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RESEARCH ARTICLE

Global negative effects of drought on instream invertebrate communities

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ABSTRACT

Global climate change has led to more frequent and severe droughts, which can negatively affect instream invertebrate communities, but we lack a perspective on the global patterns and drivers of such drought effects. Here, using meta-analysis, we synthesized 997 paired observations extracted from 94 peer-reviewed publications to assess how drought affects the biomass, density, taxonomic richness, and diversity (Shannon–Wiener, Simpson, and Pielou indices) of instream invertebrates at a global scale. We found that (i) drought significantly decreased instream invertebrate density and taxonomic richness by an average of 4.9 and 5.0%, respectively, had marginal negative effects on Shannon–Wiener index, but did not affect biomass, Simpson index or Pielou index; (ii) the effects of drought on instream invertebrate biomass, density, and diversity were not affected by taxonomic level, indicating the robustness of our results; and (iii) stream water physiochemical characteristics such as water flow velocity, pH, conductivity, discharge, total nitrogen concentration, and chlorophyll-a concentration were important moderator variables of drought effects on instream invertebrate communities. Overall, our results clearly showed the global patterns and driving factors of drought effects on instream invertebrate biomass, density, richness, and diversity, which helps scientists better understand the responses of instream invertebrate communities under ongoing global climate change.

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Biomass; density; diversity; taxonomic level; stream characteristic

1. Introduction

Global warming caused by human activities has triggered frequent extreme drought events (Vogel et al. 2019), exacerbating stream fragmentation and loss of aquatic habitats

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and resulting in reduced biodiversity and impaired ecosystem functions (Boulton and Lake 2008; Rolls et al. 2012; Vander Vorste et al. 2020). Shifts in stream flows from perennial to intermittent induced by climate change, particularly drought, will accelerate in the coming decades (Döll and Schmied 2012), resulting in significant impacts on instream biota such as invertebrate communities. Extreme drought events tend to push invertebrate communities beyond critical thresholds, and even a small environmental change can cause disproportionately large biological responses (Capon et al. 2015). Although previous studies assessed the impacts of drought on stream ecosystems (e.g. Aspin et al. 2018; Gómez-Gener et al. 2020; Sabater et al. 2018; Sarremejane et al. 2020), and found that invertebrate biodiversity was lower in drying streams (Soria et al. 2017), we still lack a deep global understanding of the impacts of drought on instream invertebrate communities.

Invertebrates are fundamental components of stream ecosystems, because they not only contribute to stream biodiversity but also play critical roles in carbon (C) and nutrient (e.g. nitrogen and phosphorus) cycling, for example, contributing to leaf litter decomposition (Yue et al. 2022), and directly or indirectly incorporating organic matter from various autochthonous and allochthonous sources into aquatic food webs (Cao et al. 2018; Cummins and Klug 1979; Hauer and Resh 2017). As a crucial component of stream ecosystems, invertebrates are highly sensitive to drought (Bogan et al. 2015). Drought results in spatially extended river flow reductions, often leading to drying of typically perennial sections (Stubbington et al. 2017). Such drying events affect invertebrate communities by eliminating species lacking drying resistance strategies locally and by limiting dispersal and thus species recolonization capacity through increasing hydrological fragmentation at the network scale. (Aspin et al. 2019; Chadd et al. 2017). Also, droughts typically are associated with high water temperature, specific conductance, and reduced dissolved oxygen concentrations, changing water characteristics critical for the survival of invertebrates (Boulton and Lake 2008; Rolls et al. 2012). However, the ways in which habitat availability and water quality changes moderate drought effects on instream invertebrates have not yet been quantitatively assessed at global scales.

Drought effects on instream invertebrate communities can be controlled by a variety of abiotic factors, including stream physicochemical properties, climate conditions, and geographical locations (Ptatscheck et al. 2020; Hussain and Ashok 2012). Water physicochemical properties such as temperature, dissolved oxygen, and current flow may directly affect the survival patterns of invertebrates, because these factors are closely related to the survival and growth rates of invertebrates, possibly with larger drought effects in streams with low current flow and dissolved oxygen but high water temperature (Arismendi et al. 2013). Hygrothermal conditions (e.g. precipitation, temperature, and evaporation) control the duration and intensity of drought and alter the flow regime (e.g. discharge, and flow velocity) of streams, thus indirectly regulating the distribution and structure of instream invertebrate communities (Datry et al. 2016). In addition, latitude, and elevation can be also important moderator variables, because they are directly or indirectly related to other environmental factors such as precipitation, and temperature that are closely related to stream characteristics and instream invertebrate communities (Aspin et al. 2018), but were not well assessed at regional or global scales.

Evidence suggested that drought can selectively and progressively eliminate some species with certain functional traits, creating new niche opportunities for the continuous replacement of species and traits (Boulton and Lake 2008; Leigh et al. 2016; Stubbington et al. 2017). For example, Leigh et al. (2019) found that invertebrates among different taxonomic groups gradually homogenized under the filter effects of drought, with decreases in diversity but increases in evenness, and the density of a small number of tolerant taxa strongly increased. This filtering effect is driven by the duration and intensity of drought, because extreme drought events usually lead to sharp declines in invertebrate biomass, and even loss of species and collapse of food webs (Ledger et al. 2012; Walters and Post 2011). In drying streams, invertebrate density and diversity may increase in a short time if different taxonomic groups congregate in reduced habitat areas (Wright and Berrie 1987). However, as drought intensity increase steadily over time, invertebrate density and diversity would decrease because competition and predation in the temporary shelters or habitats would be extremely difficult (Bae et al. 2014). In addition, the effects of drought on instream invertebrate communities may be affected by taxonomic level, because communities at higher taxonomic levels would be less sensitive to drought due to niche overlap (Broennimann et al. 2012; Saigo et al. 2016).

Here, using 997 pairwise observations (the comparison of biodiversity of stream invertebrates under drought and controlled conditions) collected from 94 publications, we systematically assessed the effects of drought on instream invertebrate communities. The objectives of our study were to: (1) quantify the effects of drought on instream invertebrate biomass, density, taxonomic richness, and diversity (Shannon-Wiener diversity index, Simpson diversity index, and Pielou evenness index); (2) evaluate whether the effects of drought on instream invertebrate communities were affected by taxonomic level, because invertebrates were identified to family, genus, and species level or unreported in different primary studies; and (3) assess the impacts of multiple moderator variables on the responses of invertebrate communities to drought. We hypothesized that (1) drought would decrease the biomass, density, taxonomic richness, and diversity of instream invertebrates, but would increase community evenness; (2) the effects of drought on instream invertebrate communities would vary among different taxonomic levels; and (3) the effects of drought on invertebrate communities would be modulated by environmental factors (e.g. geographical locations, climate conditions, and physicochemical characteristics) that are closely related to invertebrate communities.

2. Materials and methods

2.1. Data collection and complication

Following the PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analysis) statement, namely an evidence-based minimum set of items for reporting in systematic reviews and meta-analysis (Page et al. 2021; Fig. S1), we searched for peer-reviewed articles, academic theses, and book chapters published in English or Chinese before June 2022 using Web of Science (http://apps.webofknowledge.com/), Google Scholar (http://scholar.google.com/), and China National Knowledge Infrastructure (http://www.cnki.net/). The terms ("benthic invertebrate*" or "bottom invertebrate*" or "demersal invertebrate*" or macroinvertebrate*) and (drought or arid or dry or "decrease* precipitation" or "decrease* rainfall") and (stream or river) were used as the search terms, and their equivalents in Chinese. Primary studies were included in our database if they meet the following criteria: (1) control and drought conditions were not affected by pollution or human activities (e.g. water extraction and experimental manipulation), and drought in studies refers to hydrological drought caused by natural conditions; (2) the type of drying refers to an unusual drying event in a stream/river caused by an extreme drought event; (3) collection of invertebrates was carried out in at least one stream or river not affected by drought (control condition) and one comparable stream or river affected by drought (drought condition), and sampling in drought conditions were done during drought (the no-flow period); (4) at least one of the following invertebrate metrics were reported: biomass, density, taxonomic richness, Shannon–Wiener index, Simpson index, or Pielou index in both the drought and control groups; and (5) the sample size was clearly reported for both groups. Ninety-four independent publications (92 in English and 2 in Chinese) were included in our database, which contributed a total of 997 pairwise observations (Figure 1 and Table S1).

To assess the impacts of moderator variables we also extracted data of geographical locations [latitude (°) and elevation (m)] and stream physicochemical characteristics, including water width (cm), depth (cm), flow velocity (m/s), pH, conductivity (μS/cm), temperature (°C), turbidity (NTU), discharge (L/s), alkalinity (mg $CaCO_3$/L), total phosphorus (TP, mg/L), total nitrogen (TN, mg/L), dissolved O_2 (mg/L), and chlorophyll-a concentrations (μg/L), where available. Data were directly extracted from the main texts, tables, and appendices of the selected primary studies, or digitized from figures using GetData Graph Digitizer (version 2.26; http://www.getdata-graph-digitizer.com). Because many of the primary studies did not report climate data, we extracted mean annual temperature (MAT, °C), and mean annual precipitation (MAP, mm) from the *WorldClim* v2 database (Fick and Hijmans 2017), as well as aridity index (AI), and annual evapotranspiration (AET, mm/day) from the CGIAR-CSI v2 database (Trabucco and Zomer 2019).

2.2. Statistical analysis

To assess the effects of drought on instream invertebrate communities, we used the natural log response ratio (lnRR) as the effect size, because it is easily interpretable and its sampling distribution approximates normality (Hedges et al. 1999). The lnRR for each individual pairwise observation was calculated as:

$$\mathrm{lnRR} = \ln\left(\frac{\bar{X}_d}{\bar{X}_c}\right) \tag{1}$$

where $\bar{X}_d$ and $\bar{X}_c$ are the means of invertebrate metrics in the drought and control groups, respectively. Because many of the studies did not report standard deviation or

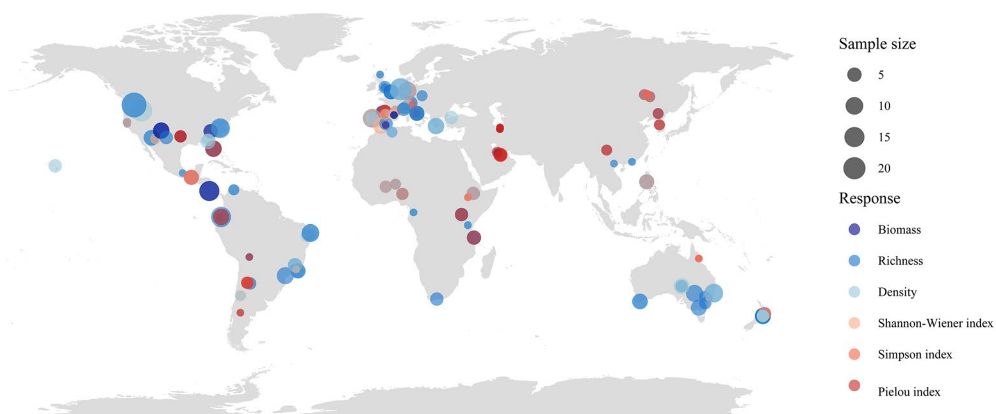

Figure 1. Global distribution of observations used in the meta-analysis. The number of pairwise observations of each study site is represented by symbol size, and different colors indicate different invertebrate metrics.

standard error, we used the number of repeats associated with each observation to calculate the weight (W_r) of the corresponding effect size as:

$$W_r = \frac{(N_c \times N_d)}{(N_c + N_d)} \tag{2}$$

in which N_c and N_d are the number of replications in the control and drought groups, respectively (Morris and DeShon 2002; Yue et al. 2021).

To calculate the overall mean effect size ($\ln RR_{++}$) of drought on invertebrate communities, we ran an intercept-only linear mixed-effects model using the *lme4* package in R (Bates et al. 2015), where lnRR was fitted as a response variable and the identity of the primary study was fitted as a random-effects factor to account for the potential non-independence of observations extracted from a single study. To further assess the impacts of moderator variables on lnRR, we used linear mixed-effects meta-regression models by fitting these variables as continuous or categorical fixed-effect factors. Because the data points varied substantially among different moderator variables, and it is impossible to evaluate their interactions, we thus only performed univariate models to evaluate the impacts of each variable individually. To aid interpretation, $\ln RR_{++}$ and the associated 95% confidence interval (CI) were back-transformed using the equation $\left(e^{lnRR_{++}} - 1\right) \times 100\%$ (Koricheva et al. 2013). The lnRRs across all observations or those for each invertebrate metric showed normal or slightly skewed normal distributions (Figure 2), indicating the robustness of our database to publication bias. All statistical analyses were performed in R version 4.1.1 (R Core Team 2021).

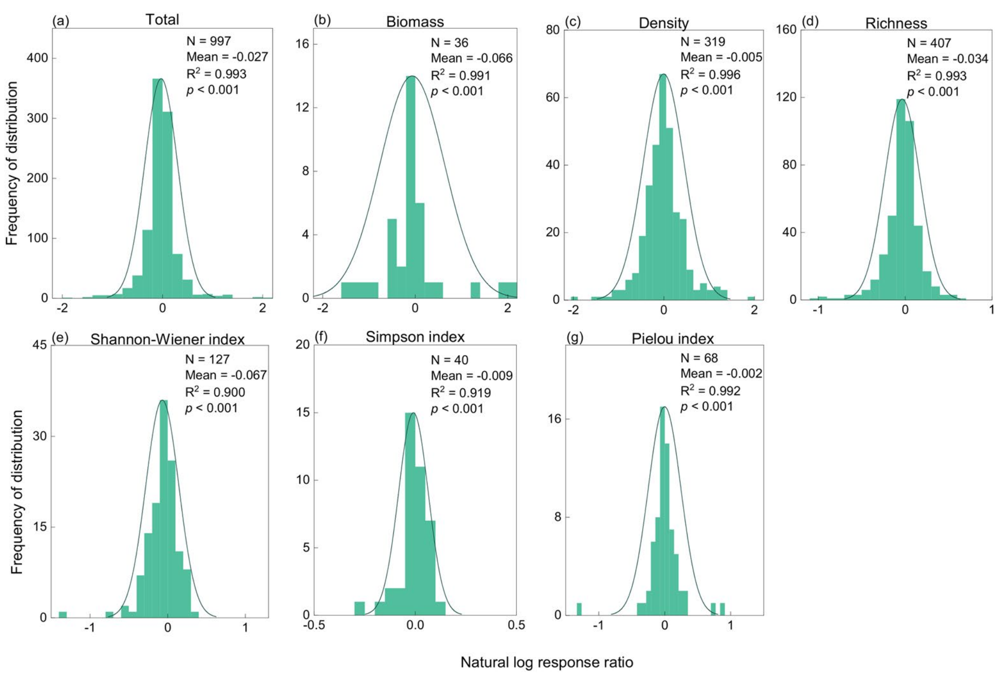

Figure 2. Frequency of the distribution of natural log response ratio of instream invertebrate total (all metrics joined; a), biomass (b), density (c), taxonomic richness (d), Shannon-Wiener index (e), Simpson index (f) and Pielou index (g). The number, means and standard error are also shown.

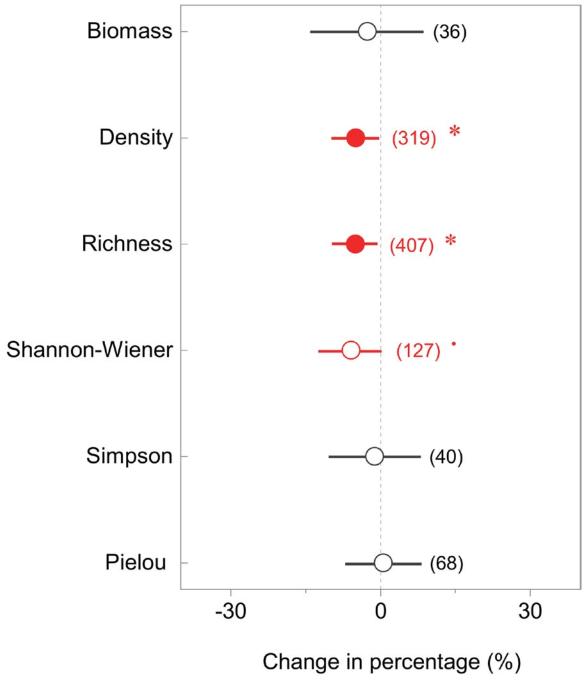

Figure 3. Overall effects of drought on instream invertebrate communities. Values are means with 95% confidence intervals of the per cent difference between drought and control groups, and numbers of pairwise observations are shown in parentheses. Grey symbols indicate statistically non-significant effects of drought on invertebrate metrics, and red symbols indicate statistically significant negative effects at $*p < 0.05$ and marginally significant negative effects at $\cdot p < 0.1$.

3. Results

3.1. Overall effects of drought

Averaged across the observations, instream invertebrate density and taxonomic richness were significantly reduced by drought by an average of 4.9% and 5.0%, respectively, while drought showed a marginally negative effect (−5.9%) on the Shannon-Wiener index of instream invertebrate communities. However, invertebrate biomass, Simpson index, and Pielou index showed non-significant responses to drought (Figures 3 and S1).

3.2. Impacts of moderator variables

The responses of invertebrate biomass and density to drought were not affected by taxonomic level, while the effects of drought on taxonomic richness were only significant at the species level, which was significantly decreased by 8.9% (Figure 4). Likewise, drought effects on invertebrate community Shannon-Wiener index and Pielou index were not affected by taxonomic level, while the responses of Simpson index to drought were only significant at unreported levels (Figure 5). The effect size of drought on invertebrate biomass was positively related to MAP, and stream water conductivity. The lnRR of density was negatively related to MAT and stream water nitrogen concentration, and the lnRR of richness was only negatively associated with latitude (Table 1). The lnRR of both Shannon-Wiener and Pielou indices were positively associated with stream water flow velocity and discharge, and negatively associated with water nitrogen concentration, and positively related to pH and chlorophyll-a concentration. The lnRR of Simpson index was positively related to stream water pH and conductivity.

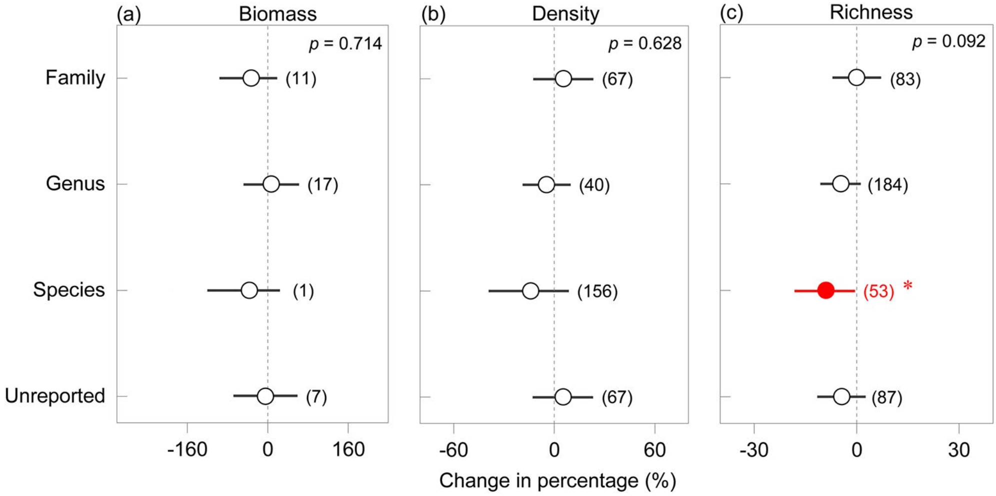

Figure 4. Effects of drought on instream invertebrate biomass (a), density (b) and taxonomic richness (c) among different taxonomic levels (family, genus, species and unreported). Values are means with 95% confidence intervals of the per cent difference between drought and control groups for different taxonomic levels, and numbers of pairwise observations are shown in parentheses. Grey symbols indicate statistically non-significant effects of drought, and red symbols indicate significant negative effects at $^*p < 0.05$.

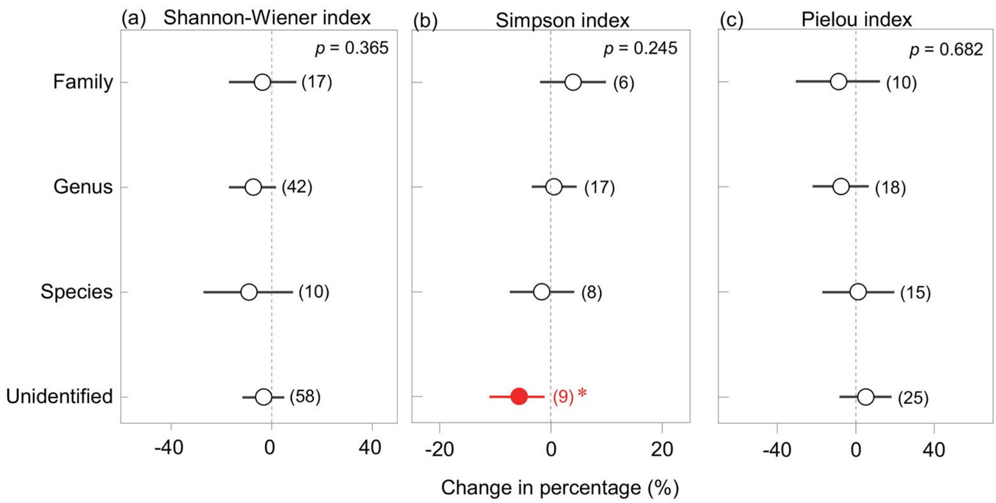

Figure 5. Effects of drought on instream invertebrate diversity [Shannon-Wiener index (a), Simpson index (b) and Pielou index (c)] among different taxonomic levels (family, genus, species and unreported). Values are means with 95% confidence intervals of the per cent difference between drought and control groups for different taxonomic levels, and numbers of pairwise observations are shown in parentheses. Grey symbols indicate statistically non-significant effects of drought, and red symbols indicate significant negative effects at $^*p < 0.05$.

4. Discussion

4.1. Negative effects of drought on instream invertebrate communities

Partly consistent with the first hypothesis, drought showed significant negative effects on instream invertebrate density, taxonomic richness, and Shannon–Wiener index (Figure 3), indicating that drought could thus profoundly modify the structure of instream invertebrate communities. First, the effects of drought typically lead to reductions in the availability of habitats, as decreased stream discharge usually results in the loss of

Table 1. Univariate linear mixed-effects models used to evaluate the impacts of moderator variables on the effect of drought (lnRR) on instream invertebrate biomass, density, taxonomic richness, Shannon–Wiener index, Simpson index, and Pielou index. Slopes and sample sizes (*N*) are reported.

	Biomass		Density		Richness		Shannon–Wiener		Simpson		Pielou	
Predictor	Slope	*N*	Slope	*N*	Slope	*N*	Slope	*N*	Slope	*N*	Slope	*N*
Geographical locations												
Latitude (°)	−0.013	36	0.001	319	**−0.001***	407	−0.001	127	0.001	40	0.001	68
Elevation (m)	0.001	35	0.001	314	0.001	402	−0.001	122	0.001	35	−0.001	58
Climate conditions												
MAT (°C)	0.024	35	**−0.011**·	309	0.004	397	0.005	122	0.001	35	−0.001	53
MAP (mm)	**−0.001**·	35	0.001	314	0.001	402	0.001	122	0.001	35	−0.001	58
AI	0.001	36	−0.001	319	−0.001	407	−0.001	127	0.001	40	−0.001	68
AET (mm/day)	0.001	35	0.001	309	0.001	397	0.001	122	−0.001	35	−0.001	53
Physicochemical characteristics												
Width (cm)	0.001	6	0.001	157	0.001	205	−0.001	58	0.001	17	−0.001	27
Depth (cm)			0.001	188	0.001	235	−0.001	63	0.001	17	−0.001	41
Flow velocity (m/s)			−0.037	161	0.051	195	**0.122***	46	0.014	16	**0.292*****	39
Discharge (L/s)	0.001	35	0.001	211	0.001	263	**0.001**·	72	0.001	15	**0.001***	29
pH	0.045	22	−0.006	245	0.011	287	**0.060**·	118	**0.034**·	33	0.081	64
Conductivity (μS/cm)	**−0.003**·	21	−0.001	256	−0.001	315	0.001	112	**0.001***	30	0.001	54
Water temperature (°C)	0.032	8	0.008	212	0.003	263	0.001	98	−0.002	30	−0.007	48
Turbidity (NTU)			0.001	45	0.001	48	0.001	14			0.001	13
Alkalinity (mg $CaCO_3$/L)	−0.005	5	−0.001	57	−0.001	71	0.002	13	−0.001	8	0.001	24
Total phosphorus (mg/L)			0.006	106	0.003	106	0.002	47	−0.001	20	−0.001	30
Total nitrogen (mg/L)			**−0.111**·	78	−0.001	81	**−0.013****	33	0.011	15	**−0.013***	30
Dissolved O_2 (mg/L)			−0.019	154	−0.004	191	0.019	89	0.014	22	0.035	38
Chlorophyll-a (μg/L)			0.001	76	−0.001	63	0.002	20	−0.001	16	**0.109****	11

Note: Bold indicates statistically significant at $\cdot p < 0.1$, $^{*}p < 0.05$, $^{**}p < 0.01$, and $^{***}p < 0.001$.
Abbreviations: AI: Aridity Index; AET: Annual Evapotranspiration; MAP: Mean Annual Precipitation; MAT: Mean Annual Temperature

lateral, longitudinal, and/or vertical connectivity, and fragmentation with drying (Boulton and Lake 2008; Chadd et al. 2017). Second, drought can significantly cause decreases in habitat qualities and increases in extremes of physical and chemical water quality parameters, for example, increase in water temperature and conductivity as well as decrease in dissolved oxygen (Magoulick and Kobza 2003). In addition, drought can also indirectly affect stream primary productivity *via* low flow and high temperature, which decrease the quantity and quality of food resources, thereby altering the structural characteristics or composition of invertebrate communities, especially of taxa adapted to fast flows and cold waters (Bonada et al. 2006; Herbst et al. 2019).

The decreases in instream invertebrate density, taxonomic richness, and diversity under drought stress may be attributed to homogenizations in invertebrate communities (Bertoncin et al. 2019; Pinna et al. 2016). It is considered to be an overarching process that includes either loss of taxonomic, genetic, or functional uniqueness over time (Olden et al. 2004). Drought can filter out instream invertebrate taxa adapted to high oxygen and low-temperature environments, while those that have adapted to lentic conditions and have been able to cope with poor water quality are able to persist (Aspin et al. 2018; Leigh et al. 2019), and thus caused an overall decrease in invertebrate density, taxonomic richness, and diversity. In addition, the selective effects of drought are also expected to have negative impacts on sensitive species having low density in streams (Vellend 2010), which can also contribute to declines in instream invertebrate density and diversity under the stress of drought. However, in contrast to our second hypothesis, we found that the effects of drought on instream invertebrate communities were not affected by taxonomic level, which may be explained by the variations in individual species that have adapted to a narrow range of drought levels that were not reflected at higher taxonomic levels (Bowman and Bailey 1997; Warwick 1993).

4.2. Impacts of moderator variables

The effects of drought on instream invertebrate communities were regulated by multiple moderator variables such as latitude, MAT, MAP, stream flow velocity, discharge, pH, conductivity, nitrogen, and chlorophyll-a concentrations. The latitudinal gradient in species richness, with species and richness declining with latitude, is widely known (Chaudhary et al. 2021; Crow 1993; Hubendick 1962). For example, Jacobsen et al. (1997) found that tropical lowland streams had an average of 2–4 times higher species richness than temperate lowland streams. The lnRR of taxonomic richness was negatively related to latitude, indicating that invertebrate species in high-latitude streams are more resistant to drought effects, which in line with previous findings on marine and terrestrial organisms (Culp et al. 2019; Musonge et al. 2020). Climate conditions shape stream environments through direct and indirect impacts on biological and abiotic factors that control the duration and intensity of drought (Dodds et al. 2019). Temperature has been found to be a major factor affecting the growth rates of invertebrates, and the smaller the individuals, the greater the impacts (Humpesch 1979). However, in our study, climate conditions only marginally impacted the effect size of drought on instream invertebrate biomass and density. Three mechanisms may explain this result: (i) the climatic condition during droughts may not be accurately described by annual average climatic indicators (Li et al. 2020); (ii) instream invertebrates present high persistence and resilience to drought-induced stressful environmental conditions (Hiddink et al. 2015; Mesa 2012); and (iii) the limited data points for each taxonomic group may limit the statistical power to generate a significant result.

Stream physicochemical properties seem obviously to affect the magnitude of drought effects on invertebrate communities, because they change the availability of food resources and availability and suitability of aquatic habitats, which control the structure and composition of invertebrate communities (Boulton and Lake 2008; Ledger et al. 2012; Stubbington et al. 2017). For example, discharge and flow velocity are often inter-related in running water. The decline of discharge and flow velocity caused by drought will lead to habitat shrinkage and connectivity reduction, which selectively eliminates some invertebrate taxa (e.g. floating, slow-breeding, and riffle groups) (Herbst et al. 2019; Lake 2003; Stubbington et al. 2017). Our results showed a negative impact of water nitrogen concentration on lnRR of Shannon-Wiener index, reflecting its effect on instream invertebrate diversity during drought (Camargo and Alonso 2006). During the drying period, nitrogen concentration in streams can increase significantly due to low-flow upwelling and microbial nitrogen fixation (Grimm and Petrone 1997), which favors high abundances and activities of microorganisms (Rosa et al. 2014). However, Camargo et al. (2005) found that ammonia and nitrite could also be toxic to invertebrates when their concentrations rose to a certain level, and the toxicity increased with increasing concentrations and exposure times. Increased nitrogen concentration and temperature can also lead to the increase of water pH, but the positive slope for pH suggested that drought effects were stronger in acidic water (low pH), which possibly indicated that invertebrates from streams with low pH are less resistant to drought-induced pH changes than those from relatively neutral streams (Bernard et al. 1990). The increased specific conductance during drought might simply be an indicator of generally lower water quality under the stress of drought, but its positive relationship with the lnRR of drought on invertebrate biomass was likely to indicate an increased tolerance of invertebrates to a temporary drying environment (Chessman and Robinson 1987). In addition, the decreased water velocity in the boundary layer declined with falling discharge limited the input of exogenous chlorophyll-a (Biggs and Gerbeaux 1993), and reduced the food source of invertebrates during drought thus affects the ingestion and nutritional relationships of invertebrate communities (Finn et al. 2009).

4.3. Major limitations and perspectives

Despite the general patterns of drought effects on instream invertebrate density and diversity found in this study, several uncertainties and knowledge gaps still exist because of the inherent limitations of experimental designs and the lack of a more complete dataset with sufficient information on instream invertebrate study. First, 253 of the 997 observations in our database did not have information on the taxonomic level, which limited the assessment of the impacts of taxonomic level on drought effects. Second, many primary studies did not report background information such as stream physicochemical characteristics, which limited our ability to generate a robust perspective on the driving factors of drought effects on instream invertebrate communities. Third, the study sites included in our database were unevenly distributed across the globe, with limited data from Asia, which reduced our ability to achieve a general pattern of drought effects on instream invertebrate communities at the global scale. Therefore, we suggest that future studies focusing on instream invertebrates should clearly identify the taxonomic levels and report background information that are directly and indirectly related to invertebrate communities, especially in regions that are less studied.

5. Conclusions

This quantitative synthesis represents the most comprehensive assessment of the global impact of drought on instream invertebrate communities, complementing a recent global study that included a few study sites (Sabater et al. 2018). The results of our systematic meta-analysis showed global negative effects of drought on instream invertebrate communities, with density and taxonomic richness significantly reduced by 4.9% and 5.0%, respectively. Drought had marginal negative effects on Shannon–Wiener index, but did not affect biomass, Simpson index or Pielou index. Taxonomic level, geographic locations, and climate conditions showed limited impacts on the response of invertebrates to drought, but stream physiochemical characteristics such as those related to aquatic habitat availability and quality (water flow velocity, discharge, pH, conductivity, nitrogen, and chlorophyll-a concentrations) were the most important moderator variables of drought effects on instream invertebrates. Overall, our study not only quantitatively synthesized the global patterns and driving factors of drought to instream invertebrate communities, but also clearly assessed the regulatory mechanisms of key moderator variables. Finally, the results also highlight the importance of precise taxonomic resolution. And we hope to design scientific experiments to further explore the effect of drought on functional traits of invertebrates.

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Author contributions

K.Y. and Q.Y. conceived of the study. Q.Y. collected the raw data. Q.Y. and K.Y. performed the data analyses and wrote the first draft. All authors contributed critically to revisions.

Data availability statement

Raw data used in the study have been deposited in figshare with a DOI (https://doi.org/10.6084/m9.figshare.22582027.v1).

Disclosure statement

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References

Arismendi I, Safeeq M, Johnson SL, Dunham JB, Haggerty R. 2013. Increasing synchrony of high temperature and low flow in western North American streams: double trouble for coldwater biota? Hydrobiologia 712(1):1–14.

Aspin TWH, Khamis K, Matthews TJ, Milner AM, O'Callaghan MJ, Trimmer M, Woodward G, Ledger ME. 2019. Extreme drought pushes stream invertebrate communities over functional thresholds. Glob Chang Biol. 25(1):230–244.

Aspin TWH, Matthews TJ, Khamis K, Milner AM, Wang Z, O'Callaghan MJ, Ledger ME. 2018. Drought intensification drives turnover of structure and function in stream invertebrate communities. Ecography 41(12):1992–2004.

Bae M-J, Chon T-S, Park Y-S. 2014. Characterizing differential responses of benthic macroinvertebrate communities to floods and droughts in three different stream types using a Self-Organizing Map. Ecohydrology 7(1):115–126.

Bates D, Mächler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4. J Stat Soft. 67(1):1–48.

Bernard DP, Neil WE, Rowe L. 1990. Impact of mild experimental acidification on short term invertebrate drift in a sensitive British Columbia stream. Hydrobiologia 203(1-2):63–72.

Bertoncin AP, dos S, Pinha GD, Baumgartner MT, Mormul RP. 2019. Extreme drought events can promote homogenization of benthic macroinvertebrate assemblages in a floodplain pond in Brazil. Hydrobiologia 826(1):379–393.

Biggs BJF, Gerbeaux P. 1993. Periphyton development in relation to macro-scale (geology) and micro-scale (velocity) limiters in two gravel-bed rivers, New Zealand. New Zealand J Marine Freshw Res. 27(1):39–53.

Bogan MT, Boersma KS, Lytle DA. 2015. Resistance and resilience of invertebrate communities to seasonal and supraseasonal drought in arid-land headwater streams. Freshw Biol. 60(12):2547–2558.

Bonada N, Rieradevall M, Prat N, Resh VH. 2006. Benthic macroinvertebrate assemblages and macrohabitat connectivity in Mediterranean-climate streams of northern California. J North Am Benthol Soc. 25(1):32–43.2.0.CO;2]

Boulton AJ, Lake PS. 2008. Effects of drought on stream insects and its ecological consequences. Aquatic Insects: Challenges to Populations (p. 81–102).

Bowman MF, Bailey RC. 1997. Does taxonomic resolution affect the multivariate description of the structure of freshwater benthic macroinvertebrate communities? Can J Fish Aquat Sci. 54(8):1802–1807.

Broennimann O, Fitzpatrick MC, Pearman PB, Petitpierre B, Pellissier L, Yoccoz NG, Thuiller W, Fortin M-J, Randin C, Zimmermann NE, et al. 2012. Measuring ecological niche overlap from occurrence and spatial environmental data: measuring niche overlap. Global Ecol Biogeogr. 21(4):481–497.

Camargo JA, Alonso Á. 2006. Ecological and toxicological effects of inorganic nitrogen pollution in aquatic ecosystems: a global assessment. Environ Int. 32(6):831–849.

Camargo JA, Alonso A, Salamanca A. 2005. Nitrate toxicity to aquatic animals: a review with new data for freshwater invertebrates. Chemosphere 58(9):1255–1267.

Cao X, Chai L, Jiang D, Wang J, Liu Y, Huang Y. 2018. Loss of biodiversity alters ecosystem function in freshwater streams: potential evidence from benthic macroinvertebrates. Ecosphere. 9(10):e02445.

Capon SJ, Lynch AJJ, Bond N, Chessman BC, Davis J, Davidson N, Finlayson M, Gell PA, Hohnberg D, Humphrey C, et al. 2015. Regime shifts, thresholds and multiple stable states in freshwater ecosystems; a critical appraisal of the evidence. Sci Total Environ. 534:122–130.

Chadd RP, England JA, Constable D, Dunbar MJ, Extence CA, Leeming DJ, Murray-Bligh JA, Wood PJ. 2017. An index to track the ecological effects of drought development and recovery on riverine invertebrate communities. Ecol Indic. 82:344–356.

Chaudhary C, Richardson AJ, Schoeman DS, Costello MJ. 2021. Global warming is causing a more pronounced dip in marine species richness around the equator. Proc Natl Acad Sci USA. 118(15):e2015094118.

Chessman B, Robinson D. 1987. Some effects of the 1982-83 drought on water quality and macroinvertebrate fauna in the lower La Trobe River, Victoria. Mar Freshwater Res. 38(2):289.

Crow GE. 1993. Species diversity in aquatic angiosperms: latitudinal patterns. Aquat Bot. 44(2-3):229–258.

Culp JM, Lento J, Curry RA, Luiker E, Halliwell D. 2019. Arctic biodiversity of stream macroinvertebrates declines in response to latitudinal change in the abiotic template. Freshw Sci. 38(3):465–479.

Cummins KW, Klug MJ. 1979. Feeding ecology of stream invertebrates. Annu Rev Ecol Syst. 10(1):147–172. http://www.jstor.org/stable/2096788.

Datry T, Fritz K, Leigh C. 2016. Challenges, developments and perspectives in intermittent river ecology. Freshw Biol. 61(8):1171–1180.

Dodds WK, Bruckerhoff L, Batzer D, Schechner A, Pennock C, Renner E, Tromboni F, Bigham K, Grieger S. 2019. The freshwater biome gradient framework: predicting macroscale properties based on latitude, altitude, and precipitation. Ecosphere 10(7):e02786.

Döll P, Schmied HM. 2012. How is the impact of climate change on river flow regimes related to the impact on mean annual runoff? A global-scale analysis. Environ Res Lett. 7(1):14037.

Fick SE, Hijmans RJ. 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int J Climatol. 37(12):4302–4315.

Finn MA, Boulton AJ, Chessman BC. 2009. Ecological responses to artificial drought in two Australian rivers with differing water extraction. fal 175(3):231–248.

Gómez-Gener L, Lupon A, Laudon H, Sponseller RA. 2020. Drought alters the biogeochemistry of boreal stream networks. Nat Commun. 11(1):1795.

Grimm NB, Petrone KC. 1997. Nitrogen fixation in a desert stream ecosystem. Biogeochemistry 37(1):33–61.

Hauer FR, Resh VH. 2017. Macroinvertebrates. In Methods in stream ecology (3rd ed., Vol. 1, p. 297–319). Academic Press.

Hedges LV, Gurevitch J, Curtis PS. 1999. The meta-analysis of response ratios in experimental ecology. Ecology 80(4):1150–1156.2.0.CO;2]

Herbst DB, Cooper SD, Medhurst RB, Wiseman SW, Hunsaker CT. 2019. Drought ecohydrology alters the structure and function of benthic invertebrate communities in mountain streams. Freshw Biol. 64(5):886–902.

Hiddink JG, Burrows MT, García Molinos J. 2015. Temperature tracking by North Sea benthic invertebrates in response to climate change. Glob Chang Biol. 21(1):117–129.

Hubendick B. 1962. Aspects on the diversity of the fresh-water fauna. Oikos 13(2):249.

Humpesch UH. 1979. Life cycles and growth rates of Baetis spp. (Ephemeroptera: Baetidae) in the laboratory and in two stony streams in Austria. Freshwater Biol. 9(5):467–479.

Jacobsen D, Schultz R, Encalada A. 1997. Structure and diversity of stream invertebrate assemblages: The influence of temperature with altitude and latitude. Freshw Biol. 38(2):247–261.

Koricheva J, Gurevitch J, Mengersen K. 2013. Handbook of meta-analysis in ecology and evolution. Princeton and Oxford: Princeton University Press.

Lake PS. 2003. Ecological effects of perturbation by drought in flowing waters. Freshw Biol. 48(7):1161–1172.

Ledger ME, Harris RML, Armitage PD, Milner AM. 2012. Climate change impacts on community resilience: evidence from a drought disturbance experiment. In Advances in ecological research (Vol. 46, p. 211–258). Academic Press.

Leigh C, Aspin TWH, Matthews TJ, Rolls RJ, Ledger ME. 2019. Drought alters the functional stability of stream invertebrate communities through time. J Biogeogr. 46(9):1988–2000.

Leigh C, Bonada N, Boulton AJ, Hugueny B, Larned ST, Vander Vorste R, Datry T. 2016. Invertebrate assemblage responses and the dual roles of resistance and resilience to drying in intermittent rivers. Aquat Sci. 78(2):291–301.

Li Q, He P, He Y, Han X, Zeng T, Lu G, Wang H. 2020. Investigation to the relation between meteorological drought and hydrological drought in the upper Shaying River Basin using wavelet analysis. Atmos Res. 234:104743.

Magoulick DD, Kobza RM. 2003. The role of refugia for fishes during drought: a review and synthesis: *refugia for fishes during drought*. Freshw Biol. 48(7):1186–1198.

Mesa LM. 2012. Interannual and seasonal variability of macroinvertebrates in monsoonal climate streams. Braz Arch Biol Technol. 55(3):403–410.

Morris SB, DeShon RP. 2002. Combining effect size estimates in meta-analysis with repeated measures and independent-groups designs. Psychol Methods. 7(1):105–125.

Musonge PSL, Boets P, Lock K, Goethals PLM. 2020. Drivers of benthic macroinvertebrate assemblages in equatorial Alpine Rivers of the Rwenzoris (Uganda). Water 12(6):1668.

Olden JD, LeRoy Poff N, Douglas MR, Douglas ME, Fausch KD. 2004. Ecological and evolutionary consequences of biotic homogenization. Trends Ecol Evol. 19(1):18–24.

Page MJ, McKenzie JE, Bossuyt PM, Boutron I, Hoffmann TC, Mulrow CD, Shamseer L, Tetzlaff JM, Akl EA, Brennan SE, et al. 2021. The PRISMA 2020 statement: an updated guideline for reporting systematic reviews. Syst Rev. 10(1):89.

Pinna M, Marini G, Cristiano G, Mazzotta L, Vignini P, Cicolani B, Di Sabatino A. 2016. Influence of aperiodic summer droughts on leaf litter breakdown and macroinvertebrate assemblages: testing the drying memory in a Central Apennines River (Aterno River, Italy). Hydrobiologia 782(1):111–126.

Ptatscheck C, Gansfort B, Majdi N, Traunspurger W. 2020. The influence of environmental and spatial factors on benthic invertebrate metacommunities differing in size and dispersal mode. Aquat Ecol. 54(2):447–461.
Hussain QA, Ashok KP. 2012. Macroinvertebrates in streams: a review of some ecological factors. Int J Fish Aquac. 4(7):114–123.
R Core Team 2021. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.
Rolls RJ, Leigh C, Sheldon F. 2012. Mechanistic effects of low-flow hydrology on riverine ecosystems: ecological principles and consequences of alteration. Freshw Sci. 31(4):1163–1186.
Rosa BJFV, Rodrigues FT, de Oliveira GS, da Gama Alves R. 2014. Chironomidae and Oligochaeta for water quality evaluation in an urban river in southeastern Brazil. Environ Monit Assess. 186(11):7771–7779.
Sabater S, Bregoli F, Acuña V, Barceló D, Elosegi A, Ginebreda A, Marcé R, Muñoz I, Sabater-Liesa L, Ferreira V. 2018. Effects of human-driven water stress on river ecosystems: a meta-analysis. Sci Rep. 8(1):11462.
Saigo M, Marchese M, Wantzen KM. 2016. A closer look at the main actors of Neotropical floodplain food webs: functional classification and niche overlap of dominant benthic invertebrates in a floodplain lake of Paraná River. Iheringia, Sér Zool. 106.
Sarremejane R, England J, Sefton CEM, Parry S, Eastman M, Stubbington R. 2020. Local and regional drivers influence how aquatic community diversity, resistance and resilience vary in response to drying. Oikos 129(12):1877–1890.
Soria M, Leigh C, Datry T, Bini LM, Bonada N. 2017. Biodiversity in perennial and intermittent rivers: a meta-analysis. Oikos 126(8):1078–1089.
Stubbington R, Bogan MT, Bonada N, Boulton AJ, Datry T, Leigh C, Vander Vorste R. 2017. The biota of intermittent rivers and ephemeral streams: aquatic invertebrates. In Intermittent rivers and ephemeral streams (p. 217–243). Academic Press.
Trabucco A, Zomer RJ. 2019. Global aridity index and potential evapo-transpiration (ET0) climate database v2. CGIAR Consort Spat Inf. 10 m9.
Vander Vorste R, Obedzinski M, Nossaman Pierce S, Carlson SM, Grantham TE. 2020. Refuges and ecological traps: extreme drought threatens persistence of an endangered fish in intermittent streams. Glob Chang Biol. 26(7):3834–3845.
Vellend M. 2010. Conceptual synthesis in community ecology. Q Rev Biol. 85(2):183–206.
Vogel MM, Zscheischler J, Wartenburger R, Dee D, Seneviratne SI. 2019. Concurrent 2018 hot extremes across Northern Hemisphere due to human-induced climate change. Earths Future. 7(7):692–703.
Walters AW, Post DM. 2011. How low can you go? Impacts of a low-flow disturbance on aquatic insect communities. Ecol Appl. 21(1):163–174.
Warwick RM. 1993. Environmental impact studies on marine communities: pragmatical considerations. Austral Ecol. 18(1):63–80.
Wright JF, Berrie AD. 1987. Ecological effects of groundwater pumping and a natural drought on the upper reaches of a chalk stream. Regul Rivers: res Mgmt. 1(2):145–160.
Yue K, De Frenne P, Van Meerbeek K, Ferreira V, Fornara DA, Wu Q, Ni X, Peng Y, Wang D, Heděnec P, et al. 2022. Litter quality and stream physicochemical properties drive global invertebrate effects on instream litter decomposition. Biol Rev. 97(6):2023–2038.
Yue K, Fornara DA, Li W, Ni X, Peng Y, Liao S, Tan S, Wang D, Wu F, Yang Y. 2021. Nitrogen addition affects plant biomass allocation but not allometric relationships among different organs across the globe. J Plant Ecol. 14(3):361–371.