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RESEARCH ARTICLE

# Disentangling responses to natural stressor and human impact gradients in river ecosystems across Europe

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## Abstract

1. Rivers are dynamic ecosystems in which both human impacts and climate-driven drying events are increasingly common. These anthropogenic and natural stressors interact to influence the biodiversity and functioning of river ecosystems. Disentangling ecological responses to these interacting stressors is necessary to guide management actions that support ecosystems adapting to global change.
2. We analysed the independent and interactive effects of human impacts and natural drying on aquatic invertebrate communities—a key biotic group used to assess the health of European freshwaters. We calculated biological response metrics representing communities from 406 rivers in eight European countries: taxonomic richness, functional richness and redundancy, and biomonitoring indices that indicate ecological status. We analysed metrics based on the whole community and on a group of taxa with traits promoting resistance and/or resilience ('high RR') to drying. We also examined how responses vary across Europe in relation to climatic aridity.
3. Most community metrics decreased independently in response to impacts and drying. A richness-independent biomonitoring index (the average score per taxon; ASPT) showed particular potential for use in biomonitoring, and should be considered alongside new metrics representing high RR diversity, to promote accurate assessment of ecological status.
4. High RR taxonomic richness responded only to impacts, not drying. However, these predictors explained little variance in richness and other high RR metrics,

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potentially due to low taxonomic richness. Metric responsiveness could thus be enhanced by developing region-specific high RR groups comprising sufficient taxa with sufficiently variable impact sensitivities to indicate ecological status.

5. *Synthesis and applications*. Metrics are needed to assess the ecological status of dynamic river ecosystems—including those that sometimes dry—and thus to identify priority sites requiring action to tackle the causes of environmental degradation. Our results inform recommendations guiding the development of such metrics. We propose concurrent use of richness-independent 'average score per taxon' indices and metrics that characterize the richness of resistant and resilient taxa. We observed interactions between aridity, impacts and drying, highlighting that these new metrics should be region specific, river type specific and adaptable, promoting their ability to inform management actions that protect biodiversity in river ecosystems responding to climate change.

**KEYWORDS**
bioassessment, biomonitoring, flow intermittence, intermittent river, macroinvertebrate, multiple stressors, resistance and resilience, temporary stream

## 1 | INTRODUCTION

Biodiversity is declining at unprecedented rates as interactions between anthropogenic activities and climatic extremes increase at local to global scales (Pereira et al., 2010). Declines are particularly severe in freshwater ecosystems, in which multiple interacting anthropogenic pressures (e.g. land-use change, pollution and climate change) result in stressors that are altering communities characterized by high biodiversity (Reid et al., 2019). Rivers experience these human impacts alongside natural flow extremes: seasonal or unpredictable disturbances in which natural stressors such as the absence of water (during drying) and fast flows (during floods) disrupt ecosystem structure and function (White & Pickett, 1985). Rivers are thus suitable ecosystems in which to explore the concurrent, independent and interacting responses of ecological communities to human impacts and natural stressors (Gutiérrez-Cánovas et al., 2015). These responses may vary across climatic gradients, due to the contrasting environmental conditions in which communities have evolved (Birk et al., 2020; Bonada et al., 2007).

The communities inhabiting river ecosystems comprise taxa which vary in their responses to human impacts. Community responses can be summarized by taxonomic and functional metrics, including biomonitoring indices that use the impact sensitivities of taxa in a community to assess ecological status. Ideal biomonitoring indices respond only to human impacts (i.e. a single response), but the concurrent effects of impacts and natural stressors on these metrics can be equal to (additive), greater than (synergistic) or less than (antagonistic) the sum of their individual effects and stressors can act in opposing directions (Côté et al., 2016), hampering the capacity of indices to assess ecological status (Stubbington et al., 2018). In particular, anthropogenic and natural stressors (such as drying in river ecosystems) can eliminate a comparable range of sensitive taxa. As a result, metrics based on taxonomic richness—including biomonitoring index totals—can experience antagonistic decreases, whereby responses to impacts weaken as community exposure to natural stressors increases (Soria et al., 2020; Figure 1a), an interactive effect which may be exacerbated by environmental harshness (e.g. climatic aridity; Piggott et al., 2015; Figure 1). In contrast to index totals, 'average score per taxon' (ASPT) indices describe community sensitivity to impacts independent of taxonomic richness, and may thus experience less pronounced decreases in response to stressors (Wilding et al., 2018; Figure 1b). However, research is needed to inform the development of metrics that respond independently to impacts and natural stressors (Gutiérrez-Cánovas et al., 2015), and thus to enable effective biomonitoring in ecosystems responding to environmental change (Nõges et al., 2016).

Taxa with common responses to environmental variability can be defined using functional traits (Suding et al., 2008). Many traits promote resistance and/or resilience to drying in freshwater ecosystems; for example, desiccation tolerance enables survival after a river dries, and strong dispersal facilitates rapid recovery after water returns (Bogan et al., 2017). The composition of community subsets comprising drying-adapted taxa may thus reflect responses to human impacts but not river drying, enabling identification of impacted conditions, including in rivers that sometimes dry (i.e. temporary rivers). Assemblages of resistant and resilient taxa can be diverse in rivers experiencing frequent, predictable drying (Bonada et al., 2007), but no large-scale studies have documented spatial variability in their responses to co-occurring natural and anthropogenic stressors.

Metrics based on the functional traits of the taxa comprising an assemblage enable comparison of regions with contrasting species

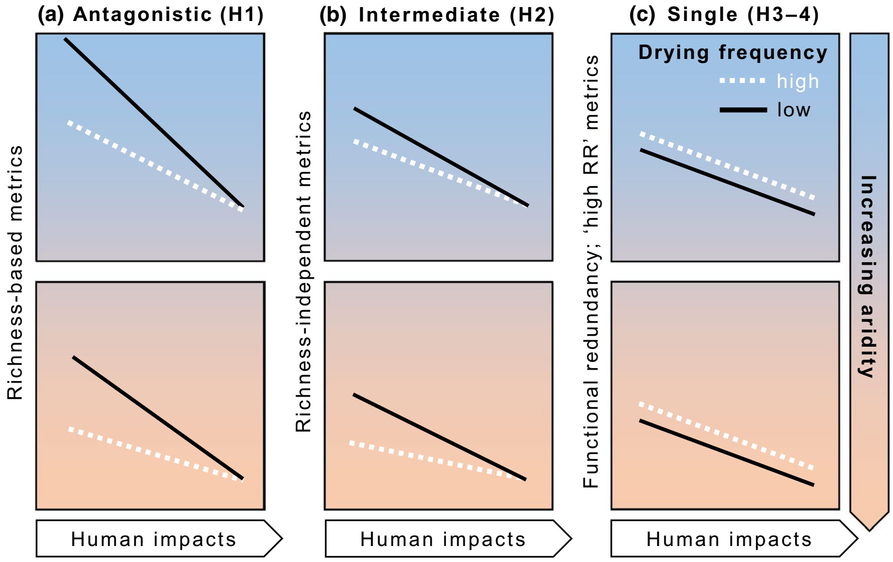

FIGURE 1 Hypothesized responses of invertebrate-based metrics to human impacts at river sites with high and low drying frequencies across a climatic gradient. Hypotheses (H) 1–4 are described in the text; (a) antagonistic, (b) intermediate and (c) single responses are sensu Côté et al. (2016)

pools (Suding et al., 2008). Different functional metrics, such as richness and redundancy, can have contrasting responses to co-occurring stressors. For example, functional richness (which quantifies the trait space filled by an assemblage) can decrease along both natural and anthropogenic stress gradients as stress-sensitive traits are lost (Gutiérrez-Cánovas et al., 2015). In contrast, functional redundancy (which indicates the number of taxa making similar contributions to ecosystem functioning) can be unresponsive to natural stressors such as river drying until high disturbance intensities are reached (Aspin et al., 2019), but declines with human impacts if drying-tolerant taxa vary in both their traits and their impact sensitivities (Soria et al., 2020). This single negative response of functional redundancy to impacts (Figure 1c) may facilitate its use in biomonitoring of temporary rivers (Bruno et al., 2016).

We characterized freshwater invertebrate community responses to human impact and natural drying gradients in European rivers. Established biomonitoring indices and the availability of trait information (Sarremejane et al., 2020; Tachet et al., 2010) make freshwater invertebrates an effective group with which to disentangle taxonomic and functional responses to multiple stressors (Statzner & Bêche, 2010). Our aim was to identify metrics that distinguish between responses to impacts and drying. Specifically, we identified metrics with single responses to impacts and those with independent or interactive responses to both impacts and drying.

We hypothesized antagonistic decreases in response to human impacts and drying for richness-based metrics (H1; Figure 1a); less pronounced decreases for richness-independent ASPT indices (H2; Figure 1b); and single negative responses to impacts for functional redundancy (H3) and metrics describing a 'high RR' group comprising taxa with traits promoting resistance and/or resilience to drying (H4; Figure 1c). We examined how responses vary across Europe in relation to variability in climatic aridity (Figure 1). As global change increases the spatial and temporal extent of river drying, our goal is to describe general principles that inform development of metrics to assess the ecological status of dynamic rivers.

## 2 | MATERIALS AND METHODS

### 2.1 | Datasets and their assignment to groups

We compiled 15 datasets describing invertebrate assemblages, flow permanence and human impacts in 406 rivers in eight European countries (Figure 2; see Appendix S4, Table S1). We analysed all datasets in one *all-region* dataset, which identified interactions between aridity, impacts and river drying, and we therefore also analysed three *regional* datasets (based on biogeographical classifications; EEA, 2002, 2009; Figure S1). We used nonmetric multidimensional scaling ordinations to visualize assemblage composition (Figure S2) and to define coherent regional groups, removing one dataset characterized by exceptional compositional variability. Three datasets (GB_NE, GB_SE and GB_SW) represent Great Britain within the Atlantic biogeographical region (hereafter, *Atlantic*). Five *West Mediterranean* datasets (ES_E, ES_NE1, ES_NE2, ES_S and PT) represent the Ibero-Macronesian ecoregion of the Mediterranean biogeographical region. Three *East Mediterranean* datasets (CY, GR_NW and GR_SE) are from western Balkan ecoregions within the Mediterranean biogeographical region and Cyprus, which had comparable communities (Figure S2c). Three datasets were not assigned to regional groups due to insufficient replication and/or impact gradient length (Figure S1; Table S1). We also analysed four *individual* datasets (CY, ES_NE1, ES_NE2 and ES_S), which represented all datasets with sufficient impact and drying gradients to warrant individual analysis (Feld et al., 2016; Figure S1).

All samples were collected during wet phases using standard quantitative or semi-quantitative methods designed to capture the taxa present in all habitat types (Table S1). We excluded samples collected during non-flowing wet phases because flow cessation alters community composition (Chadd et al., 2017; Appendix S1.1). We retained flowing-phase samples from all months to characterize responses to variability in environmental conditions across time, and explored seasonal differences in supporting analyses

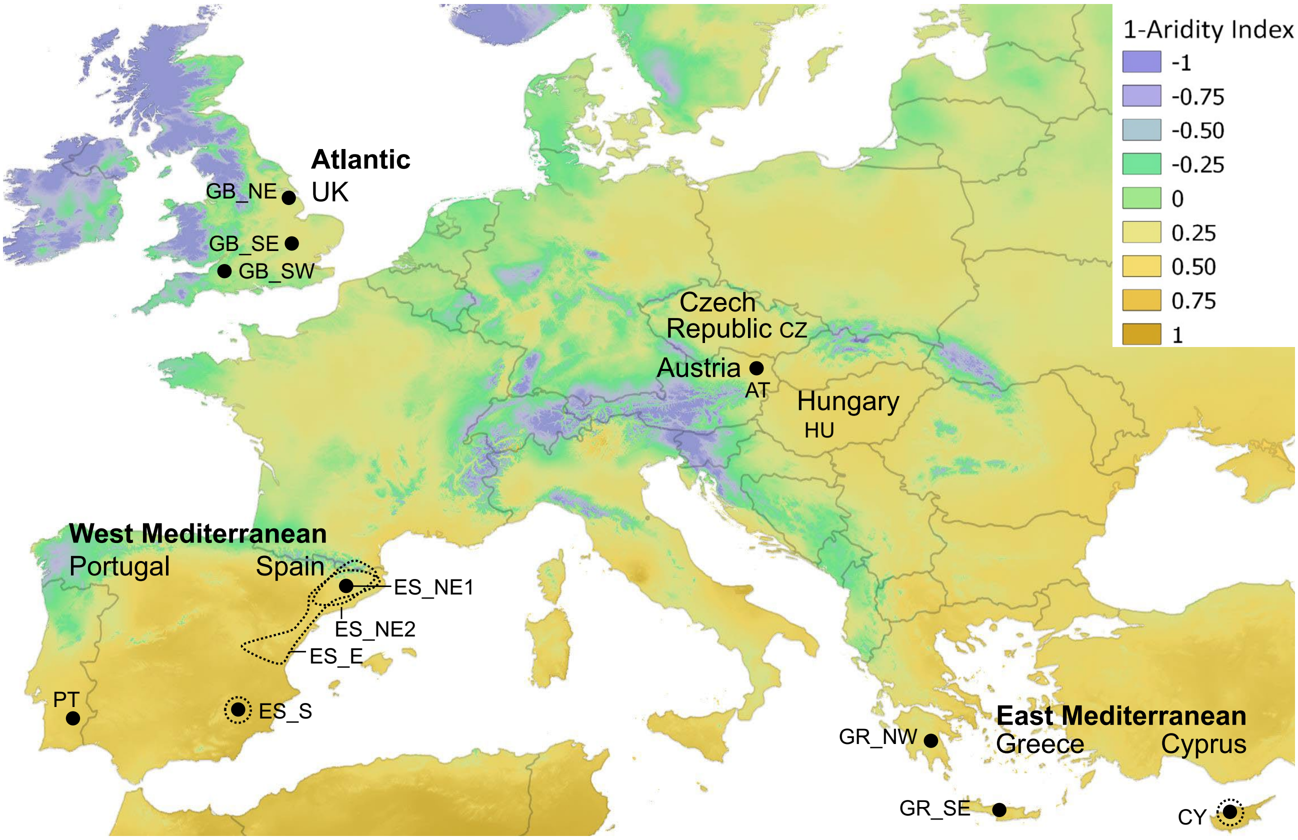

**FIGURE 2** Study areas characterized by the 14 datasets used in all-region analyses, three regional analyses (bold text) and four individual analyses (dotted lines); freeform lines enclose larger study areas; CZ and HU datasets are nationwide. Datasets are labelled using ISO two-letter country codes, with abbreviated cardinal points describing the location relative to other national datasets (Table S1). 1–Aridity index is the inverted ratio of precipitation to potential evapotranspiration; values increase with aridity

(Appendix S1.2). We retained samples from perennial sites to encompass a full drying frequency gradient (0–1), and validated this approach in supporting analyses (Appendix S1.3).

We harmonized biological datasets to family level, which all datasets achieved for most taxa. We excluded Oligochaeta, which were typically identified to this coarser resolution, and excluded meiofauna and semi-aquatic taxa, which were recorded inconsistently. Family-level data can effectively characterize taxonomic and functional responses to human impacts and drying (Datry et al., 2014; Gayraud et al., 2003), and we validated this approach by comparison with genus-level analyses (Appendix S1.4). We converted abundance data to presence–absence, to facilitate comparison of samples collected using different field methods (Gayraud et al., 2003; Table S1), and validated this approach in supporting analyses (Appendix S1.5).

## 2.2 | Characterization of human impact, river drying and climatic gradients

To provide a broad measure summarizing overall site-specific human impact levels (i.e. general degradation, sensu Poikane et al., 2020), we adapted criteria proposed by Sánchez-Montoya et al. (2009). We calculated the number of impacts per site from a maximum of 21 human influences relating to riparian vegetation, invasive species, pollution, land use, river morphology and hydrological alteration (Table S2), then converted numbers to proportions, where 0 indicates unimpacted sites. We described site-specific flow permanence using three candidate variables, with field observations confirming that no-flow conditions equated to a dry bed with or without disconnected pools (Table S3). We used four candidate variables to describe climate (Table S3), including an aridity index (AI, i.e. precipitation/potential evapotranspiration). AI was calculated using WorldClim data (http://www.worldclim.org) then inverted (1–AI) so that values increase with aridity.

## 2.3 | Functional trait assignment

To identify traits promoting resistance and/or resilience to drying, we considered biological response traits in Tachet et al. (2010), plus female wing size and type, which describe the dispersal potential of aerial adult insects which have aquatic juveniles (Sarremejane et al., 2020). Informed by literature and expert opinion, we selected 22 trait categories across nine traits as responsive to drying

(Tables S4–S5). We weighted each category from 1 to 4, with higher scores indicating greater resistance and/or resilience to drying (Table S4). For each genus, traits were coded using a fuzzy approach (Chevenet et al., 1994), in which affinities between 0 (no affinity) and 4 (strong affinity) were assigned to each trait category. Affinities were then converted to percentage affinities within each trait and averaged across all genera with each family. We calculated family-specific resistance/resilience (RR) scores as the sum of each trait affinity multiplied by the corresponding trait category weight (Table S4). Family scores were then ranked to identify the high RR group for each dataset, comprising its top 33% of families (Table S6).

### 2.4 | Calculation of biological response metrics

We used five metrics to characterize the responses of the whole community and the high RR group. For both groups, we calculated three family-level taxonomic metrics: richness (*FamRich*) and two biomonitoring indices of ecological status. In all-region models, we used the Whalley, Hawkes, Paisley and Trigg (WHPT) and WHPT-ASPT indices (Paisley et al., 2014). WHPT updates the widely used BMWP index (Armitage et al., 1983), which was developed for UK rivers and has been demonstrated as responsive to environmental degradation across and beyond Europe (e.g. Mustow, 2002). We validated its capacity to represent all-region responses in supporting analyses (Appendix S1.6). We used region-specific indices in regional and individual models, that is, WHPT in the Atlantic region, the Iberian BMWP (IBMWP; Alba-Tercedor et al., 2002) in the West Mediterranean region and STAR-ICMi (Buffagni et al., 2006) in the East Mediterranean region.

We calculated two functional metrics, redundancy (*FuncRed*) and richness (*FuncRich*), as described in Appendix S2. In brief, FuncRed was calculated as the difference between taxonomic diversity and functional diversity and represents the extent to which an assemblage is 'saturated' by taxa with comparable traits (de Bello et al., 2007). FuncRich was calculated as the multidimensional trait space representing each assemblage (Villéger et al., 2008). We also calculated functional metrics and taxonomic richness at genus level for selected datasets (Atlantic, ES_E, ES_S), and calculated FuncRed and FuncRich at a mixed subfamily level for the all-region dataset (Appendix S1.4).

### 2.5 | Modelling

We analysed the whole community and the high RR group for each of the eight (one all-region, three regional, four individual) datasets, that is, 16 models (Figure S1). Following Zuur et al. (2010), we used variance inflation factors (VIF) to identify collinearity among candidate predictor variables representing river drying and, in all-region models, climate (Table S3). We retained three predictor variables with VIF <2: aridity (as 1–AI), drying frequency and the proportion of human impacts (Table S3), with their non-collinearity evidencing the limited influence of hydrological alteration on the human impact gradient. We calculated skewness values to assess the distribution of each response variable, then used square-root or log transformations to reduce values >0.5.

We ran linear mixed-effects models to characterize metric responses to the three predictor variables and their pairwise interactions. To account for the non-independence of samples from the same site and dataset, we included *site* nested within *dataset* as random factors in all-region and regional models and *site* as a random factor in individual models. We used a multi-model inference approach to quantify the size and significance of metric responses (Anderson & Burnham, 2002). We assessed model performance using Akaike information criteria (AIC), considered models with a ΔAIC <2 as equally good, and averaged these models (Anderson & Burnham, 2002). We partitioned the variance explained by predictors and their interactions in the top all-region models. We used marginal and conditional goodness-of-fit statistics ($R^2_m$ and $R^2_c$, respectively) to evaluate model performance (Mac Nally et al., 2018). Independent (single, additive) and interactive (antagonistic, opposing, synergistic) response types were classified using the sign and significance of responses to predictors and their interactions (Feld et al., 2016). We used significance levels of $p < 0.01$ and $<0.001$ for response variables violating one or both of the assumptions of normality and homoscedasticity, respectively.

Analyses were conducted in R (R Core Team, 2019) using the packages *biomonitoR* (Laini et al., 2020), *lme4* (Bates et al., 2015), *MuMIn* (Bartoń, 2019), *usdm* (Naimi et al., 2014) and *variancePartition* (Hoffman & Schadt, 2016). Our study did not require ethical approval.

## 3 | RESULTS

The environmental and biological characteristics of each dataset are described in Appendix S3 and Table S7.

### 3.1 | Community responses to human impacts and river drying

In the all-region model, all community metrics decreased independently in response to both human impacts and drying (i.e. additive responses; Figure 3; Table 1h). The proportion of variance explained by impacts was highest for the two biomonitoring indices (4.0%–4.6%) and particularly low for functional redundancy (<1%; Table 1a; Table S15). Plotted slopes indicated the greater independence of WHPT-ASPT compared to the WHPT index total (Figure 3b,c), and effect sizes (Table 1b,c) and explained variance (Table S15c,d) were higher for impacts compared to drying for WHPT-ASPT but not the WHPT total. Responses were largely comparable at family and mixed subfamily taxonomic levels (Appendix S1.4).

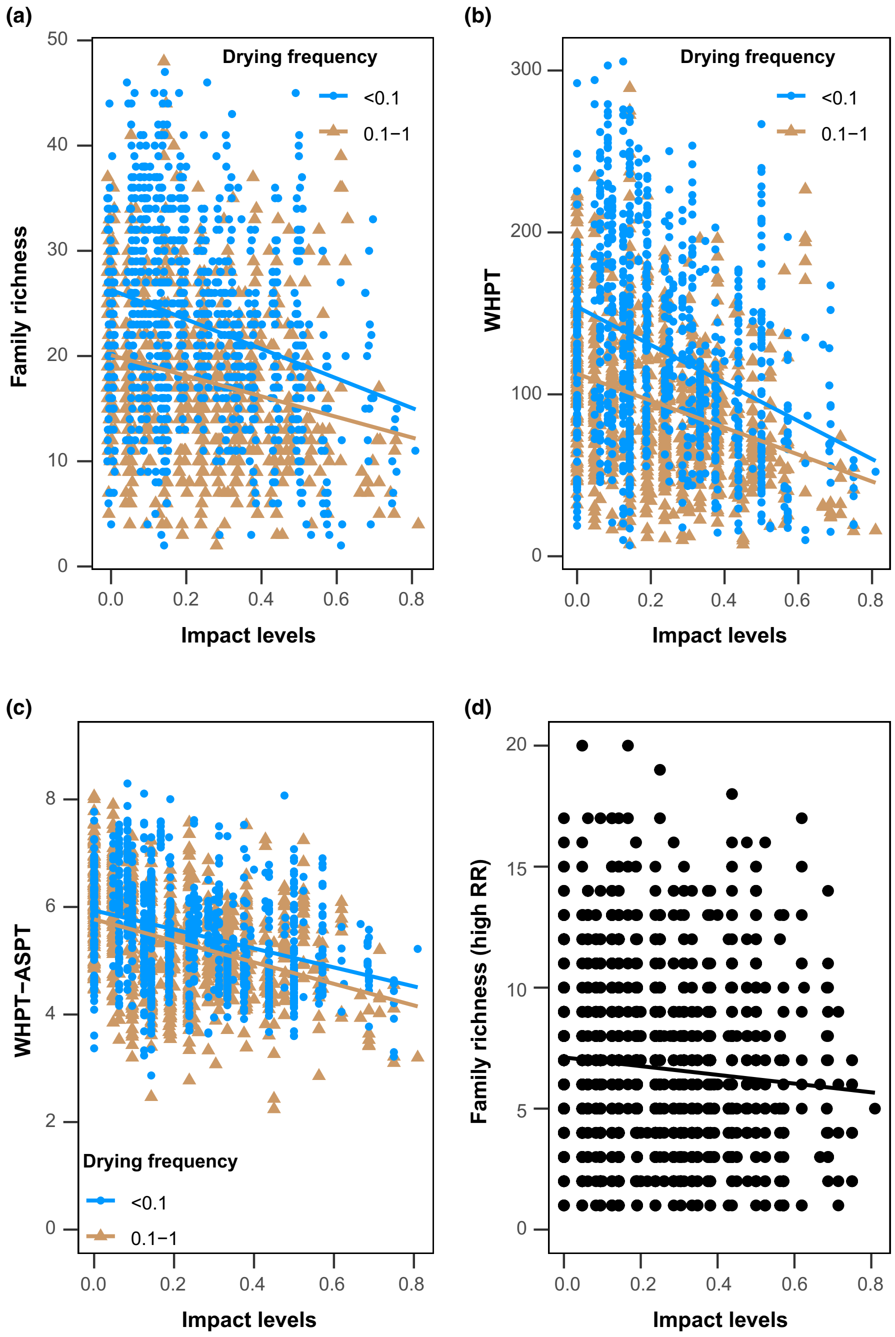

**FIGURE 3** Metric responses to human impact levels: community (a) family-level taxonomic richness (FamRich); (b) WHPT; and (c) WHPT-ASPT at high and low drying frequencies; (d) high RR FamRich

Of the regional models, the two Mediterranean models included most independent (i.e. single or additive) responses (Tables S9e–S10e): all community metrics decreased with impacts, and most variance was explained for biomonitoring indices (Tables S9a–S10a). In the Atlantic region, FamRich and the WHPT total experienced antagonistic declines in response to impacts and drying (Table S8), and responses were largely comparable at family and genus levels (Table S16a). Of the individual models (Tables S11–S14), a particularly high proportion of variance (34%–52%) was explained for taxonomic metrics in the ES_S model, in which FamRich declined only in response to impacts (i.e. a single response), and IASPT and IBMWP both decreased independently with impacts and drying (i.e. additive responses; Table S11). Genus- and family-level responses were comparable in both the ES_E and ES_S models (Table S16a). Response types for all models are summarized in Table S17.

## 3.2 | High RR responses to human impacts and river drying

In the all-region high RR model, FamRich decreased only in response to human impacts (i.e. a single response; Figure 3d; Table S18h), and both biomonitoring indices declined independently in response to

**TABLE 1** Linear mixed-effects model results: (a) goodness-of-fit (marginal $R^2$, $R^2_m$; conditional $R^2$, $R^2_c$); (b–g) significance ($p$) and effect size (ES) of (b) human impacts, (c) river drying, (d) aridity and (e–g) their interactions for response metrics summarizing the all-region community dataset ($n = 1{,}763$); and (h–j) the independent (additive) and interactive (antagonistic, synergistic) response types

| | | | | Individual effects | | | | | | Interactions | | | | | | Response types | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Intercept ($p < 0.001$) | (a) Goodness-of-fit | | (b) Impacts | | (c) Drying | | (d) Aridity | | (e) Impacts × drying | | (f) Aridity × impacts | | (g) Aridity × drying | | | | |
| Response metric | ES | $R^2_m$ | $R^2_c$ | $p$ | ES | $p$ | ES | $p$ | ES | $p$ | ES | $p$ | ES | $p$ | ES | (h) Impacts and drying | (i) Aridity and impacts | (j) Aridity and drying |
| Family richness | 19.8 | 0.236 | 0.795 | <0.001 | −2.02 | <0.001 | −2.63 | <0.001 | −3.30 | 0.385 | 0.214 | 0.051 | −0.712 | <0.001 | 1.25 | Additive | Additive | Antagonistic |
| Functional redundancy | 0.296 | 0.190 | 0.566 | <0.001 | −0.005 | 0.008 | −0.004 | <0.001 | −0.019 | 0.628 | −0.001 | 0.388 | −0.002 | <0.001 | 0.006 | Additive | Additive | Antagonistic |
| Functional richness | 0.247 | 0.103 | 0.677 | <0.001 | −0.024 | <0.001 | −0.018 | 0.006 | −0.031 | 0.069 | 0.007 | 0.026 | −0.013 | 0.095 | 0.007 | Additive | Synergistic | Additive |
| WHPT | 10.1 | 0.339 | 0.869 | <0.001 | −0.778 | <0.001 | −0.866 | <0.001 | −1.66 | 0.596 | 0.041 | 0.040 | −0.234 | <0.001 | 0.417 | Additive | Synergistic | Antagonistic |
| WHPT-ASPT | 5.59 | 0.370 | 0.913 | <0.001 | −0.283 | <0.001 | −0.240 | <0.001 | −0.765 | 0.175 | −0.034 | 0.666 | −0.017 | 0.126 | 0.042 | Additive | Additive | Additive |

impacts and drying (i.e. additive responses; Table S18h). The proportion of variance explained by impacts was very low, exceeding 1.0% only for WHPT and WHPT-ASPT (Table S15). In all regional and individual models, most variance in impact-responsive high RR metrics was explained for biomonitoring indices (Tables S8a–S14a). Genus-level analysis of the ES_S high RR assemblage increased the response strength ($R^2_m$) of all metrics, and produced a single impact-driven decline in FuncRed (Table S16).

## 3.3 | Effects of aridity on all-region responses to impacts and drying

In the all-region community model, all metrics declined with aridity (Table 1d), which explained between 4.9% (FuncRich) and 30% (WHPT-ASPT) of variance in metric responses (Table S15). Impact- and aridity-driven decreases in FamRich and WHPT-ASPT were independent (i.e. additive responses; Figure 4a), whereas an impact-related decrease in the WHPT total increased with aridity (i.e. a synergistic response, Table 1i), but this interaction explained negligible variance (Table S15a). In contrast, aridity reduced the strength of some drying-driven decreases (i.e. antagonistic responses; Table 1j), reflecting metric stability at arid sites (Figure 4b). In the all-region high RR model, interactions between impacts and aridity explained negligible variance (Table S15), whereas interactions between aridity and drying frequencies were antagonistic for FamRich and WHPT (Table S18i,j). WHPT-ASPT was the only metric for which decreases in response to aridity, impacts and drying did not interact, in either the community or the high RR model (Tables 1h–j and S18h–j).

# 4 | DISCUSSION

Taxon absences caused by natural disturbances can compromise interpretation of biomonitoring data collected to inform management actions that protect biodiversity. This challenge is particularly pronounced in dynamic ecosystems including temporary rivers, which fluctuate between wet and dry states. Despite this dynamism, we identified metrics representing invertebrate communities that had independent, negative responses to drying and human impacts, and these responses were strongest for biomonitoring indices. However, limited variance was explained in our Europe-wide analyses, likely reflecting context-dependent metric responses to environmental variability among rivers. In addition, the taxonomic richness of families with traits promoting resistance and/or resilience to drying (our 'high RR' group) responded only to impacts—not drying—but this response was weak, due to low taxonomic richness. As rivers experience increasing climate-driven drying (Tramblay et al., 2021), our results highlight the need to develop region-specific indices for use in ecological status assessments. By identifying priority sites for further investigation, such assessments can inform management actions that support biodiversity within dynamic river ecosystems.

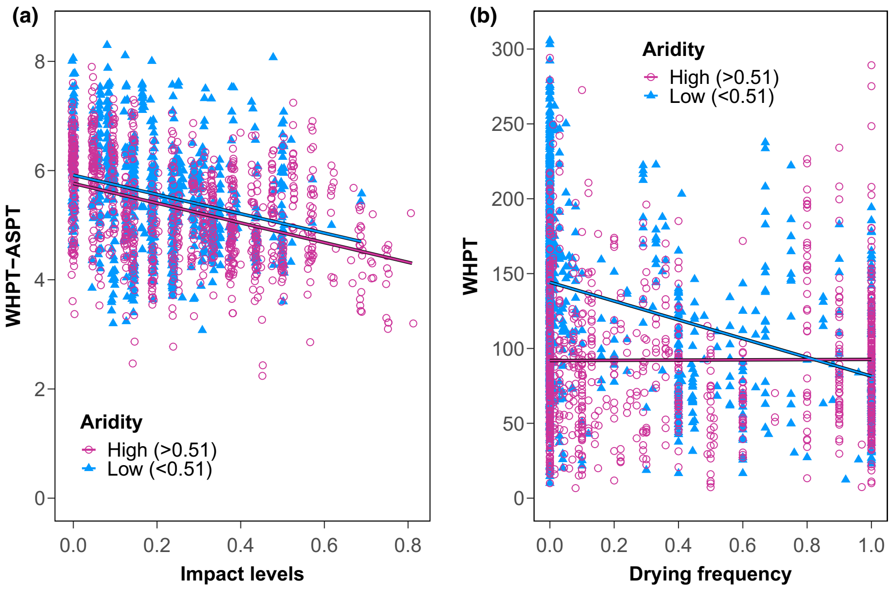

FIGURE 4 Community metric responses in relation to aridity: (a) WHPT-ASPT response to human impacts and (b) WHPT response to drying frequency

## 4.1 | Community metrics decreased in response to human impacts and river drying

Our first hypothesis was that richness-based metrics including biomonitoring index totals would experience antagonistic declines in response to increasing human impacts and drying frequencies, because drying-driven reductions in impact-sensitive taxa can limit community responses to impacts (Datry et al., 2014; Gutiérrez-Cánovas et al., 2015). In contrast to this hypothesis, all community-based metrics experienced independent, additive declines with impacts and drying in the all-region model. As such, we found limited support for our second hypothesis, that decreases would be less pronounced for richness-independent ASPT indices, although in the all-region model, impacts explained more variance than drying in WHPT-ASPT but not the index total. ASPT indices assess assemblages based on the impact sensitivities of their constituent families independently of taxonomic richness, thus facilitating impact discrimination in both temporary rivers (Wilding et al., 2018) and perennial rivers that experience seasonal flow variability (Álvarez-Cabria et al., 2010).

Metrics with additive responses can be used in ecological status assessments if values are adapted to recognize the communities expected at unimpacted sites exposed to a natural stressor, in our case, drying (Soria et al., 2020). Identifying taxa which are associated with perennial flow—and which are therefore absent from temporary rivers regardless of their impact levels (Chadd et al., 2017)—could guide expectations of community composition and thus interpretation of metrics such as ASPT indices. However, ASPT indices can overestimate ecological status if fewer taxa than expected contribute to index values (Clarke et al., 2003). An ASPT should thus be considered alongside a measure of taxonomic richness—or potentially alongside a functional metric such as redundancy, which, despite our third hypothesis, responded to both impacts and drying in this study. As such, we recommend the development of richness metrics based on taxa representative of specific river types, a process which could be enabled by our high RR group—and also by genus- or species-level characterization, to recognize within-family variability in responses to both impacts and drying (see Section 4.2; Bonada et al., 2004; Chadd et al., 2017).

The limited variance in biological response metrics explained by human impacts and drying in the all-region models likely reflects variability introduced by the spatiotemporal breadth of our pan-European analysis. Accordingly, our goodness-of-fit statistics (and specifically, conditional $R^2$) indicate that site-specific habitat conditions explained considerable variance in metric responses. Furthermore, we analysed uncalibrated biomonitoring indices, which failed to represent variability among the communities expected in different river types (Clarke et al., 2003). Index calibration was not possible because only one (Mediterranean) temporary river type is officially classified in European biomonitoring (van de Bund, 2009). This situation overlooks the considerable environmental and biological variability among temporary river types and hampers characterization of distinctive, type-specific communities indicative of unimpacted reference conditions and of deviations from such conditions (Cid et al., 2020; Stubbington et al., 2018). Characterization of distinctive regional river types and their associated communities is a priority to underpin improvements in temporary river biomonitoring and management (Clarke et al., 2003; Stubbington et al., 2018). In addition, our capacity to detect biological responses to impacts was hampered by a short impact gradient in the Atlantic region (Feld et al., 2016), highlighting the need to collect data representing the full range of impact levels experienced across the breadth of European temporary rivers.

## 4.2 | Resistant and resilient taxa responded mainly, but weakly, to impacts

Our fourth hypothesis, that metrics characterizing assemblages of taxa with traits promoting resistance and/or resilience to drying would respond only to human impacts, was partly supported. First, in all models in which high RR taxonomic richness responded significantly to impacts, it decreased only in response to increasing impacts—not drying. However, such responses reflected only West Mediterranean assemblages, in which taxonomic richness was relatively high, reflecting the greater range of adapted taxa that occur in temporary rivers in which disconnected pools persist during seasonal dry phases (Bonada et al., 2007). In addition, impacts consistently explained little variance in metrics representing the high RR group, likely because—for metrics including WHPT-ASPT—values varied little among some taxon-poor assemblages. Ensuring representation of sufficient taxa with sufficiently variable impact sensitivities (Hering et al., 2006) within high RR groups defined for specific regional river types (van de Bund, 2009) could thus strengthen metric responsiveness, using the approaches outlined below.

First, to improve representation of impact-sensitive high RR taxa within region-specific groups, temporary river specialists could be better represented. For example, the traits conferring resistance to drying on specialist insect species associated with small, lowland, temporary rivers (Armitage & Bass, 2013) in our Atlantic dataset were obscured by the traits of dominant generalists in our family-level assignment. As also indicated by our genus-level ES_S analyses, such examples highlight that finer-resolution taxonomic identification can enhance characterization of biological responses to natural stressors (Chadd et al., 2017; England et al., 2019), and thus the selection of taxa to include in high RR metrics. In addition, although beyond our scope, novel metrics based on the abundance of specialist taxa may be more responsive to impact levels than presence–absence-based metrics (Gutiérrez-Cánovas et al., 2019).

Second, representation of high RR families—and genera and species—within certain high-potential taxonomic groups could be expanded. For example, human impact detection by indices developed for small temporary Mediterranean rivers is enhanced by inclusion of true fly and beetle families alongside selected mayflies, stoneflies and caddisflies (Munné & Prat, 2009). True flies, which dominated our high RR group, have diverse environmental preferences (Paisley et al., 2014) and can increase in relative abundance with drying duration in temporary rivers (Datry et al., 2014), due to their prevalent resistance traits (Tachet et al., 2010). We also identified beetles and true bugs as common high RR families, reflecting resilience traits including strong aerial dispersal (Sarremejane et al., 2020). In particular, the single, strong responses to human impacts identified for the beetle and bug-rich ES_S dataset from semi-arid Spain evidences the potential use of these taxa in temporary river biomonitoring (Bilton et al., 2006). However, metric performance is constrained by representation of sufficient taxa with sufficiently variable sensitivities to impacts, restricting the potential of these groups to regions with adequate taxonomic richness (Gutiérrez-Cánovas et al., 2019).

Third, the performance of high RR metrics could be improved by recognizing that traits conferring resistance and/or resilience to drying vary among river types. For example, the ‘interstitial’ ‘substrate relation’ trait (which reflects use of wet subsurface sediments; Tachet et al., 2010) only promotes persistence at sites with permeable sediments; the resilience conferred by dispersal traits depends on site-specific connectivity to colonist sources (Cid et al., 2020); and traits may encompass irrelevant subtypes such as resistance forms that confer cold tolerance (Ditrich & Papáček, 2009).

Finally, representation of high RR taxa could be maximized by using field methods designed to promote consistent, comprehensive sampling of temporary river taxa, including those inhabiting marginal habitats (England et al., 2019). Collectively, these recommendations could enable characterization of taxonomic assemblages specific to distinctive river types, informing the development of richness metrics that enhance ecological status assessments in temporary rivers.

## 5 | CONCLUSIONS

We outline principles upon which to develop biomonitoring schemes that recognize variability among river types—and in particular, among highly diverse temporary rivers (Stubbington et al., 2018). Our community-level results suggest that biomonitoring indices can identify responses to human impacts despite concurrent responses to drying, but require adaptation to reflect the values representative of rivers with contrasting flow permanence (Soria et al., 2020). Richness-independent ASPT indices show promise as indicators of impact levels, but considered alone, could overestimate ecological status. An ASPT should thus be considered alongside a metric representing the richness of the assemblages of resistant and/or resilient taxa characteristic of specific regional river types. Our high RR group provides a basis for adaptation and development of such responsive, region-specific richness metrics. Finally, our all-region models identified interactions with aridity and drying that influenced metric responses to impacts (Piggott et al., 2015), suggesting that climate-driven shifts in river flow regimes may concurrently alter ecosystems and our capacity to manage them effectively. Flexible approaches are therefore needed to monitor, manage and protect river ecosystems as they respond to global change.

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### CONFLICT OF INTEREST

The authors have no conflicts of interest to report. Thibault Datry is an Associate Editor of the *Journal of Applied Ecology*, but took no part in the peer review and decision-making processes for this paper.

## AUTHORS' CONTRIBUTIONS

R.St., R.Sa., N.C., T.D. and A.L. conceived the ideas and designed the methodology; all authors except A.L., C.G.-C. and R.Sa. acquired the data; R.St., R.Sa., A.L., I.T., M.P. and Z.C. analysed the data; R.St. led the manuscript writing; A.L., A.M., C.G.-C., D.B., D.S.-F., N.B., N.C., J.W., P.P., R.Sa., T.A., T.D. and Z.C. contributed to drafts; and all authors gave final approval for publication.

## DATA AVAILABILITY STATEMENT

Data are available via the Dryad Digital Repository https://doi.org/10.5061/dryad.08kprr53j (Stubbington et al., 2021).

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