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Extreme drought effects and recovery patterns in the benthic communities of temperate streams

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ABSTRACT

Extreme drought effects and recovery patterns in the benthic communities of temperate streams

Portugal faced an uncharacteristic hydrological drought in the fall/winter of 2011-2012. Small, typically perennial streams were affected by this extreme event and many dried out. Five of these streams were examined during six sampling events between spring 2011 (pre-drought) and spring 2012 (post-drought) to analyse the effects of this disturbance on the macroinvertebrate and diatom communities. Two weeks after dewatering, macroinvertebrate metrics exhibited accentuated decreases in the total abundance, EPT taxa and the scores of the Portuguese Index of Invertebrates but exhibited increases in equitability. The post-drought diatom assemblages showed no significant difference in abundance or evenness in relation to pre-drought conditions, but the diatom quality index ("Indice de Polluosensibilité Spécifique-IPS") decreased. Four weeks after the drought, the invertebrate communities progressively recovered, whereas the diatom metrics were already at pre-drought values, except for the IPS, which improved slowly over time. The benthic communities recovered faster in streams with higher Habitat Quality Assessment scores. The EPT taxa, *Echinogammarus* spp., *Hydroporus* spp. and *Ancylus fluviatilis*, did not recover to pre-drought values, whereas Lumbricidae and Orthocladiinae increased. For diatoms between the pre- and post-drought years, there was a shift from more sensitive to more tolerant taxa (e.g. the disappearance of *Cocconeis euglypta* and the appearance of *Nitzschia palea*). This study showed that an extreme off-season drought had immediate effects on both of the analysed benthic communities, but the diatoms recovered faster. Over one year, none of the studied benthic communities returned to the same pre-drought conditions, but the differences were stronger for invertebrates. In both cases, the *a priori* habitat condition of streams appeared to control the reaction and recovery patterns of the benthic communities to drought in the studied temperate streams.

Key words: Diatoms, invertebrates, climate change, dewatering, precipitation.

RESUMEN

Efecto de la sequía extrema y patrones de recuperación de las comunidades bentónicas de ríos templados

Portugal sufrió una sequía hidrológica atípica en el otoño/invierno de 2011-2012. Pequeños arroyos, generalmente permanentes, se vieron afectados por este evento extremo y muchos se secaron. Cinco de esos ríos fueron muestreados en seis ocasiones, entre la primavera de 2011 (antes de la sequía) y la primavera de 2012 (después de la sequía) con el fin de analizar los efectos de esta perturbación en las comunidades de macroinvertebrados y diatomeas. Dos semanas después de la sequía, las métricas de los macroinvertebrados mostraron disminuciones acentuadas en la abundancia total, en los taxones EPT y en las puntuaciones del Índice Portugués de Invertebrados, pero un aumento en la equidad. La comunidad de diatomeas post-sequía no presentó diferencias significativas en la abundancia y la equidad en relación a las condiciones pre-sequía, pero el índice de calidad de diatomeas ("Indice de Polluosensibilité Spécifique-IPS") disminuyó. Cuatro semanas después de la sequía la comunidad de invertebrados comenzó a recuperarse progresivamente, mientras que las métricas de las diatomeas ya estaban en los valores de pre-sequía, a excepción de los valores de IPS que mejoraron lentamente con el tiempo. Las comunidades bentónicas se recuperaran más rápido en arroyos con valores de Evaluación de la Calidad del Hábitat *("HQA") más altos. Los taxones EPT,* Echinogammarus *spp.,* Hydroporus *spp. y* Ancylus fluviatilis *no alcanzaron los* *valores anteriores a la sequía, mientras que Lumbricidae y Orthocladiinae aumentaron. En el caso de las diatomeas, entre los años pre-y post-sequía, hubo un cambio de especies más sensibles a especies más tolerantes (por ejemplo desaparición de* Cocconeis euglypta *y aparición de* Nitzschia palea*). Este estudio demostró que la sequía extrema, fuera de temporada, tuvo efectos inmediatos en ambas las comunidades bentónicas analizadas, pero las diatomeas se recuperaron más rápido. Un año después, ninguna de las comunidades bentónicas estudiadas volvió a presentar la composición que tenía antes de la sequía, pero las diferencias fueron mayores en los invertebrados. En ambos casos, la condición* a priori *del hábitat de los arroyos parece controlar la reacción y los patrones de recuperación de las comunidades bentónicas a la sequía en los arroyos templados estudiados.*

Palabras clave: *Diatomeas, invertebrados, cambio climático, deshidratación, precipitación.*

INTRODUCTION

The increasing atmospheric concentrations of greenhouse gases and aerosols due to anthropogenic activities have been causing climate changes (Forster *et al*., 2007), which have global implications for all ecosystems. Sea levels are expected to continue rising as the snow and ice extents decrease (IPCC, 2012). In addition, precipitation amounts and patterns are changing, and there are major alterations in the timing of wet and dry seasons (Arnell, 1999a, b). Climate change consequences, such as higher temperatures, more frequent floods and drought, clearly need further attention from both scientists and managers (Bond *et al*., 2008).

Freshwater ecosystems are particularly vulnerable to climate change (Schindler, 1997; Heino *et al*., 2009; Whitehead *et al*., 2009). Shifts in river flow regimes and groundwater recharge are determined by changes in temperature, evaporation, and particularly precipitation (Chiew, 2006; IPCC, 2012). Modifications in river runoff will decrease the recharging of groundwater supplies (Mandal & Zhang, 2012; Thampi & Raneesh, 2012) and will be enhanced by increased evaporation rates. Moreover, this climatic alteration leads to an increase in extreme climate events such as floods and droughts, which can be exacerbated by anthropogenic factors such as streambed alterations and deforestation (e.g. Hauer *et al*., 1997). According to Christensen *et al*. (2007), diverse future climatic scenarios for Europe predict an increase in annual mean temperatures (more than the global mean) and greater heterogeneity in precipitation patterns; for example, increases in the annual precipitation are forecasted for northern Europe, whereas decreases are forecasted for southern Europe and the Mediterranean. In addition, seasonal precipitation is expected to increase in winter and spring and decrease in summer and autumn (Johns *et al*., 2003; Giorgi *et al*., 2004).

The northern and central Portuguese coastline and adjacent regions have a temperate Atlantic climate with typically wet winters. Despite these climatic characteristics, the country experienced a severe and uncharacteristic drought in the autumn/winter period of 2011/2012. Throughout the territory, the total monthly precipitation observed in this period was extremely low when compared with the same seasons from previous years. More particularly, in central Portugal, the mean precipitation between October 2011 and March 2012 was 58.5 mm, compared to 126.6 mm for the same period between 1980 and 2013 according to the Portuguese National Information System of Hydric Resources (SNIRH at http://snirh.pt). In fact, February 2012 was the driest month since 1931, and the monthly precipitation was only 3.3 mm, which largely contrasts with the 128.6 mm registered for the monthly average in February of previous years (period of 1980 to 2013; SNIRH; http://snirh.pt). This absence of precipitation led to a severe dewatering drought event in some streams of the Portuguese Atlantic humid climate. The intermittence of flow is a characteristic of Mediterranean streams where communities have adaptations for desiccation (Steinman & McIntire, 1990; Lake,

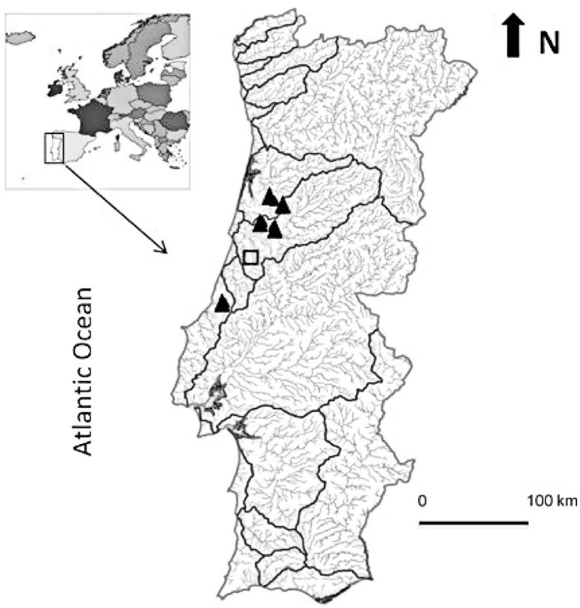

Figure 1. Locations of the study stream sites in Portugal (▲) and the precipitation gauge station (□) used in this study. *Localización de las estaciones de los ríos estudiados en Portugal (▲) y de la estación meteorológica (□) usada en este estudio.*

2003; Bonada *et al.*, 2006) but constitutes an anomaly in Atlantic temperate areas, where streams are typically perennial.

In previous studies, extreme droughts have caused sharp decreases in the total biomass of aquatic insects (e.g. Walters & Post, 2011) and alterations in assemblages (e.g. Thomson *et al.*, 2012), as well as triggered species loss and the collapse of food webs, with important decreases in secondary production (Ledger *et al.*, 2011). Indeed, rapid or unpredicted drying does not provide the necessary amount of time for the development of desiccation-resistant structures or physiological adjustments (Stanley *et al.*, 2004). In this case, the ability of biota to recover from drought relies on the environmental features (e.g. substratum type; Wright *et al.*, 2003), availability of refugia (e.g. Magoulick & Kobza, 2003), intensity and/or duration of the hydrological event (e.g. Lake, 2003), and the taxonomic assemblage considered (e.g. Acuña *et al.*, 2005; Ledger *et al.*, 2008; Boix *et al.*, 2010). Primary producers with short life cycles, such as diatoms, usually recolonise faster after a disturbance when compared with secondary producers (e.g. invertebrates) with longer life cycles (Gasith & Resh, 1999).

Other studies have addressed the impact of extreme climatic events such as droughts in shaping communities of freshwater systems under an intermittent hydrological regime (e.g. Bond *et al.*, 2008; Feio *et al.*, 2010; Marchetti *et al.*, 2011; Thomson *et al.*, 2012). However, little is known about the effects of extreme and uncharacteristic off-season dewatering events (but see Caramujo *et al.*, 2008) in the benthic communities of temperate streams.

This study aims to analyse the effect of an unusually (seasonally and geographically) extreme dewatering drought event in Atlantic temperate streams by comparatively assessing the recovery responses of two distinct benthic communities (macroinvertebrates and diatoms) from the progression of dewatering to rewetting.

METHODS

Study sites

Five permanent streams were selected for this study, which are located near the coast of central Portugal (<40 km from the Atlantic Ocean). This area has an Atlantic-humid temperate climate, with a mean annual precipitation within the period of 1971-2000 ranging from 800 to 1200 mm (Belo-Pereira *et al.*, 2011; IPMA, Portuguese Institute of the Sea and Atmosphere at http://www.ipma.pt). These streams have mild temperatures and moderate summers and winters, and all five streams have similar environmental characteristics (size, altitude, geology). These streams, named Ribeira de Boialvo (Boialvo), Rio da Serra (Serra), Ribeira de Eiras (Eiras), Ribeira de Ança (Ança), and Nascente do Rio Alcoa (Alcoa), are located in the Mondego, Vouga and Ribeiras do Oeste catchments in the centre of Portugal (Fig. 1). This study region is dominated by flatlands with sedimentary rocks (limestone and sandstone). The altitude of the study sites is relatively low, ranging from 36 (Ança) to 111 metres (Serra). The distance to source varied between 4.2 and 12.0 km. All sites are influenced by mild organic pollution, mainly derived from agriculture activities and housing.

In mid-fall 2011 (late October), all stream sites were found completely dry (without any visible water or remaining pools) because of an unusual climatological drought that occurred throughout 2011. The mean average precipitation registered until October was lower than the historical mean monthly precipitation for the period of 1980-2013, except for two months, May and August (Fig. 2). In November 2011, a peak of precipitation occurred that allowed a break in the dewatering period of the streams; however, the flow level was still low. Afterwards, the recorded precipitation was still considered low in the following months in comparison to previous years (until March 2012; Fig. 2), and the flow level was also low. The total monthly precipitation between October 2011 and March 2012 was 50 % lower than the precipitation recorded in previous years for the same period (Fig. 2). It was not until April/May 2012 that the streams appeared to recover to a typical average discharge for that season (based on the observed mean precipitation, which was closer to the historical reference values for the same period).

Sample collection and processing

The streams were first sampled in spring 2011 (Sample 1-s1; May). This sample was considered as the pre-drought condition, as the selected streams were not yet completely dewatered. The post-drought condition was assessed by four biweekly sampling events after rewetting during winter (between November 2011 and January 2012; Sample 2-s2, Sample 3-s3, Sample 4-s4, Sample 5-s5) and then again in spring 2012 (Sample 6-s6; May; Fig. 2). Sampling was only conducted when the streams had visible water in their streambeds. For each sampling event, measurements of pH, conductivity (μS/cm), total dissolved oxygen (DO; mg/L) and current velocity (m/s) were performed using in situ using field metres (Multiparameter Probe 3430 WTW®; Current Meter 108MKIII VALEPORT). The

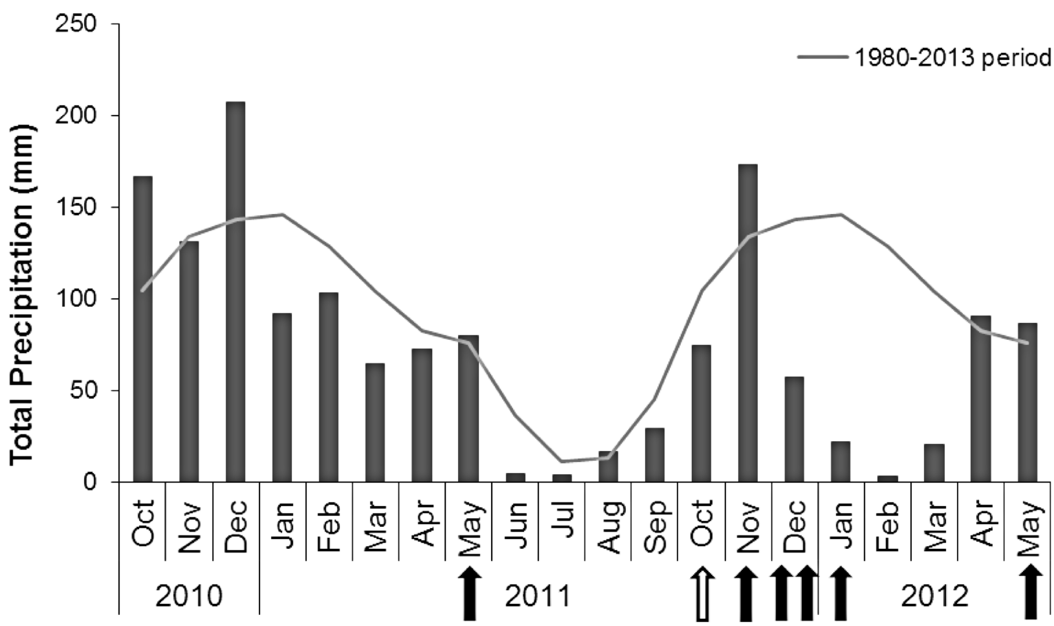

Figure 2. Total monthly precipitation (mm) in the central territory region, Portugal, recorded during the study period (bars) and the historical mean monthly precipitation for the period of 1980-2013 (line). Black arrows represent the sampling events, and the open arrow indicate the time when the streams completely dried out. *Precipitación mensual total (mm) en la zona del territorio central, Portugal, en el periodo de estudio (barras) y precipitación mensual media histórica referente al periodo de 1980-2013 (línea). Las flechas negras representan la toma de muestras y la flecha blanca representa el momento en que los ríos se han secado totalmente.*

water samples were collected in spring 2011 and spring 2012 (s1 and s6) for the laboratory determination of the chemical oxygen demand (COD; mg/L), biochemical oxygen demand (BOD_5; mg/L), phosphates (PO_4^{3-}; mg/L), total phosphorus (P; mg/L), total nitrogen (N; mg/L), nitrates (NO_3^-; mg/L) and alkalinity ($CaCO_3$; mg/L). In addition, all stream sites were geomorphologically characterised according to River Habitat Survey methodology (RHS-Environmental Agency, 2003) to determine the Habitat Quality Assessment (HQA scores). The HQA index reflects the overall habitat diversity through the assessment of the flow types, diversity of channel substratum, in-channel vegetation, and the extent of bank-top trees and near-natural land uses adjacent to the river. The final HQA score results from the sum of the individual scores attributed to those features; a higher score indicates a site with a better habitat condition (36 is the Excellent-Good boundary for the HQA of littoral streams).

Macroinvertebrates were sampled with a hand net (500 μm mesh size) by kicking and sweeping the benthos, following a multi-habitat approach described in INAG (2008). Each sample was composed of six sub-samples distributed proportionally to the most representative habitats and defined by an area of 1 m × 0.25 m (hand net side) upstream. The samples were preserved in formaldehyde (4 %) and conserved in ethanol (90 %) after sorting for future identification and counting. Taxonomic identification using a stereomicroscope was typically performed to the genus level; however, Chironomidae and Oligochaeta were identified to the sub-family or tribe level.

The diatoms were sampled and processed based on European standards (European Committee for Standardization, 2003, 2004, 2006) and on the recommendations of Kelly *et al.* (1998). Whenever stones (preferred sampled substrate) were absent or unavailable, stream sediment was sampled as a substitute. A previous study (Mendes *et al.*, 2012) showed that alternative substrates can be used for water quality assessment in the absence of a certain substrate, disregarding the substrate variability. The epilithic biofilm was scraped with a toothbrush from the upper surface of submerged stones, comprising an area of approximately 100 cm^2. For sampling the epipsammon/epipelon, a syringe (50 ml) was used to collect streambed sediment. The samples were preserved with formaldehyde (4 %) and oxidised using concentrated nitric acid and potassium dichromate for approximately 24 hours for organic matter digestion. The samples were mounted on permanent slides using Naphrax®. Under a light microscope (100 × objective and 1.32 numerical aperture), up to 400 diatom valves for each sample were counted and identified to species or infra-specific rank mainly using Krammer and Lange-Bertalot's flora (1986, 1988, 1991a,b).

Community analyses and biological metrics

To assess differences in the macroinvertebrate and diatom communities between the different sampling times, non-parametric multidimensional scaling analysis (MDS) were run for each biological element based on a Bray-Curtis similarity matrix. We used taxa abundances from sites in spring 2011 pre-drought (s1) and spring 2012 post-drought (s6; diatom data transformed by fourth root). In addition, the ANOSIM global test (analysis of similarities; 126 permutations) was used to test for significant differences between the above groups of samples for both biological elements. ANOSIM is a non-parametric, randomisation-based multivariate test analogous to a standard univariate ANOVA.

To determine the taxa contributing the most to the dissimilarity between pre-drought (May 2011: s1) and post-drought conditions (May 2012: s6), a SIMPER analysis (with Bray-Curtis similarity) was used based on the total abundance of diatoms and invertebrates for all sites at the corresponding sampling dates. In addition, widely used metrics were applied to evaluate the eventual responses to drought. The metric values were represented by the mean (± standard error; SE) from all sites at each sampling event. The differences between sampling events were tested for each metric by running PERMANOVA pairwise tests (permutational univariate analysis of variance; based on Euclidean distance matrix; 999 permutations).

For macroinvertebrates, we used the following metrics: total number of individuals, richness (number of taxa), Pielou's evenness, EPT taxa, Coleoptera and Diptera richness (number of families) and the multimetric index IPtI (Portuguese Index of Invertebrates). The IPtI was expressed in an Ecological Quality Ratio (EQR), in which the values represent the relationship between the observed biological parameters in a river type and the expected for that same river type in reference conditions, assigning a quality classification as High, Good, Moderate, Poor and Bad, according to the Water Framework Directive (WFD; Directive 2000/60/EC, 2000). For diatoms, we used the following metrics: richness (number of taxa), Pielou's evenness and the IPS index ("Indice de Polluosensibilité Spécifique"; Cemagref, 1982) expressed in EQR.

For the macroinvertebrates, the metrics and indices were determined using the Amiib@ software developed by Instituto da Água, I.P. (http://dqa.inag.pt/documenacaoficial_PORTUGAL_invertebradosbentonicos.html), whereas the OMNIDIA software v. 5.3 (Lecointe *et al.*, 1993) was used for the diatoms. All statistical tests were performed using PRIMER 6 & PERMANOVA+ for Windows.

RESULTS

Abiotic characterisation of the sites

The physical and chemical parameters recorded in the streams confirmed that they were all affected by mild organic pollution. The COD values ranged from 2.1 mg/L to 9.8 mg/L, and the phosphate values ranged from 0.25 to 0.97 mg/L PO_4^{3-} (Table 1). The HQA scores varied from 22 to 42, indicating that the Eiras and Alcoa streams had a low habitat quality (lowest scores), whereas the Serra and Boialvo streams had a high habitat quality (highest scores), thus revealing an excellent classification according to the Portuguese limits established for the types of rivers under study (INAG, 2009).

Table 1. Mean values (± standard error) of the measured and calculated variables for each study site. *Valores medios (± error estándar) de las variables medidas o calculadas para cada estación de estudio.*

Parameters	Ribeira de Boialvo (B)	Ribeira de Eiras (E)	Rio da Serra (S)	Nascente do Rio Alcoa (Al)	Ribeira de Ança (An)
Latitude (*y*)	40.5844	40.254	40.4124	39.5366	40.2675
Longitude (*x*)	−8.3358	−8.4238	−8.3486	−8.9457	−8.5153
Distance to source (km)	7.1	6.8	6.9	13	12
Altitude (m)	44	38	111	44	36
Current velocity (m/s)**	0.38 (± 0.09)	0.41 (± 0.15)	0.76 (± 0.20)	0.78 (± 0.16)	0.04 (± 0.02)
Depth (cm)**	21.00 (± 6.42)	8.80 (± 3.25)	21.60 (± 2.98)	25.50 (± 2.35)	36.33 (± 7.12)
pH **	6.80 (± 0.05)	8.20 (± 0.14)	7.35 (± 0.24)	6.92 (± 0.04)	7.10 (± 0.08)
Oxygen (mg/L)**	9.38 (± 0.36)	10.10 (± 0.64)	11.44 (± 1.07)	6.50 (± 0.18)	6.18 (± 0.94)
Conductivity (μS/cm)**	132.72 (± 8.49)	275.40 (± 19.58)	83.78 (± 4.26)	619.33 (± 32.83)	697.17 (± 36.79)
COD (mg O_2/L)*	6.90 (± 1.42)	5.97 (± 0.54)	7.09 (± 2.69)	< 2.1	4.08 (± 3.03)
BOD_5 (mg O_2/L)	< 3.3	< 3.3	< 3.3	< 3.3	< 3.3
Phosphates (mg PO_4^{3-}/L)*	0.50 (± 0.25)	0.45 (0.00)	0.64 (± 0.33)	0.33 (± 0.03)	0.46 (± 0.05)
Total P (mg P/L)*	0.39 (± 0.07)	0.49 (± 0.26)	0.69 (± 0.45)	0.34 (± 0.09)	0.46 (± 0.18)
Total N (mg N/L)*	0.64 (± 0.23)	0.23 (± 0.16)	0.28 (± 0.21)	0.26 (± 0.20)	0.13 (± 0.07)
Nitrates (mg NO_3/L)*	2.28 (± 0.58)	2.01 (± 0.24)	0.78 (± 0.41)	2.61 (± 0.38)	3.03 (± 0.63)
Alcalinity (mg $CaCO_3$/L)*	116.35 (± 96.45)	71.54 (± 12.40)	70.35 (± 60.75)	208.85 (± 16.95)	282.35 (± 69.55)
HQA score	41	22	42	24	33

* spring values.

** all sampling values.

Table 2. Macroinvertebrate taxa contributing 88.3 % to the mean dissimilarity (SIMPER analysis) between s1 and s6 (spring 2011 pre-drought and spring 2012 post-drought, respectively) with their percentage contribution, average dissimilarity and standard deviation (SD). The increase (I) or decrease (D) in the mean abundance of each taxon from s1 to s6 is also shown. *Taxones de macroinvertebrados que más contribuyen a la disimilitud media de 88.3 % (análisis SIMPER) entre s1 y s6 (primavera de 2011 antes de la sequía y primavera de 2012 después de la sequía), con su porcentaje de contribución, disimilitud media y desviación estándar (SD). También se muestra el incremento (I) o la disminución (D) de la abundancia media de cada taxón de s1 a s6.*

Taxon	Av. Diss.	SD Diss.	Contrib. %	I/D
Baetis spp.	16.7	1.1	18.9	D
Echinogammarus spp.	12.8	0.5	14.5	D
Simuliidae	10.2	0.5	11.6	D
Ancylus fluviatilis	9.1	0.5	10.3	D
Leptophlebiidae	6.2	0.8	6.4	I
Perlodidae	4.8	0.5	5.2	D
Hydroporinae	3.3	0.7	3.6	D
Ephemerella spp.	3.3	0.7	3.6	D
Oligochaeta	2.7	0.6	3	I
Dugesia spp.	2	0.7	2.2	I
Orthocladiinae	2.0	0.7	2.2	I
Physa spp.	2	0.5	2.2	D
Chironominae	1.8	0.6	2	D
Oulimnius spp.	1.7	0.9	1.8	D
Ecdyonurus spp.	1.4	0.6	1.6	I

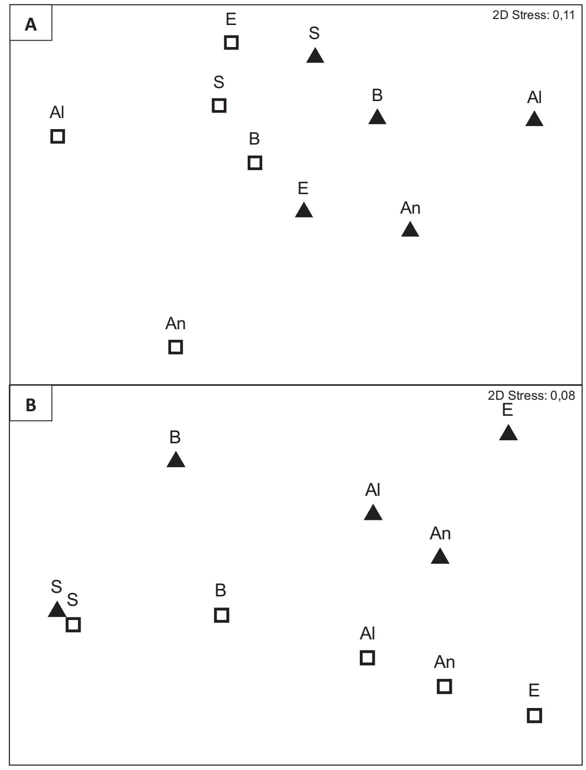

Figure 3. Multidimensional Scaling Analysis ordination for the macroinvertebrate (A) and diatom (B) communities of all study sites sampled in the pre-drought (spring 2011, s1: ▲) and post-drought (spring 2012, s6: □) conditions. Site codes are also indicated (Al: Alcoa; An: Ança; B: Boialvo; E: Eiras and S: Serra). *Análisis de Escalamiento Multidimensional de las comunidades de macroinvertebrados (A) y diatomeas (B) muestreadas antes de la sequía* (primavera de 2011, s1: ▲) y *después de la sequía (primavera 2012, s6: □). Los códigos de las estaciones también se indican (Al: Alcoa; An: Anca; B: Boialvo; E: Eiras; S: Serra).*

Macroinvertebrate patterns

A total of 114 different macroinvertebrate taxa were identified for all sites throughout the present study, comprising a total of 26 631 individuals. Taxa such as *Ancylus fluviatilis* (Planorbidae; Gastropoda), *Baetis* spp. (Baetidae; Ephemeroptera), *Echinogammarus* spp. (Gammaridae; Amphipod), Orthocladiinae (Chironomidae; Diptera), Perlodidae (Plecoptera), *Oulimnius* spp. (Elmidae; Coleoptera) and Simulidae (Diptera) were among the most abundant (over 1100 individuals).

The MDS (stress 0.13) analysis showed a partial segregation between macroinvertebrate communities from pre-drought (s1) and post-drought (s6) conditions; however, for two sites (Boialvo and Serra), the s1 and s6 communities were more similar to each other than in the other cases (Fig. 3A). The ANOSIM test confirmed differences in the macroinvertebrate community composition between 2 sampling events: s1 was different from s6 (Global $R = 0.3$, $p\text{-value} = 0.024$), despite the high variability within groups.

The SIMPER analysis revealed 88.3 % dissimilarity in the macroinvertebrate community between samples in the pre-drought year (s1) and the post-drought year (s6). This high dissimilarity was mainly due to a decrease in s6 (post-drought) of the mean abundance of taxa such as *Baetis* spp., *Echinogammarus* spp., *Ancylus fluviatilis*, Simuliidae, *Hydroporus* spp. (Dytiscidae; Coleoptera) and Perlodidae and an increase of Leptophlebiidae, Oligochaeta, *Dugesia* spp. (Dugesiidae; Turbellaria) and Orthocladiinae (Table 2).

When analysing all sampling events, metrics such as the richness (number of taxa), number of EPT taxa, Coleoptera richness and IPtI index followed a similar short-term recovery pattern (Fig. 4b, d, f, g), i.e. values obtained in spring 2011 (s1) generally decreased after the drought event (s2) and progressively recovered over time along the sampling events (s3, s4, s5) until spring 2012 (s6). For the remaining metrics (evenness and Diptera richness), the values increased or did not change immediately after the drought event (s2) and remained generally unchanged over

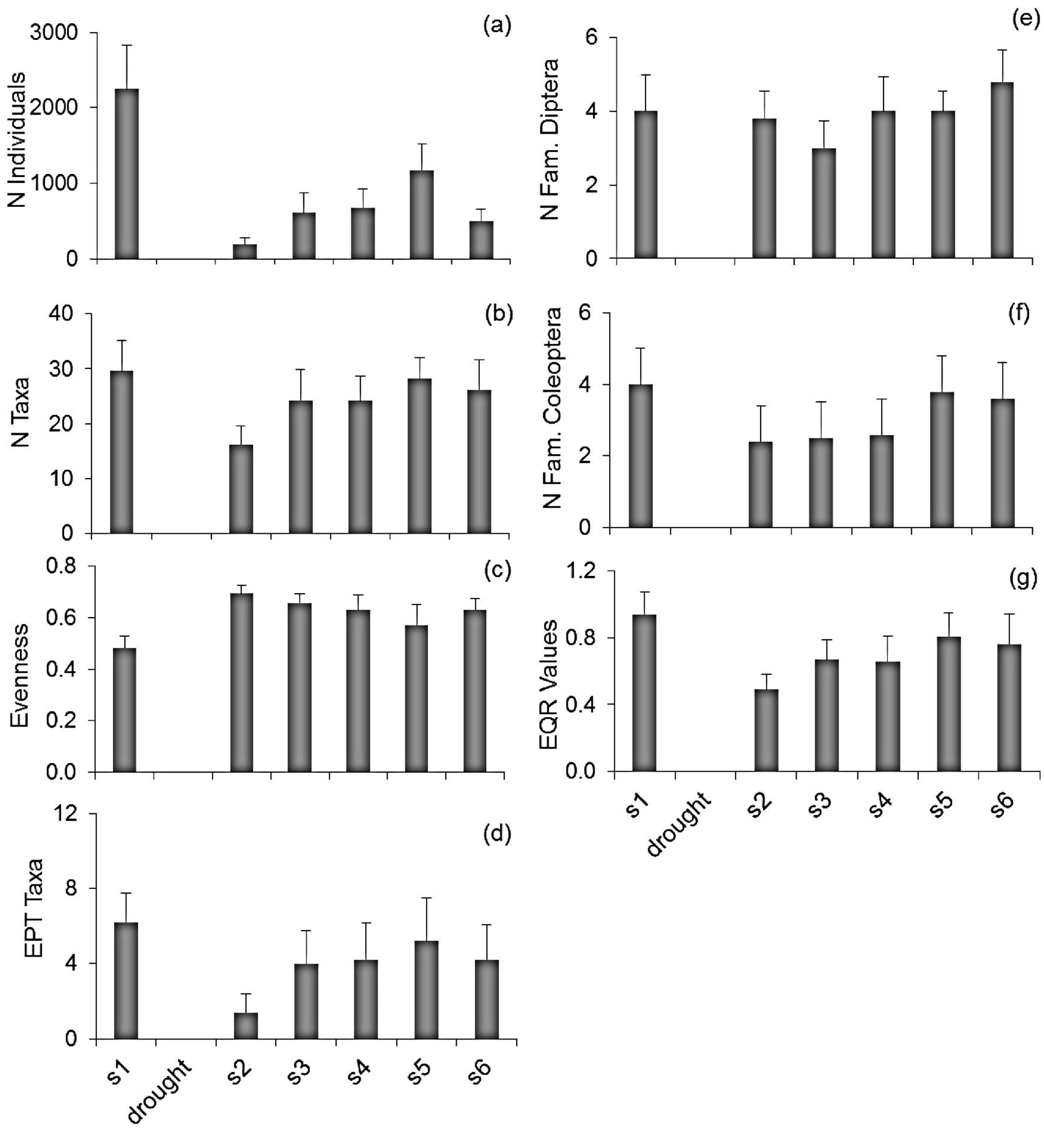

Figure 4. Macroinvertebrate metrics for all study sites (mean ± SE) at each sampling event from spring 2011 (s1) until spring 2012 (s6); a) total number of individuals, b) number of taxa, c) evenness, d) EPT taxa, e) number of Diptera families, f) number of Coleoptera families and g) IPtI index (expressed in Ecological Quality Ratios). *Métricas de los macroinvertebrados para todas las estaciones estudiadas (media ± SE) en cada muestreo desde primavera de 2011(s1) hasta primavera de 2012(s6); a) número total de individuos, b) número de taxones, c) equidad, d) taxones EPT, e) número de familias de Diptera, f) número de familias de Coleoptera y g) Índice IPtI (expresado en proporciones de calidad ecológica).*

12 months until s6 (Fig. 4c, e). However, when evaluating the significant differences among sampling events (PERMANOVA pair-wise test), the total abundance in s1 was different from s2 ($t = 3.48$; $p = 0.007$), s4 ($t = 2.47$; $p = 0.033$) and s6 ($t = 2.89$; $p = 0.010$). Moreover, the abundance in s2 was different from s5 ($t = 2.76$; $p = 0.013$). Further, the total number of macroinvertebrates decreased sharply by 91.5 % from s1 to s2 and recovered by 83.7 % from s2 to s5. However, when comparing spring 2011 and spring 2012, the total number of macroinvertebrates decreased by 77.6 % (from s1 to s6; Fig. 4a).

Although we found no significant differences in richness ($p < 0.05$, PERMANOVA), the richness decreased by 45.3 % from s1 to s2 (sampling just after the drought event) but recovered again in s5 (42.6 %). After one year (s6), the taxa richness was 12.5 % lower compared with the pre-drought condition (s1; Fig. 4b).

Pielou's evenness in s1 was different from s2 ($t = 3.90$; $p = 0.016$), s3 ($t = 2.86$; $p = 0.040$) and s6 ($t = 2.42$; $p = 0.038$) according to the PERMANOVA pair-wise test results. The evenness increased by an average of 30.5 % for all sites from s1 to s2. Overall, from s1 to s6, the community evenness presented an increase of 23.7 % (Fig. 4c).

No significant differences were found in the EPT taxa and Coleoptera and Diptera richness ($p > 0.05$, PERMANOVA pair-wise test) among the sampling events; however, a pattern was detected. In s2, rheophilic taxa such as Ephemeroptera, Plecoptera and Trichoptera decreased abruptly by 77.4 % from s1 but progressively recovered over the duration of the sampling events, increasing by 73.1 % until s5. After one year, these specific taxa had decreased 32.7 % (from spring 2011 to spring 2012; Fig. 4d). As for Diptera, in the majority of sites, the tendency was to maintain or increase the number of families (mean increase of 16.7 %) after one year (Fig. 4e). In addition, Diptera richness in s2 only decreased by 5 % when compared to s1. In the case of Coleoptera, the number of families decreased by 40 % in s2 from s1 but recovered progressively by 38.8 % until s5. Over one year of sampling, the Coleoptera richness decreased by approximately 10.0 % from s1 to s6 (Fig. 4f).

Finally, regarding the IPtI (macroinvertebrate index) given by the EQR values, the quality status in s1 was different from s2 ($t = 3.48$; $p = 0.01$), s4 ($t = 2.47$; $p = 0.033$) and s6 ($t = 2.89$; $p = 0.017$); this indicates that the EQR values after one year (s6) had not recovered their initial status of high ecological quality. In addition, s2 was different from s5 ($t = 2.76$; $p = 0.009$). The lowest quality status for all streams was observed in s2 (first sampling just after the drought event), with a mean EQR value of 0.49 (± 0.09), which indicates a moderate quality status (Fig. 4g).

Diatom patterns

A total of 181 diatom species were identified in all the samples. However, only 66 species presented a relative abundance above or equal to 1 % in at least one sample. The species *Achnanthidium minutissimum* (Kützing) Czarnecki, *Planothidium frequentissimum* (Lange-Bertalot) Lange-Bertalot, *Achnathidium* cf. *kranzii* (Lange-Bertalot) Round and Bukhtiyarova and *Karayevia oblongella* (Oestrup) M. Aboal were the most abundant.

The MDS (stress 0.12) showed an apparent segregation between s1 and s6 samples but also a high variability among sites, except for the Serra site (Fig. 3B). However, no significant differences were confirmed (Global $R = 0.1$, p-value > 0.05; ANOSIM). The dissimilarity was 65.4 % (SIMPER analysis) between spring 2011 (s1) and spring 2012 (s6), which was mainly due to the disappearance of species in post-drought samples such as *Cocconeis euglypta* Ehrenberg, *Amphora pediculus* (Kützing) Grunow, *Reimeria sinuata* (Gregory) Kociolek and Stoermer and *Cocconeis placentula* Ehrenberg var. *lineata* (Ehr.) Van Heurck and the appearance of others such as *Nitzschia palea* (Kützing) W. Smith var. *debilis* (Kützing) Grunow in Cl. and Grun. and *Fragilaria gracilis* (Oestrup). In addition, *Gomphonema rhombicum* Fricke and *Eolimna minima* (Grunow) Lange-Bertalot were among the species that contributed the most to this dissimilarity by decreasing, whereas species such as *Planothidium frequentissimum* (Lange-Bertalot) Lange-Bertalot, *Planothidium lanceolatum* (Brébisson ex Kützing) Lange-Bertalot, *Navicula veneta* and *Karayevia oblongella* increased in s6 compared to s1 (Table 3).

When analysing the selected metrics in all streams, we found that the richness and evenness for the diatom assemblages showed the same recovery trend over the sampling events from s2 to s6 (Fig. 5a, b), despite there being no significant differences ($p > 0.05$; PERMANOVA pair-wise test). For these metrics, an increase of 11.5 % (in richness) and 14.3 % (in evenness) was observed from s1 to s2; and over one year (from s1 to s6) an increase of 11.5 % (richness) and 15.9 % (evenness) was also recorded.

When analysing the IPS index scores, the good water quality status observed in s1 was not altered in s2 (before and immediately after the drought event). However, the index values dropped in s3, changing the status to moderate. In s4 and s5, the status recovered to good again. Despite these results, the average of the study sites in spring 2012 did not recover to the pre-drought values of spring 2011 (the quality status changed from good in s1 to moderate in s6; Fig. 5c).

Table 3. Diatom taxa contributing 65.4 % to the mean dissimilarity (SIMPER analysis) between s1 and s6 (spring 2011 pre-drought and spring 2012 post-drought, respectively), with their percentage contribution, average dissimilarity and standard deviation (SD). The increase (I) or decrease (D) in the mean abundance of each taxon from s1 to s6 (spring 2011 pre-drought and spring 2012 post-drought) is also shown. *Taxones de diatomeas que más contribuyen a la disimilitud media de 65.4 % (análisis SIMPER) entre s1 y s6 (primavera de 2011 antes de la sequía y primavera de 2012 después de la sequía, respectivamente), con su porcentaje de contribución, disimilitud media y desviación estándar (SD). También se muestra el incremento (I) o la disminución (D) de la abundancia media de cada taxón de s1 a s6.*

Taxon	Av. Diss.	SD Diss.	Contrib. (%)	I/D
Nitzschia palea	3.3	1.2	5	I
Planothidium frequentissimum	3.2	1.1	4.9	I
Planothidium lanceolatum	3.2	1.1	4.9	I
Cocconeis euglypta	3.1	1.1	4.7	D
Navicula veneta	3.1	1.1	4.7	I
Karayevia oblongella	2.9	1	4.4	I
Gomphonema rhombicum	2.8	0.7	4.3	D
Amphora pediculus	2.5	1.1	3.8	D
Eolimna minima	2.4	1.2	3.7	D
Reimeria sinuata	2.4	0.8	3.6	D
Nitzschia palea var. debilis	2.3	0.8	3.5	I
Fragilaria capucina	2.1	0.9	3.3	I
Cocconeis placentula	2.1	0.8	3.2	D
Achnanthidium minutissimum	2.1	1.5	3.2	D
Fragilaria vaucheriae	2	0.9	3.1	I
Mayamaea atomus var. *permitis*	1.9	1	3	I
Gomphonema acuminatum	1.8	0.9	2.8	I
Melosira varians	1.8	0.9	2.7	D
Eunotia minor	1.8	0.9	2.7	D
Gomphonema parvulum	1.8	0.9	2.7	I
Navicula gregaria	1.7	0.7	2.6	I
Fragilaria gracilis	1.7	0.8	2.6	I
Fragilaria biceps	1.7	0.9	2.6	I
Nitzschia capitellata	1.7	0.9	2.6	I
Nitzschia inconspicua	1.6	0.8	2.5	I
Encyonema minutum	1.5	0.7	2.4	D
Nitzschia fonticola	1.3	0.7	2	I

DISCUSSION

Diatom and macroinvertebrate community recovery differences

The macroinvertebrates and diatoms differed in their recovery response after dewatering. The macroinvertebrates significantly decreased their abundance when the water first resumed, whereas the diatoms apparently did not differ from the pre-drought-sampled community. In fact, the same pattern prevailed after a year. The diatom biodiversity was not significantly altered over the rewetting progression. This could be because, when compared to macroinvertebrates, diatoms have a rapid life cycle and a consequently rapid ability to colonise a habitat. Oemke and Burton (1986) concluded that a period between 14 days to one month was adequate to complete the colonisation of artificial substrates, attaining the equivalent to mature diatom communities, which was quite similar to the recovery time that we found in the present study (approximately two weeks). Despite their short life cycle, diatoms are capable of persisting in refuges during the dry period (Robson *et al.*, 2008). Furthermore, many benthic algal species are able to resist desiccation due to physiological adaptations such as thick cell walls or resistant propagules, facilitating recolonisation (Steinman & McIntire, 1990). Regarding benthic invertebrates, the reduced flow and decreased water velocity were not beneficial to taxa strongly dependent on flowing water, such as the EPT taxa (Boulton, 2003; Lake, 2003), whereas it had no effect on Diptera or Coleoptera. The latter taxa are most likely able to better tolerate extreme drought because they have desiccation-resistant stages (Coleoptera) or are capable of surviving in moist streambeds (Diptera; Lake, 2003; Boulton & Lake, 2008). Indeed, we found an increase of taxa resistant to drying and typically characteristic of intermittent systems, such as Oligochaeta and several Diptera (Frouz *et al.*, 2003; Dumnicka & Koszalka, 2005).

For both studied benthic elements, the increase in evenness immediately after the dewatering event followed the pattern of the first colonisation stages of empty niches (Begon *et al.*, 1996). In the particular case of diatoms, the dominant species were generally characteristic

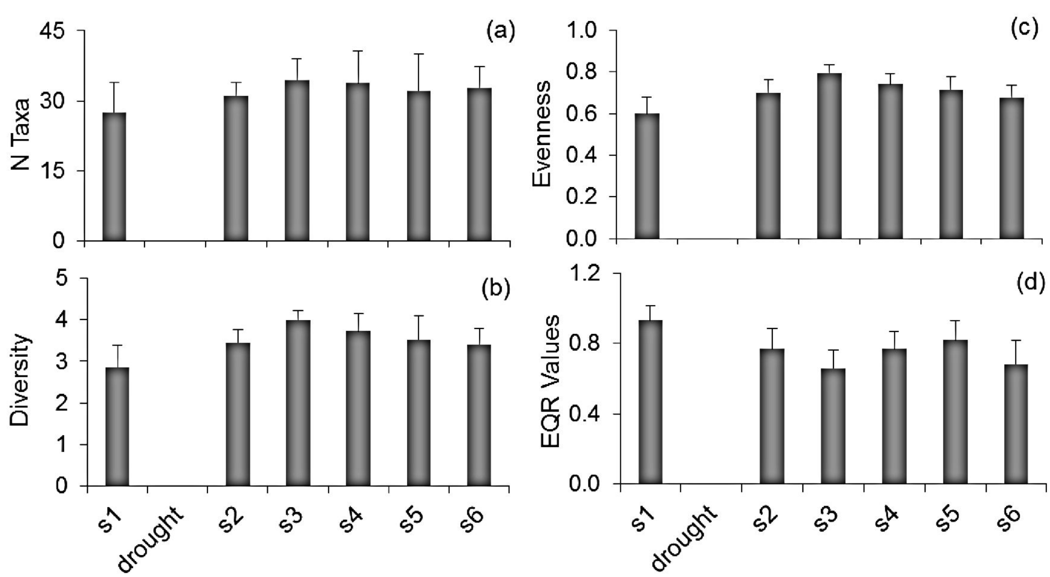

Figure 5. Diatom metrics for all study sites (mean ± SE) at each sampling event from spring 2011 (s1) until spring 2012 (s6); a) number of taxa, b) evenness and c) IPS index (expressed in Ecological Quality Ratios). *Métricas de las diatomeas para todas las estaciones estudiadas (media ± SE) en cada muestreo desde primavera de 2011 (s1) hasta primavera de 2012 (s6); a) número de taxones, b) equidad y c) Índice IPS (expresado en proporciones de calidad ecológica).*

of oligo- to eutraphentic environments, suggesting that the community shifted from the first colonisation stages to a stage of response from the stress affecting the site (van Dam, 1994).

Drought effects on the evaluation of the ecological status

Regarding the biological quality, the IPS index for diatoms was similar over the rewetting progression, but the quality status decreased after one year; this indicates that a shift in species occurred. Indeed, there was a shift from more sensitive species such as *R. sinuata* and *C. placentula* var. *lineata* in spring 2011 to less sensitive or even tolerant species such as *Nitzschia palea* (Kützing) W. Smith. *palea* and *Nitzschia palea* var. *debilis* in spring 2012. Moreover, despite the initial similarity between the studied streams, the drought appeared to induce different environmental (physical and chemical) changes in the streams that led to an irregular response of the diatom communities to the drought. Similarly, Boix *et al*. (2010) did not find linear or uniform changes in the taxonomic composition or structural physiognomy of diatom communities in streams affected by hydrological alteration. Contrary to diatoms, stream water quality, given by the macroinvertebrate IPtI index, decreased with the drought event, and although it did not reach the initial reference values after one year, our streams gradually recovered during the winter season. Both communities provide reliable information on water quality (e.g. Alba-Tercedor *et al*., 2002; Rimet *et al*., 2005). Diatoms are more sensitive to changes in water chemistry, whereas invertebrates are more susceptible to channel morphological changes and habitat conditions (Passy *et al*., 2004). Under drought effects, their simultaneous use for bioassessment should be considered, as their responses are different and appear to be complementary (Feio *et al*., 2007), particularly if considering responses at different temporal scales. In addition, these structural bioassessment measures using taxonomic composition may be complemented by adding trait-based metrics (e.g. body size, life cycle duration, dispersal ability, respiration type), which indirectly provide information on the ecological functioning of streams (Dolédec & Statzner, 2010) and could therefore yield accurate insights into the assessment of extreme events such as droughts.

The role of habitat features in drought resistance and resilience

The river habitat characteristics appeared to play an important role in the recovery of macroinvertebrate and diatom communities. Our study showed that the initial condition of streams was important in the recovery process, as the communities of streams displaying better environmental conditions (e.g. riparian corridors, valley form, HQA) recovered faster and easier from extreme disturbances, which is in agreement with other authors (e.g. Sponseller *et al*., 2001; Elosegi *et al*., 2010; Thomson *et al*., 2012). It is known that benthic communities are strongly influenced by local riparian conditions (Lammert & Allan, 1999; Sponseller *et al*., 2001; Poole & Berman, 2001; Elias *et al*., 2012), which might generate a buffer favouring humidity and lower temperatures by shading. Moreover, the heterogeneity of habitats within the channel and the availability, size and the spatial distribution of refugia during drought likely played a crucial role not only in the communities' resistance but also in their resilience (Magoulick & Kobza, 2003; Lake, 2003) to the dewatering event in the streams of this study. By moving to moist leaf litter or to the moisture under rocks and bark, migrating to the hyporheic zone or burrowing into the bed of the water body (Boulton *et al*., 1992; Clinton *et al*., 1996; Magoulick & Kobza, 2003), the communities found drought refugia that enabled them to survive and progressively recover.

Under the current climate change scenario and consequent unpredictability of extreme events such as the occurrence of dewatering droughts in small, typically perennial streams, the maintenance of morphological riverine features that enhance habitat quality (e.g. continuous riparian corridors, channel habitat heterogeneity) constitutes a determining factor in the continued resilience of aquatic ecosystems (Lake, 2003).

In conclusion, our study revealed that isolated, unusual dewatering drought events in temperate streams affected primary and secondary producers despite their differences in reaction and recovery patterns. The ability of diatom assemblages to recover faster than macroinvertebrates after a drought is most likely due to their shorter life cycles, capability to remain in refuges and physiological adaptations to dryness. We also found that the quality of the habitat appears crucial to minimise the impact and accelerate the recovery processes of these key riverine biological communities as soon as water returns to the channel. With increasing anthropogenic pressures and climatic alterations, we expect biological communities of temperate streams to change through time to comprise more pollution-tolerant taxa and those with a higher resilience to extreme drought events.

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