological model in the study of plant invasions. *Critical Reviews in Plant Sciences*, 23, 415–429.
- 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>
- Mommer, L., & Visser, E. J. (2005). Underwater photosynthesis in flooded terrestrial plants: A matter of leaf plasticity. *Annals of Botany*, 96, 581–589.
- Mouquet, N., Moore, J. L., & Loreau, M. (2002). Plant species richness and community productivity: Why the mechanism that promotes coexistence matters. *Ecology Letters*, 5, 56–65.
- Myers, J. A., & Harms, K. E. (2009). Seed arrival, ecological filters, and plant species richness: A meta-analysis. *Ecology Letters*, 12, 1250–1260.
- National River Flow Archive (2022). 28031 – Manifold at Ilam. Available under <https://nrfa.ceh.ac.uk/data/station/info/28031>
- Nilsson, J., & D'Hertefeldt, T. (2008). Origin matters for level of resource sharing in the clonal herb *Aegopodium podagraria*. *Evolutionary Ecology*, 22(3), 437–448.
- O'Donnell, J., Fryirs, K., & Leishman, M. R. (2014). Digging deep for diversity: Riparian seed bank abundance and species richness in relation to burial depth. *Freshwater Biology*, 59, 100–113.
- Pollux, B. J. A., Santamaria, L., & Ouborg, N. J. (2005). Differences in endozoochorous dispersal between aquatic plant species, with reference to plant population persistence in rivers. *Freshwater Biology*, 50, 232–242.
- Questad, E. J., & Foster, B. L. (2008). Coexistence through spatiotemporal heterogeneity and species sorting in grassland plant communities. *Ecology Letters*, 11, 717–726.
- R Development Core Team. (2021). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

- Rascio, N. (2002). The underwater life of secondarily aquatic plants: Some problems and solutions. *Critical Reviews in Plant Sciences*, 21, 401–427.
- Rawls, W. J., Pachepsky, Y. A., Ritchie, J. C., Sobecki, T. M., & Bloodworth, H. (2003). Effect of soil organic carbon on soil water retention. *Geoderma*, 116, 61–76.
- Rose, R., & O'Reilly, C. (2006). *The wild flower key. How to identify wild flowers and shrubs in Britain and Ireland*. London: Penguin Books Ltd.
- Royal Horticultural Society. (2022). Wild garlic and crow garlic. Available under <https://www.rhs.org.uk/weeds/wild-garlic-and-crow-garlic>
- Sabater, S., Timoner, X., Bornette, G., De Wilde, M., Stromberg, J. C., & Stella, J. C. (2017). The biota of intermittent river and ephemeral streams: Algae and vascular plants. In T. Datry, N. Bonada, & A. J. Boulton (Eds.), *Intermittent Rivers and ephemeral streams: Ecology and management* (pp. 189–216). Amsterdam: Elsevier.
- Sand-Jensen, K. (1998). Influence of submerged macrophytes on sediment composition and near-bed flow in lowland streams. *Freshwater Biology*, 39, 663–667.
- Sand-Jensen, K., & Frost-Christensen, H. (1998). Photosynthesis of amphibious and obligately submerged plants in CO₂-rich lowland streams. *Oecologia*, 117, 31–39.
- Saxton, K. E., & Rawls, W. J. (2006). Soil water characteristic estimates by texture and organic matter for hydrologic solutions. *Soil Science Society of America Journal*, 70, 1569–1578.
- Shiple, B., De Bello, F., Cornelissen, J. H. C., Laliberté, E., Laughlin, D. C., & Reich, P. B. (2016). Reinforcing loose foundation stones in trait-based plant ecology. *Oecologia*, 180, 923–931. <https://doi.org/10.1007/s00442-016-3549-x>
- Skoulikidis, N. T., Sabater, S., Datry, T., Morais, M. M., Buffagni, A., Dörflinger, G., ... Rosado, J. (2017). Nonperennial Mediterranean rivers in Europe: Status, pressures, and challenges for research and management. *Science of the Total Environment*, 577, 1–18.
- Song, K.-Y., Zoh, K.-D., & Kan, H. (2007). Release of phosphate in a wetland by changes in hydrological regime. *Science of the Total Environment*, 380, 13–18. <https://doi.org/10.1016/j.scitotenv.2006.11.035>
- Stace, C. A. (2010). *New Flora of the British Isles* (Third ed.). Cambridge: Cambridge University Press. ISBN 9780521717725.
- Stanley, E. H., Fisher, S. G., & Grimm, N. B. (1997). Ecosystem expansion and contraction in streams. Desert streams vary in both space and time and fluctuate dramatically in size. *Bioscience*, 47, 427–435.
- Stromberg, J. C., & Merritt, D. M. (2016). Riparian plant guilds of ephemeral, intermittent and perennial rivers. *Freshwater Biology*, 61, 1259–1275. <https://doi.org/10.1111/fwb.12686>
- Stubbington, R., Chadd, R., Cid, N., Csabai, Z., Miliša, M., Morais, M., ... Datry, T. (2018). Biomonitoring of intermittent rivers and ephemeral streams in Europe: Current practice and priorities to enhance ecological status assessments. *Science of the Total Environment*, 618, 1096–1113. <https://doi.org/10.1016/j.scitotenv.2017.09.137>
- Stubbington, R., England, J., Acreman, M., Wood, P. J., Westwood, C., Boon, P., Mainstone, C., Macadam, C., Bates, A., House, A., & Jorda-Capdevila, D. (2018). The Natural Capital of Temporary Rivers: Characterising the value of dynamics aquatic-terrestrial habitats. Valuing Nature Natural Capital Synthesis Report VNP12.
- Tockner, K., Pennetzdorfer, D., Reiner, N., Schiemer, F., & Ward, J. V. (1999). Hydrological connectivity, and the exchange of organic matter and nutrients in a dynamic river-floodplain system (Danube, Austria). *Freshwater Biology*, 41, 521–535.
- UK Meteorological Office (2022). UK climate averages. Available under <https://www.metoffice.gov.uk/research/climate/maps-and-data/uk-climate-averages/gcqw4zw62>
- UK-TAG (Task Advisory Group). (2014). *UK-TAG River assessment method Macrophytes and Phytobenthos: Macrophytes (river LEAFACS2)*. Water Framework Directive–United Kingdom Advisory Group. Available under <https://www.wfduk.org/sites/default/files/Media/Characterisation%20of%20the%20water%20environment/Biological%20Method%20Statements/River%20Macrophytes%20UKTAG%20Method%20Statement.pdf>
- van der Valk, A. G. (2005). Water-level fluctuations in North American prairie wetlands. *Hydrobiologia*, 539, 171–188.
- van Geest, G. J. V., Coops, H., Roijackers, R. M. M., Buijse, A. D., & Scheffer, M. (2005). Succession of aquatic vegetation driven by reduced water-level fluctuations in floodplain lakes. *Journal of Applied Ecology*, 42, 251–260.
- van Geest, G. J. V., Wolters, H., Roozen, F. C. J. M., Coops, H., Roijackers, R. M. M., Buijse, A. D., & Scheffer, M. (2005). Waterlevel fluctuations affect macrophyte richness in floodplain lakes. *Hydrobiologia*, 539, 239–248.
- van Groenendael, J. M., Klimeš, L., Klimešová, J., & Hendriks, R. J. J. (1996). Comparative ecology of clonal plants. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 351, 1331–1339.
- Waggy, M. A. (2010). *Phalaris arundinacea: Fire Effects Information System*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. Available under <https://www.fs.fed.us/database/feis/plants/graminoid/phaaru/all.html>
- Walczak, R., Rovdan, E., & Witkowska-Walczak, B. (2002). Water retention characteristics of peat and sand mixtures. *International Agrophysics*, 16, 161–165.
- Westwood, C. G., England, J., Dunbar, M. J., Holmes, N. T. H., Leeming, D., & Hammond, D. (2017). An approach to setting ecological flow thresholds for southern English chalk streams. *Water and Environment Journal—Promoting Sustainable Solutions*, 31, 528–536.
- Westwood, C. G., England, J., Johns, T., & Stubbington, R. (2020). A revised classification of temperate lowland groundwater-fed headwater streams, based on their flora. *Water Environment Journal*, 34, 573–585. <https://doi.org/10.1111/wej.12561>
- Westwood, C. G., Teeuw, R. M., Wade, P. M., & Holmes, N. T. H. (2006). Prediction of macrophyte communities in drought-affected groundwater-fed headwater streams. *Hydrological Processes*, 20, 127–145. <https://doi.org/10.1002/hyp.5907>
- Westwood, C. G., Teeuw, R. M., Wade, P. M., Holmes, N. T. H., & Guyard, P. (2006). Influences of environmental conditions on macrophyte communities in drought-affected headwater streams. *River Research and Applications*, 22, 703–726. <https://doi.org/10.1002/rra.934>
- Wood, P. J., & Armitage, P. D. (1997). Biological effects of fine sediment in the lotic environment. *Environmental Management*, 21, 203–217.
- Xiao, S., Zobel, M., Szava-Kovats, R., & Partel, M. (2010). The effects of species pool, dispersal and competition on the diversity-productivity relationship. *Global Ecology and Biogeography*, 19, 343–351.
- Zelený, D., & Schaffers, A. P. (2012). Too good to be true: Pitfalls of using mean Ellenberg indicator values in vegetation analyses. *Journal of Vegetation Science*, 23, 419–431.

SUPPORTING INFORMATION

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

How to cite this article: Milner, V. S., Dutton, J. S., & Hayes, C. (2022). Colonisation of terrestrial vegetation in an intermittent river: Diversity responses to seasonal drying. *River Research and Applications*, 1–15. <https://doi.org/10.1002/rra.4085>