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A comparison of biotic groups as dry-phase indicators of ecological quality in intermittent rivers and ephemeral streams

Rachel Stubbington[a,*], Amael Paillex[b], Judy England[c], Amélie Barthès[d], Agnès Bouchez[e], Frédéric Rimet[e], María Mar Sánchez-Montoya[f], Christian G. Westwood[g], Thibault Datry[h]

[a] Nottingham Trent University, Clifton Campus, Clifton Lane, Nottingham NG11 8NS, UK
[b] Eawag, Swiss Federal Institute of Aquatic Science and Technology, Ueberlandstrasse 133, CH-8600 Dübendorf, Switzerland
[c] Environment Agency, Red Kite House, Howbery Park, Crowmarsh Gifford, Wallingford OX10 8BD, UK
[d] EUROFINS Hydrobiologie France, 75D, Avenue de Pascalet, 30310 Vergeze, France
[e] UMR CARRTEL, Institut National de la Recherche Agronomique, FR-74200 Thonon les Bains, France
[f] Department of Ecology and Hydrology, Regional Campus of International Excellence "Campus Mare Nostrum" – University of Murcia, Campus de Espinardo, 30100 Murcia, Spain
[g] Environmental Research Associates, 21 Meadowbrook Close, Exeter EX4 2NN, UK
[h] Irstea, UR RiverLy, Centre de Lyon-Villeurbanne, 69616 Villeurbanne Cedex, France

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ABSTRACT

Intermittent rivers and ephemeral streams (IRES) are dynamic ecosystems that shift between aquatic and terrestrial states. IRES are widespread, abundant and increasing in extent, but developing biomonitoring programmes to determine their ecological quality is challenging. To date, quality assessments have focused on the aquatic organisms present during wet phases, whereas dry-phase communities remain poorly characterized. We examined multiple biotic groups present in dry IRES channels, to compare assemblages at sites impacted and unimpacted by human activity and to evaluate the potential of each group as an ecological quality indicator. We explored existing, unpublished data for three biotic groups: an aquatic microflora (diatoms), an aquatic fauna (the invertebrate 'seedbank'), and a mixed flora (aquatic and terrestrial plants); notably, we did not source data for terrestrial assemblages with high potential to act as indicators. Diatom and plant assemblage composition differed between impacted and unimpacted sites, and the latter assemblages were more diverse and included more indicator taxa. Invertebrate seedbank taxa richness was higher at unimpacted sites but compositional differences were not detected, probably due to the coarse taxonomic resolution to which abundant taxa were identified. Performance of standard indices of ecological quality was variable, but differences were identified between impacted and unimpacted conditions for all biotic groups. Our results can inform the enhancement of biomonitoring programmes designed to characterize IRES ecological quality in relation to legislative targets. We highlight the need to integrate wet- and dry-phase survey data in holistic quality assessments. Although we suggest diatoms, aquatic plants and the aquatic invertebrate seedbank as having the potential to inform assessment of dry-phase ecological quality, we highlight the need for research to further characterize these aquatic groups and, crucially, to explore terrestrial assemblages with high potential to act as dry-phase quality indicators.

1. Introduction

Intermittent rivers and ephemeral streams (IRES) are defined by freshwater ecologists as lotic ecosystems in which water sometimes stop flowing, and many systems also experience partial or complete loss of surface water (Datry et al., 2017a). IRES encompass a diverse range of ecosystems, from rivers that stop flowing only during severe droughts, through to headwater channels that are usually dry and flow only occasionally after heavy rain. As such, IRES are not only aquatic ecosystems that sometimes lose all flowing surface water, but are also transition zones in which aquatic and terrestrial habitats can occur both successively and simultaneously (Datry et al., 2016). Depending on the extent and pattern of drying, IRES may also be conceptualized as linear terrestrial habitats that experience periodic inundation (Stubbington

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*Abbreviations:*IRES, Intermittent rivers and ephemeral streams

* Corresponding author at: School of Science and Technology, Nottingham Trent University, Clifton Campus, Clifton Lane, Nottingham NG11 8NS, UK.
E-mail address: rachel.stubbington@ntu.ac.uk (R. Stubbington).

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et al., 2017). These coupled aquatic-terrestrial ecosystems can dominate dendritic networks in drylands, are common in temperate regions, and are increasing in global extent in response to water resource demands, land use change and climatic drivers (Datry et al., 2017a; Stubbington et al., 2017).

The communities present in IRES during flowing phases are relatively well-studied, and include vertebrates, invertebrates, microorganisms and aquatic plants (i.e. macrophytes), with spatial and temporal variation in community composition promoting high beta-diversity (Schriever and Lytle, 2016; Stubbington et al., 2017). Dry channels can also support high terrestrial biodiversity including invertebrates, diatoms and plants. These communities are far less well-known, but terrestrial invertebrates include both generalists and dry-channel specialists (Steward et al., 2011; Corti and Datry, 2015) that may have adaptations such as inundation tolerance (Adis and Junk, 2002). Some desiccation-tolerant aquatic invertebrate life stages also persist as a 'seedbank' within the drying sediments (Stubbington and Datry, 2013), and other biotas include diatom-rich biofilms (Barthès et al., 2015) and plant communities in which the dominance of terrestrial taxa increases over time (Holmes, 1999; Westwood et al., 2006).

International legislation such as the EU Water Framework Directive (WFD) and the US Clean Water Act require biomonitoring to assess ecological quality. Although it encompasses IRES, this biomonitoring has to date relied almost exclusively on aquatic biota present during flowing phases (Sheldon, 2005; Stubbington et al., 2018a; but see Steward et al., 2018). This activity includes recent evaluation of indices developed for perennial systems in IRES (Mazor et al., 2014; Prat et al., 2014) and development of IRES-specific indices to characterize the responses of flowing-phase biota to ecological quality (Munné and Prat, 2011). However, difficulties in timing sampling to coincide with peak aquatic diversity in systems with short, unpredictable flowing phases (Sheldon, 2005) and inappropriate calculation of IRES ecological quality using indices designed for perennial ecosystems (Wilding et al., 2018) may both prevent accurate assessment of ecological quality (Stubbington et al., 2018a). Elsewhere, if channels are dry no samples are collected, and absent samples often compromise quality assessments in drylands and during droughts (Steward et al., 2012). A robust suite of aquatic *and* terrestrial indicators that collectively reflect the physicochemical determinants of ecological quality during both wet *and* dry phases therefore requires development (Steward et al., 2012).

We evaluated the potential of multiple biotic groups present in dry IRES channels to act as indicators of ecological quality, potentially of the quality of an IRES in general (i.e. also representing wet phases) and/or of dry phases in particular. We sought dry-phase data from participants in a European research network (Datry et al., 2017b), acquiring data for the aquatic invertebrate seedbank, diatoms, and aquatic and terrestrial plants. We evaluated each group's response to specific human impacts i.e. its ability to distinguish between sites of contrasting ecological quality, with 'quality' defined in relation to the geomorphological, hydrological and/or physicochemical conditions at sites impacted and unimpacted (or minimally impacted) by human activity. We identify biotic groups warranting further study, with the long-term goal of establishing robust dry-phase indicators of IRES quality.

2. Materials and methods

2.1. Data collection

We gathered existing data from 69 members representing 24 countries in a European research network (COST Action *CA15113 Science and Management of IRES*; Datry et al., 2017b). We requested data comprising samples or surveys of one taxonomic group collected from multiple sites within one river type during dry phases. River types could be classified using official typologies (for example under the WFD; EC, (2000)) or comparable descriptions (e.g. UK chalk rivers, which fall within the *lowland, small, calcareous* WFD river type; EC, 2000). Within a river type, sites had to vary in specific aspects of ecological quality, with: at least two states characterized (i.e. unimpacted and impacted); the driver(s) responsible for deviations from unimpacted conditions determined by legislation-driven regulatory monitoring or academic research projects; and each state represented by at least three replicate samples per site / date. Differences in quality could be among multiple sites sampled at one time and/or at repeatedly sampled individual sites. Taxonomic identification was required to a sufficient resolution to infer environmental preferences, preferably genus or species level, with some exceptions made for taxonomically challenging groups.

Data meeting most or all of our criteria were acquired for each of three groups: an aquatic microflora (diatoms; Bacillariophyceae), an aquatic fauna (the invertebrate seedbank), and a mixed flora (aquatic and terrestrial plants; Appendix A, Supplementary Material).

2.1.1. Diatoms

The diatom data comprised 12 biofilm samples collected on 1–3 dates from six sites across five rivers in the temperate (oceanic-mediterranean climate) Adour-Garonne catchment, France, during single, continuous dry phases of 4–30 weeks (Appendix B, Supplementary Material; A. Barthès, unpublished data). Field sampling and laboratory processing methods followed the French national standard (AFNOR, 2007; Appendix B, Supplementary Material). Ecological quality was categorized using WFD *status* classes and spanned *high* (i.e. unimpacted conditions, $n = 8$), *good* (i.e. slight deviation from unimpacted conditions; $n = 2$) and *moderate* (i.e. moderate deviation; $n = 2$) classes. Deviations from high status reflected elevated phosphate concentrations (mean ± SE, 0.15 ± 0.04 mg L^{-1} compared to $\leq 0.10 \pm 0.01$ mg L^{-1}). Low replication was a notable limitation of this data set.

2.1.2. Aquatic invertebrate seedbank

In total, 19 dry sediment samples were collected across three rivers in a semi-arid region of Bolivia (Figs. S1–S2) to examine the aquatic macroinvertebrate and meiofauna taxa persisting within the seedbank (Appendix B, Supplementary Material; T. Datry, unpublished data). In each river, 3–5 replicate sediment samples were taken at unimpacted sites ($n = 11$) and 2–3 replicates were collected from sites impacted by sediment mining ($n = 8$), following methods described by Datry et al. (2017c; Appendix B, Supplementary Material). Data set limitations were covariation of ecological quality and intermittence, i.e. ten of 11 unimpacted sites had longer flowing phases (> 8 months year^{-1}) than impacted sites (< 6 months year^{-1}), and the coarse taxonomic resolution to which three abundant taxa (Chironomidae [Diptera], Hydrachnidia, Oligochaeta) were identified (Appendix B, Supplementary Material).

2.1.3. Macrophytes and terrestrial plants

The plant data reported 137 surveys conducted during dry phases in 15 headwater sites across six chalk rivers in two catchments in temperate (oceanic climate) England, between 1992 and 2013 (Fig. S3, Appendix B, Supplementary Material). These surveys represent a subset of the data set reported by Holmes (1999) and Westwood et al. (2006), with our dry-phase focus complementing these previous explorations of community responses across wet and dry phases. Dry-phase durations prior to sampling varied between 3 months and 4 years, but were otherwise unknown. Surveys followed Holmes (1999), with aquatic and semi-aquatic macrophytes identified to species or genus, and terrestrial plants recorded as *non-aquatic grasses* and *non-aquatic herbs*. Data collected by regulatory agencies informed characterization of environmental variables influencing ecological quality at spatiotemporally relevant scales: sediment heterogeneity, shading by riparian vegetation, bank slope, livestock poaching (i.e. physical disturbance of bank and bed sediments by hooves), and water quality. Additional information regarding the extent of habitat modification and instream habitat quality was also available (Appendix B, Supplementary Material).

2.2. Data analysis

To visualize variability in assemblage composition in relation to characterized determinants of ecological quality, we used non-metric multi-dimensional scaling (NMDS) ordinations based on Bray-Curtis dissimilarity matrices, with 95% confidence ellipses used to aid visualization of groups for the plant data. We tested the significance of compositional differences using analysis of similarities (ANOSIM), supplemented where necessary by pairwise comparisons to identify quality categories between which assemblages differed. For plants, NMDS ordinations were plotted for different environmental drivers, with *slope* and *poaching* combined to distinguish between communities at gently sloping sites with and without poaching impacts. Preliminary analyses of plant assemblages showed clustering of surveys dominated by (unidentified) terrestrial plants and widely dispersed macrophyte-dominated assemblages (Fig. S4 in Appendix B, Supplementary Material). Therefore, to facilitate observation of variability in macrophyte assemblages, NMDS and ANOSIM were repeated with terrestrial plants (and therefore 36 samples containing only these groups) excluded ($n = 101$). NMDS and ANOSIM were conducted using square-root transformed abundance data (for diatoms, first rarefied to 839 individuals to account for unequal sample sizes [Appendix B, Supplementary Material] and the invertebrate seedbank) or total cover values (for plants, with macrophyte and terrestrial cover analysed in combination and separately).

To summarize assemblages, we calculated the metrics: total abundance (for the invertebrate seedbank only); abundance (invertebrate seedbank), cover (plants) or rarefied abundance (diatoms) of each common taxon, with 'common' defined as comprising > 5% of all individuals, rarefied individuals or cover; taxa richness; evenness (*J'*); and Shannon–Weiner diversity (*H'*, hereafter, *diversity*) for each sample.

We calculated the most suitable ecological quality index for each group. For French diatom assemblages, we used OMNIDIA v6 (Lecointe et al., 1993) to calculate the *Biological Diatom Index* (BDI; AFNOR, 2007), which reflects organic and inorganic nutrient pollution. For the Bolivian invertebrate seedbank, the BMWP-based *Andean Biotic Index* (ABI) score, number of scoring taxa (NTAXA) and average score per taxon (ASPT) were used as presence-absence-based indicators of responses to environmental degradation (Ríos-Touma et al., 2014). For UK plant assemblages, we calculated the *Mean Trophic Rank* (MTR) index of trophic status, which also responds to physical habitat characteristics including sediment composition, shading, bank slope and poaching (Holmes et al., 1999); these results should be interpreted in light of the adapted MTR field protocol used (Holmes, 1999; Appendix B, Supplementary Material).

We used one-way ANOVA supplemented as necessary by Tukey's post-hoc tests to identify differences in summary metrics and quality indices between impacted and unimpacted conditions. Abundance data were ln(x + 1)-transformed prior to analysis. For diatom assemblages, good and moderate-status classes were combined, to improve replication and to identify differences between these ($n = 4$) and unimpacted sites ($n = 8$). For plants, five aspects of ecological quality were used to distinguish impacted (stated in italics) and unimpacted conditions: sediment heterogeneity (*none*; some), the extent of shading (*unshaded*; light; heavy), cross-sectional bank slope and livestock poaching (*gentle, poached*; gentle, unpoached; moderate; *steep*), and water quality during preceding wet phases (good; *poor* WFD status classes; Appendix B, Supplementary Material). Light shading and moderate bank slopes are indicative of semi-impacted conditions in these IRES, but were coded as unimpacted in this analysis to facilitate observation of patterns.

Indicator value analysis (IndVal; Dufrêne and Legendre, 1997) based on abundance (invertebrate seedbank), rarefied abundance (diatoms) or % cover (plants) was used to identify taxa indicative of unimpacted and impacted conditions, with quality categories defined as for ANOVA. Indicator values reflect *specificity*, i.e. the probability of a taxon occurring in a group, and *fidelity*, i.e. the relative abundance of the taxon in that group. Following Dufrêne and Legendre (1997), taxa with indicator values ≥0.25 were considered sufficiently common to warrant consideration, with a maximal score (1) indicating taxa found in all unimpacted but not impacted samples, or vice versa. In the plant analysis, 36 surveys including only terrestrial taxa were excluded due to inadequate taxonomic resolution. Taxa restricted to 1–2 rivers or ≤10% of samples are not reported, to avoid inaccurate suggestion of indicator value.

All analyses were performed in R version 3.2.2 (R Development Core Team, 2010): ANOSIM, ANOVA, NMDS and rarefaction using the *vegan* package (Oksanen et al., 2018) and IndVal using the *multipatt* function in the *indicspecies* package (De Cáceres and Jansen, 2016).

3. Results

3.1. Diatoms

In total, 34 diatom taxa were identified, including 28 species and 19 genera, with one genus not also identified to species level (mean ± SE, 9.0 ± 0.84 taxa sample^{-1}; Appendix A, Supplementary Material). Four taxa were common: the *Achnanthidium minutissimum* complex (29% of all individuals counted), *Amphora pediculus* (16%), *Nitzschia amphibia* (7.2%) and *Mayamaea* (5.2%). Assemblage composition differed among quality categories (ANOSIM, global $R = 0.47$, $P = 0.007$), with NMDS showing dispersed high-status samples and a lower-status cluster (Fig. 1).

Identification of diatom indicator taxa is preliminary due to low replication in both impacted ($n = 4$) and unimpacted ($n = 8$) categories. The *A. minutissimum* complex occurred across categories, was particularly abundant in high-status samples (363 ± 79 compared to 9.8 ± 4.1 individuals sample^{-1}; one-way ANOVA, $F_{1,10} = 37.86$, $P < 0.001$; Fig. 2a), and was identified as indicative of these unimpacted conditions (Appendix C, Supplementary Material). *Encyonopsis minuta* was among 16 taxa restricted to high-status samples and occurred at a mean abundance of 72 ± 22 individuals sample^{-1}, but was not a high-status indicator. *Amphora pediculus* abundance was higher in good and moderate-status samples (303 ± 101 individuals sample^{-1} compared to 46 ± 26 individuals sample^{-1}; one-way ANOVA,

Fig. 1. Non-metric multidimensional scaling ordination of diatom assemblages in dry bed-sediment samples of contrasting ecological quality from five rivers (1–5; Appendix B, Supplementary Material). *High*, *good* and *moderate* are EU Water Framework Directive ecological status classes describing unimpacted, slightly impacted and moderately impacted conditions, respectively (EC, 2000). Stress = 0.05.

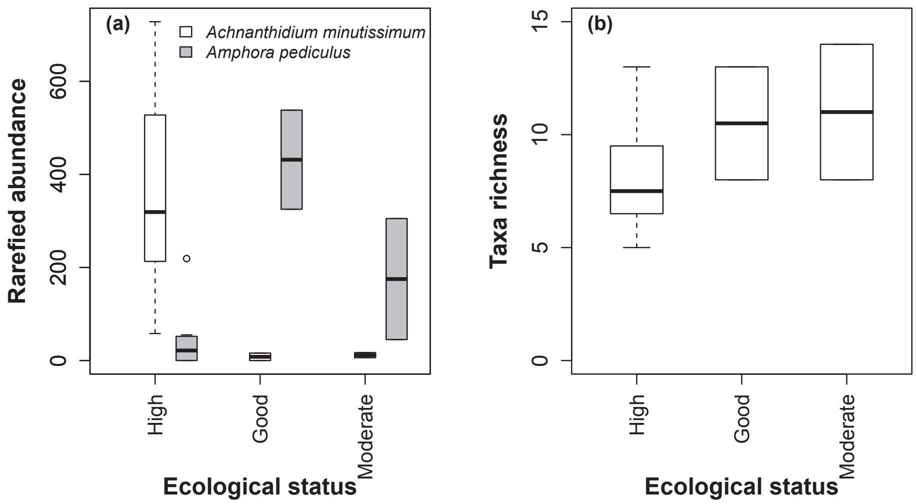


Fig. 2. Metrics summarizing diatom assemblages in dry bed-sediment samples ($n = 12$) from five rivers of contrasting ecological quality: (a) rarefied abundance of the *Achnanthidium minutissimum* complex and *Amphora pediculus*; (b) richness (taxa sample^{-1}). *Ecological status* classes are defined in Fig. 1. Boxes represent the interquartile range (Q75–Q25) around the median, the upper and lower whisker represents (Q75 + 1.5*[Q75–Q25]) and (Q25 + 1.5*[Q75–Q25]) of the data, respectively, and the circle represents an outlier.

Table 1

Ecological quality index scores in unimpacted and impacted site conditions, based on: (a) the Biological Diatom Index (diatoms, France); (b) the Andean Biotic Index (aquatic invertebrate seedbank, Bolivia); (c) the Mean Trophic Rank (MTR; macrophytes, UK). Differences between assemblages sampled in unimpacted and impacted conditions were identified using one-way ANOVA, with the MTR related to five aspects of ecological quality; significant differences are in bold.

Biotic group	Index	Site condition		F	P
		Unimpacted	Impacted		
Diatoms	Biological Diatom Index	18 ± 0.63	14 ± 0.86	9.96	**0.010**
Invertebrate seedbank	Andean Biotic Index	21 ± 4.3	9.6 ± 1.7	4.56	**0.048**
	Number of scoring taxa	5.6 ± 0.77	3.5 ± 0.42	4.82	**0.042**
	Average score per taxon	3.4 ± 0.26	2.7 ± 0.27	3.90	0.065
Macrophytes	MTR – sediment	25 ± 2.5	17 ± 2.6	3.95	**0.049**
	MTR – shading	26 ± 2.7[1]	17 ± 2.4	3.03	**0.032**
	MTR – bank slope[2]	28 ± 2.5[3]	18 ± 4.0	2.29	0.107
	MTR – poaching[4]	29 ± 2.8	12 ± 3.0	18.74	< **0.001**
	MTR – water quality	26 ± 3.2	19 ± 2.2	3.27	0.073

[1] *Light* and *heavy* shade categories.

[2] Excluding poached sites.

[3] *Gentle* and *moderate* slope categories.

[4] *Gently* sloping sites only.

$F_{1,10} = 6.81$, $P = 0.026$; Fig. 2a) and was among six taxa indicative of these impacted conditions (Appendix C, Supplementary Material). Richness (Fig. 2b), diversity and evenness were comparable across status classes (one-way ANOVA, $P \geq 0.150$). BDI scores were higher in high-status compared to good and moderate-status samples (Table 1).

3.2. Aquatic invertebrate seedbank

In total, 1077 invertebrates (mean ± SE 57 ± 17, range 2–319 individuals L^{-1}) from 35 viable macroinvertebrate and meiofauna taxa (4.9 ± 0.5, 2–11 taxa L^{-1}) were recorded from 19 1-L samples (Appendix A, Supplementary Material). Chironomidae, Oligochaeta, Hydrachnidia and Planariidae (Tricladida) were common, accounting for 37%, 27%, 12% and 5% of all individuals, respectively. Diptera was the most diverse of 10 orders, represented by 12 families, with Coleoptera, Ephemeroptera and Hemiptera represented by four, three and two families, respectively. Of the 35 taxa, 24 are exclusively aquatic, whereas 11 are semi-aquatic or include aquatic, semi-aquatic and/or terrestrial representatives. Assemblage composition was comparable at impacted and unimpacted sites (ANOSIM, global $R = -0.013$, $P = 0.489$; Fig. 3).

Abundance was comparable at unimpacted and mining-impacted sites, in total (one-way ANOVA, $P = 0.108$; Fig. 4a) and for each common taxon ($P \geq 0.163$). Richness was higher at unimpacted sites (5.9 ± 0.8 taxa L^{-1}) than at impacted sites (3.6 ± 0.5 taxa L^{-1}; $F_{1,17} = 5.21$, $P = 0.036$; Fig. 4b), whereas evenness ($P = 0.796$) and

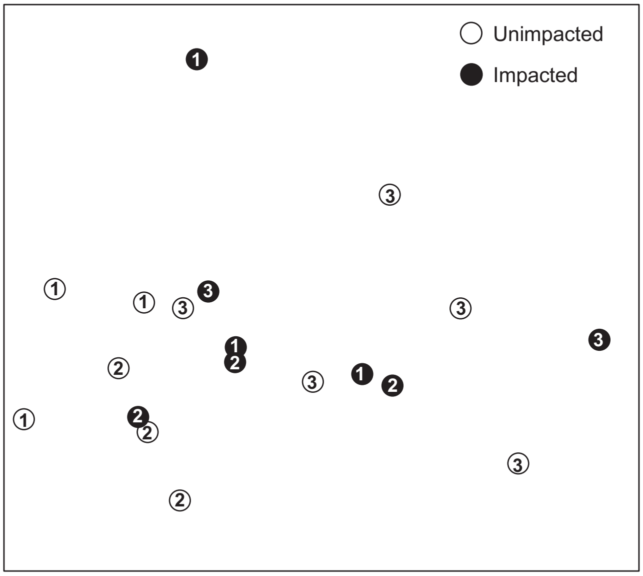


Fig. 3. Non-metric multidimensional scaling ordination of aquatic invertebrate seedbank. assemblages in dry bed-sediment samples collected from unimpacted ($n = 11$) and mining-impacted ($n = 8$) reaches of three rivers (1–3) and rehydrated. Stress = 0.09.

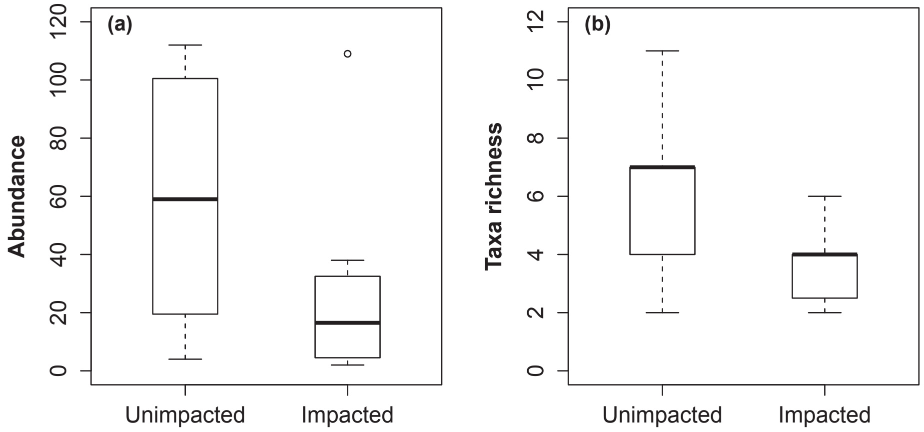


Fig. 4. Metrics summarizing aquatic invertebrate seedbank assemblages in dry bed-sediment samples collected from unimpacted ($n = 11$) and mining-impacted ($n = 8$) reaches of three rivers and rehydrated: (a) total abundance (individuals L^{-1}) and (b) richness (taxa L^{-1}). An outlier (319) in the abundance unimpacted category was excluded to facilitate observation of patterns. Boxes represent the interquartile range (Q75–Q25) around the median, the upper and lower whisker represents (Q75 + 1.5*[Q75–Q25]) and (Q25 + 1.5*[Q75–Q25]) of the data, respectively, and the circle represents an outlier.

diversity ($P = 0.065$) were comparable across sites.

Taxa occurring only at unimpacted sites comprised all Elmidae (Coleoptera), Ephemeroptera, Hirudinea and Tricladida, and at low abundance, Amphipoda, Dytiscidae (Coleoptera), Hemiptera, Nematomorpha and six Diptera families (Appendix A, Supplementary Material). No taxa were identified as significant indicators of either unimpacted or impacted sites. However, Hydrachnidia had a high IndVal score (0.802; Appendix C, Supplementary Material) and this taxon was particularly abundant in three unimpacted samples (10, 23, and 72 individuals L^{-1}) whereas its abundance at impacted sites was consistently low (maximum 4 individuals L^{-1}). ABI and NTAXA scores were higher at unimpacted than impacted sites, whereas the ASPT was comparable across sites (Table 1).

3.3. Macrophytes and terrestrial plants

Vegetation cover (mean ± SE, 83 ± 2.3% survey^{-1}) was recorded for 29 taxa: two terrestrial groups (grasses, herbs), and 27 macrophyte taxa comprising 24 species and 24 genera, with three genera not also identified to species level (5.7 ± 0.3 taxa survey^{-1}; Appendix A, Supplementary Material). Terrestrial grasses (51% of cover), terrestrial herbs (17%) and *Phalaris arundinacea* (7.4%) were common. Compositional differences in macrophyte assemblages were observed between sites with: gentle poached and both gentle unpoached and moderate bank slopes (ANOSIM, $P = 0.002$; Fig. 5a); homogeneous (i.e. fine-sediment dominated) and heterogeneous sediments ($P = 0.002$; Fig. 5c); and no, light and heavy shading ($p \leq 0.008$, Fig. 5d); comparable patterns were observed when all taxa were analysed. Compositional differences between water quality categories ($P = 0.001$) and between sites with gentle poached and steep banks ($P = 0.001$) were not apparent when terrestrial taxa were excluded ($P \geq 0.35$; Fig. 5a-b). Considerable overlap in assemblage composition was observed among categories in all analyses (ANOSIM, global $R \leq 0.251$; Fig. 5).

Fig. 6 shows differences in richness, diversity, terrestrial grass and macrophyte cover between quality categories, with one-way ANOVA results presented for these and other assemblage metrics in Appendix D (Supplementary Material). Sites with some sediment heterogeneity had higher richness, diversity, macrophyte and *P. arundinacea* cover, and lower terrestrial grass cover compared to sites with homogeneous fine sediments, whereas total and terrestrial herb cover and evenness were comparable between sediment categories. Richness, diversity, evenness, total cover, macrophyte cover and *P. arundinacea* cover all peaked at sites with light shading, whereas terrestrial grass cover was highest at unshaded sites, and terrestrial herb cover was comparable among shade categories. Considering combined bank slope and livestock poaching categories, sites with gently sloping poached banks had lower richness, diversity, macrophyte cover and *P. arundinacea* cover, and higher terrestrial grass cover than other sites, whereas the highest richness, diversity, macrophyte and *P. arundinacea* cover and the lowest cover of terrestrial grasses occurred at sites with moderate bank slopes. Richness, diversity, macrophyte cover and *P. arundinacea* cover were higher and terrestrial grass cover was lower at sites with good water quality, whereas evenness, total cover and terrestrial herb cover were comparable between water quality categories (Fig. 6).

MTR scores were higher at sites with some sediment heterogeneity and light-to-heavy shading, and lower at sites with gently sloping poached banks, but were comparable among unpoached bank slope groups and water quality categories (Table 1).

Multiple indicator taxa were identified for each unimpacted ecological quality category, and *Veronica beccabunga* was identified indicative of unimpacted conditions in all categories. Three taxa were indicative of two impact types, including *Alopecurus geniculatus* (Appendix C, Supplementary Material).

4. Discussion

To date, few published studies have explored IRES dry-phase assemblages, and of these, most have examined only terrestrial (Corti and Datry, 2015; Sánchez-Montoya et al., 2016) and/or aquatic (e.g. Stubbington and Datry, 2013) invertebrate communities, and all except Steward et al. (2018) have characterized only unimpacted sites. Our study represents the start of a new stage: comparing dry-phase assemblages at sites impacted by human activity to those at minimally impacted sites (i.e. a reference condition approach; Birk et al., 2012). Our aim was to identify effective indicators of ecological quality: assemblages of widely distributed taxa whose variable spatiotemporal occurrence reflects their known, taxon-specific environmental preferences, thus indicating the impacts of specific human activities (Niemelä, 2000). Our ultimate goal is to inform the development of dry-phase biomonitoring programmes that determine whether IRES meet legislative and other ecological quality targets.

4.1. Aquatic groups have potential as dry-phase quality indicators

Our results suggest aquatic-terrestrial plant assemblages and aquatic diatoms as potential dry-phase quality indicators. Diatom samples collected during preceding and subsequent flowing phases (Appendix A, Supplementary Material) included eight taxa not observed during the dry phase, meaning that 81% of the assemblage remained viable during drying events lasting 4–30 weeks. Similarly, only five macrophyte taxa recorded during flowing phases were absent during dry phases, i.e. 84% of the assemblage persisted for at least 12 weeks. Presence during dry phases suggests desiccation tolerance in these aquatic taxa, although variable dry-phase durations prevent confirmation of specific, persistent indicator taxa. Organisms may have adaptations that promote long-term persistence, for example Barthès et al. (2015) noted diatom

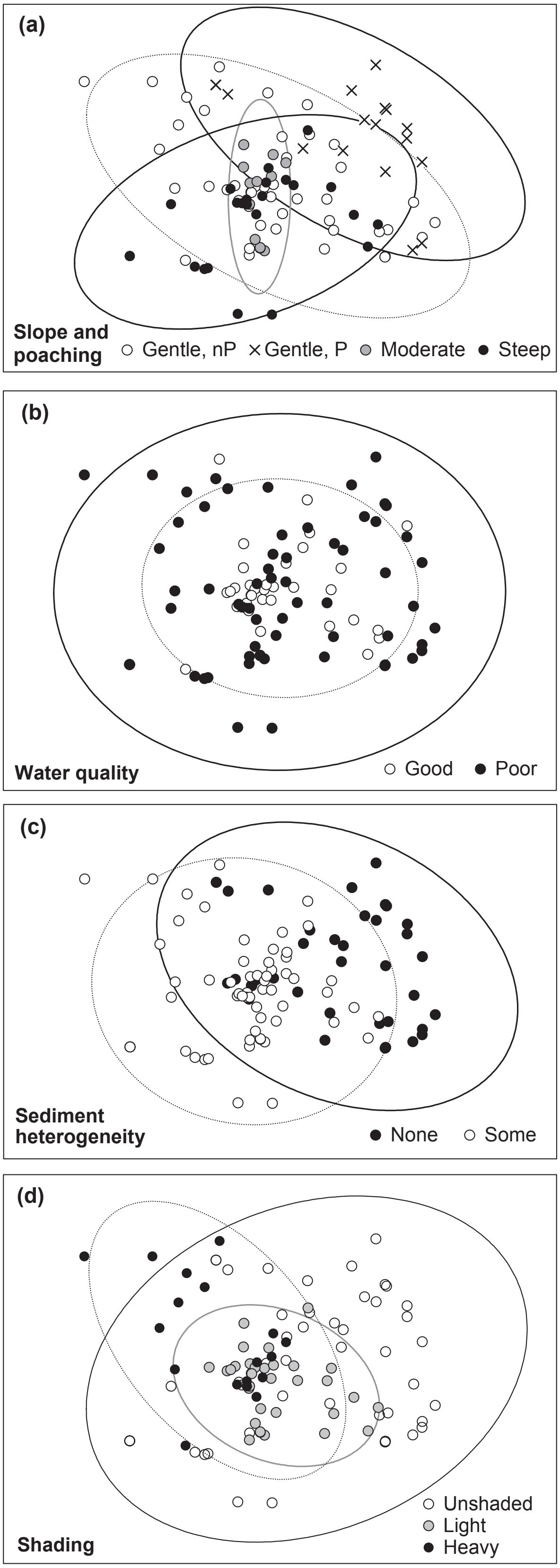


Fig. 5. Non-metric multidimensional scaling ordination of macrophyte assemblages in the dry channels of six rivers, showing differences based on: (a) bank slope (nP, not poached; P, poached); (b) water quality; (c) sediment heterogeneity; (d) shading. Ellipses represent 95% confidence intervals; black, grey and faint dotted lines indicate impacted, semi-impacted and unimpacted sites, respectively. Stress = 0.12.

mortality rates of only 45% and 36% for 4-day and 4-week dry phases, respectively, and site-specific characteristics that locally maintain saturated interstices may promote persistence of diatoms, rooted macrophytes, and other organisms.

Both desiccation-tolerant diatom and macrophyte taxa have known, and contrasting, environmental preferences. In particular, nutrient preferences of species in both groups inform their widespread use in freshwater biomonitoring (Holmes et al., 1999; Kelly et al., 2008). Specifically, we distinguished between diatom assemblages (comprising ≥30 species; Appendix A, Supplementary Material) at unimpacted sites and at sites with elevated phosphate concentrations. Based on our small data set, the *A. minutissimum* complex was indicative of unpolluted sites, as observed in IRES during flowing phases (Delgado et al., 2012) and in perennial rivers (Kelly et al., 2008). In addition, *E. minuta* occurred exclusively at unimpacted sites, reflecting its known organic and inorganic nutrient sensitivities (Coste et al., 2009; Delgado et al., 2012). Equally, four of the five diatom species identified as indicative of nutrient-enriched IRES (*Amphora inariensis*, *A. pediculus, Navicula tripunctata*, *Rhoicosphenia abbreviata*) are recognized as moderately pollution tolerant (Kelly et al., 2008; Coste et al., 2009; Delgado et al., 2012), and their dominance contributed to the homogeneous community composition observed across good and moderate quality classes.

We also identified distinct plant assemblages at sites exposed to varying anthropogenic impacts. Less-impacted sites with some sediment heterogeneity, some shading, gentle unpoached or moderate bank slopes and good water quality supported assemblages with higher richness, diversity and macrophyte cover, and lower terrestrial grass cover. Thirteen compared to three taxa were indicative of unimpacted compared to impacted sites for at least one aspect of ecological quality, suggesting that the latter sites supported a tolerant subset of the taxa present at less-impacted sites. *Veronica beccabunga* was indicative of all unimpacted quality categories, this competitive herb being characteristic of UK 'winterbourne' IRES (Mainstone et al., 1999), associated with unimpacted conditions during flowing phases (Szoszkiewicz et al., 2010), and capable of rapid recovery following disturbance. The grass *A. geniculatus,* associated with non-perennial flow regimes (Holmes, 1999; Mainstone et al., 1999), was indicative of homogeneous, fine sediments and its presence may prove informative in dry-phase quality assessments.

Although unimpacted aquatic invertebrate seedbank assemblages were taxonomically richer, we identified no indicators of mining-impacted or unimpacted sites, probably because the coarse identification level did not distinguish genus- and species-specific responses to environmental drivers within three abundant taxa: Chironomidae, Oligochaeta and Hydrachnidia. In particular, Hydrachnidia abundance was considerably higher at unimpacted sites, this taxon distinguishing between sites of contrasting quality when identified to family during flowing phases (Miccoli et al., 2013) and therefore warranting further investigation during dry phases. Harsh environmental conditions may have reduced persistence in the seedbank at all sites in the semi-arid study area. These invertebrate assemblages are more diverse and abundant where interstitial moisture reduces desiccation (Stubbington and Datry, 2013), and the persistence of aquatic organisms in temperate seedbanks may increase this group's potential as a dry-phase indicator of impacts (such as organic pollution; see Fig. 8) in such regions.

4.2. Dry-phase performance of aquatic biomonitoring indices is variable

Indices calculated to summarize ecological quality based on assemblage composition performed variably. The diatom BDI (AFNOR, 2007) was higher at unimpacted sites than at nutrient-enriched sites, reaching values comparable to those at perennial sites of equivalent status. Equally, macrophyte MTR scores reached values expected at perennial sites, but only where site-specific environmental characteristics (e.g. a flat channel profile and high water table) maintained sediment moisture. Such results highlight that existing indices require

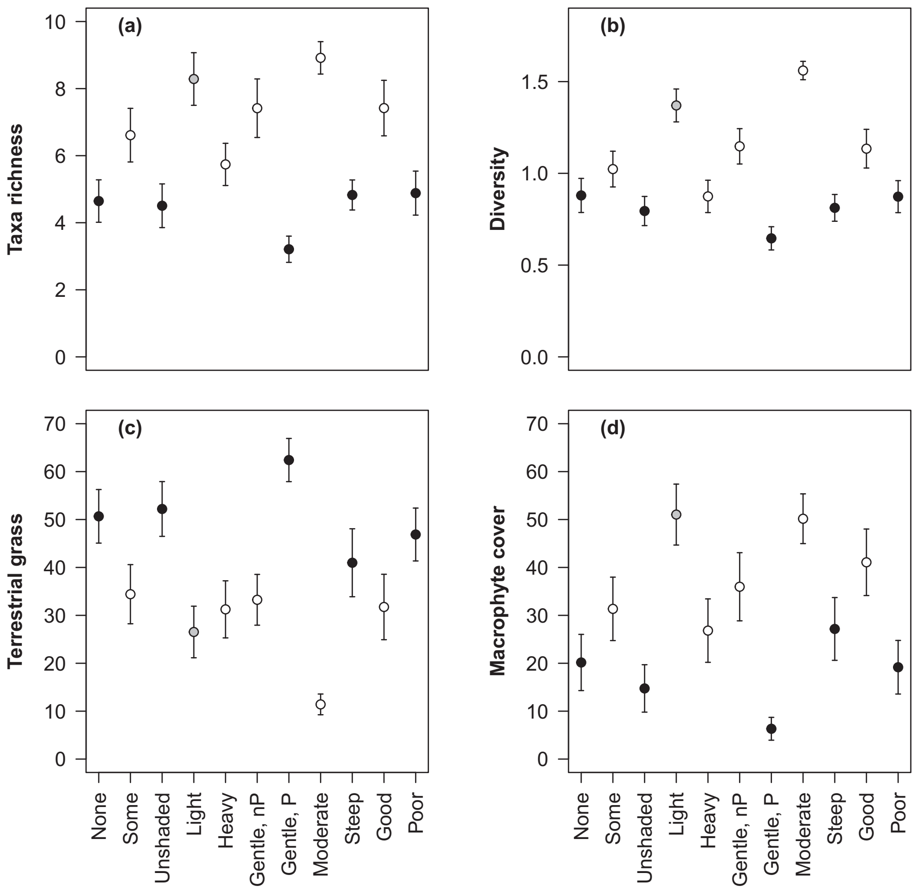


Fig. 6. Mean ± 1 SE metrics for plant assemblages surveyed in the dry channels of six rivers ($n = 137$), in relation to five aspects of ecological quality: sediment heterogeneity (none, some), extent of shading (unshaded, light, heavy), bank slope (gentle, moderate, steep) and poaching (nP, not poached; P, poached), and water quality (good, poor): (a) richness (taxa survey^{-1}); (b) Shannon–Weiner diversity (*H'*); (c) terrestrial grass cover (%); (d) macrophyte cover (%). Black, grey and white-fill symbols indicate impacted, semi-impacted and unimpacted conditions, respectively.

further evaluation to establish their potential for use in dry-phase biomonitoring, and that potential may vary in time in relation to dry-phase durations, and in space, both within and among regions with contrasting environmental conditions. Given such variation, interpretation of assemblage composition and index scores should be informed by site-specific field observations and, where available, hydrological data for the period preceding sampling. Expected scores reflective of different ecological quality categories may need adapting for IRES, to recognize the absence of desiccation-sensitive taxa (Chadd et al., 2017; Stubbington et al., 2018a) and temporal changes in assemblage composition after dry-phase onset.

The MTR, primarily a descriptor of nutrient enrichment (Holmes et al., 1999), did not distinguish between plant assemblages in good and poor water quality categories, possibly because terrestrial grasses dominated enriched sites, and/or because quality was classified during preceding wet phases, *not* in conjunction with dry-phase plant surveys. This result highlights that dry-phase-specific abiotic conditions require characterization in channels of contrasting ecological quality, including temporal changes as ecosystems transition between wet and dry conditions (Fig. 7). Such research is crucial to indicate whether a characterized dry-phase assemblage could represent IRES quality throughout a hydrological cycle, is dry-phase-specific, or is restricted to particular periods within a dry phase. Fig. 7 suggests temporal patterns for four anthropogenic stressors, with each pattern requiring confirmation by new research that represents a sufficient range of IRES types. Outcomes of such research could inform enhancements to IRES biomonitoring by guiding the interpretation of data collected at different times after dry-phase onset, including identification of periods in which biotic assemblages are sufficiently responsive to impacts to render the findings of a quality assessment valid.

Assuming stable release rates, reduced dilution means that organic pollution increases as discharge declines, and effluent may ultimately provide all surface water, limiting natural transitions to dry phases and fundamentally impacting dry-phase ecological quality by preventing establishment of terrestrial assemblages (Fig. 7a). If inputs cease, aquatic organisms in pools slowly consume accumulated organic resources, whereas minimal decomposition by terrestrial biota occurs in dry sediments (Baldwin and Mitchell, 2000; von Schiller et al., 2017). Inorganic nutrient enrichment from point sources also increases during flow recession due to reduced dilution, whereas diffuse inputs decrease due to reduced runoff (Fig. 7b). When flow ceases, high nutrient concentrations in pools increase further due to release from decomposing accumulated material (Acuña et al., 2005; von Schiller et al., 2017). Interstitial concentrations may then decline during dry phases due to uptake by primary producers, but spatial heterogeneity is considerable (Baldwin and Mitchell, 2000; von Schiller et al., 2017; Fig. 7b). Organic and/or inorganic nutrient enrichment may allow low-diversity assemblages of competitive generalists thrive, as we observed for diatoms in response to inorganic nutrient pollution, with the taxonomic composition of terrestrial plant assemblages requiring characterization.

Fine sediment increases as declining velocities deposit increasingly small particles on the bed (Fig. 7c). Inputs and flow cease simultaneously, with accumulated sediments (including those of anthropogenic origin) persisting throughout a dry phase, with localised redistribution by terrestrial invertebrates (Steward et al., 2017). As for organic and inorganic nutrient inputs, dry-phase assemblages may be disproportionately affected by the timing of peak impacts; accordingly, we observed taxon-poor, grass-dominated plant assemblages at sites with homogeneous fine sediments. Finally, poaching may be restricted to channel margins during flowing phases, with impact intensity depending on livestock densities and access points (Fig. 7d). As discharge declines, livestock encroach on an increasing channel area, and their impacts may peak around contracting pools if other drinking water is scarce (Stubbington et al., 2018b). During dry phases, unlimited

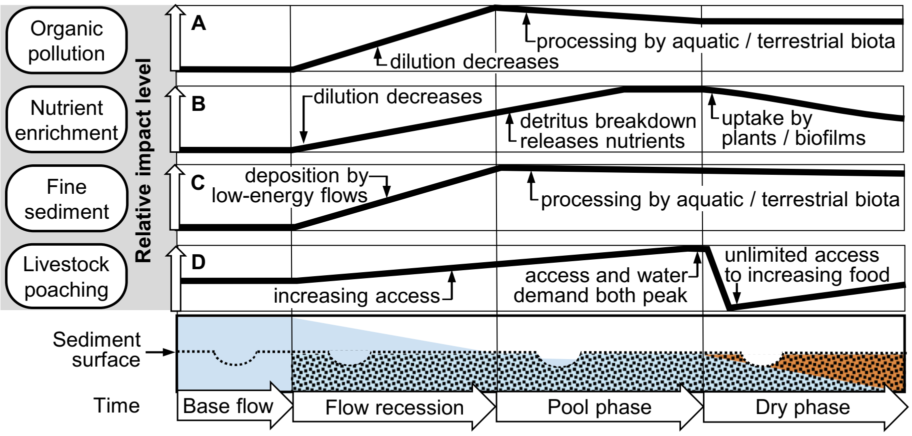


Fig. 7. Hypothesized changes in the severity of (A) organic pollution; (B) inorganic nutrient enrichment; (C) fine sediment deposition; (D) livestock poaching, in an impacted IRES transitioning from a flowing to a dry phase. Changes are relative to the range of conditions experienced at a location. Light blue (light grey) and dark brown (dark grey) indicate free water and unsaturated interstices, respectively.

channel access can spread impacts over a wider area, with plant consumption (Fig. 7d) increasing impacts during dry phases; such activity could prevent plants from acting as a biomonitor of livestock pressures.

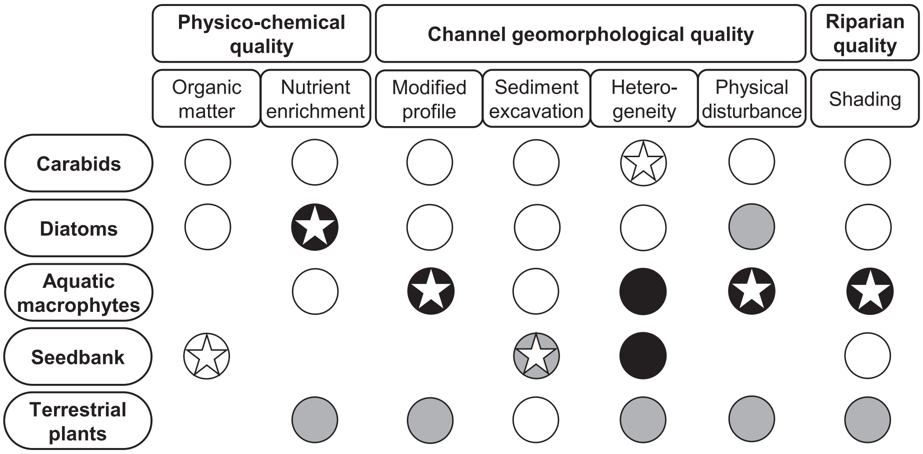
4.3. Terrestrial communities need incorporating into IRES biomonitoring

The communities inhabiting IRES during dry phases include both persisting aquatic and colonizing terrestrial taxa. Our suggested use of aquatic biota in dry-phase quality assessments may be justifiable, due to the persistence of desiccation-tolerant taxa, and the availability of protocols informed by the environmental preferences of freshwater biota. In addition, more available data characterize aquatic than terrestrial dry-phase biotas: we only sourced suitable data for groups dominated by aquatic taxa. However, taxon-specific desiccation tolerances typically cause temporal declines in aquatic diversity (Datry et al., 2014), while terrestrial richness increases as colonists arrive (Sánchez-Montoya et al., 2016). Terrestrial taxa therefore have increasingly high potential as quality indicators as dry-phase durations increase.

Terrestrial grasses dominated dry-channel plant assemblages, their cover peaking at unshaded, nutrient-enriched, fine-sediment dominated sites with gently sloping poached banks. Although low diversity assemblages dominated by generalist ruderals *may* characterize such impacted sites (Mainstone et al., 1999; Fig. 8), suggesting ‘terrestrial grasses’ as indicative of anthropogenic impacts may overlook variability in assemblage composition, including temporal changes in response to colonization by riparian taxa, and emergence of dry-channel specialists (Steward et al., 2011) from inundation-tolerant seeds. Species-level characterization of spatiotemporal variability in terrestrial plant assemblages is needed to evaluate their potential as dry-phase quality indicators (Fig. 8): their potential is high, due to known environmental preferences (Hill et al., 1999). Extension of macrophyte-based indices (such as the MTR; Holmes et al., 1999) to encompass terrestrial flora could create a flexible protocol for consistent application to assemblages comprising variable proportions of taxa spanning the continuum from aquatic to terrestrial environmental preferences, generating comparable data sets that integrate wet and dry-phase information in holistic ecological quality assessments.

Dry-phase diatom assemblages exclusively comprised taxa associated with freshwaters, but terrestrial diatoms are also potential ecological quality indicators, their utility reflecting taxon-specific responses to nutrient concentrations and physical disturbance (Zancan et al., 2006; Fig. 8). Some diatoms span terrestrial and freshwater habitats, for example members of the *A. minutissimum*complex, identified as indicative of unimpacted conditions, also inhabit terrestrial soils (Blanco et al., 2017). Reports of comparable taxon-specific environmental preferences in populations from terrestrial and aquatic habitats (Antonelli et al., 2017) require evaluation, because differences in dispersal within and between aquatic and terrestrial metacommunities may alter the balance of spatial and environmental factors driving assemblage composition (Tonkin et al., 2016; Sarremejane et al., 2017). Specifically, low dispersal ability may limit the potential of terrestrial diatoms as in-channel quality indicators, and desiccation-tolerant taxa that span wet and dry phases may have greater potential, unless their tolerance of desiccation and human impacts covaries.

Although use of established aquatic quality indicators such as diatoms and macrophytes may be appropriate in systems with long, predictable flowing phases, the exclusion of terrestrial biota from IRES biomonitoring is inappropriate – especially where infrequent, unpredictable flow resumptions prevent wet-phase quality assessments.



	Physico-chemical quality		Channel geomorphological quality				Riparian quality
	Organic matter	Nutrient enrichment	Modified profile	Sediment excavation	Hetero-geneity	Physical disturbance	Shading
Carabids	○	○	○	○	☆	○	○
Diatoms	○	★	○	○	○	◍	○
Aquatic macrophytes		○	★	○	●	★	★
Seedbank	☆			✪	●		○
Terrestrial plants		◍	◍	○	◍	◍	◍

Fig. 8. Potential indicators of physico-chemical, geomorphological and riparian aspects of dry-phase ecological quality in IRES, based on: cited literature or author experience (open symbols), our results (grey-fill symbols), or both literature and our results (black-fill symbols). Stars indicate the group considered to have the greatest potential to indicate an aspect of quality, and gaps indicate insufficient evidence to propose potential indicators. *Heterogeneity* includes sediment characteristics; *physical disturbance* includes livestock poaching; and *seedbank* refers to the aquatic invertebrate seedbank.

Dry-phase characterization of terrestrial biota represents an opportunity to incorporate such streams in biomonitoring programmes, especially in dryland IRES with long-lasting dry phases (Sheldon, 2005; Stubbington et al., 2018a). Sampled assemblages will reflect dry-phase duration, and as for aquatic invertebrates in IRES flowing phases (Prat et al., 2014), sampling should be done long enough after a phase begins (i.e. here, after drying onset) to allow a stable assemblage representing peak diversity to establish. Where quantitative hydrological data are unavailable, alternative information is needed to estimate the timing of dry-phase onset, and approaches including the collection of observational data by citizen scientists may be informative (Datry et al., 2016; Puntenney et al., 2017).

Assemblages not explored in our study are also potential dry-phase quality indicators that warrant characterization across unimpacted and impacted sites. In particular, based on our exploration of offered data which did not meet our criteria, our unpublished data (including those provided in Stubbington et al., 2018b), and their ecological preferences in other habitats, we highlight ground beetles (Carabidae, Coleoptera) as high-potential dry-phase indicators. In aquatic-terrestrial habitats such as exposed riverine sediments and floodplains, carabid assemblages can be diverse and abundant (Rainio and Niemelä, 2003); include specialists that tolerate inundation (Adis and Junk, 2002); and can act as indicators of both heterogeneous, complex sediments (Sadler et al., 2005) and livestock poaching (Bates et al., 2007; Fig. 8), if patterns can be disentangled from responses to hydrological drivers.

5. Conclusions

The early developmental stage of dry-phase biomonitoring provides an opportunity to move beyond the typical approach: comparison of metrics summarizing site-specific, morphologically identified taxonomic assemblages with a benchmark (Birk et al., 2012). Such approaches may be inappropriate in IRES if environmental fluctuations and metacommunity dynamics prevent establishment of stable, characteristic assemblages (Ruhí et al., 2017). Novel tools to characterize ecological quality require exploration, potentially including molecular tools that allow concurrent taxonomic characterization of an assemblage spanning the aquatic-terrestrial spectrum (Keck et al., 2017), and encompassing spatial scales from site-specific communities to catchment-wide metacommunities. Depending on phase durations, aquatic, and/or terrestrial biotas may provide appropriate target groups for characterization. Elsewhere, information collected during multiple phases may require integration to provide holistic assessments that inform management interventions to enhance wet and/or dry phase quality. It is therefore crucial to that new research characterizes terrestrial assemblages across quality classes, starting with groups that we and previous studies have identified as having high potential, such as carabid beetles (Bates et al., 2007) and Hydrachnidia mites (Miccoli et al., 2013).

Once dry-phase assemblages are sufficiently well-characterized, summary metrics and indices will require adaptation or development, including new, IRES-specific indices that integrate lotic, lentic and/or terrestrial information. Our results suggest that informative dry-phase metrics should be abundance-weighted and should recognize the value of indicator taxa. In addition, because sensitivities to anthropogenic stressors and natural intermittence covary (Hughes et al., 2009), improved characterization of taxon-specific desiccation tolerance is crucial if aquatic taxa are used as dry-phase indicators, to avoid inaccurate suggestion that absences reflect poor ecological quality (Stubbington et al., 2018a). Collaboration between academic researchers and regulatory stakeholders needs to underpin implementation of our recommendations, to develop flexible, cost-effective biomonitoring tools that effectively represent the biotic complexity of dynamic aquatic-terrestrial ecosystems.

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Appendices A-D. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2018.09.061.

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