



Review

Ecological responses of freshwater macroinvertebrates to augmented drought: A literature review and projections

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ARTICLE INFO

Keywords:

Drought
Macroinvertebrate diversity
Bioassessments
Field-based studies
Experimental approaches

ABSTRACT

Drought significantly impacts freshwater ecosystems, disrupting all biological levels. In particular, freshwater macroinvertebrates undergo significant changes in taxonomic and functional diversity bioassessments. The effects often synergize with other stressors, such as pollution that drought can exacerbate. Several techniques have been well-developed (traditional) or have the potential (innovative) to address this issue. This review provides a comprehensive description of the impact of drought as a primary stressor on macroinvertebrate diversity. An overview of the research and projections are presented. Three conceptual pillars drive this study: taxonomic-functional responses, simultaneous pressure dynamics, and innovative techniques. Few studies have been conducted on lentic water bodies, arid and semi-arid systems, and on multiple continents. Common research keywords across continents are observed less frequently in experimental than in field studies. Most analyzed studies examine community structure, which is more common in field-based than experimental studies. Agricultural land use effect, urbanization, and invasive species are the stressors most associated with drought. Integrating traditional with advanced/innovative techniques that have hardly been applied makes it challenging to understand ecological responses comprehensively. If innovative techniques are employed to consider the dynamics of multiple stressors and to consistently estimate taxonomic and functional diversity, promising avenues for future research could be uncovered.

1. Introduction

The reduction in biodiversity within freshwater environments is an ecological issue mostly resulting from climate change and human activities (Jourdan et al., 2018; Roobavannan et al., 2018; Cid et al., 2020). Diversity is a fundamental metric of ecosystems (Chapin et al., 2000), and it is important to consider this attribute (Bonada et al., 2006) and its relationship with the degree of anthropogenic disturbance. This is necessary for ecological analysis and bioassessment practices (Hil-senhoff, 1988; Irfan and Alatawi, 2019). Macroinvertebrate diversity

has been recognized as an indicator of the status of freshwater ecosystems (Vannote et al., 1980; Rosenberg and Resh, 1993). Studies in this area have been continuously reported, primarily through identifying taxa at different scales, bioassessments, and monitoring routines (Verkaik et al., 2013). Such feedback began to consider taxonomic and functional groups together regarding morphological, physiological, and behavioral traits, among others (Merritt et al., 2002). Bioassessments examine direct responses to environmental changes caused by effects such as pollution or land use change (Figuerola et al., 2003; Fierro et al., 2021).

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<https://doi.org/10.1016/j.ecolind.2024.112153>

Received 18 January 2024; Received in revised form 15 May 2024; Accepted 16 May 2024

Available online 23 May 2024

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Drought is related to anomalous flow intermittency, posing a significant issue to bioassessment frameworks (Crabot et al., 2021). The consensus is that drought is a water deficit condition below normal levels (White et al., 2022). According to Slette et al. (2019), drought has several definitions used by ecologists, such as quantifying differences between a reference and an abnormal condition, synonymous with dry conditions, reduced rainfall, characterized by low water flow, associated with low soil moisture, etc. Severity, defined as the degree of water deficit, and intensity, defined as the ratio of severity to the duration of the event (Cavus and Aksoy, 2020), are key variables in these definitions. Significant intensity and severity events of drought can have complex consequences, including reducing hydrological connectivity, enhancing siltation, changing the structure of aquatic vegetation, altering channel shape, increasing water temperature, decreasing dissolved oxygen availability, affecting water chemistry, and altering nutrient cycles (Ledger et al., 2011; Chessman, 2015). Also, drought has been noted for various characterizations used to describe its consequences in intermittent and regular systems, such as drying patterns (Wilding et al., 2018), extremely low flow levels (White et al., 2022), watershed water scarcity (Karaouzas et al., 2018), permanent drying (Carey et al., 2021), and others. In Mediterranean climate zones, intermittent watercourses denote a temporary or reduced flow in specific locations and periods (Banegas-Medina et al., 2021). Depending on climate-induced factors, drought has been increasing in frequency and intensity over the last few decades, as reported by Cunha et al. (2019) and Adámek et al. (2022). Additionally, the impact of drought on biota is influenced by several factors, including the chronic or semi-chronic duration, the severity and intensity of the disruption, and the availability of drought refuges (Boulton, 2003).

Hydroclimatic events, or natural intermittency, can be anomalous due to more severe and intensified droughts, leading to loss of macroinvertebrate diversity (Trenberth et al., 2014). Diversity can also be influenced by low flows, which can affect various processes, including migration, speciation, niche selection, and ecological drift (Green et al., 2022); it can also affect the life cycle, body size, biomass, and secondary production of macroinvertebrates (Ledger et al., 2011). There is evidence of changes in the trophic web resulting from certain functional feeding groups of macroinvertebrates being more sensitive than others (Piano et al., 2019; Ruiz et al., 2022). In this way, certain taxonomic groups, including crustaceans, leeches, and many species of Ephemeroptera, Plecoptera, and Trichoptera, are often the most vulnerable to drought (Aspin et al., 2019a). Therefore, each taxonomic and functional group responds differently to critical flow regimes with distinctive durations and intensities related to local aspects (Aspin et al., 2019a; McDaniel et al., 2019; Mormul et al., 2022). Drying patterns as natural processes have also been affected by drought, compromising resistance, resilience, and dispersal capacity, which is distinguishable among macroinvertebrates found in intermittent and perennial watercourses (Sarremejane et al., 2021; Hill et al., 2019).

There are numerous publications about field and controlled laboratory analyses for disentangling the effects of drought on abiotic and biotic changes in different freshwater systems. The study of macroinvertebrates has been more frequent in Mediterranean and temperate zones, both field-based and experimental approaches (Wilding et al., 2018). Using macroinvertebrate-based studies in field or controlled experiments involves primarily modeling the effects of anthropogenic pressures (Menbohan et al., 2022). Considering anthropogenic impacts as an important issue, especially given the increased risk of droughts that can exacerbate the damage to freshwater organisms, the complexity of responses and impacts in ecological processes also increases (Let et al., 2021). The multidimensional dynamics of the effects of stressors on communities pose a challenge, particularly for management planning and diagnostic purposes (Ormerod et al., 2010; Soria et al., 2017). In this context, advanced/innovative techniques represent a promising methodology that could complement traditional bioassessments (White et al., 2022). For example, biomonitoring 2.0 (Baird and Hajibabaei, 2012),

“omics” techniques (Blackman et al., 2021), behavioral assessments (Guo et al., 2021), and physical/modelled simulations (Verdonschot et al., 2015; Patrick and Yuan, 2017) are some of the methods that can be used to tackle that complexity.

This review seeks to describe the most common ecological responses of freshwater macroinvertebrates to the increasing severity and intensity of droughts. The review is organized on three pillars of discussion that represent the most critical issues related to the topic: i) the responses of taxonomic and functional diversity, ii) the concurrent effect of drought with other stressors, and iii) the advanced/innovative diversity assessment techniques. It also provides an overview of the research, focusing on field-based and controlled experimental studies. Different types of analyses, such as overviews, reviews, empirical data analyses, and modeling techniques, are included. This knowledge would provide a comprehensive understanding of the effects of drought on macroinvertebrates based on evidence from multiple case studies. To account for the complexity of the responses of individual biotic groups and their diversity, this paper briefly outlines how research should proceed in the coming years.

2. Methods

As a first step, a comprehensive literature search was conducted including different types of scientific papers, such as primary research articles and reviews. The search was conducted using the Web of Science database provided by Clarivate Analytics. The Boolean search algorithm used was as follows: “macroinvertebrate OR *benthic OR macrozoobenthic AND drought AND *monitoring OR assess*”, for highly cited articles only. The filters identified articles that matched the specified date and topic parameters. The selected papers were published between 1982 and May 2022. Also, articles mainly address the following issues, lead into three conceptual pillars: differential responses between taxonomic and functional groups, concurrent effects with other stressors, and potential applications related to advanced techniques. Each section relates to one of these pillars. Research on flow regulation, such as water abstraction during droughts, was included. Regarding macroinvertebrates, no filter was applied to the set of studies that analyzed their interactions with other communities such as microalgae or fish. Our analysis is also based on a systematic review of both field-based and experimental studies. Specific analysis in detail are as follows: i) for taxonomic and functional diversity, we quantified community versus one/few taxa analyzed in the studies, and ii) we ranked the most explores stressors analyzed simultaneously with drought events. Also, we described advanced/innovative techniques mostly recommended in the papers. First, this article provides a synoptic representation of the chronological development of research and a global map illustrating the number of studies conducted in each country. In addition, a heat map of the most frequently used study areas worldwide has been created. A brief overview of the current state is provided by a network map, to illustrate the relationships between the studies conducted in different locations and the progress made over the years. The network map, classified according to the co-occurrence of keywords, shows the main research objectives and identifies relationships between work focusing on field-based and experimental approaches. We used the programs R (<https://www.R-project.org>), VOSviewer (<https://www.vosviewer.com>) and QGIS (<https://www.qgis.org>) to perform all analyzes and create figures.

3. Results

3.1. Synoptic view of research

The 283 articles selected address the conceptual pillars in great detail and were reviewed to support the discussion. Fig. 1 summarizes the temporal distribution of articles for each year, considering the approach (field-based or experimental) they followed.

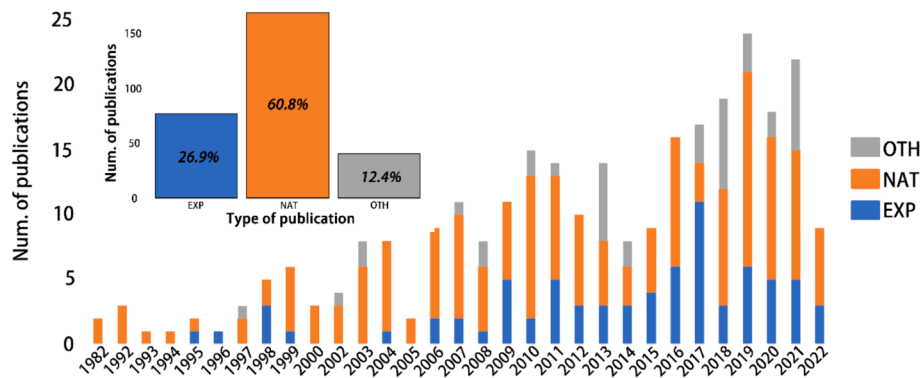


Fig. 1. Number of publications taken into account for this review, categorized by year of publication and type of assessment: direct assessments in natural environments (NAT), experimental (EXP), and other types of works (OTH). At the top left are the percentages associated with each type of publications.

Field-based studies constituted 60.8 % of the total, whereas experimental works accounted for 26.9 %. Other types of articles, such as reviews, overviews, empirical data evaluations, life history records, and modeling procedures, accounted for 12.4 % (Fig. 1). Hydrological conditions or freshwater systems include lotic systems (rivers, streams, channels, creeks, and springs) (75.2 % of the total), lentic systems (lagoons, lakes, ponds, pools, and floodplains) (11.4 %), coastal systems (estuaries and mangroves) (3.3 %), and wetland systems (10.2 %). Similarly, when it comes to climatic regions according to the Köppen climate classification, most field and experimental analyses were conducted in the Mediterranean (30.8 %) and temperate regions (30.3 %). This was followed by tropical/subtropical regions (19.2 %), arid/semi-arid regions (11.7 %), multiple regions simultaneously (5.6 %), and cold (high-altitude) regions (2.1 %). Fig. 2 illustrates all of these proportions across freshwater systems and climates.

The response of macroinvertebrates in terms of taxonomic and functional diversity is the first conceptual pillar to be addressed. Research development has primarily focused on assessing this response at the community level, with the main objective being to estimate the effect on ecological status that is either entirely or partially damaged by the consequences of drought. 10.6 % of the reviewed articles analyze one specific taxon or a few taxa. In Fig. 3, the analysis summarizes the community and taxa levels, including experimental, in-field, and other types of studies (represented as percentages of the total).

To determine the consequences on benthic macroinvertebrates, the dynamics of drought in combination with other stressors or anthropogenic pressures have been studied successively. This topic is discussed in 24.7 % of the articles reviewed. Overexploitation of certain human activities, such as the impacts of land use (mainly agricultural activities), urbanization, and invasive species (28.6 %, 12.5 %, and 12.5 %, respectively), are the most reported. Fig. 4 summarizes the most observed effects in research regarding experimental, in-field, and other types of works, expressed as percentages.

Fig. 5 presents a heat map that synthesizes the number of publications produced between 1982 and 2022 across different study areas and locations of experiments achieved. Given the high ecosystem diversity of Asia and Africa and their vulnerability to drought, very limited research has been conducted.

The network maps across keywords are illustrated in Fig. 6. In addition to words such as “drought”, “benthic macroinvertebrates”, and “stream,” there is a high prominence of concepts such as “climate change”, “traits”, “intermittent/temporary streams/rivers”, “environmental flow”, “reference conditions”, “water quality”, “resilience”, and “flow alteration”. Field-based research (Fig. 6A) has recently begun to use the keyword “climate change” more frequently in opposition to the early 2010 s. In these years, “flow permanence”, “headwater stream”, “variability”, and “disturbance” are commonly utilized. “Resilience” is a keyword associated with recent works as well. This is similar to experimental research, where “resilience” and “resistance” become more well-known. Interestingly, in the experiments, the keyword “climate change” was employed more before field-based works.

Lastly, we cover a range of advanced techniques, including those already applied and those with potential for application in a projected understanding. This review considers advanced or innovative techniques as catalysts for technological, social, and cultural change within a defined thematic scheme (Edwards-Schachter, 2018). Therefore, we chose the following advanced/innovative techniques described because they are related to freshwater bioassessment and are frequently utilized in the literature acquired and revised. Consequently, we have decided to choose the following: molecular techniques, experiments of behavior movement, and physically modeled simulated drought. They include key articles on specific topics, their main findings, and associated disciplines or approaches. In this section, we describe some case studies from reviewed articles that comprehensively examine the three conceptual pillars from the two approaches explored and ecoregions.

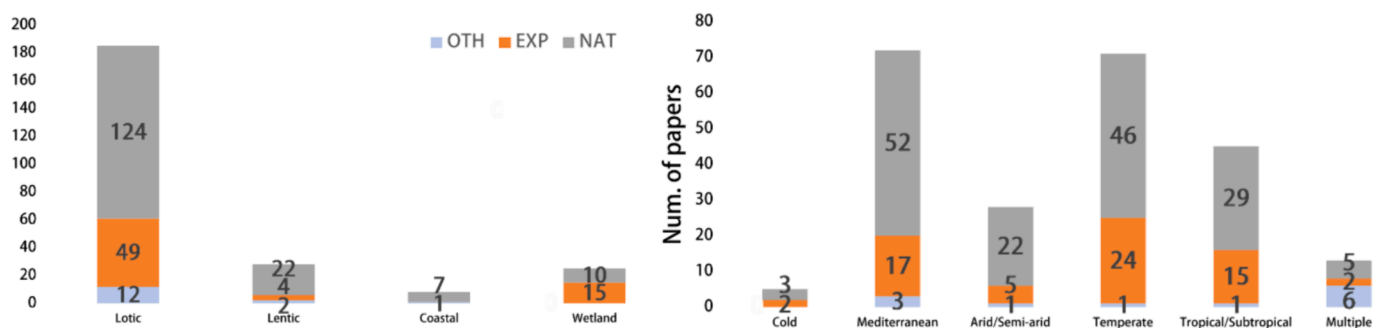


Fig. 2. Types of freshwater systems (lotic, lentic, coastal and wetland) (left) and climatic regions (Mediterranean, temperate, tropical/subtropical, arid/semi-arid, multiple, and cold regions) (right) in direct assessments in natural environments (NAT), experimental (EXP), and other types of works (OTH).

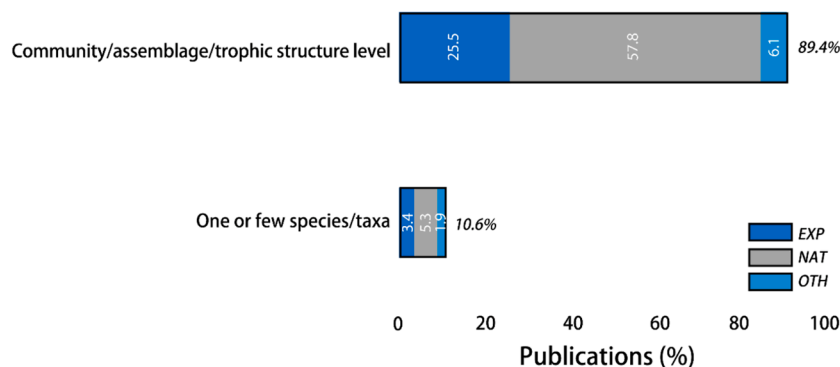


Fig. 3. Number of studies (in percentages) related to analysis addressed to community/assembly/trophic structure level and one/few macroinvertebrates species or taxa, with respect to direct assessments in field or natural environments (NAT), experimental (EXP), and other types of works (OTH).

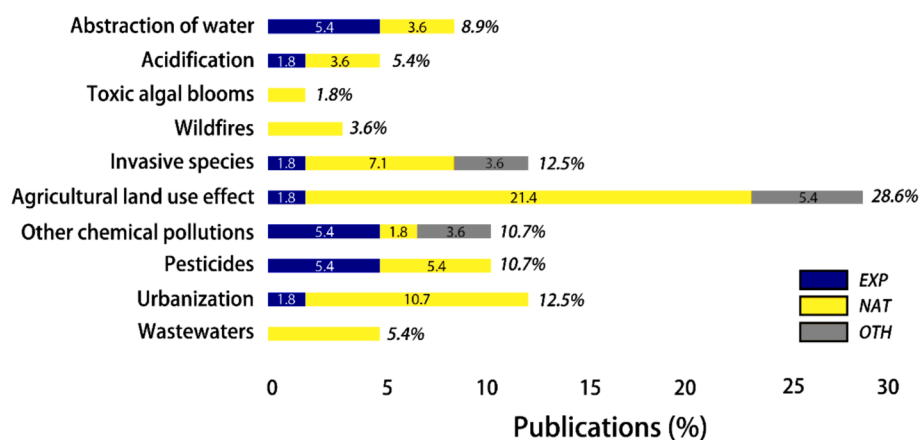


Fig. 4. Percentage of publications that focus directly on effects from several types of stressors simultaneously with drought. Of the total number of articles reviewed, 24.7% directly examine the effects of drought and at least one other stressor, from direct assessments in natural environments (NAT), experimental (EXP), and other types of work (OTH).

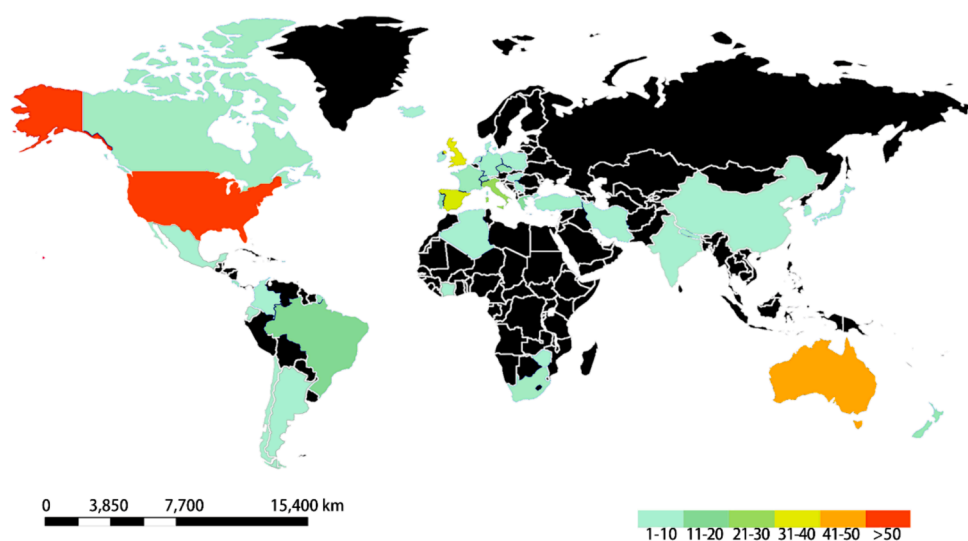


Fig. 5. Distributional geographic heat map of the study areas analyzed for the number of papers published. Black color represents countries without data or available data or studies.

3.2. Insights of taxonomical and functional responses

We describe some study cases from reviewed articles related to taxonomical and functional responses from macroinvertebrates to drought, mostly arthropods (Insecta and Crustacea class), followed

secondarily by non-insects. Given the community or individual taxonomic levels of study, members of the phylum Arthropoda are the primary group explored. The complexity of responses between species, even within the same genus or family, makes it tremendously difficult to clarify specific trends of groups concerning increased drought severity

A

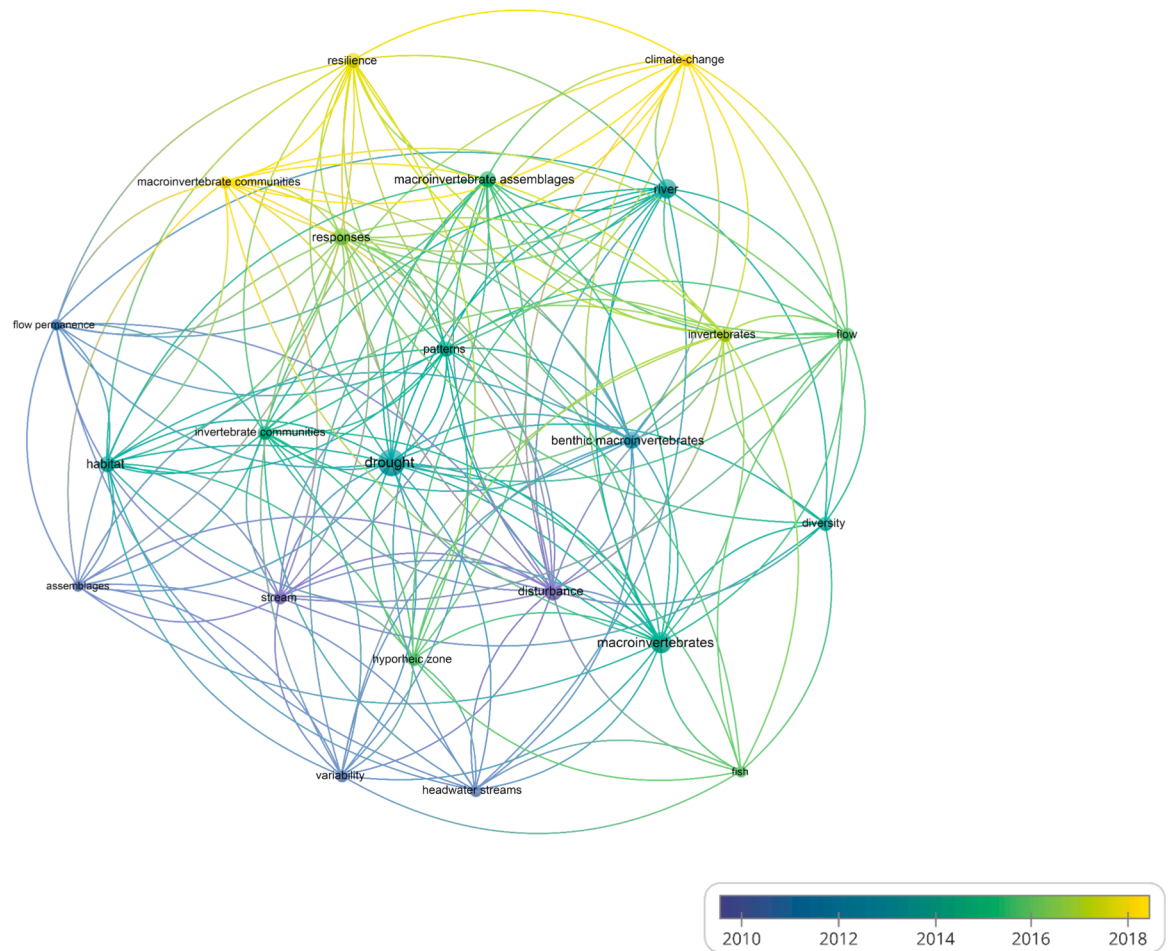


Fig. 6. Keyword analysis A) from works that emphasize field-based approaches, and B) which emphasize experimental approaches. Colors indicate the average publication year (from 2010 to 2018) in Fig. 6-A. Occurrences are related to the size of keywords and the size of circles.

and intensity. This is mainly due to differences in habitat conditions in different hydrological systems, climates, and biogeographical contexts.

Ephemeroptera, Plecoptera, Trichoptera, Diptera, and Coleoptera are the most commonly studied in relation to the effects of increased drought severity. The families Ephemeroptera, Plecoptera, and Trichoptera are primarily associated with perennial streams, widely found in riffles rather than pools (Verdonschot et al., 2015). Ephemeroptera, Plecoptera, and Trichoptera have been reported as drought-sensitive taxa in headwater intermittent streams of temperate climates (Storey, 2016). For example, drought incidents dramatically reduce the taxon richness of larval caddisflies, making them one of the most sensitive macroinvertebrates (Doretto et al., 2018). Nonetheless, in semi-arid intermittent streams, Ephemeroptera and Trichoptera show elevated richness compared to ephemeral sites (Chakona et al., 2008). This trend has been supported by experimental approaches, specifically in the effects of increased fine sediment on the silk of Hydropsychids, which are generally resilient to various environmental changes, such as drying events (Albertson and Daniels, 2016). Also, species of the genera *Hydropsyche* and *Rhyacophila*, which typically thrive in faster currents, can survive in altered habitats with reduced flow conditions (Dunbar et al., 2010). The main similarity among Ephemeroptera, Plecoptera, and Trichoptera is their dependence on water flow, sensitivity to dissolved oxygen, and intolerance to intensified drying events (Connolly et al., 2004; King et al., 2016; Peterson et al., 2017; Herbst et al., 2019).

As a basic finding from the reviewed articles, certain authors state that members of Diptera and Coleoptera can adapt well to temporary streams (López-Rodríguez et al., 2012; Verdonschot et al., 2015; Menció

and Boix, 2018). In the case of Diptera, many authors have found that they are the most abundant and ubiquitous in different habitat types (García-Roger et al., 2011; Karaouzas et al., 2011; White et al., 2012; De Jong et al., 2015). For example, Dipterans can survive in reduced oxygen concentrations during extreme drought, increasing their capacity to colonize different habitats (Jovem-Azevêdo et al., 2019; Popović et al., 2022). The adaptability of Diptera and their life strategies to many environments allow them to persist in the cover of riparian vegetation in perennial sites during extreme droughts (Griswold et al., 2008; Cooper et al., 2021). Therefore, Chironomidae members can tolerate extreme environmental conditions, including drought (Irons et al., 1993; Frouz et al., 2003). The diversity of Chironomidae increases during low water-level periods but decreases during high water-level periods (Mormul et al., 2022). Some blackflies and midges dominate after rewetting (Bogan et al., 2013) and tanyponid *Zavrelimyia* (Ledger and Hildrew, 2001). Nonetheless, under experimental stagnant and drought conditions in the field, an abundance of Chironomidae increased, while other taxa, such as Simuliidae, decreased (Hille et al., 2014). Determining a general disposition is complicated by additional elements related to the effects of drought, such as ecological succession, dispersion capacities, and life span in chironomids (Cañedo-Argüelles and Rieradevall, 2011). In Coleoptera, most groups show adaptative reactions to drying in lentic water environments (Chadd et al., 2017). Coleoptera can exhibit unique behavior, such as consuming vertebrate carrion (some Dytiscids) in contracting pools (McDaniel et al., 2019). Particular taxa of Coleoptera can thrive in hypoxic conditions when a low flow scenario leads to fragmented habitats (disconnected pools) experiencing an increased

B

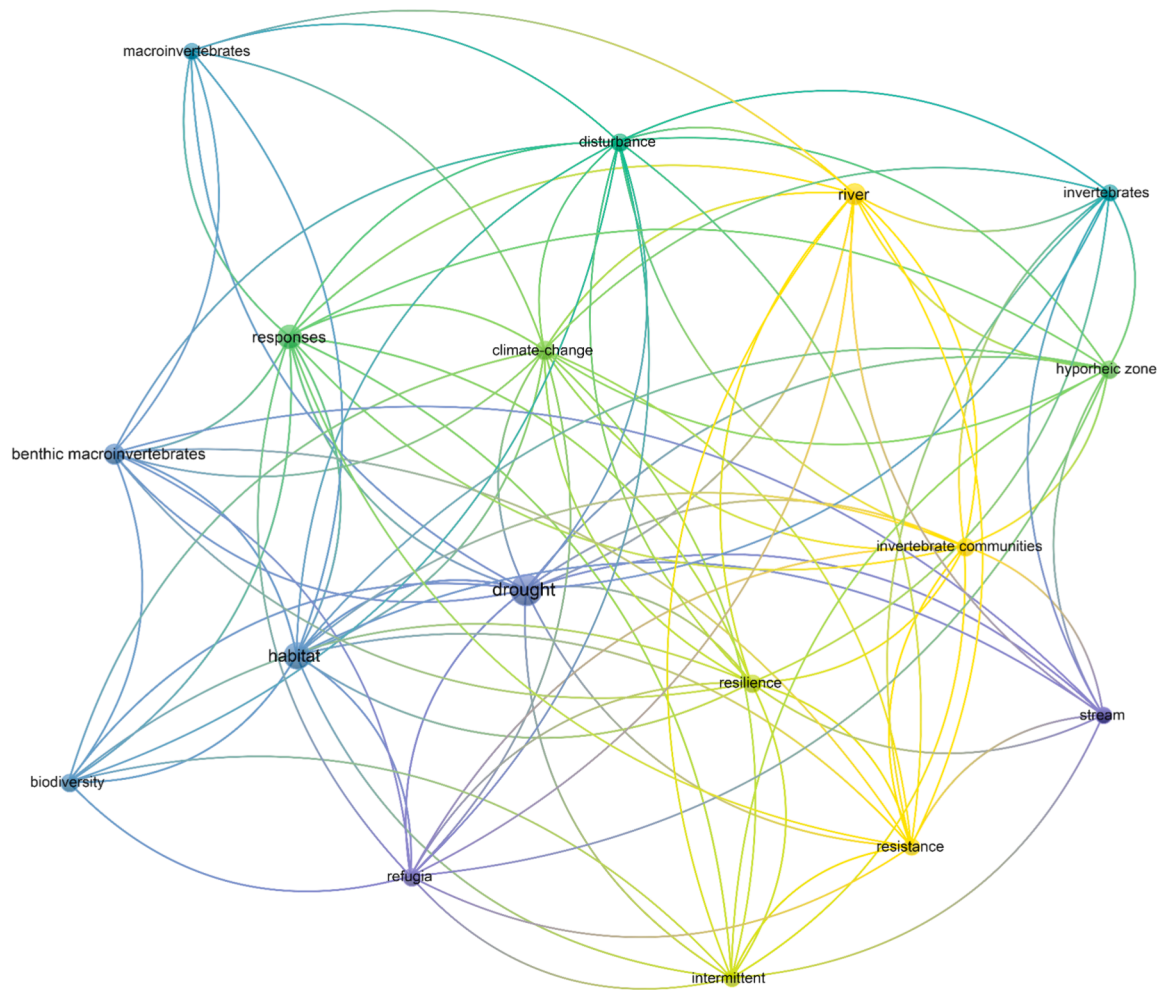


Fig. 6. (continued).

oxygen deficit (Buffagni, 2021). Together with Odonata species, a recolonization process in ponds is displayed within a couple of weeks of re-flooding (Chase and Knight, 2003).

The cases of non-insects such as Crustacea and Malacostraca are relevant examples of species models affected by drought that have been studied in terms of their recolonization dynamics (Adams and Warren, 2005). *Asellus aquaticus* dominates after dry episodes in ephemeral streams and *Gammarus pulex* in near perennial streams (Hill et al., 2019). Crayfish can survive desiccation through several strategies, involving vertical burrowing in the hyporheic zone (Kouba et al., 2016), sediment cracks for refugees (Strachan et al., 2015), and physiological limitations (Xu et al., 2022). Regarding amphipods, body size is important for migration processes, which can be affected by reduced water levels (Patel et al., 2021). According to Martínez et al. (2015), Oligochaetes dominate the community composition after rewetting but are presumed to have lower densities and biomasses than permanent streams. Other groups, such as bivalves, experience mortality during drought events, which is more remarkable in invasive species than native species (McDowell and Sousa, 2019). A myriad of responses are evidenced; the severity and intensity of drought alter ecological succession by recolonization, thermal tolerances, and hypoxic stress processes.

The taxonomic characteristics of macroinvertebrates in response to drought stressors are strongly influenced by their functional feeding conduct, as demonstrated in experimental (Ledger et al., 2011) and field-based research (Pinna et al., 2013). Some cases of shredders, collectors, scrapers, and predators are listed here. First, shredders are

highly sensitive to episodes of drought disturbance; they are often replaced by other taxonomic groups (Carey et al., 2021). Shredders can be influenced by the biomechanical and stoichiometric characteristics of plants that grow on low-flow surfaces (Dehedin et al., 2013). After a drought event in perennial temperate streams, the recolonization process by shredders differs depending on the riparian vegetation type (Monroy et al., 2017). Direct and indirect consequences of drought, such as wildfires (Cooper et al., 2021), algal blooms resulting from hydrological variations (Burgazzi et al., 2020), and inter-seasonal drought periods (Reznickova et al., 2007), also have a negative impact on shredders. Notwithstanding the presence of shredders, the decline in leaf litter breakdown has also been directly attributed to drought conditions (Leberfinger et al., 2010). Hence, the loss of shredder taxa is presumed to alter the decomposition rate of leaf litter in streams, resulting in a modification of ecosystem functions (Wenisch et al., 2017). In the case of collectors, feed fine particulate organic matter has been extensively studied in the context of low-flow disturbances in seasonal variations (Boulton and Lake, 1992; Merritt et al., 2017). Collector-gatherers and filter feeders are the most dominant groups in terms of biomass in wetlands; however, they exhibit distinct temporal dynamics and recovery patterns (Meyer and Whiles, 2008). In tropical streams, drought causes an increase in the overall density of collector-gatherers (and some grazers) at the peak of the event, but the overall taxonomic richness remains unchanged (Gutiérrez-Fonseca et al., 2020). In mountain-Mediterranean streams, the relative abundance of collector-gatherers and predators increases during late drought, mainly tolerant Chironomidae that can benefit from enhanced food resources (Herbst et al.,

2019). In experiments in wetlands disconnected from rivers, where coarse organic matter was manipulated during a severe drought, collector-gatherers were significantly modified in their trophic dynamics (Bush et al., 2017). Another study suggests a relationship between post-fire disturbance and drought conditions, which affects the composition of gathering collector assemblages in their functional characteristics (Verkaik et al., 2014). Other relevant functional feeding groups, such as scrapers, filterers, and predators, are closely linked to algal biomass and hydrological changes (DeColibus et al., 2017; Pardo and García, 2016). Scrapers are more common in streams where they rely on autotrophic materials for food, as noted by Sabater et al. (2008). Wright et al. (2003) and Let et al. (2021) report the effects of drought and other stressors for grazer-scrapers. Scrapers and attached algae form a robust trophic relationship, influenced by factors such as organism distribution and density, water flow, temperature, and sedimentation (Fenoglio et al., 2020). Scrapers are more abundant in permanent Mediterranean ponds than in temporary ones, which can affect the growth and diversity of algae and/or macrophytes (Bazzanti et al., 2009). Predator macroinvertebrates can be affected by extreme variations in water flow. For instance, López-Rodríguez et al. (2012) observed changes in food webs between wet and dry periods; the most remarkable is that the predators' role shifts to detritivores at the end of the wet season. Large specialist predators prefer isolated pools because deposit feeders' prey consume the organic matter that accumulates there (Gallardo et al., 2014). Table 1 summarizes the most recurrent characteristics and lessons of taxonomic and functional responses from the detailed study cases.

3.3. Drought synergistic effect with other stressors

The synergistic effect of drought with shifts in water chemistry caused by pesticides, wastewater discharge, and thermal pollution have

a significant impact on the physical characteristics of habitats, some considered drought refugia (Humphries and Baldwin, 2003). Also, severely low flow events alter nutrient dynamics more than the wet years (Wetzel and Likens, 2000). For example, in regions with a semi-arid climate, the limited variety of species is associated with the quality of water, primarily influenced by total ammonia nitrogen, nitrate, total phosphorus, and total suspended solids. These factors alter the community structure of macroinvertebrates and other autotrophic groups (da Rocha et al., 2016). It has been evidenced that macroinvertebrate assemblages can be affected by anomalies in nutrient dynamics in eutrophic lowland rivers in a transition from a dry to a wet year (Parr and Mason, 2003). An increase in high concentrations of ammonium in low-flow contexts has a negative effect on overall diversity and the relative abundance of shredders (Menéndez et al., 2011). A study found a negative correlation between arthropod and non-arthropod taxa in this context; however, a positive correlation was observed only for the collector-gatherer feeding group (Let et al., 2021). The presence of temperature fluctuations and pesticides in water is associated with negative impacts on Trichoptera, but net-spinning caddisflies are an exception, as it has shown tolerance and a positive response in drought scenarios (Waite et al., 2020). Additionally, the negative correlation between organophosphates and the macroinvertebrate community structure is a result of the damage caused by low flows, worsening the risk of pollutant effects (Bollmohr and Schulz, 2009; Kalogianni et al., 2017). A specific example of this is the aerial application of glyphosate to willow canopies, which affects macroinvertebrates, particularly during intense and severe droughts (Wech et al., 2018).

The concentration of pollutants in urban wastewater increases during dry seasons, exacerbated by droughts, which leads to a homogenization of functional trait composition by the type of river substrate and stream size (Figuerola et al., 2003; Mor et al., 2019). The stream

Table 1

Most recurrent responses of different taxonomic and functional groups of benthic macroinvertebrates associated with increasing drought severity and/or intensity in the literature reviewed here.

Taxonomic or functional feeding groups	Hydrologic or climatic system	Response to increasing drought severity and/or intensity	Possible ecological concerns	Reference
Ephemeroptera, Plecoptera, and Trichoptera	Headwater intermittent streams in temperate climates	Sensible to drought condition due to anomalous rates of low flow	Migration, drift, and emergence can be deteriorated	Storey, 2016
Some Trichoptera families	Lowland temperate streams	Can endure in diminished numbers within modified habitats characterized by reduced flow conditions	Maintained dominance in more altered state from these taxa	Dunbar et al., 2010
Diptera	Semi-arid watersheds	During the extreme drought period, they survive in environments with reduced oxygen concentrations, and colonize diverse habitats	Aridity scenarios can pulse predictable dynamics for intense drought events, with Diptera as bioindicator	Jovem-Azevêdo et al., 2019
Chironomidae	Shallow lake in a wetland area	Various factors linked to drought effects, and others such as ecological succession, dispersal abilities, and lifespan in chironomids contribute to the ambiguity in establishing a common trend	Micro-habitat structure such as algal mat or type of sediments play a key role in the multiple responses from Chironomidae	Cañedo-Argüelles and Rieradevall, 2011
Coleoptera	Temporary rivers	Can prosper in hypoxic conditions when a low-flow scenario results in fragmented habitats	An elevated oxygen deficit, caused by disconnected pools, would determine a decreasing habitat function	Buffagni, 2021
Oligochaeta	Calcareous streams under oceanic climate	Pioneer taxa dominate the community structure following rewetting, although it is presumed that they exhibit lower densities and biomasses compared to those in permanent streams	Hypoxic environment with low organic material processing in post-drought conditions could be evidenced	Martínez et al., 2015
Shredders	Streams of oceanic-temperate climate	If drought event is severe/intense, the recolonization process will depend on the hazards of vegetation in catchment area	Modified flux energy between terrestrial to fluvial ecosystem	Monroy et al., 2017
Collectors	Floodplain wetlands	In experimental settings where coarse organic matter was manipulated during a severe drought, there were significant modifications observed in the trophic dynamics of collector-gatherers	Adaptability times between flood pulses periods may be altered together with food webs	Bush et al., 2017
Scrapers	Riverbed sites	Water flow, temperature, and sedimentation influence organism distribution and density	Likely shift of size and morphology of scrapers, and algal susceptibility to grazing in biofilm dynamics	Fenoglio et al., 2020
Predators	Mediterranean intermittent streams	Discernible alterations in food webs between wet and dry periods can be observed, at the onset of the wet season, only a limited number of predator species are present	Changes in their diet during wet and dry periods	López-Rodríguez et al., 2012

environment downstream from wastewater treatment plant discharges can serve as a stable living habitat for some macroinvertebrates. However, these organisms are still affected by episodic drought perturbations (Canobbio et al., 2009). When examining lotic systems with comparable hydrology, it has been observed that land use significantly influences the variation in biota, but drought has a greater impact on invertebrates than the type of land use (Cowell et al., 2004). The impervious surfaces of channelized urban streams and the crops grown have a homogenizing effect on Odonata specimens. This effect is less frequent in warmer regions but more common in dry summers (Ball-Damerow et al., 2014). Furthermore, streams with an intact catchment area, minimal land use change, and undisturbed riparian vegetation offer more favorable conditions for preserving habitats during drought (Thomson et al., 2012). Ganong et al. (2021) demonstrate that poorly buffered streams experience seasonal acidification and are vulnerable to drought. However, larval midges have a remarkable tolerance for extreme pH levels. During a severe drought, changes in land use within a subtropical catchment resulted in a sudden shift in chemical parameters, including electrical conductivity, which decreased macroinvertebrate richness (Pacheco et al., 2017).

Another significant stressor contributing to shifts in macroinvertebrate communities is the presence of invasive species, which have been shown to resist extreme environmental conditions (Scharler et al., 2020). One of the most extensively researched alien organisms is crayfish, which have a significant impact on native aquatic species, especially during drought. Crayfish are generally larger, longer-lived, and more mobile than most other invertebrates and can dramatically affect the ecosystems they inhabit (Martínez, 2012). In the case of gammarids, most native species are capable of longitudinal migration (Pařil et al., 2019). Aquatic invasive species, however, can overcome specific environmental constraints; for example, they can rapidly migrate to a previously dry area and possess the ability to move both upstream and downstream (Meyer et al., 2004). In arid streams, drought-tolerant species develop a breakdown rate that does not affect that provides drought-tolerant crustaceans, despite the fact that these decrease alpha diversity of colonizing macroinvertebrates (Moody and Sabo, 2013). It is important to conduct long-term surveillance on the dynamics of invasive species, with a focus on controlling their intra- and inter-specific responses. Thus, to determine its distribution and correlation with climate factors, it is important to consider the effects of seasonal drying (Resh et al., 2013), which can be prolonged during intense droughts.

Other directly or indirectly anthropogenic-induced activities can negatively impact on macroinvertebrate diversity and may be exacerbated by drought. Examples of such activities include wildfires (Beganyi and Batzer, 2011), toxic algal blooms (Gérard and Lance, 2019), highway construction (Akay and Dalkiran, 2020), water abstraction (Miller et al., 2007; Skoulikidis et al., 2011), deposition of nutrients (Figueroa et al., 2003; Peralta-Maraver et al., 2018), acidification (Bowman et al., 2006), among others). Climate change affects various levels of ecological structure, associated with changes in temperature and atmospheric conditions, and interacts with the impacts of local or regional disturbances (Ledger et al., 2011). For instance, climate change is related to severe and intense droughts, and its impact leads to extreme events, which in turn lead to long-term disruptions (Nichols et al., 2010). Furthermore, climate change is predicted to increase the frequency and severity of drought events and threats to diversity on a larger spatial scale (Dodemaide et al., 2018). It is expected that species distributions may change or decrease due to future climate change scenarios. For instance, this could impact Griopterygidae members in neotropical catchments (Silva et al., 2019). The challenges related to the ecological effects of climate change are addressed through the response of species and communities. They may either adapt quickly to environmental variability or face a situation where the severity of the stressor exceeds their capacity to adapt (Parmesan, 2006). Similarly, stress caused by changes in water flow is expected to reduce the effectiveness and success

of restoration efforts due to the inadequate recovery period after disturbances (Veríssimo et al., 2013). Numerous studies have concluded that hydrologic changes leading to water scarcity have a greater impact on aquatic communities than chemical pollution (Arenas-Sánchez et al., 2016). Therefore, taking into account all the above-mentioned antecedents, it is reasonable to consider water quantity as a crucial factor when assessing diversity. It is also necessary to consider thermal pollution, which shaped the biomass of detritivores and shredders in harsh drought scenarios (Rivera-Usme et al., 2015). Given the persistent nature of climate change, it is anticipated that drying patterns with erratic weather will significantly shift the bioassessments (de Necker et al., 2022). As already stated, it is recommended that both water quality and quantity considerations be systematically integrated into bioassessments to achieve a comprehensive understanding and effective management.

3.4. Advanced techniques already or potentially applied

We describe only three selected advanced techniques already mentioned: molecular techniques, movement-behavioral response setups, and drought simulation methods. Their function has brought or would bring significant shifts in both theoretical and practical knowledge. The advanced/innovative methods discussed in this section are provided in Table 2.

Bioassessments based on “big data” using next-generation sequencing (NGS) can process huge amounts of data, such as metagenomics, to characterize diversity. This technology can also help clarify community structure and functioning in extreme stress situations, such as drought, which can lead to the response analysis (Woodward et al., 2013). The responses of diversity to community-level stressors and the associated functional aspects are not yet fully understood. However, the next generation of biomonitoring programs, known as biomonitoring 2.0, can help achieve these goals. This is due to their ability to generate a more comprehensive range of operational taxonomic units (OTUs) and their respective response to stressors (Leese et al., 2018). In particular, DNA metabarcoding facilitates high-throughput taxonomic identification through automatized processing pipelines, expanding the ability to detect changes in macroinvertebrate communities (Bush et al., 2019). In interpreting diversity patterns in intermittent streams, metabarcoding techniques have been evaluated for taxonomic resolution improvements. These techniques have been shown to provide more accurate information on species-specific habitat preferences due to desiccation events (Laini et al., 2020).

From the same root, omics techniques are innovative evaluations that utilize molecular tools to comprehensively understand ongoing processes at all levels of biological organization in the presence of stressors (Mierzejewska and Urbaniak, 2020). The most commonly used omics approaches include transcriptomics, proteomics, and metabolomics (Mortimer et al., 2022), applied in toxicology to identify biomarkers and clarify mechanisms of toxicity. Metabolomics has been used to diagnose stressors in a multi-stressor environment. However, further research is needed to establish a link between specific combinations of responses and specific stressors (Pomfret et al., 2020). Additionally, multi-omics or omics-based monitoring may be best suited to provide comprehensive linkages between sub-individual biomarker responses and multiple stressor scenarios (Liang et al., 2020). Applications of omics-based monitoring in specific stressors, such as drought, may involve greater complexity than the search for bioindicators. Blackman et al. (2021) suggest that the population size and dynamics of intermittent rivers and related species have not been thoroughly assessed using genomic markers. This approach could help identify specialist species and determine their relative speed of adaptation to desiccation. Another significant contribution of multi-omics is identifying drought-resistant forms of macroinvertebrates, which can be used to estimate the survival rates of specific adaptations (Pařil et al., 2019).

Experimental ecology behavior has expanded its relevance to

Table 2

Innovative techniques condensed here with the main articles containing this information, main findings related to them (innovations are already or potentially applied), and each discipline associated with their research development.

Type of innovation	Articles	Main findings	Disciplines associated
Molecular techniques	Leese et al., 2018 ; Stubbington et al., 2018 ; Laini et al., 2020 ; Blackman et al., 2021 .	<ul style="list-style-type: none"> ● Assessment of biomarkers for the recognition of specialist species and their adaptation to desiccation ● Expansion of ecosystem monitoring scope to detect changes in ecological communities ● Gain understanding of the ongoing processes on all levels of biological organization ● Next-generation sequencing (NGS) to characterize diversity in changing environments 	Genetics, –omics, Big data management
Behavioral-response assessments	Aspin et al., 2019a ; Patel et al., 2021 ; Gallegos-Sánchez et al., 2022	<ul style="list-style-type: none"> ● Colonization patterns in pre, during and post drought events ● Growth rates in altered conditions by pollution enforced by direct consequences of drought ● Movement traits and other related to determine the resistance and resilience strategies 	Engineering, Ecotoxicology, Ethology
Drought simulation	Ledger et al., 2011 ; Dézerald et al., 2015 ; Le et al., 2020 ; Waite et al., 2020	<ul style="list-style-type: none"> ● Environmental flows simulations to identify habitat suitability in groundwater and surface water ● Experimental setups for community structure organization and response ● Measurement of taxonomic compositional turnover across several environmental gradients ● Prediction of total benthic biomass reduction by several orders of magnitude of hydrologic regimes 	Engineering, Informatics, Hydrology, Mathematical modelling

multiple aspects of organisms, including intraspecific variability such as fitness, response to seasonality, and body size. This topic has been studied by several authors, including [Mancinelli \(2010\)](#). Nonetheless, progress in this matter should be addressed to deal with the direct consequences of more severe and/or intense drought events. Locomotion, dispersal, and feeding habits are the most commonly analyzed traits in bioassessment schemes and toxicological bioassays ([De Castro-Català et al., 2017](#); [Mor et al., 2019](#)). Movement behavior is easily observable in macroinvertebrates, and numerous studies have developed sophisticated methodological procedures using experimental assessments ([Longo and Mancinelli, 2014](#); [Shokri et al., 2021](#)). Migration and colonization behavior can create adverse conditions for physiological, morphological, life strategy, or behavioral adaptations aimed at seeking refuge ([Durkota et al., 2019](#)). The dispersal of organisms during emergency or submerged migration processes is hindered by drought, particularly in lotic compared to lentic systems ([Rosset et al., 2017](#)). A highly saturated substratum influences vertical migration of organisms into deeper sediment layers, as it enhances their survival ([Poznańska-Kakareko et al., 2017](#); [Vadher et al., 2017](#); [Loskotová et al., 2019](#); [Pernacker et al., 2020](#)). Survival strategies are directly related to an organism's movement or type of locomotion. In this regard, traits-based bioassessments have been incorporated into Mediterranean streams to evaluate diversity and the effects of drought. This protocol directly indicates how anomalies of ecological integrity are manifested ([García-Roger et al., 2011](#); [Elias et al., 2015](#)). Information garnered utilizing movement-behavior setups can enhance comprehension regarding the dynamics of populations across expansive spatial scales. Also, it can clarify the ramifications of various management methodologies shaped by drought on the dispersal capacity of macroinvertebrates ([Augusiak and Van den Brink, 2015](#)). Thus, a potential assessment involves the response of dispersal capacity to drought conditions aligned with ecotoxicological procedures in the pursuit of physiological constraints and potential biomarkers. This will aid in recognizing benchmarks and model responses with hydrological atypical patterns linked to specific stressors like pollution.

Cutting-edge methodologies have been developed to simulate physical drought, providing valuable insights. Simulations range from assessing the impact on water temperature to examining community structure and even studying the behavior of species ([Ledger et al., 2011](#);

[Gallegos-Sánchez et al., 2022](#)). For instance, the trophic behavior of macroinvertebrates has been extensively studied through experimental mesocosms in the field. For example, the predatory behavior of control cages may be affected by intensified droughts ([Dorn et al., 2006](#)). In recent decades, innovative methods such as mathematical modeling have been implemented in laboratory or field mesocosm environments ([Dézerald et al., 2015](#)) and through hydrological models ([Le et al., 2020](#)). The development of models of simulation specifically designed for intermittent Mediterranean river reaches has been reported. These models incorporate environmental flows and baseflows to simulate the habitat suitability of macroinvertebrates ([Theodoropoulos et al., 2019](#)). In experimental subtropical wetlands, a physical simulation was carried out on the effects of a drying-to-rewetting sequence on predation pressure responses of dragonflies and crayfish ([Knorp and Dorn, 2014](#)). Similarly, [Ledger et al. \(2011\)](#) conducted a controlled experiment using stream mesocosms to examine the impact of repeated drought disturbances on macroinvertebrate assemblages and their functional groups. Through a covariance structure analysis model, it was possible to predict that severe hydrological regimes can reduce the total benthic biomass ([Riseng et al., 2004](#)). Furthermore, a “gradient forest” modeling technique has been developed to evaluate potential species-specific thresholds and quantify taxonomic compositional turnover across environmental gradients. This technique considers substrate size, dissolved oxygen levels, and contaminants ([Waite et al., 2020](#)). Mathematical modeling has been used in hydrology and engineering to analyze the hydrodynamic interactions between groundwater and surface water. In the field of hyporheic zone ecology, implementing this technique has resulted in significant advancements and progress ([Peralta-Maraver et al., 2018](#)). As noted above, the mentioned techniques have facilitated advancements in diversity assessments. In detail, specific improvements in taxonomic determination, movement behavior responses, and interactions between physical variables and ecology of macroinvertebrates.

4. Discussion

Responses of macroinvertebrates should be assessed, taking into account different severities and intensities of drought, although this becomes more complex when combined with the synergistic effects of

other stressors. This approach provides a realistic assessment of the likely consequences of drought (White et al., 2022). From numerous climatic regions and hydrological conditions, significant progress has been made in understanding how the responses of macroinvertebrates are due to drought. First and foremost, methods for disentangling responses are focused and more efficient by functional traits. Such a perspective supports the analysis of organisms ranging from rheophilic and lentic tolerances, respiration forms, locomotion, etc. Work on both taxonomic and functional diversity is being organized and integrated using modern techniques for efficient assessment (Skoulikidis et al., 2011). Taxonomic and functional groups respond to drought events with specific trends, each with high variability. However, further research is needed on this matter.

Accordingly, lotic systems are generally the best studied. Conversely, water bodies from arid and semi-arid regions are relatively understudied (see Fig. 2). Further research is also needed in arid and semi-arid regions extending beyond developed countries' borders and encompassing several climatic regions simultaneously. Compared to taxonomic diversity, the literature on functional diversity in unexplored areas can still progress today and seems to receive more attention and consolidation. Agricultural land use, invasive species, and the effects of urbanization are the topics most analyzed in relation to drought hazards. Historical impacts have led to the accumulation of a considerable amount of data on these topics (Fig. 4). It is noteworthy that few studies have investigated these threats using experiments (in the field or other), which can be challenging to conduct at large spatial and temporal scales. The qualitative analysis of innovative techniques aims to determine their consistency using continuously improving methods. Toxicological and monitoring frameworks could serve as examples where bio-indicators and biomarkers can be used jointly in standardized methods. This enables the assessment of concurrent stressors that directly contribute to exacerbating drought conditions. For instance, trait-based assessments, increasingly used in different fields (see Fig. 6), could significantly improve by integrating with molecular techniques, such as biomonitoring 2.0 and other related ones. Considering the context of aggravated stressors by drought, bioassessments, management proposals for restoration, mitigation, and other areas on a global scale, it is essential to foster collaboration among multiple countries and organizations.

It is feasible to provide valuable insights for assessing the different variations in the dynamics of drought and extreme dryness under several conditions of perturbations. For example, it may be stated that research conducted in IRES (intermittent rivers and ephemeral streams) take an initial and important role in identifying the factors contributing to severe droughts in macroinvertebrates. It is a useful comparable framework for arid and semi-arid regions to integrate research and resource management with Mediterranean and temperate ecoregions. Moreover, it provides a basis for analysis in experimental contexts conducted in the field. Subsequently, the dynamics of carbon cycling in riparian ecosystems, as an indicator of the trophic capacity of watercourses, are concepts frequently discussed in the articles reviewed. It is important to measure the negative effects of drought on the processing of large organic matter in freshwater systems in different climatic regions. In this way, community structure patterns involved in this ecosystem function, decimated by drought, have been evaluated. Also, water extraction/diversion is a derived stressor that rarely appears in the results of the overall studies examined. This highlights that only 29.4 % of the studies specifically consider the effects of other stressors in combination with drought. This is emphasized because the damage suffered by macroinvertebrates is not solely associated with a single stressor. Therefore, gaining a more detailed understanding of the complexity of freshwater systems in an increasingly anthropogenic context is important.

Experimental analyses are needed to focus on specific species or taxa, as their number is currently limited. It is important to note that integrating community analyses and experimental approaches is still underdeveloped. This is understandable, given the significant resources

required to conduct such integrated studies (Vadher et al., 2017). The water quantity factor shows a synergistic interaction with water quality, which amplifies the overall impact. However, existing techniques are insufficient to capture this synergy. Therefore, such techniques should probably be applied using a system of multiple perspectives, including taxonomic, trait-based, and biomonitoring 2.0 methods. Interconnected techniques can shed light on the combined effects, as Aspin et al., (2019b) mentioned. For example, ecotoxicological assessments with molecular techniques to identify biomarkers could be valid where quantity and quality have been altered jointly. The upcoming challenge is to identify biomarkers specifically related to drought impacts. In this sense, only living organisms were sampled to assess the impact dynamics based on the data collected. However, the study of inactive stages (resistant forms) with molecular techniques has hardly been studied.

It is important to understand and recognize that the responses of macroinvertebrates to climate regions vary greatly, as do the potentially unknown effects of extreme conditions. For example, there are marked differences in the combinations of traits observed (Gallardo et al., 2014). Conducting these studies concurrently would improve our ability to predict potentially detrimental effects in these regions. Such predictions could then be extrapolated to other areas, considering the context of fluctuating climate patterns attributed to global change.

As for innovative techniques described, it is clear from the reports and background articles reviewed that including field methods to complement model-based simulations can improve the accuracy of diversity assessments. It would also facilitate the creation of a practical basis for implementing specific measures to protect or mitigate impacts on freshwater systems. This is similar to the extensive use of mathematical models to study, for example, in hyporheic dynamics (Peralta-Maraver et al., 2018). Molecular techniques can potentially uncover hidden information and clarify the characteristics of the biota affected. Non-destructive molecular methods such as eDNA or omics have well-structured methodological protocols for sampling. However, these protocols must be refined for rivers or streams affected by extreme desiccation, such as disturbed ephemeral streams. In such cases, the water may not be the medium through which biological material (e.g., sediments) is recovered (Blackman et al., 2021). This way, we can improve our understanding of the differences between field and experimental methods and develop tools to help organisms withstand challenging drought conditions. Furthermore, integrated strategies at all ecological levels, including ethology (i.e., movement patterns) and biological aspects (i.e., forms of resistance such as cocoons), can help to further address this complexity.

5. Conclusions

To fully understand the impact of extreme drought scenarios and distinguish between regular and abnormal episodes, it is necessary to carry out diversity assessments simultaneously across multiple continents and freshwater systems globally. In addition, simulated droughts, jointly with natural weather anomalies, are expected to be mostly addressed in the long term. This scenario requires introducing new mitigating tools to address altered water flow/volume changes. Therefore, it is necessary to propose diversity assessments with methodological protocols explicitly designed for a scenario with more intense and severe droughts. This includes formulating clear objectives, implementing simple sampling protocols, ensuring optimal specimen fixation or treatment, conducting efficient laboratory investigations, streamlining data extraction, managing databases, and performing meta-analysis. All of these steps should inevitably include the most innovative techniques to enhance a realistic understanding of the synergistic effects of drought with other stressors, as described in this review. It is essential to develop manuals, instructions, and practical tools that prioritize assessments during droughts of different intensities, while accounting for the concomitant pressures. For instance, one of the most important challenges is identifying the types of biomarkers that can be used to

detect irreversible damage at the physiological level in both the most sensitive and least sensitive species. This involves the basic information already identified, such as morphological and functional traits and life form strategies covered by molecular methods or advanced experimental setup. Based on our results, future studies should focus on these topics (conceptual pillars) separately in more depth. If novel methodologies are utilized to account for the interactions among multiple stressors and reliably bioassessments, potential pathways to future investigations could be revealed, particularly in contexts characterized by progressive climate change and weather anomalies.

Funding

This research was funded by ANID (Agencia Nacional de Investigación y Desarrollo) scholarship, grant number 21210601 and FAPESP-UFRO N°2020/06982-3.

Authors' contributions

J.M-S: idea for the article, literature search, data analysis, original draft preparation, and editing. J.G.F, M.L, P.F: idea for the article, critical revision of the work, supervision, writing, and editing. J.F.B, J-A. N, M.Z, R. P. S. O: critical revision of the work and editing. All authors have read and agreed to the published version of the manuscript.

CRediT authorship contribution statement

Jorge Machuca-Sepúlveda: Writing – review & editing, Writing – original draft, Investigation, Formal analysis, Conceptualization. **Matilde López:** Resources, Investigation, Formal analysis, Conceptualization. **Pablo Fierro:** Writing – review & editing, Supervision, Resources, Formal analysis, Data curation, Conceptualization. **Jorge F. Beltrán:** Supervision, Conceptualization. **Juan-Alejandro Norambuena:** Supervision, Conceptualization. **Ricardo Pinheiro S. Oliveira:** Writing – review & editing, Supervision, Resources. **Mauricio Zamorano:** Writing – review & editing, Writing – original draft, Supervision, Resources, Methodology, Conceptualization. **Jorge G. Farias:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

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

Data availability

Data will be made available on request.

Acknowledgements

Thanks to ANID (Agencia Nacional de Investigación y Desarrollo) scholarship grant 21210601, São Paulo Research Foundation (FAPESP) grant 2018/25511-1, and the National Council of Scientific and Technological Development (CNPq) grants 312923/2020-1 and 408783/2021-4.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2024.112153>.

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