

Drying niches of aquatic macroinvertebrates identify potential biomonitoring indicators in intermittent and ephemeral streams

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ARTICLE INFO

Keywords:

Biomonitoring
Ecological niche
Ecological status
Intermittent rivers and ephemeral streams
Macroinvertebrates

ABSTRACT

Intermittent rivers and ephemeral streams (IRES) compose the majority of draining networks on Earth, supporting a unique fraction of biodiversity. Despite their high ecological value, IRES are increasingly threatened by global change and require appropriate biomonitoring and restoration tools. However, indices and indicators used in routine biomonitoring programs are often confounded by drying effects. This occurs because most pollution-sensitive taxa are lost over drying gradients, limiting the utility of current biomonitoring tools in IRES. To address this challenge, there is a need to evaluate which taxa should be used to calculate biomonitoring metrics and indicators over the different portions of the drying gradient. Here, using high-resolution drying data from 33 unpolluted streams, we explored the drying preferences of macroinvertebrates to identify their potential as biomonitoring indicators in IRES. To do this, we characterized macroinvertebrate drying niches and identified those with drying resistance and sensitivity preferences. Next, we evaluated the capacity of functional traits to predict drying specialization and affinity. Finally, to identify potential biomonitoring metrics and indicators for IRES, we evaluated how drying influenced the density, relative abundance and richness of taxa in drying-sensitive and drying-resistant niches. Our results identified three macroinvertebrate groups with drying-resistant niches (partly tolerant, generalist and specialist taxa) and one group of drying-sensitive taxa. We also found that functional traits had a limited capacity to represent differences in drying niches, with shredding trophic preferences and body size showing the strongest correlations. In addition, we observed that the density, relative abundance and richness of drying-resistant taxa were less influenced by drying intensity than those of drying-sensitive taxa. Finally, we found that some pollution-sensitive taxa with partial (e.g., *Lepidostoma*), moderate (e.g., *Corduliidae*) or high drying tolerance (e.g., *Nemoura*) can serve as potential indicators in IRES. Taken together, our results demonstrate that characterizing drying niches can be a useful strategy for developing biomonitoring tools in IRES and for highlighting the limitations of taxonomic and trait-based approaches.

1. Introduction

Running waters sustain a disproportional fraction of biodiversity relative to their extent and provide key benefits to people (Dudgeon et al., 2006). However, widespread environmental degradation is threatening their biological and societal values at unprecedented rates (Gutiérrez-Cánovas et al., 2022; Reid et al., 2019). There is a growing consensus that drainage networks are mainly composed of intermittent rivers and ephemeral streams (IRES) that are periodically dry (Messager et al., 2021) and they are expanding due to climate change and water

extraction (Döll and Schmied, 2012; Scheider et al., 2017). IRES range from watercourses that flow only for a short period after intensive rainfall followed by a quick drying process (ephemeral streams) to streams and rivers that flow most of the year but drying up periodically (intermittent streams and rivers). Thus, preserving healthy IRES is fundamental for biodiversity conservation and to maintain human well-being in the Anthropocene (Cid et al., 2022; Datry et al., 2018). However, IRES have been traditionally overlooked in biomonitoring and conservation programs due to the difficulty of establishing reference conditions and indicators for these highly dynamic systems (Cid et al.,

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<https://doi.org/10.1016/j.ecolind.2022.109263>

Received 5 June 2022; Received in revised form 21 July 2022; Accepted 1 August 2022

Available online 5 August 2022

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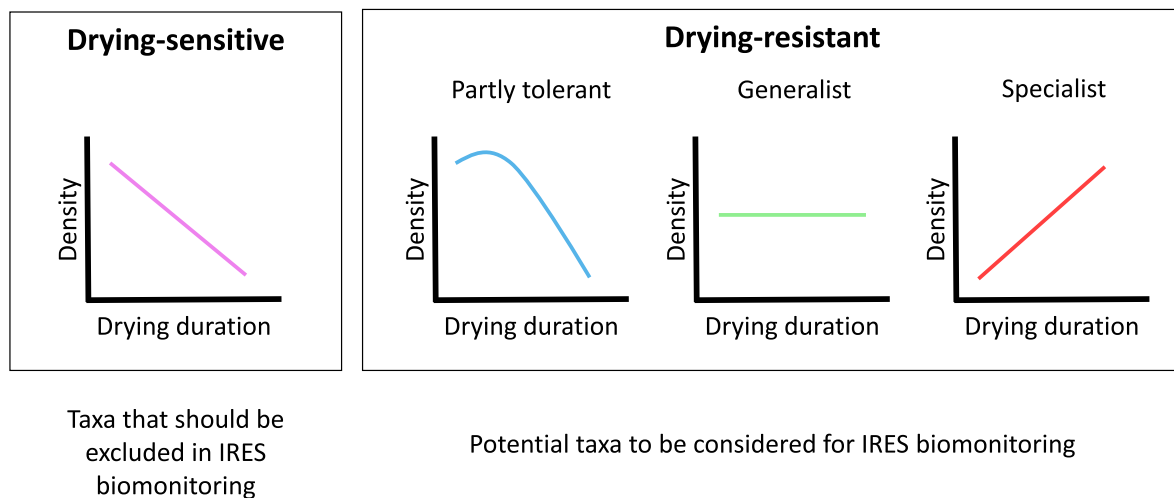


Fig. 1. Hypothetical expectations of taxon density responses for each drying niche-based group.

2017; Stubbington et al., 2018). For example, the extirpation of drying-sensitive taxa causes most indices used in river biomonitoring to yield lower scores for IRES than for permanent-flowing watercourses (Crabot et al., 2021; Munné et al., 2021). Additionally, biomonitoring indicators often result in ineffective detection of abiotic degradation in IRES because drying-resistant taxa may cotolerate other impacts (Crabot et al., 2021; Pallarés et al., 2017b; Soria et al., 2020). Therefore, there is an urgent need to identify taxa and indicators that respond to anthropogenic impacts and not to drying stress.

Exploring the drying niches of aquatic taxa has emerged as a promising way to address these challenges by revealing drying niche-based groups of taxa with similar specialization and affinity over the drying gradient (Aspin and House, 2022; Devictor et al., 2010). For example, identifying taxa with drying-resistant niches will help to find suitable bioindicators for IRES and to predict reference conditions over the drying gradient (e.g., richness and abundance patterns). Additionally, investigating which taxa have drying-sensitive niches will aid in adapting current indices to taxa occurring in IRES (Soria et al., 2020; Stubbington et al., 2022). However, despite their potential to improve IRES biomonitoring, the use of drying niches has remained elusive due to the lack of in situ information on drying stress (drying duration, frequency, or timing) and on the communities inhabiting ephemeral streams.

As hydrological data are unavailable for most watercourses, functional traits have been used as surrogates for drying niches due to their potential to predict responses to abiotic stress (Bonada et al., 2007; Devictor et al., 2010). Applications typically evaluate how functional traits linked with resistance and resilience capacities respond to flow intermittence and/or drying stress (Arias-Real et al., 2021; Aspin et al., 2019; Soria et al., 2020; Stubbington et al., 2022). However, conflicting outcomes and recent criticisms have cast some doubt on the degree to which traits can be accurate predictors of drying responses (Carey et al., 2021; Hamilton et al., 2020), calling for further empirical evidence to clarify this issue.

Recent progress in developing indicators for IRES has focused on benthic macroinvertebrates due to their wide use in routine biomonitoring and well-known responses to anthropogenic impacts (Bonada et al., 2006; Metcalfe, 1989). Due to their contrasting vulnerability to drying stress (Arias-Real et al., 2021; Aspin et al., 2019), macroinvertebrates have a variable potential to act as bioindicators in IRES (Miliša et al., 2022; Soria et al., 2020). Traditionally, biomonitoring indices have focused on Ephemeroptera, Plecoptera and Trichoptera taxa (EPT) due to their sensitivity to anthropogenic impacts, but their diversity in IRES is limited (Stubbington et al., 2017; Stubbington et al., 2009), constraining the development of suitable metrics.

Recent studies have suggested new trait-based metrics and adaptations of conventional indices based on drying-resistant taxa (Crabot et al., 2021; Soria et al., 2020; Stubbington et al., 2022), but their effectiveness in capturing anthropogenic impacts is still limited. Despite this progress, the availability of biomonitoring indicators for the most intermittent and ephemeral watercourses is still constrained due to the scarcity of hydrological and community data and the focus on spring and summer surveys when flow fragmentation is more frequent.

Here, we characterized the drying niches of aquatic macroinvertebrates to identify potential taxa to be used as bioindicators in IRES and those that should be excluded from indices due to their vulnerability to drying. To do this, we performed an extensive survey of 33 streams over a wide drying gradient (annual drying duration ranged from 0 to 257 days), including perennial, intermittent and ephemeral watercourses. Specifically, our goals were i) to characterize the drying niches of macroinvertebrates and identify drying niche-based groups holding taxa with similar niche specialization and affinity; ii) to evaluate the capacity of functional traits to explain variability in macroinvertebrate drying niches; and iii) to identify potential metrics and bioindicators for IRES based on taxa with drying-resistant niches. We expect to find two main niche-based aggregations of taxa (Fig. 1): (i) drying-sensitive taxa that only occur in perennial watercourses, i.e. perennial-flow specialists with high sensitivity to drying stress and (ii) drying-resistant taxa with a greater affinity for intermittent and ephemeral watercourses. In addition, we expect to find different groups of drying-resistant taxa showing varying specialization and affinities over the drying gradient: (i) partly tolerant taxa with affinity for low-intensity drying conditions, (ii) generalist taxa able to develop their life cycles over an ample range of drying conditions and (iii) drying specialists showing the highest affinities for intense drying conditions, including ephemeral watercourses (Fig. 1). Our findings can assist water managers in establishing reference conditions and biomonitoring indicators for IRES.

2. Materials and methods

2.1. Study sites

This study was conducted at 33 independent, low-impacted streams located in nine river basins in Catalonia (NE Spain) along a wide flow intermittence gradient (annual drying duration: 0–257 days; annual drying frequency: 0–8 drying periods). Local land cover was dominated by forest, scrubland, grassland and extensive agriculture (mainly olive groves and vineyards) (based on Corine Land Cover 2006 data in a buffer area of 1 km around each sampling site). Water electrical conductivity

Table 1

Ecological strategy, specialization (OMI) and affinity (OMI Axis 1) of macroinvertebrate taxa over the drying gradient. *p* is the percentage of permutations (out of 1000) that produced a higher value than the observed OMI (in bold, those showing a nonsignificant departure from mean affinity over the drying gradient). The IBMWP score represents a proxy for pollution tolerance.

Taxon	Drying niche-base groups	OMI	OMI Axis 1	<i>p</i>	IBMWP score
<i>Calopteryx</i>	Sensitive	42	-1.26	0.01	8
<i>Onychogomphus</i>	Sensitive	55	-1.55	0.00	8
<i>Polycentropus</i>	Sensitive	60	-1.59	0.02	7
Gammaridae	Sensitive	55	-1.59	0.00	6
<i>Elmis</i>	Sensitive	53	-1.43	0.00	5
<i>Hydropsyche</i>	Sensitive	66	-1.67	0.00	5
<i>Oulimnius</i>	Sensitive	72	-1.80	0.00	5
Athericidae	Partly tolerant	34	-1.05	0.03	10
<i>Habroleptoides</i>	Partly tolerant	13	-0.65	0.06	10
<i>Lepidostoma</i>	Partly tolerant	16	-0.69	0.13	10
<i>Leuctra</i>	Partly tolerant	29	-0.99	0.02	10
<i>Boyeria</i>	Partly tolerant	30	-1.17	0.00	8
Simuliidae	Partly tolerant	15	-0.63	0.00	5
<i>Baetis</i>	Partly tolerant	17	-0.71	0.00	4
<i>Gerris</i>	Partly tolerant	30	-1.04	0.06	3
Corduliidae	Generalist	4	0.29	0.78	8
Ancyliidae	Generalist	1	0.08	0.63	6
<i>Limnius</i>	Generalist	7	-0.47	0.05	5
Tipulidae	Generalist	1	-0.08	0.76	5
<i>Caenis</i>	Generalist	2	-0.25	0.52	4
<i>Centropitulum</i>	Generalist	1	-0.16	0.91	4
Ceratopogonidae	Generalist	2	-0.19	0.38	4
Empididae	Generalist	5	-0.27	0.41	4
Limoniidae	Generalist	6	-0.43	0.08	4
Psychodidae	Generalist	4	-0.30	0.32	4
Stratiomyidae	Generalist	4	-0.33	0.22	4
Dytiscidae	Generalist	2	0.17	0.47	3
Lymnaeidae	Generalist	0	0.01	0.96	3
Planorbidae	Generalist	1	0.15	0.53	3
Scirtidae	Generalist	10	-0.30	0.63	3
Chironomidae	Generalist	0	-0.06	0.11	2
Lumbricidae	Generalist	0	-0.07	0.75	1
Lumbriculidae	Generalist	0	-0.06	0.37	1
<i>Nemoura</i>	Specialist	13	0.40	0.28	7
Asellidae	Specialist	33	0.80	0.05	3
Hydrobiidae	Specialist	18	0.67	0.25	3
<i>Hydrobius</i>	Specialist	11	0.72	0.33	3
Physidae	Specialist	8	0.35	0.36	3

ranged from 151 to 827 μm^{-1} , dissolved inorganic nitrogen ranged from 0.180 to 5.576 mg L^{-1} and soluble reactive phosphorus ranged from 0.006 to 0.175 mg L^{-1} . Stream order ranged from two to four over an altitudinal range of 81–920 m a.s.l. The climate is typically Mediterranean with dry and warm summers, and precipitation mainly occurs during spring and autumn, ranging from 427 to 1038 mm within a year. See Appendix A for more details regarding the study sites.

2.2. Macroinvertebrate data collection

We collected macroinvertebrates immediately after the rainy season (February 2017) to ensure that all streams were in the flowing phase, including those with ephemeral regimes. At each stream site, we collected macroinvertebrates using three quantitative Surber samples (area: 0.04 m^2 , mesh size: 250 μm) in riffle habitats. All samples were preserved in formalin (4%). Individuals were counted and identified in the laboratory until the lowest possible taxonomic level, i.e. to the genus or to the family level (e.g., Diptera), resulting in a total of 66 invertebrate taxa. Over the drying gradient, macroinvertebrate communities varied in their taxonomic richness (6–39 taxa) and total abundance (750–212,825 ind. m^{-2}).

We applied statistical analyses to a subset of 38 taxa, which occurred in at least five out of 33 sites (occurrence $\geq 15\%$) to avoid an imprecise characterization of drying responses. We removed 12 taxa occurring once, six taxa occurring twice, seven taxa occurring three times and

three occurring four times. The 28 discarded taxa included alderflies (*Sialis*), caddisflies (*Crunoecia*, *Oecetis*, *Myastacides*, Limnephilidae, *Limnephilus*, *Mesophylax*, *Philopotamus*, *Rhyacophila*, *Schizopelex*, *Sericostoma*), beetles (*Esolus*, *Hydraena*), dipterans (Culicidae, Dixidae, *Dicranota*, Ephidryidae), true bugs (*Nepa*), mayflies (*Ephemera*, *Ephemarella*, *Heptagenia*), molluscs (Bithyniidae), dragonflies (*Cordulegaster*) and stoneflies (*Brachyptera*, *Capnia*, *Chloroperla*, *Rhabdiopteryx*). These taxa cover a range of potential responses to drying, suggesting no bias in the taxon subset used to perform the final analyses. All statistical analyses were performed using R statistical software Version 3.4.1 (R Development Core Team, 2020).

2.3. Characterization of macroinvertebrate drying niches and ecological strategies

To calculate drying we calculated three different aspects of the drying process: annual drying duration, annual drying frequency and the duration of the last drying event. These metrics were calculated using in situ hydrological information from levelloggers (Solinst Levellogger Edge, full-scale reading precision of 0.05%) placed in the streambed in lotic and lentic habitats for water level and temperature recording. These dataloggers allowed us to infer water presence (and drying) during the 12 months preceding biological sampling (for details, see Appendix B). Previous studies found that the combination of these drying metrics effectively explained variations in macroinvertebrate diversity and abundance in IRES (Arias-Real et al., 2021; Pond et al., 2022).

Based on drying characteristics and taxon abundances, we calculated the drying niche specialization and affinity values for each macroinvertebrate taxon using the outlying mean index (OMI) (Doledec et al., 2000) through the *ade4* R package. Drying niche specialization (OMI) represents the deviation between the mean drying conditions where a taxon occurs and the average drying conditions in the study area (represented by a uniform distribution over the drying gradient). Thus, the OMI ranges from 0 to 100, where greater OMI values represent a more specialized strategy for a given portion of the drying gradient as opposed to generalist strategies (low OMI values). Taxa constrained to either perennial-flowing or drying conditions will show high OMI values, indicating their specialist behaviour. Drying niche affinity is represented by the first axis of the drying space, which was positively correlated with annual drying duration ($r_p = 0.91$). To reduce distribution skewness, annual drying durations were squared-root-transformed, the duration of the last drying event was fourth-root-transformed, and taxon abundances were log-transformed before analyses.

In addition, to identify drying niche-based groups of taxa with similar drying niches, we classified taxa according to their drying specialization and affinity through a *k*-means clustering procedure. Drying niche variables were standardized before analysis. We evaluated the statistical performance (sum of squares) and ecological meaning of a range of potential clusters, representing two to ten macroinvertebrate drying niche-based groups. Finally, we decided to retain the cluster splitting taxa into four drying niche-based groups, as this shows a good explanatory capacity (sum of squares = 91.5%) and a coherent ecological grouping according to our expectations (Fig. 1): drying-sensitive (i.e. perennial-flow specialists with high sensitivity to drying stress), partly tolerant-to-drying, generalist and drying-specialist taxa.

2.4. Evaluating functional traits as surrogates of macroinvertebrate drying niches

To assess whether functional traits are good surrogates of macroinvertebrate drying niches, we compiled information on nine fuzzy-coded functional traits (and 64 categories, see Appendix C), which are commonly used to explain macroinvertebrate ecological responses to flow intermittence (Aspin et al., 2019; e.g., Bonada et al., 2007; Chessman, 2015). Our compilation included maximum body size, life cycle duration, number of generations per year, aquatic stage,

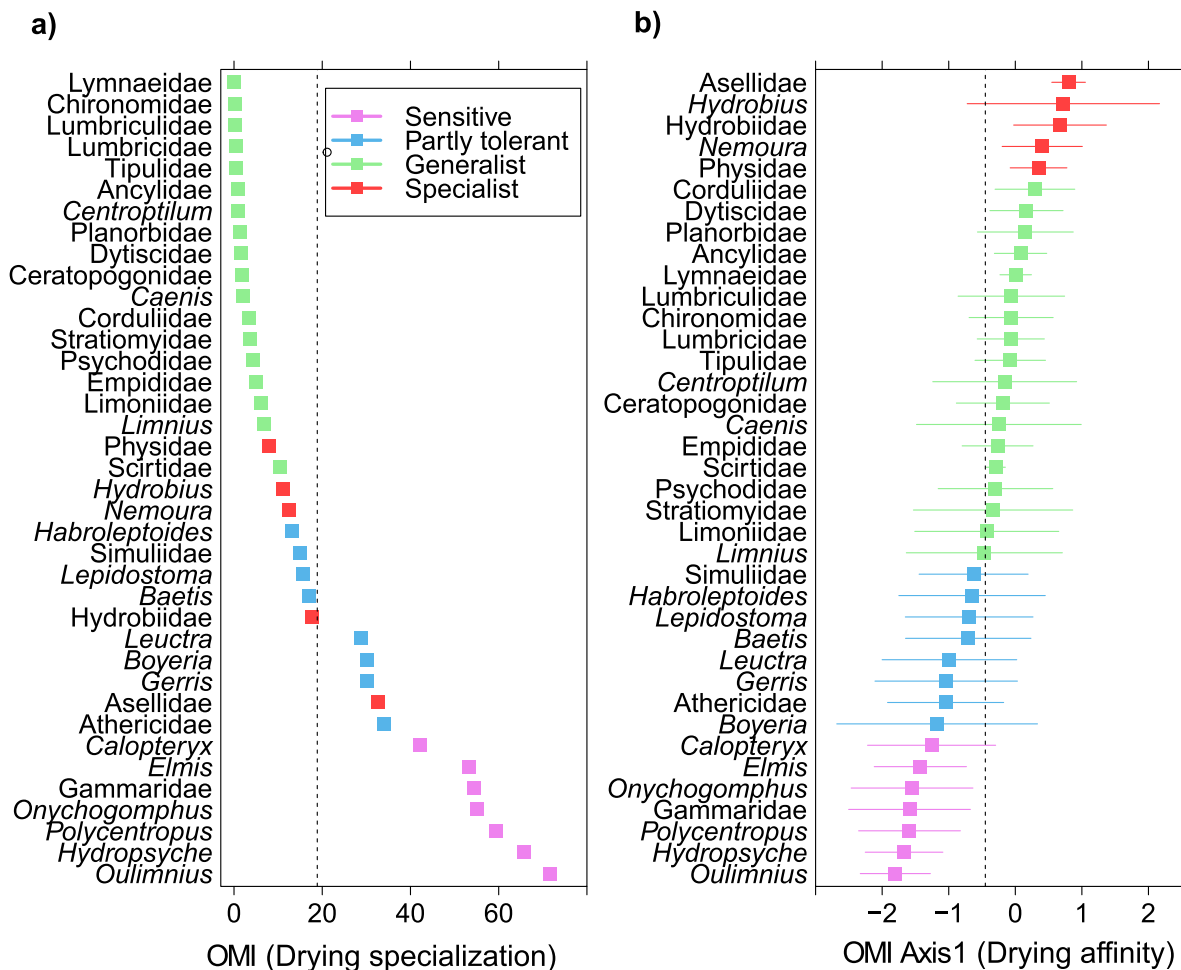


Fig. 2. Specialization (OMI; a) and affinity (OMI Axis 1; b) of macroinvertebrate taxa over the drying gradient. The different colours represent the four drying niche-based groups. Horizontal bars represent the drying niche breadth (drying tolerance).

reproduction, dispersal mode, resistance strategy, respiration, locomotion (Bonada et al., 2011; Tachet et al., 2002) and trophic preferences (<https://www.freshwaterecology.info>; Moog, 2002; Schmidt-kloiber and Hering, 2015). These traits were fuzzy coded, i.e., for each macroinvertebrate taxon, a degree of affinity (ranging from 0 to 10) was assigned to each trait category according to the frequency of occurrence within the genus or family. For macroinvertebrate taxa identified at family level, we averaged trait values for the genera belonging to a given family to obtain a mean trait profile at family-level (Kunz et al., 2022). Prior to analysis, fuzzy coded data were converted into percentages of affinity for each trait. To quantify their value as surrogates of macroinvertebrate drying niches, we calculated Spearman rank correlations between traits and drying niche specialization and affinity. Positive correlation values between drying niche specialization and traits indicate macroinvertebrate features that may favour ecological specialization (in either perennial-flowing or drying conditions). In contrast, positive correlations between drying niche affinity and traits suggest features enabling resistance or resilient capacities to cope with drying stress.

2.5. Identifying macroinvertebrate taxa as potential bioindicators in IRES

To illustrate the advantages of our proposal and identify potential biomonitoring metrics for IRES, we calculated total density, relative abundance and taxon richness for drying-resistant taxa and evaluated their responses to drying (annual drying duration) by means of Spearman correlations. Our expectation is that these metrics based on

drying-resistant taxa should be less dependent on drying than those including sensitive taxa. In addition, we selected drying-resistant taxa sensitive to pollution based on the scores of the Iberian Working Monitoring Party (IBMWP) index (Alba-Tercedor et al., 2002; Munné and Prat, 2009). IBMWP scores range from 1 (pollution-tolerant taxa) to 10 (pollution-sensitive taxa). Thus, we selected taxa with an IBMWP > 5 as potential bioindicators in IRES. The IBMWP index is one of the core elements used by Portuguese and Spanish managers to evaluate the ecological status of Iberian surface waters.

3. Results

3.1. Ecological preferences and strategies over the drying gradient

The OMI results showed that drying space was explained by two axes associated with annual drying duration (OMI Axis 1, 93.9% explained variance) and annual drying frequency (OMI Axis 2, 3.24% explained variance). Fourteen out of 38 taxa showed a significant deviation from the average affinity for drying (global test of marginality < 0.001), indicating the co-existence of several ecological strategies over the drying gradient (Table 1; Fig. 2).

Our cluster analysis identified four drying niche-based groups showing contrasting distributions over the drying gradient (Fig. 3). The first drying niche-based group was composed of taxa sensitive to drying stress; that is, taxa confined to sites with perennial flow (mean OMI: 57; mean OMI Axis 1: -1.56). Drying-sensitive macroinvertebrates had moderate mean densities (4476 ind. m⁻²) (Fig. 4) and included seven

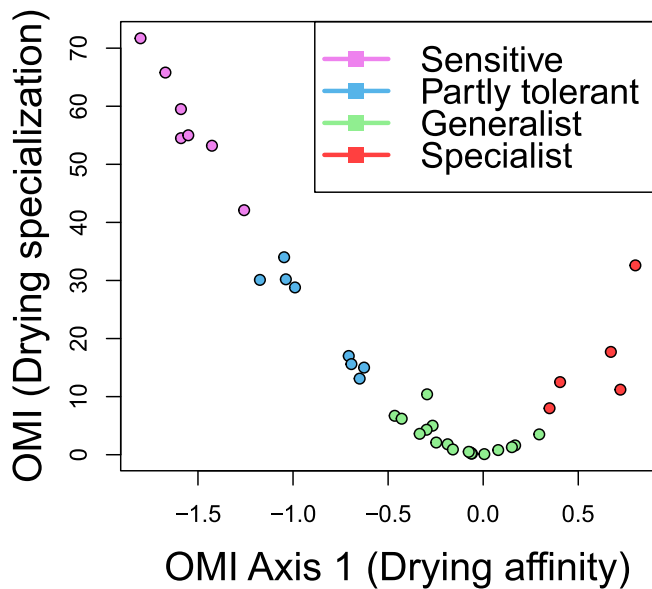


Fig. 3. Distribution of the four drying niche-based groups over gradients of drying affinity (OMI Axis 1) and specialization (OMI). Greater OMI values represent a more specialized strategy for a given portion of the drying gradient as opposed to generalist strategies (low OMI values). Drying niche affinity is represented by the first axis of the drying space, which was positively correlated with annual drying duration.

taxa showing significant departures from average drying affinity (*Calopteryx*, *Elmis*, Gammaridae, *Hydropsyche*, *Onychogomphus*, *Oulimnius* and *Polycentropus*) (Table 1; Fig. 2). The second drying niche-based group contained taxa with a wider distribution over the drying gradient (mean OMI: 23) and a certain tolerance to short drying periods (mean OMI Axis 1: -0.83) (Table 1; Fig. 2). This group of partly tolerant-to-drying macroinvertebrates included eight taxa (Athericidae, *Baetis*, *Boyeria*, *Gerris*, *Habroleptoides*, *Lepidostoma*, *Leuctra* and Simuliidae), which had moderate abundances (mean density: 4227 ind. m^{-2}) (Fig. 4). Five of these taxa showed significant departures from mean affinities over the drying gradient. The third drying niche-based group encompassed 18 generalist taxa showing the widest distributions over the drying gradient (mean OMI: 3, mean OMI Axis 1: -0.12) (Table 1; Fig. 2). This generalist group included several flies (e.g., Chironomidae, Ceratopogonidae, Empididae, and Tipulidae), along with some beetles (e.g., Dytiscidae), some dragonflies (Corduliidae), earthworms (e.g., Lumbricidae) and molluscs (e.g., Ancyliidae) (Table 1; Fig. 2). Generalist taxa composed the majority of individuals over the drying gradient (mean density: $43,338 \text{ ind. m}^{-2}$) (Fig. 4). Finally, the fourth drying niche-based group was composed of drying specialists (mean OMI: 16, mean OMI Axis 1: 0.59) (Table 1; Fig. 2) with moderate abundances (mean density: 4365 ind. m^{-2}) (Fig. 4). Drying specialists included Asellidae, Hydrobiidae, *Hydrobius*, *Nemoura* and Physidae. In the generalist and drying-specialist groups, we found no taxa departing from mean affinities over the drying gradient (Table 1; Fig. 2).

3.2. Functional traits as surrogates of drying niches

Functional traits showed a limited capacity to explain differences in drying niches. Drying specialization was positively related to taxa with small body sizes ($0.5\text{--}1 \text{ cm}$; $r_S = 0.40$), nymph aquatic stages ($r_S = 0.40$), reproductive strategies laying eggs in the terrestrial environment ($r_S = 0.36$) and shredder trophic strategies ($r_S = 0.45$). Drying affinity was positively related to taxa laying eggs in vegetation ($r_S = 0.35$) and those with predatory strategies ($r_S = 0.30$). Drying affinity was negatively correlated with shredder ($r_S = -0.50$), grazer ($r_S = -0.34$) and active filterer ($r_S = -0.30$) trophic strategies, taxa with one reproductive cycle

per year ($r_S = -0.32$) and surface swimmers ($r_S = -0.30$).

3.3. Identifying macroinvertebrate taxa as potential bioindicators in IRES

Generally, the density, relative abundance and richness of sensitive taxa showed stronger negative responses over the drying gradient than those of drying-resistant taxa. For example, density, abundance and richness metrics based on partly resistant taxa had less pronounced declines over the drying gradient than those for sensitive taxa. Metrics based on generalist taxa experienced both moderate negative and positive responses, whereas those for drying-specialist taxa showed weak or moderate increases over the drying gradient (Fig. 4 and Appendix D).

Among drying-resistant taxa, we identified eight potential bioindicators in IRES according to their high IBMWP scores (i.e., sensitive to organic pollution). Among these, the densities of Ancyliidae ($r_S = -0.03$), Corduliidae ($r_S = 0.04$) and *Nemoura* ($r_S = 0.23$) were less affected by drying than those of *Lepidostoma* ($r_S = -0.32$), Athericidae ($r_S = -0.36$), *Habroleptoides* ($r_S = -0.40$), *Leuctra* ($r_S = -0.41$) and *Boyeria* ($r_S = -0.47$).

4. Discussion

Our results revealed three groups of macroinvertebrates with drying-resistant niches, which represent a promising target for identifying metrics and bioindicators to track anthropogenic impacts in IRES. In parallel, our analyses found a group of drying-sensitive taxa that should be excluded in IRES biomonitoring to avoid confounding effects on indices. On the other hand, we found that functional traits had a limited capacity to represent differences in drying niches, thus challenging their utility for anticipating macroinvertebrate responses to drying. Taken together, our results can help to advance the development of biomonitoring indicators in IRES and can highlight limitations of taxonomic and trait-based approaches.

By combining in situ hydrological information with a niche-based approach, we identified macroinvertebrate groups with contrasting specializations and affinities over a wide drying gradient. As occurs with other natural stressors (Gutiérrez-Cánovas et al., 2013; Pallarés et al., 2017a), long-term exposure to recurrent drying events has favoured the development of contrasting ecological strategies that segregate niches and taxa over the drying gradient. In most cases, and despite widespread flow intermittence in semiarid river networks (Munné et al., 2021; Stubbington et al., 2019), most macroinvertebrates have a limited capacity to cope with flow intermittency or complete desiccation. This might be a result of phylogenetic constraints in the adaptation to challenging abiotic or trophic conditions in IRES. For example, in our study, the majority of EPT taxa had drying-sensitive or partly tolerant strategies, as observed elsewhere (Miliša et al., 2022; Stubbington et al., 2017). The drying sensitivity of EPT taxa can be attributed to their life histories, reduced dispersal capacity and vulnerability to desiccation, which collectively constrain evolutionary or phenotypical adaptations to IRES conditions. In addition, rheophilic water beetles (Elmidae) and some dragonflies are also highly sensitive to drying because their preferential habitats are easily lost with flow contraction and disruption (Aspin and House, 2022). Notably, generalist taxa have a successful strategy in IRES based on their dominance in terms of abundance and richness. Similar results were found in other regions (Aspin et al., 2019; Leigh et al., 2019; Miliša et al., 2022) and organisms (diatoms; Tornés and Ruhí, 2013), suggesting that generalist strategies—rather than drying specialists—dominate IRES. This clearly contrasts with the patterns observed for other natural stressor gradients (e.g., salinity, altitude), where stress specialists are common (Gutiérrez-Cánovas et al., 2013). In our study, the generalist group was composed of flies, beetles, dragonflies and molluscs with the widest drying niches. Some of these organisms, such as Chironomidae, Ceratopogonidae, Limoniidae and other flies, tend to show rapid development, strong fecundity and recolonization capacities, making them capable of increasing their

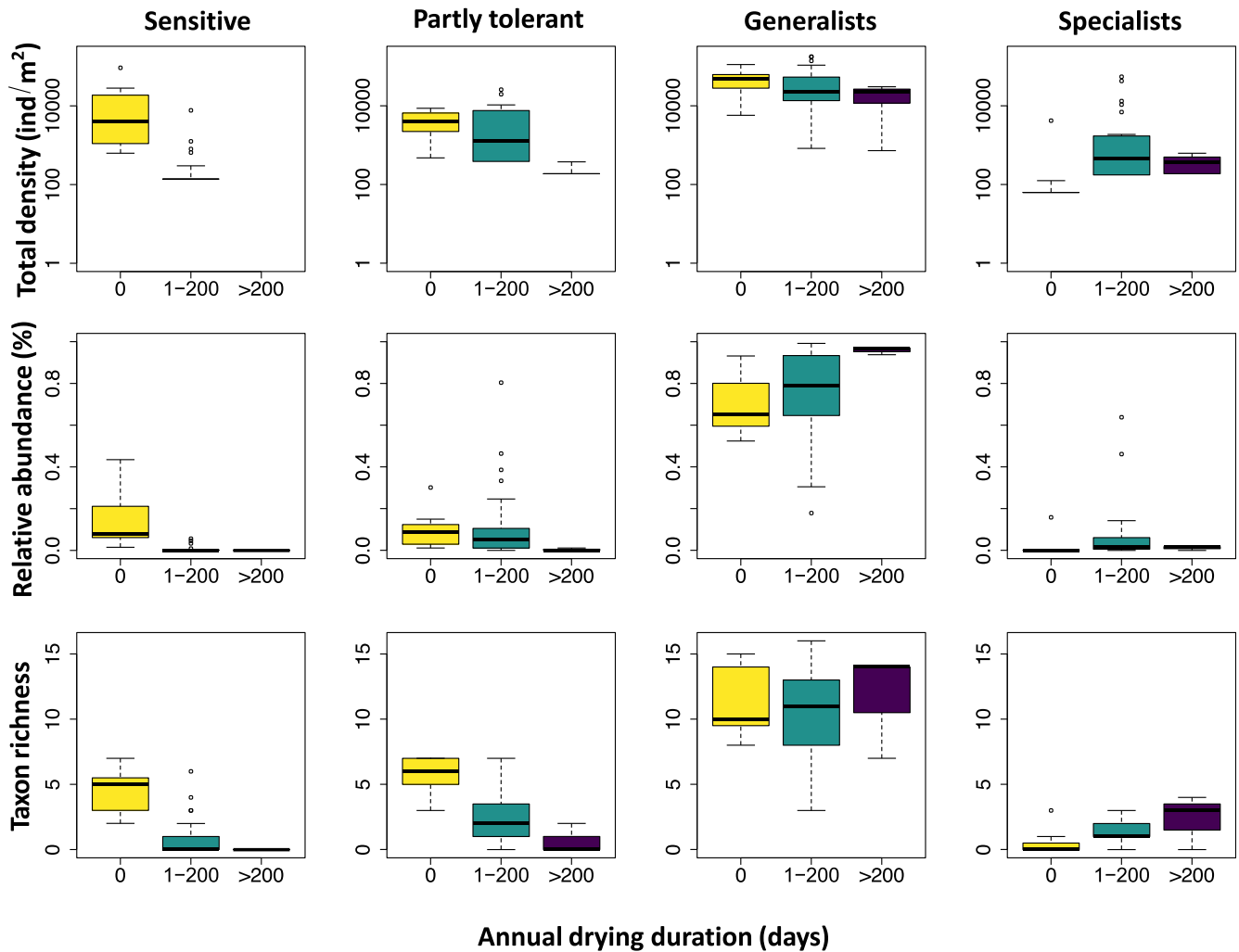


Fig. 4. Boxplots illustrating responses of each drying niche-based group to annual drying duration. Annual drying duration was divided into three groups to represent total density, relative abundance and total richness values for sites with perennial-flow (0 dry days), low to medium drying stress (1–200 dry days) and ephemeral-type streams (>200 dry days). Scatterplots showing responses of raw data are shown in Appendix D.

numbers immediately after flow resumption (Aspin et al., 2019). In other cases, aerial respiration and strong dispersal capacities make Dytiscidae able to recolonize streams after flow resumption from adjacent ponds in flowing waters. It is also important to note that our observed patterns for generalists might be partly attributed to the coarse taxonomic levels of some identifications. Thus, we expect to find a greater degree of specialism for species within these families or genera (Miliša et al., 2022), but this should be explored in future studies. Finally, our results showed a reduced number of drying-specialist taxa compared to the large number of generalists, which might reflect the fact that the most ephemeral streams are challenging habitats for macroinvertebrates.

Despite their potential, functional traits had a limited capacity to explain macroinvertebrate drying niches. Among them, only shredding trophic preferences and body size showed some capacity to track changes in drying specialization and affinity. These findings reinforce doubts about the way in which drying stress sorts species traits (Hamilton et al., 2020). Traditionally, to understand species sorting patterns, researchers have explored trends in individual trait modes over drying gradients (Aspin et al., 2019; Bonada et al., 2007). However, adaptation to IRES conditions seems to not converge into directional trait shifts but into different trait combinations conferring drying resistance or resilience capacities. For example, both small and large organisms can inhabit IRES depending on additional traits. Small organisms can

migrate into the hyporheic zone during drying but require physiological and resistant adaptations to withstand potential desiccation or starvation periods (Stubbington et al., 2017). On the other hand, large organisms can have stronger dispersal, recolonization and competitive capacities, but they require either rapid maturation or adult aquatic stages (Bogan et al., 2015). Although drying reduces the quality and quantity of food resources (Arias-Real et al., 2018), even specialized shredders or predators can occur in IRES but typically at reduced abundances (Arias-Real et al., 2021; Leberfinger et al., 2010; Ledger et al., 2013). Future research should be directed to identifying which trait combinations are associated with increased drying resistance and resilient capacities.

Our results are consistent with those of previous studies, suggesting the need to adapt and develop biomonitoring tools for IRES based on drying-resistant taxa (Miliša et al., 2022; Stubbington et al., 2016). Recent evidence suggests that indices used in routine river biomonitoring can be confounded by drying stress, providing misleading results (Crabot et al., 2021; Munné et al., 2021; Soria et al., 2020). This occurs because these biomonitoring tools are based on pollution-sensitive indicators, which are lost over drying gradients. Similarly, in our study, most of the drying-sensitive and partly tolerant taxa were pollution-sensitive taxa according to their high IBMWP scores. Thus, our results highlight the utility of characterizing drying niches to understand which taxa should be used over the different portions of the drying

gradient. Four main biomonitoring implications arise from our results. First, we recommend extending the identification of drying-sensitive taxa and adapting biomonitoring tools targeting IRES. This will help to reduce confounding effects caused by natural drying. Second, the estimation of IRES reference conditions should consider which taxa can potentially occur given the drying conditions. Thus, as done in this study, the density, relative abundance or richness of the drying-resistant groups can be calculated from wider datasets to estimate regional reference conditions for different drying intensities and IRES typologies (Stubbington et al., 2018). Third, the abundance of certain pollution-sensitive taxa with partial (e.g., *Lepidostoma*), moderate (e.g., Corduliidae) or high drying tolerance (e.g., *Nemoura*) can be used as indicators for IRES depending on drying characteristics. This type of abundance-based metric can track anthropogenic impacts in naturally stressed rivers more effectively than those based on diversity measures (Gutiérrez-Cánovas et al., 2019). Fourth, given the limitations observed here and in other studies (Hamilton et al., 2020), trait information should be used cautiously to represent drying resistance and resilience capacities. Although recent studies have made promising advances (Soria et al., 2020; Stubbington et al., 2022), there is still a need to better exploit trait information by identifying which trait combinations enable drying resistance and resilience capacities.

In conclusion, our study showed that the combination of niche-based approaches and high-resolution hydrological information can be useful in characterizing potential biomonitoring metrics and indicators in IRES. These findings can assist water managers in the adaptation and development of biomonitoring tools for IRES. Future developments of biomonitoring tools can benefit from the combination of niche-based data, such as those presented here, with metacommunities elements (e.g., dispersal capacity, river network structure; Cid et al., 2020) to enable a better predictive capacity of IRES reference conditions.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

We gratefully acknowledge to the field assistance of Verónica Granados and to Ariadna Fabà and Priscila N. Heredia for their help in invertebrate sample processing.

Funding

This work was funded by MCIN/AEI/10.13039/501100011033 through the project RIVSTRESS (PID2020-115708RB-C21). RA-R held a post-doctoral grant “Margarita Salas” from the Spanish Ministry of Universities and the Next Generation EU – Recovery, Transformation and Resilience Plan. CG-C was supported by a “Juan de la Cierva – Incorporación” contract (MINECO, IJC2018-036642-I).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2022.109263>.

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