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Abstract

Intermittent rivers and ephemeral streams (IRES), those watercourses that periodically cease to flow or dry, are the world's most widespread type of river ecosystem. Our understanding of the natural hydrology and ecology of IRES has greatly improved, but their responses to extreme events such as drought remains a research frontier. In this review, we present the state of the art, knowledge gaps, and research directions on droughts in IRES from an ecohydrological perspective. We clarify the definition of droughts in IRES, giving recommendations to promote transferability in how ecohydrological studies characterize droughts in non-perennial stream networks. Based on a systematic search of the literature, we also identify common patterns and sources of variation in the ecological responses of IRES to droughts and provide a roadmap for further research to enable improved understanding and management of IRES during those extreme hydrological events. Confusion in the terminology and the lack of tools to assess the hydrological responses of IRES to drought may have hindered the development of drought research in IRES. We found that 44% of studies confused the term drought with seasonal drying and that those that measure droughts in a transferable way are a minority. Studies on ecological responses to drought in IRES networks are still rare and limited to a few climatic zones, organisms and mainly explored in perennial sections. Our review highlights the need for additional research on this topic to inform IRES management and conservation.

Keywords: fragmentation, extreme events, non-perennial rivers, population, communities, hydrology

Significance Statement

Drought severity and frequency is increasing due to climate change, affecting river ecosystems around the world. Here, we review the current understanding, knowledge gaps, and research directions for investigating ecohydrological responses to droughts in intermittent rivers and ephemeral streams, i.e., those streams that naturally cease to flow at some point in time. Studies assessing the effects of droughts in IRES networks are still limited to a few climatic zones, countries and organisms, most probably because disentangling ecological responses from natural flow intermittence to those from drought remains a challenge.

1. Introduction

Intermittent rivers and ephemeral streams (IRES), those watercourses that periodically cease to flow or dry, are the world's most widespread type of river ecosystem (Thibault Datry, Bonada, & Boulton, 2017; Messager et al., 2021). IRES comprise 51-60% of the global river and stream network by length (Thibault. Datry, Larned, & Tockner, 2014; Messager et al., 2021), and range from ephemeral streams that occasionally flow for a few days after heavy rain to intermittent rivers that may recede to isolated pools or dry out completely. While most prevalent in arid and semi-arid regions, IRES naturally occur in all climates, biomes, and continents, including in the humid tropics and polar regions (Thibault Datry et al., 2017; Messager et al., 2021; Stubbington, England, Wood, & Sefton, 2017).

Anthropogenic global change has affected the hydrology of IRES (Hammond et al., 2021; Sauquet et al., 2021; Tramblay, Llasat, Randin, & Coppola, 2020). The duration, frequency, timing, and spatial extent of flow cessation is changing in many IRES globally due to climate change, water abstraction and land-use changes (de Graaf, Gleeson, van Beek, Sutanudjaja, & Bierkens, 2019; Larned, Datry, Arscott, & Tockner, 2010). While climate-driven shifts from perennial to intermittent flow are predicted to increase in the next decades for streams and rivers across global regions (Döll & Schmied, 2012), naturally intermittent watercourses have also become perennial due to flow regulation and effluent recharge (Halaburka et al., 2013; Hamdhani, Eppehimer, & Bogan, 2020). Our understanding of the natural hydrology and ecology of IRES has greatly improved in the past decade, but their responses to extreme events such as drought and to climate change remains a research frontier.

Contrasting with the predictable cycles of flow cessation and resumption that are typical of most IRES, hydrological droughts are unpredictable and severe events characterized by long-lasting and spatially extended deficit in surface water (Tallaksen & Van Lanen, 2004). During droughts, water discharge decreases and aquatic habitats contract beyond their long-term seasonal averages (Boulton, 2003). Droughts can cause drying conditions to extend temporally and spatially within IRES networks (Jaeger, Olden, & Pelland, 2014). During such events, perennial or near-perennial reaches may dry out partially or completely and intermittent reaches may experience longer and more severe dry periods (Lake, 2011).

Hydrological droughts lead to a cascade of abiotic changes that alter the ecological and biogeochemical functioning of IRES networks. For instance, increasing drying extent can increase river network fragmentation, which decreases dispersal capacities and thus compromises the resilience and survival of aquatic organisms (Jaeger et al., 2014). The biotic communities of IRES are typically hypothesized to be more resistant and resilient to droughts than perennial communities based on the assumption that species adaptations to regular drying provide advantages under drought conditions (Hill et al., 2019). However, there is limited evidence to date for such subdued responses to drought in IRES (Bogan & Lytle, 2011), as unpredictable and severe drying events may overcome any seasonal adaptations.

Until recently, the ecohydrology of droughts in IRES has received little attention (Hill et al., 2019; Lake, 2011). Most research on IRES has focused on understanding how seasonal drying influences ecological processes and patterns in river networks (Thibault Datry et al., 2017; Leigh & Datry, 2017; Vander Vorste, Sarremejane, & Datry, 2020). While Lake (2011) provided an extensive overview of the ecological literature of droughts in IRES, little distinction was made between studies that focus on regular flow intermittence from those on anomalous drying. Since then, a growing body of literature has documented ecological responses to droughts at individual sites or for individual ecosystem components, yet a global overview of the ecohydrology of droughts in IRES is still lacking.

Here, we review the current understanding, knowledge gaps, and research directions for investigating droughts in intermittent rivers and ephemeral streams from an ecohydrological perspective. Based on a systematic search of the literature, we first identify trends and gaps in the ecohydrology of IRES during droughts. Second, we define droughts in IRES and give recommendations to promote transferability in how ecohydrological studies characterize droughts in non-perennial stream networks. Third, we summarize knowledge on the ecohydrology of IRES, focusing on how physical, biological and ecological processes are naturally and seasonally affected by varying spatial and temporal drying patterns. Fourth, we review the ecological consequences of droughts on riverine biotic communities as well as the impact of anthropogenic stressors on ecosystem responses to droughts in IRES. Last, we provide a roadmap for further research to enable improved understanding and management of IRES during droughts. Our review highlights the need for additional research on this topic to inform conservation of IRES in the Anthropocene given the ongoing increase in frequency and severity of droughts (Cook et al., 2020; Lehner et al., 2017; Pokhrel et al., 2021; Spinoni, Vogt, Naumann, Barbosa, & Dosio, 2018) .

We performed a systematic search on Web of Science to identify literature on ecohydrological responses in IRES during droughts (see Appendix 1 for the search terms). This search combined a term related to intermittence (e.g. temporary, intermittent), a descriptor of a lotic waterbody (e.g. river, stream) and the word drought. Our word list was limited to the most specific terms used to refer to IRES to avoid collecting unspecific literature (but see Bush et al. 2020 for a more exhaustive list of terms). Whereas we obtained 12206 hits when searching for a waterbody term and drought, we only received 904 hits (i.e., 7.4% of the former) when searching for literature specifically addressing IRES and drought (Appendix 1). Of these 904 articles, 109 addressed ecohydrological responses to drought in IRES, of which 43% (n=46) used the term "drought" to refer to seasonal drying and were thus excluded from further analysis. Of the 63 remaining studies, 3 were reviews, 4 were experiments and the rest were field studies that looked at community (73%), population (23%), and/or hydro-biogeochemical processes and ecosystem function (9%) responses to drought in IRES (some studies investigated multiple types of responses, organisms, and climates). Most experiments and field studies looked at macroinvertebrate (57%) or fish (32%) responses, and 85% of studies focused on Mediterranean and semi-arid to arid climates even though 53% of IRES, by length, occur outside of those climates (**Figure 1**; see **Appendix 1**, **Fig. S1** for a map of climate zones). Knowledge on the ecohydrology of IRES during drought is thus limited. In this review, we summarize available evidence when possible but present hypotheses for those processes and scales for which little information exists.

2. Defining and describing droughts in IRES

2.1. Common definitions of drought

A drought can be most concisely defined as "a deficit of water relative to normal conditions" (Sheffield & Wood, 2011). Droughts are classified into four major types based on the impacted system of interest (Wilhite & Glantz, 1985): (1) a meteorological drought (also called climatological drought) is a deficiency in precipitation, sometimes together with increased potential evapotranspiration, that is long-lasting and spans a large area; (2) an agricultural drought (also called soil moisture drought) is a deficit in plant-available water, usually impacting crops; (3) a hydrological drought is a deficit in surface or subsurface water levels or flows (see Van Loon, 2015 for a recent review); and (4) a socio-economic drought expresses a failure of water resources systems to meet water demands by society, often combining the three other types of droughts (Mishra & Singh, 2010). A fifth kind of drought has long been subsumed under the socio-economic category but is increasingly recognized as a distinct category: ecological drought (Crausbay et al., 2017; Tallaksen & Van Lanen, 2004). An ecological drought is “an episodic deficit in water availability that drives ecosystems beyond thresholds of vulnerability, impacts ecosystem services, and triggers feedbacks in natural and/or human systems” (Crausbay et al., 2017).

The reason for such specificity in defining droughts is that management actions and policies are influenced by which type of drought is defined and how (Lloyd-Hughes, 2014). Drought response strategies vary according to the severity and extent of water deficit, and must be adapted to the differences in temporal and spatial characteristics among drought types (e.g., hydrological droughts are spatially more heterogeneous than meteorological droughts; (Changnon, 1987; Eltahir & Yeh, 1999; Van Loon, 2015). Defining drought is also needed to avoid conflation between meteorological droughts and climatic aridity (Wilhite, 1992). A meteorological drought is a finite event, an anomalous precipitation deficit, whereas aridity is a climate normal expressing a continual negative water balance due to evapotranspiration exceeding precipitation. As such, these two phenomena require distinct policies and water resource management actions. In this section, our aim is first to assess the usage of the term drought in IRES research, thus focusing mostly on meteorological and hydrological droughts, and second, to better define hydrological droughts in IRES.

2.2. Limitations of current definitions of droughts in IRES

The term drought is loosely handled in freshwater ecology. Few studies in this field define their use of the term or quantitatively describe the drought at hand (Humphries & Baldwin, 2003; Lake, 2011). Those studies that mention a type of drought usually do so by distinguishing between seasonal and supra-seasonal types of hydrological droughts (Lake 2003; Kovach et al., 2019). Seasonal droughts are seen as predictable, periodic and of limited severity, while supra-seasonal droughts are unpredictable, aseasonal or extending beyond one season, with greater magnitude and severity (Boulton, 2003; Humphries & Baldwin, 2003; Lake, 2003). Lake (2003) differentiated seasonal droughts as “press” disturbances (i.e., arising sharply, and rapidly reaching a level that is maintained constant over time; (Lake,

2000) from supra-seasonal droughts that he conceptualized as “ramp” disturbances (i.e., progressively and steadily increasing over time; Lake, 2000).

Here we contend that the use of the term “seasonal drought” is not beneficial to the scholarship of freshwater ecology, particularly as it relates to IRES. Just as meteorological droughts must be distinguished from aridity, hydrological droughts must be distinguished from natural flow intermittence in IRES. Flow cessation by itself is not an anomaly in IRES. On the contrary, water flows for only a few weeks or days every year in many non-perennial rivers (Vidal-Abarca et al., 2020). Dryland stream catchments typically exhibit great intra- and inter-annual variability in rainfall (Tooth, 2000), so flow does not necessarily follow regular seasonal patterns in non-perennial rivers — further invalidating the relevance of the term seasonal drought. Whether seasonal drought is a legitimate term is not a new debate in hydrology and meteorology (e.g., McBryde, 1982; Steila, 1981), yet we believe that its usage is particularly counter-productive to the study and conservation of IRES. Of the 109 studies returned by our initial literature search (Appendix 1), nearly half used the term drought synonymously with flow intermittence or called it only ‘drought’ rather than ‘seasonal drought’. Its usage muddles the literature on droughts in IRES (as exemplified in this review), but also harms public perception of IRES by perpetuating negative connotations associated with flow intermittence (Leigh, Boersma, Galatowitsch, Milner, & Stubbington, 2019; Rodríguez-Lozano, Woelfle-Erskine, Bogan, & Carlson, 2020).

Beyond definitions, we found that few studies characterized the droughts that they investigated in hydrological terms. Of the 55 articles we reviewed that examined a specific drought in IRES, 5 omitted to describe it altogether, 20 only provided a description of the associated meteorological drought, 22 only described the drought hydrologically, and 8 provided both meteorological and hydrological descriptors of the drought. Describing the flow conditions of a system under drought is an important first step. However, transferable measures of the attributes of droughts are also needed to enable comparison across studies, time periods, regions and watersheds — such attributes include the severity (or intensity), timing, duration, and spatial extent of the drought. In **Table 1**, we provide definitions of common flow regime and drought attributes (and see the following Section 2.3 on quantitative indices used in deriving these attributes). Of those studies that described the drought meteorologically, 64% relied on established, transferable indices (e.g., Standardized Precipitation Index, Palmer Drought Severity Index). By contrast, only 4 studies in total provided an established, transferable measure of the hydrological drought under study (e.g., hydrological return period of annual flow, Palmer Hydrological Drought Index). This lack of description of droughts by ecological studies is a long-standing issue which limits the generalizability of their findings and impedes comparative analyses (Lake, 2011). And while reporting the characteristics of the meteorological drought associated with the hydrological drought under study provides valuable information, it does not enable a standardized comparison across localities because identical meteorological droughts can result in significantly different hydrological conditions across regions and watersheds.

How meteorological anomalies translate to hydrological droughts is a complex phenomenon that depends on climate, each river's flow regime, catchment characteristics, streambed substrate, reach geomorphology, antecedent conditions, and human responses to droughts (Van Loon, 2015; **Figure 2**). Hydrological droughts tend to be spatially much patchier than meteorological droughts, which are driven by large-scale atmospheric processes (Tallaksen, Hisdal, & Lanen, 2009). Woelfle-Erskine, Larsen, & Carlson (2017) documented considerable variability in flow intermittence between stream sections less than one kilometre apart on Fay Creek, California in response to the drought of 2011-2017; these observed differences had population-level consequences on the viability of salmon habitat. Flow intermittence in IRES is also strongly linked to groundwater dynamics, whose response to droughts is mediated by additional local characteristics, so that these watercourses exhibit even greater variability in their responses to precipitation deficits (Fennell, Geris, Wilkinson, Daalmans, & Soulsby, 2020; Lovill, Hahm, & Dietrich, 2018; Shanafield, Bourke, Zimmer, & Costigan, 2021). As such, the recovery of normal baseflow is not only slow but also notoriously difficult to predict; discharge often returns to pre-drought levels years after precipitation resumes following supra-seasonal droughts (Deitch, van Docto, Obedzinski, Nossaman, & Bartshire, 2018). In about one third of unregulated watersheds across south-eastern Australia, runoff had not returned to pre-drought levels seven years after the end of the Millennium Drought, indicating a shift to an alternative stable state (Peterson, Saft, Peel, & John, 2021). In human-impacted systems, reactive over-withdrawal for irrigation and domestic uses can aggravate the effects of a mild meteorological drought into a severe hydrological drought (Van Loon et al., 2016). Given that meteorological drought attributes cannot be consistently translated to hydrological terms, descriptions of the hydrological character of droughts in case studies are needed to promote a broader understanding of the ecohydrology of droughts in IRES.

2.3. Quantitative hydrological drought indices for IRES

Hydrological anomalies are rarely quantified in IRES studies partly because existing drought indices are ill-fitted to intermittent flow regimes. More than 150 indices have been developed to describe the magnitude, duration, intensity, severity, frequency, and geographic extent of droughts (Haile, Tang, Li, Liu, & Zhang, 2020; Van Loon, 2015; Zargar, Sadiq, Naser, & Khan, 2011). These metrics can be broadly categorized between threshold level methods and standardized indices (Van Loon, 2015).

Threshold level methods rely on the establishment of a specific value for a hydrometeorological variable below which the system is considered to be in a drought (Zelenhasić & Salvai, 1987; Hisdal et al. 2004). Flow duration curves displaying the relationship between any discharge value and the percentage of time (frequency) that this discharge is equalled or exceeded form the basis of threshold indices (Smakhtin, 2001; Yevjevich, 1967). Based on this curve, a threshold discharge is picked below which a drought is deemed to occur. The threshold frequency usually ranges between Q70 and Q95 (the discharges that are exceeded 70% and 95% of the time respectively) for perennial rivers (Smakhtin, 2001; Van Loon, 2015). Additional refinements exist, including the use of temporally varying thresholds (Hisdal et al. 2004). Threshold indices enable the calculation of drought duration, severity, and frequency, and do not require that a parametric distribution be fit to the data. However, drought statistics cannot easily be transferred across geographies because there is no standard threshold in use (Van Loon 2015).

Standardized drought indices represent anomalies from a normal situation in a standardized way, thus enabling comparison across regions (Mishra & Singh, 2010). The most widely used meteorological drought index is the Standardized Precipitation Index (SPI). SPI fits long-term precipitation records to a probability distribution that is subsequently transformed to a normal distribution with zero mean and unit standard deviation (Mckee, Doesken, & Kleist, 1993). SPI can be computed over different time periods (e.g., 1, 6, 24 months), but its interpretation remains invariant to temporal and spatial scales, geographic regions, and climates. For instance, SPI12 month < -2 reflects a deficit in precipitation over 12 months that is more than two standard deviations below the long-term mean. Such a drought should theoretically occur only a handful of times every 100 years (< 5% of the time) and is usually labelled as "extremely dry" (Hayes, Svoboda, Wiihite, & Vanyarkho, 1999). The hydrological equivalent to SPI is the Standardized Streamflow Index (SSI), calculated from observed or simulated long-term discharge records (Vicente-Serrano et al., 2012).

Common drought indices, whether standardized or threshold-based, imperfectly quantify the hydrological disturbances that drive ecological responses to drought in IRES (**Figure 3**). Threshold-based methods as currently implemented are even less relevant than standardized drought indices for studying IRES because thresholds between Q70 and Q95 would result in considering any zero-flow event as a drought (**Figure 3a**, Lake, 2011; Van Loon, 2015). Higher thresholds have been proposed, between Q5 and Q20, to describe droughts in IRES (Gustard & Demuth 2008; Ko & Tarhule, 1994; Tate & Freeman, 2000), but their relevance to ecohydrological studies is questionable. In terms of standardized indices, the SPI only characterizes meteorological droughts, and the SSI cannot fully characterize the fundamental shift that occurs when a watercourse falls dry for abnormally long periods of time (**Figure 3b**). Due to this shortcoming, several global drought studies have altogether excluded arid regions from their analysis (e.g., Prudhomme et al., 2014; Wanders & Wada, 2015). While adaptations to standardized indices exist (Stagge, Tallaksen, Gudmundsson, Van Loon, & Stahl, 2015), a single index, to our knowledge, adequately characterizes hydrological droughts in IRES. Developed by Van Huijgevoort, Hazenberg, Van Lanen, & Uijlenhoet (2012), this approach combines i) a temporally variable threshold-level method, with ii) thresholding based on consecutive zero-flow days, to identify droughts that span across periods of zero and non-zero discharge, and exceed natural flow intermittence **(Figure 3)**.

We propose that a new set of indices be used to improve our understanding of the linkages between hydrological disturbance and ecological responses during droughts in IRES. We briefly present three possible indices: the threshold-level method developed by (Van Huijgevoort et al., 2012), a standardized index, and a spatially-explicit index. The first two methods require long-term streamflow records while the last one is more appropriate for intensively monitored catchments. These indices could complement existing composite hydrological drought indices (Hayes, Svoboda, Wall, & Widhalm, 2011) to improve our accounting of the effect of droughts on IRES.

The threshold-level method by Van Huijgevoort et al. (2012) yields a continuous time series of estimated percentiles for both flowing and non-flowing conditions. Periods with percentile values below or equal to a defined threshold (e.g., 10th or 20th percentile) are then considered to be droughts, from which start- and end-dates can be computed as well as the magnitude, severity, and duration of the drought. See Appendix 1 for details on how to calculate this index.

A standardized drought index for IRES only requires adapting the SSI by using flow intermittence (i.e., the number of zero-flow days) instead of mean discharge over the period of interest (see calculation in Appendix 1). The resulting time series could complement the SPI or SSI with, for example, values under -1.5 being considered severe droughts. Compared to the threshold-level method by (Van Huijgevoort et al., 2012), this approach is more comparable across regions and enables analysis at multiple time scales. However, it is likely sensitive to the choice of probability distribution and fitting method, similarly to SSI (Tijdeman, Stahl, & Tallaksen, 2020; Vicente-Serrano et al., 2012), and does not account for depressed peak and average flow. The same procedure could also be applied to describe hydrological droughts in terms of aquatic phases beyond flow cessation by instead using the proportion of days with flowing water, non-flowing water and connected pools, disconnected pools, or a dry channel (when this information is available, e.g., Sefton, Parry, England, & Angell, 2019).

Considering the importance of the spatial dynamics of wetting and rewetting in IRES networks, droughts should ideally also be described with spatially explicit indices at the catchment scale. Similarly to indices based on discharge or flow intermittence, spatial drought indices for IRES can rely on the probability of exceedance of landscape metrics computed at regular intervals. An example landscape metric is the Dendritic Connectivity Index (DCI). DCI is a network-wide indicator of longitudinal connectivity based on the expected probability of an organism being able to move freely between two random points in the network (Cote, Kehler, Bourne, & Wiersma, 2009). Reaches are considered to be disconnected from the rest of the network when pools become disconnected or dry, or because of physical barriers (e.g., waterfalls, weirds, dams). DCI was used by Jaeger et al., (2014) to quantify watershed-scale changes in connectivity resulting from increased flow intermittence under climate change in the Verde River Basin, United States. Aside from DCI, ecologically-scaled landscape indices tailored to IRES, like the average patch carrying capacity and connectivity, can also be employed to express the potential effect of droughts on network structure for a specific group of species of interest (Cid et al., 2020; Thibault Datry, Bonada, & Heino, 2016; Vos, Verboom, Opdam, & Ter Braak, 2001). Monitoring data on the aquatic state of all reaches within an IRES network can be acquired from sensor arrays (e.g., electrical resistance sensors; Jaeger & Olden, 2012), field observations by the general public and scientists (Allen et al., 2019; Gallart et al., 2017; Sefton et al., 2019; van Meerveld, Kirchner, Vis, Assendelft, & Seibert, 2019), or remote sensing (for larger streams and watercourses with limited riparian vegetation, e.g., Bishop-Taylor, Tulbure, & Broich, 2018), all of which can be complemented by spatiotemporal infilling procedures (Eastman, Parry, Sefton, Park, & England, 2021).

Long-term data are essential for all drought indices to determine what constitutes normal versus anomalous water levels (Van Loon, 2015). However, streamflow gauging data for IRES are scarce and their interpretation is error-prone (van Meerveld et al., 2020; Zimmer et al., 2020). IRES in semi-arid and arid zones are difficult to gauge, while in wetter climates, flow intermittence occurs mostly in under-monitored low-order streams (Zimmer et al., 2020). Although IRES comprise more than half of the global river network (Messager et al., 2021), less than a fifth of gauging stations monitor flow in IRES (based on the Global Streamflow Indices and Metadata archive; Do, Gudmundsson, Leonard, & Westra, 2018; Gudmundsson, Do, Leonard, & Westra, 2018). The average record length for IRES gauging stations is also 7 years shorter than for stations on perennial water courses globally (25 and 32 years for IRES and perennial stations, respectively). In comparison, drought indices usually require a minimum of 30 years of continuous data (Jain, Jain, & Pandey, 2014; Link, Wild, Snyder, Hejazi, & Vernon, 2020). Synthetic time series of historical flow intermittence can be generated (e.g., Jaeger et al., 2019; Yu, Bond, Bunn, Xu, & Kennard, 2018) but come with significant uncertainty, especially given the intrinsically anomalous nature of droughts. Further improvements in hydrometric monitoring, remote sensing, and hydrological monitoring will thus be key to improve our ability to monitor droughts in IRES.

3. The ‘typical’ ecohydrology of IRES

3.1. Temporal patterns of flow intermittence and ecological responses.

During a typical drying-rewetting cycle, IRES shift from flowing conditions to pool and dry riverbed phases. Whereas some IRES remain under a non-flowing pool phase throughout the flow cessation event (e.g. Anna, Yorgos, Konstantinos, & Maria, 2009), others shift directly from flowing to dry phases (e.g. Datry, 2012). During dry phases, some IRES maintain an active underlying hyporheic zone (Boulton & Lake, 1992), while in others, the water level of the hyporheic zone decreases quickly and becomes dry as well (Thibault Datry, 2012). Flow resumption can happen as a sudden rewetting event with an advancing wetted front driven by high discharge following rainfall (Cohen & Laronne, 2005; Corti & Datry, 2012), instigating a rapid reversal of the sequence from dry to flowing phases. But rewetting can also occur more steadily, when rainfall is localised to headwaters or when rewetting is driven by rising groundwater levels (Stanley, Fisher, & Grimm, 1997; Tockner, Malard, & Ward, 2000).

During these temporal sequences of phases, strong environmental constraints occur on aquatic organisms with typical steps (Thibault Datry et al., 2017). When flow recedes in flowing channels, lateral aquatic habitats with fringing vegetation in the riparian zone become isolated, which removes key habitats for animals that feed, shelter, spawn or emerge in these areas (**Figure 4**). When drying continues, riffles are the first in-stream habitats to disappear as pools become isolated in the channel. This represents an important step because it virtually eliminates most rheophilic fish and invertebrates from local communities (Anna et al., 2009). When a channel shifts from lotic to lentic conditions, biological communities also change abruptly towards pond-like communities (Anna et al., 2009; Bonada et al., 2020; Hill & Milner, 2018). However, if pools remain disconnected, many can become unviable for most organisms due to high temperatures, low dissolved oxygen and concentrated nutrients (Thibault Datry, 2017; Woelfle-Erskine et al., 2017). In some cases, active hyporheic inflow can replenish pools with cool and oxygenated water (Anna et al., 2009; Bonada et al., 2020). When drying continues, pools dry up and the complete disappearance of surface water is clearly the most critical stage for most aquatic organisms, from microbes to fish (**Figure 4**). Many organisms die, providing considerable pulses of food for terrestrial scavengers and predators (Corti, Larned, & Datry, 2013; Steward, von Schiller, Tockner, Marshall, & Bunn, 2012). A subset of species have developed physiological adaptation to cope with desiccation and can form a “seedbank” in the moist sediments, awaiting flow resumption to become active again (Stubbington & Datry, 2013). Last, some organisms can seek refuge in the underlying hyporheic zone (Stubbington, 2012; Vander Vorste, Malard, & Datry, 2016). However, this is true only for hyporheic zones which do not desiccate completely as the dry period persists (Pařil, Polášek, et al., 2019).

Hydrological signatures of flow cessation in IRES are strong and universal determinants of aquatic biodiversity (Arscott, Larned, Scarsbrook, & Lambert, 2010; Bonada, Rieradevall, &

Prat, 2007; Leigh & Datry, 2017). This is particularly the case for flow intermittence, defined as the proportion of the year without surface water flow. Flow intermittence has been shown to be the main driver of invertebrate taxonomic richness in rivers and streams across different continents and climate zones (Thibault. Datry, Larned, Fritz, et al., 2014). More generally, the taxonomic richness of many aquatic phyla linearly decreases with increasing flow intermittence (Thibault. Datry, Larned, & Tockner, 2014). At a given site, the duration of drying events controls the survival of stranded aquatic organisms during dry phases (Pařil, Polášek, et al., 2019) and the ability of the invertebrate seedbank to contribute to the resilience of aquatic communities upon rewetting (Stubbington & Datry, 2013).

3.2. Spatial patterns of flow intermittence and ecological responses.

The spatial organisation of habitats has critical roles for biodiversity dynamics in IRES networks. Notably, the co-occurrence at the network scale of flowing, non-flowing and dry reaches leads to the simultaneous presence of lotic, lentic, and terrestrial communities in the landscape (Thibault. Datry, Larned, & Tockner, 2014). The spatial arrangement, temporal turnover, and connectivity of these three habitat conditions constantly vary with surface water discharge and groundwater level fluctuations, in turn generating multiple colonisation and extinction events in the landscape (Crabot, Heino, Launay, & Datry, 2020). Theoretical work indicates that the distance between adjacent flowing sections within a river network is a pivotal determinant of the distribution of aquatic organisms with low dispersal abilities (Thibault Datry, Pella, Leigh, Bonada, & Hugueny, 2016). Recent empirical studies further demonstrated that network fragmentation by drying influences invertebrate community diversity and composition (Gauthier et al., 2020; Sarremejane et al., 2020). For example, Gauthier et al. 2020 showed that physical distances among habitat patches that accounted for drying better explained metacommunity dynamics in a set of ten intermittent river networks than environmental distances.

More recently, research has explored the influence of the longitudinal configuration and extent of drying on the aquatic biodiversity of river networks (Crabot et al., 2020; Sarremejane et al., 2020; Sarremejane, Stubbington, et al., 2021). The dynamics of aquatic invertebrate communities in river networks where drying occurs in headwaters, for example, is very different from those in rivers in which drying occurs in downstream sections (Crabot et al., 2020). Higher connectivity and refuge availability in downstream river sections may promote a higher local richness, but lower beta diversity, in river networks where drying occurs primarily in downstream sections compared to those where drying is predominantly constrained to headwaters (Crabot et al., 2020). This is because connectivity to colonisation sources such as refuges is higher in mainstems than in isolated headwaters (Brown and Swan 2010). Passive downstream drift from upstream habitats is more likely if drying occurs in the downstream sections of a river network (Vander Vorste, Malard, et al., 2016). In contrast, drying headwaters may only be recolonized through active upstream dispersal, which is rare and ineffective for most aquatic taxa. Insect species with strong aerial dispersal capacities can however overcome dispersal limitations among isolated headwaters (Sarremejane, Mykrä, Bonada, Aroviita, & Muotka, 2017) and their assembly may not be impacted by the configuration of drying (Cañedo-Argüelles et al., 2015). The presence of refuges such as pools and hyporheic zones also tends to increase downstream, due to increased geomorphological complexity (Jaeger, Sutfin, Tooth, Michaelides, & Singer, 2017), increased mean annual discharge (Messager et al., 2021) and enhanced surface water-groundwater interactions (Malard, Tockner, Dole-Olivier, & Ward, 2002).

4. Ecohydrological interactions in IRES during droughts

4.1. Abiotic implications of hydrological droughts

The effects of droughts on river ecosystems, including flow cessation and riverbed drying can be comparable to those occurring seasonally in intermittent rivers (Bogan, Boersma, & Lytle, 2015; Boulton, 2003). However, droughts increase the severity, duration, and spatial extent of drying beyond usual seasonal drying conditions in IRES (Lake, 2011). During droughts, rivers that typically stop to flow in scattered reaches for a few weeks per year may shrink to disconnected pools or dry across their entire length for months (**Figures 5 & 6**; e.g., Hill et al., 2019); reaches that normally recede into isolated pools from mid-summer until early autumn may fully dry by early summer, rewetting only in winter; and ephemeral streams may not flow for multiple years (e.g., 620 days; De Soyza, Killingbeck, & Whitford, 2004). During a drought, the proportion of pools that dry and the distance between pools increase compared to normal years, the size of remaining pools decreases (Vander et al., 2020), sediment and litter desiccate further and deeper, and perennial springs may dry out as the groundwater table falls.

The ecological response to drying during drought follows a ‘stepped’ pattern (Boulton, 2003) whereby periods of gradual change are punctuated by rapid transitions as each shift of state leads to the abrupt loss or fragmentation of a habitat (Boulton, 2003). During droughts, IRES may reach new states in which ecosystems are pushed past additional steps, potentially crossing irreversible thresholds.

Between shifts in aquatic states, the degradation of water quality is the primary driver of ecological responses (Lake, 2011). Prolonged water deficit during a drought induces a suite of physicochemical changes (Gómez, Arce, Baldwin, & Dahm, 2017) that occur faster and are more severe than during regular flow cessation events, thus exposing the biota to extreme conditions compared to normal years. For example, during a drought, temperature rose from 14 to 25°C and dissolved oxygen decreased from 12 to 4 mg L^{-1} in 2 weeks in three pools of the Albarine river in France (Datry, 2017), exceeding physiological thresholds for many aquatic species (Vander Vorste, Mermillod-Blondin, Hervant, Mons, & Datry, 2016a). Typically, dissolved oxygen, sediment size, and pool volume quickly decrease once riffle become disconnected while temperature and conductivity increase, with salinity sometimes reaching exceptionally high levels (Bae & Park, 2019; Golladay, Gagnon, Kearns, Battle, & Hicks, 2004; Lind, Robson, & Mitchell, 2006; Obedzinski, Nossaman Pierce, Horton, & Deitch, 2018; Woelfle-Erskine et al., 2017). As a supra-seasonal drought progressed in the Wimmera River (Australia), for example, electrical conductivity in downstream reaches increased from 4×10^3 µS cm^{-1} during the summer of the first year to 35×10^3 µS cm^{-1} the third year (Lind et al. 2006; typical sea water conductivity: ~50×10^3 µS cm^{-1}). Dissolved oxygen may initially increase due to higher light penetration conditions (e.g., Kalogianni, Vourka, Karaouzas, Vardakas, & Skoulikidis, 2017), but rising water temperature, stratification, and the accumulation of organic matter and nutrients in stagnant pools eventually lead to hypoxic events beyond the tolerance of species adapted to shorter flow cessation events (Larimore, Childers, & Heckrotte, 1959; Woelfle-Erskine et al., 2017). In Fay Creek in California, pools remained disconnected nearly twice as long during the third year of the drought (2014) compared to the first year, pushing minimum dissolved oxygen in several pools below 2 ppm, the lethal limit for resident salmonids (Woelfle-Erskine et al., 2017). Animal-mediated nutrient cycling changes over time, P and N excretion steeply declining owing to large reductions in biomass and shifts in assemblage structure of macroconsumers (Hopper, Gido, Pennock, Hedden, Guinnip, et al., 2020). The concentration of organic pollutants and toxicants increases (Boulton, 2003). Pools can also become filled with exceptional amounts of terrestrial leaf litter during longer periods of flow disconnection lasting into Autumn or if riparian plants become water stressed, further lowering oxygen levels and causing ‘blackwater’ conditions when the water turns a deep brown colour from leached dissolved organic carbon (Larimore et al., 1959; McMaster & Bond, 2008). Under drought conditions, habitat availability, dissolved oxygen levels, temperature, groundwater depth, and salinity may cross lethal thresholds for an increasing number of animal and plant species (Aspin, Hart, et al., 2019; Garssen, Verhoeven, & Soons, 2014; Gough, Landis, & Stoeckel, 2012; Hopper, Gido, Pennock, Hedden, Frenette, et al., 2020; Woelfle-Erskine et al., 2017).

As a drought continues and pools shrink to abnormally low levels, the distribution and physicochemical properties of groundwater sources increasingly drive abiotic conditions (Larsen & Woelfle-Erskine, 2018; Schlief & Mutz, 2011). Pool temperature can remain stable throughout the drought, or may even decrease as cold groundwater inflow becomes a dominant source (Larsen & Woelfle-Erskine, 2018; Schlief & Mutz, 2011). Most critical for the survival of resident organisms, however, is the contribution of groundwater to dissolved oxygen levels. Groundwater typically contributes low-oxygen water to watercourses (Hansen, 1975; Malard & Hervant, 1999). In a German lowland IRES under drought, Schlief & Mutz (2011) attributed severe reductions in oxygen concentrations following pool disconnection to the inflow of deoxygenated groundwater. However, temperature, oxygen, and conductivity are highly variable across groundwater sources. For instance, inflows of young groundwater (with DO > 5 mg L^{-1}) maintained relatively high dissolved oxygen in pools and promoted water movement in salmon-bearing IRES during the great California drought (2011-2017), potentially enhancing gas exchange across the air-water interface and preventing stratification (Larsen & Woelfle-Erskine, 2018). Groundwater seeps have also been shown to provide the only available habitat for rheophilic taxa after flow cessation (Bogan, Leidy, Neuhaus, Hernandez, & Carlson, 2019). Groundwater sources that maintain tolerable habitat conditions during regular flow cessation events and in the early stages of a drought may, however, disappear as a drought slowly propagates from surface water to groundwater (Van Loon, 2015).

Once pools have dried, and without flow resumption, sediment moisture decreases and temperature increases as drought condition persist. Gough, Landis, & Stoeckel (2012) recorded daily peaks in dry streambed temperature of 45°C to 50°C in Opintlocco Creek, Alabama (U.S.). Deeper sediment is characterized by lower temperatures and greater thermal inertia, buffering organisms from large diel variations in temperature (Gough et al., 2012).

Eventually, however, even deeper sediment, litter, and cavities that usually provide perennial refuge during regular flow intermittence become fully dry.

Abiotic conditions generally follow typical trajectories after flow cessation in normal years, but during droughts, contrasting responses can be observed from year to year, between neighbouring catchments, among reaches within a catchment, and even from pool to pool. In constrained river reaches with impervious substrate, overhanging vegetation, and upstream influx of groundwater, pools may subsist for much longer, while other sections may fully dry out (Obedzinski et al., 2018). As a drought progresses, heterogeneity in abiotic conditions first increases among habitat patches when flow ceases and pools become disconnected. Each pool follows a different trajectory that is contingent on microhabitats (e.g., pool geometry, shading, groundwater influx) and community assemblage (Hopper, Gido, Pennock, Hedden, Guinnip, et al., 2020). Woelfle-Erskine et al. (2017) documented lethal dissolved oxygen levels together with high conductivity in most pools, yet some pools maintained relatively high dissolved oxygen despite high conductivity. The bottom of pools may be microsites of high dissolved oxygen (Woelfle-Erskine et al., 2017) or completely anoxic and stratified (Schlief & Mutz, 2011). Owing to this heterogeneity in site responses, reaches and pools whose usual trajectory in abiotic conditions makes them refuges during periods of seasonal flow intermittence may become ecological traps during droughts (Vander et al., 2020).

4.2. Ecological resistance and local processes

As drought progresses, discharge, water level and aquatic habitat size and connectivity decrease, leading to successions of habitat losses that may lead to changes in community composition in both perennial and intermittent reaches of a river network (Chadd et al., 2017; Herbst, Cooper, Medhurst, Wiseman, & Hunsaker, 2019). The responses of IRES-inhabiting organisms to droughts depend on their traits and ability to withstand or avoid severe drying conditions (Robson, Chester, & Austin, 2011). Traits promoting resistance to predictable drying events may include strategies such as aerial respiration, low-oxygen and high-temperature tolerances, desiccation-resistances, and short life-cycle (Bonada et al., 2007; Matthews & Marsh-Matthews, 2003; Richards, 2010). Typically, these traits have been found in greater abundances in communities exposed to drought (Aspin, Khamis, et al., 2019; Bêche & Resh, 2007; Herbst et al., 2019) and in greater proportion in IRES than perennial communities (Leigh et al., 2016; Timoner, Colls, Acuña, & Sabater, 2019). Therefore, IRES communities are sometimes thought to be more resistant and/or resilient to drought than perennial communities because adaptations to drying could confer advantages during droughts (Hill et al., 2019; Sarremejane et al., 2020). However, aquatic communities in IRES are assembled depending on species capacity to persist during, or recolonize between, drying phases of given characteristics, including severity, duration, timing and frequency. Droughts, by modifying intermittent phase characteristics, could strongly alter IRES communities adapted to such a predictable drying regime (Bogan & Lytle, 2011; Jaeger et al., 2014).

In IRES, the duration of the dry phase is a key driver of organism persistence (Colls, Timoner, Font, & Sabater, 2020; Pařil, Polášek, et al., 2019; Pernecker, Mauchart, & Csabai, 2020; Vadher, Millett, Stubbington, & Wood, 2018). How much a drought extends this phase therefore strongly determines organism survival and post-drying community composition in IRES. Desiccation-resistance strategies can allow organism persistence during dry phases of several months to years. These strategies include dormancy at different life stage for insects (e.g. Stoneflies: Bogan, 2017; fishflies: Cover, Seo, & Resh, 2015, caddisflies: Salavert, Zamora-Muñoz, Ruiz-RodríGuez, Fernández-Cortés, & Soler, 2008) or fish (African lungfish; Fishman, Pack, Delaney, & Galante, 1986) or protective pigment and cell structures in algal and bacterial biofilms (Colls et al., 2019; Gionchetta, Oliva, Menéndez, Lopez, & Anna, 2019; Robson, 2000). For example, Jenkins & Boulton (2007) showed that microorganisms such as Rotifers and Cladoceran could be found in sediments rewetted after a 20-yr dry phase, but Cladoceran abundances decreased drastically between their 6-yr and 20-yr dry phase treatments. These strategies, conceptualized as temporal dispersal (Buoro & Carlson, 2014), allow organisms to persist locally and recolonize quickly at rewetting, but strongly depend on the duration of the dry period. Some organisms with no specific dormancy forms such as fishes (Kawanishi, Inoue, Dohi, Fujii, & Miyake, 2013; Rodríguez-Lozano, Leidy, & Carlson, 2019) and invertebrates (Golladay et al., 2004; Gough et al., 2012; Pařil, Polášek, et al., 2019; Pernecker et al., 2020; Stubbington, Gunn, Little, Worrall, & Wood, 2016; Stubbington, Sarremejane, & Datry, 2019) may find refuge in the humid subsurface sediment where they can subsist for a few days to months. For example, Pařil et al., (2019) showed that 80% of the invertebrate species of an intermittent river community could persist in dry sediments but richness decreased exponentially with the duration of the dry phase and half of the species died within the first 60 days of drying. Similarly, small benthic fishes of the genus *Cobitis* sp. can survive up to 40 days in dry sediments (Kawanishi et al., 2013) and *Uniomerus tetralasmus* mussels up to 30 weeks in moist sediment (Gough et al., 2012). If the dry phase extends beyond these thresholds, mass mortality events are likely.

Droughts could thus induce important community and population changes in IRES if drying exceeds the duration or intensity that organisms experience seasonally and have developed adaptation for (**Figure 7**, Aspin, Hart, et al., 2019; Aspin, Khamis, et al., 2019). Crossing these critical thresholds could lead to long-term and irreversible changes in population dynamics and community composition, particularly if negative responses are synchronized within the river network (Sarremejane, Stubbington, et al., 2021). Such changes can be sudden, and few instances have been documented. Identifying thresholds after which communities or population dynamics shift is therefore a pressing research need.

Survival during a drought also depends on the severity of drying, which usually increases with drought duration. Remnant pools serve as refuge for many invertebrates (Burk & Kennedy, 2013), fishes (Vander et al., 2020) and amphibians (Zylstra, Swann, & Steidl, 2019), whose populations rely on the persistence of these habitats to survive as the river network contracts. During severe droughts, pools may fully dry, after which the only *in situ* refugia left for aquatic animals are damp sediment and litter, crayfish burrows, and the hyporheic zone (Chester & Robson, 2011). Sediment moisture can be an important factor determining organism persistence in the substrate during a dry phase for biofilms (Gionchetta et al., 2019), invertebrates (Stubbington & Datry, 2013) and fishes (Coleman, Raadik, Pettigrove, & Hoffmann, 2017). During droughts the water table may recede below the hyporheic zone, leading to increased mortality of invertebrates that typically find refuge in the subsurface (Pernecker et al., 2020; Vadher et al., 2018; Vander Vorste, Mermillod-Blondin, et al., 2016b). For example, Vander Vorste, Mermillod-Blondin, et al. (2016) showed in a mesocosm experiment that the survival of Gammarids decreased by 39% as the water table decreased below 30 cm. Riparian vegetation also plays a key role in preserving streambed moisture through shading, which promotes invertebrate (Lymbery et al., 2021) and biofilm (Colls et al., 2019) survival during dry periods. Intense droughts can lead to earlier riparian tree defoliation and mortality, which increase streambed solar exposition and drying severity, causing higher mortalities of the stream biota. As groundwater levels decrease beyond the reach of roots during severe drought, the mortality of riparian trees may increase (Zhou et al., 2020).

The success of desiccation-resistance strategies may also depend on the timing of a drying event. Life cycles of IRES-inhabiting organisms are often synchronized with a predictable drying phase (Williams, 1996). The earlier onsets of drying during drought could hence affect species with specific phenology, leading for example to earlier insect emergence and shortened aquatic life cycles (Leberfinger, Bohman, & Herrmann, 2010). In the Mediterranean climate, where dry phases are considered highly seasonal and predictable (Tonkin, Bogan, Bonada, Rios-Touma, & Lytle, 2017), caddisflies of the genus *Mesophylax* sp. emerge before the onset of the drying phase, aestivate as adults in karstic caves and then recolonize intermittent streams at rewetting in autumn (Salavert et al., 2008). The success of such strategies could be compromised if drought induces earlier drying events, not allowing species to complete their aquatic larval stages. Similarly, *Demosgnathus fuscus* salamander larvae (North Carolina, U.S.A.) are strictly aquatic from the time they hatch (August to October) until metamorphosis the following spring, such that free-flowing water is critical for larval survival during this period of the year (Price, Browne, & Dorcas, 2012). Finally, by altering river network connectivity earlier in the year, droughts can also prevent longitudinal migration, stopping fish from reaching in-stream refugia and resulting in reproductive failure (e.g., anadromous *Oncorhynchus kisutch* coho salmon, Woelfle-Erskine et al., 2017; potamodromous *Chasmistes cujus* Cui-ui, Scoppettone et al., 2015).

The indirect role of biotic interactions like predation and competition in shaping the ecological impacts of drought in IRES is poorly studied (Bond, Lake, & Arthington, 2008; Boulton, 2003). While the relative role of local and regional processes in shaping community assembly is increasingly well-studied in IRES (Cañedo-Argüelles et al., 2020; Rolls, Heino, & Chessman, 2016), the relative strength of environmental filters versus biotic interactions in determining population and community responses to drying has received comparatively little attention. As habitats shrink, animal densities increase in remnant pools and refugia, leading to crowding, increased predation and competition (Matthews & Marsh-Matthews 2003). Competition and predation may even prevent species from accessing refuges (Magoulick & Kobza, 2003). For instance, competitive exclusion of steelhead salmon (*Oncorhynchus mykiss*) from deeper pools by coho salmon may drive differences in response to drought among these two species in intermittent streams of California (Woelfle-Erskine et al. 2017). This phenomenon is also evidenced by shifts in dominance between native and non-native species after droughts (see Section 4.5). As the ratio of aquatic to terrestrial habitat decreases in the channel, aquatic organisms become increasingly vulnerable to terrestrial predation as well (Magoulick & Kobza, 2003). Terrestrial predation of smaller freshwater mussels was an important driver of mortality in *Westralunio carteri* after emersion and may explain size-based differences in burrowing behavior observed during a drought in south-western

Australia (Lymbery et al., 2021). We expect that shifts in biotic interactions observed during seasonal drying are amplified by more intense and prolonged drying, yet the potential crossing of tipping points during droughts (e.g., local extirpation of a predator or competitor) may lead to a deeper reshuffling of interspecific relationships.

4.3. Ecological resilience and regional processes

Droughts are spatially extended events that impact entire river networks, inducing extended changes in aquatic habitat configurations and increased fragmentation (**Figure 6**, Allen et al., 2019; Jaeger et al., 2014; Sefton et al., 2019). Such extended changes hinder organism resilience — i.e., their capacity to recolonize and re-establish viable populations post-drought (Chester & Robson, 2011) — by affecting survival in refuges and connectivity to potential recolonization sources. Organism resilience depends on functional attributes like dispersal capacity, life-cycles and reproductive strategies (Robson et al., 2011). For example, multivoltine organisms with strong dispersal capacity and/or high number of propagules may be able to recover from drought more quickly than long-lived organisms with weak dispersal capacity (Bogan et al., 2017; Robson et al., 2011). Algae and bacteria constituting biofilms can recover within a few days/weeks of water resumption from dormant forms and through drift (Romaní & Sabater, 1997). Aquatic invertebrate community recovery from drought in IRES typically takes from six months to a few years, longer than recovery from regular flow intermittence (Hill et al., 2019; Pařil, Polášek, et al., 2019). Recolonization by invertebrates may occur through drift, active aquatic migration (Eveleens, McIntosh, & Warburton, 2019; Pařil, Leigh, et al., 2019), and/or overland aerial dispersal (Bogan & Boersma, 2012; Cañedo-Argüelles et al., 2015). Fish mainly recolonize from downstream or perennial pool refuges (Davey & Kelly, 2007), usually within a few days to months (Magalhães, Beja, Schlosser, & Collares-Pereira, 2007; Magoulick & Kobza, 2003). However, biological resilience to drought in IRES also depends on local resistance (see previous section), connectivity to and distance from regional refuges, and time between drought events (Jaeger et al., 2014; Sarremejane, Stubbington, et al., 2021).

Increasing drying extent may reduce recovery potential by increasing the proportion of populations impacted by low flow and drying conditions across the river network and thus limiting rescue effects post-disturbance (Crabot et al., 2020; Sarremejane, Stubbington, et al., 2021; Zelnik, Arnoldi, & Loreau, 2018). Sarremejane et al. (2021) showed that increasing drying extent during drought could lead to synchronous declines in invertebrate populations across an intermittent river network, particularly for species with low resistance and/or resilience capacity. Such decline drastically increased population extinction risks after three drought years with 50% of the network fragmented by drying. Drought may particularly impede community and population recovery if perennial refuges become intermittent and disconnected (Bogan & Lytle, 2011; Hopper, Gido, Pennock, Hedden, Frenette, et al., 2020; Vander et al., 2020). Many mobile organisms such as amphibians, fish and insects may find refuge in specific perennial pools or perennial river sections, sometimes with strong fidelity, and recolonize intermittent sections post rewetting (Bogan et al., 2019; Chester & Robson, 2011; Davey & Kelly, 2007). Thus, the contraction and loss of those habitats may have long term impacts on community and population structures at local and regional scales (Bêche, Connors, Resh, & Merenlender, 2009; Bogan et al., 2015; Bogan & Lytle, 2011; Sponseller, Grimm, Boulton, & Sabo, 2010).

The connectivity and distance of a community to perennial refuge is an important driver of post-drying community composition (Bogan & Boersma, 2012; Bogan et al., 2015; Sarremejane et al., 2020; White et al., 2018). Community recovery from drying and drought therefore vary among sites within a network depending on their connectivity (Gauthier, Le Goff, Launay, Douady, & Datry, 2021; Sarremejane, Truchy, et al., 2021). Isolated headwaters, for instance, are likely to take longer to recover from disturbance than more connected downstream sections (Tornwall, Swan, & Brown, 2017). Whether a drought predominantly affects headwaters or downstream reaches may thus have contrasting outcomes on the composition of communities, their spatial variability (i.e. β diversity; Crabot et al., 2020) and resilience. Therefore, increasing drying extent during drought could affect regional processes, leading to important changes in metacommunities and metapopulation dynamics, particularly if refuges are lost or if drought is too extended or frequent to allow resilience.

The frequency of drying and rewetting events can alter population and community persistence, by affecting the time between drying events and thus resilience capacity (Crabot et al., 2020; Leigh & Datry, 2017). If the frequency of drying events is high, many species may not have time to recover during short flowing phases, hence, diversity typically declines with increasing drying frequency (Leigh & Datry, 2017). The proportion of multivoltine organism abundances typically increases or remain constant compared to semivoltine insects during droughts (Aspin, Khamis, et al., 2019; Herbst et al., 2019), indicating that organism with shorter and multiple cycles per year could be better able to cope with droughts, as they can recolonize and develop quickly between drying events. Short rewetting events during droughts often caused by precipitation could also allow the invertebrate seedbank (Stubbington & Datry, 2013) and biofilms (Gionchetta et al., 2019) to persist by maintaining moisture within the sediment (**Figure 7**). More frequent droughts may however lead to long term changes in community compositions within IRES networks if the time between drought events is too short to allow long-lived organism populations to recover between drought events.

4.4. Community responses across flow intermittence regimes

Comparisons of stream community responses to drought across reaches with different intermittence regimes have yielded mixed evidence (Bêche et al., 2009; Cañedo-Argüelles et al., 2020; Herbst et al., 2019; Hill et al., 2019; Rolls et al., 2016; Sarremejane et al., 2020; Sarremejane, Stubbington, et al., 2021; Westwood, England, Johns, & Stubbington, 2020). Several studies found congruent drought-induced changes in community composition across streams with different permanence regimes (Bêche et al., 2009; Herbst et al., 2019). For example, Bêche et al. (2009) showed that invertebrate community composition of perennial, intermittent and ephemeral streams in semi-arid California all shifted during a drought and had not returned to an initial (pre-drought) state even 8 years after the end of the drought. In the same study, fish populations were equally affected by drought across intermittence regimes but recovery differed; whereas fish populations recovered within 2 years in perennial sections, they took 5 years in ephemeral streams and did not recover in intermittent sites, likely due to differences in connectivity to refuges among sites. Elsewhere, responses to drought have been shown to vary across permanence regimes. Hill et al. (2019) and Sarremejane et al. (2019) observed that the responses of invertebrate communities to drought in English streams with different permanence regimes differed, and that near-perennial communities (i.e., experiencing drying only during drought events) took longer or did not completely recover by the end of their study compared to communities in more intermittent sites (which also showed variable recovery trajectories). These studies therefore suggest that intermittent river communities can, in some instances, be more resilient to droughts than those of perennial rivers. What drives these contrasts in long-term responses to drought among locations remains unresolved — community resilience may depend on the studied organism (e.g., fish vs. macroinvertebrate; Bêche et al., 2009) and their traits, the influence of additional stressors, or on the severity of the drought compared to that experienced over evolutionary times. Further research is needed to determine under which biotic and abiotic conditions community response to drought may differ along a gradient of intermittence.

From a metacommunity perspective, variable responses among reaches of distinct permanence regimes across a river network may enhance recovery because asynchronous responses between communities promote rescue effects post-disturbance (Sarremejane, Stubbington, et al., 2021). Increasing variability among communities (i.e., beta diversity) may occur at the network scale during drought if habitat conditions become more heterogeneous and connectivity decreases (Rolls et al., 2016). Alternatively, extreme droughts may also induce declines in beta diversity if communities become spatially homogeneous due to the selection of a resistant subset of taxa from the regional species pool (γ diversity; Chase, 2007).

Most research on community response to drought in IRES networks have focussed on responses of perennial sections and refuges (Bogan & Lytle, 2011; Sponseller et al., 2010). For example, Bogan & Lytle (2011) showed that the drying of permanent pools in a formerly perennial river network during a supra-seasonal drought caused drastic shifts in invertebrate communities. Following the drought, community composition did not recover and instead reached a new stable state: large-bodied top predators present before the drought were replaced by more abundant and smaller meso-predators. Permanent shifts in the flow regime of river sections from perennial to intermittent following a drought are likely to have long-term impacts on aquatic communities in IRES networks, particularly if perennial refuges run dry (**Figure 7**). Rapidly improving our understanding of these shifts from perennial to intermittent regimes is key as they become more common with climate change and increasing water demands.

4.5. Droughts in interaction with anthropogenic stressors

Droughts in IRES often co-occur with anthropogenic stressors (Thibault. Datry, Larned, & Tockner, 2014). These stressors include climate change, fragmentation by dams, biological invasions, water abstraction and pollution, and land-use alterations. The impacts of droughts on IRES are likely to accentuate — or be accentuated by — the effect of other anthropogenic stressors as multiple interacting stressors may lead to synergistic impacts on the ecosystems (but see Jackson, Loewen, Vinebrooke, & Chimimba, 2016). However, while the multi-stressor environments framework has bloomed in the past decade, particularly in freshwater ecosystems (Ormerod, Dobson, Hildrew, & Townsend, 2010), its application in IRES is still in its infancy (Marshall & Negus, 2018), so that there is a dearth of evidence on how drought interacts with other stressors in these ecosystems.

As the climate is changing, droughts may not only become more frequent and severe, but also be more frequently associated with other extreme events, including floods and heatwaves (Derouin, 2021). For example, drought and floods are two extremes with contrasting characteristics, and traits conferring resistance to drought may differ from those conferring resistance to floods (Eveleens et al. 2019). The combined occurrence or succession of these contrasting extreme events may thus strongly impact freshwater ecosystems (Woodward, Bonada, Feeley, & Giller, 2015). Heatwaves may also accentuate the effect of droughts by leading to faster drying of — and increased temperatures in — aquatic habitats remaining after flow cessation (e.g., disconnected pools). Such warming may induce increased and premature organism mortality, as well as changes in microbial (Arias Font, Khamis, Milner, Smith, & Ledger, 2021) and fish activity (Mameri, Branco, Ferreira, & Santos, 2020). Drought can also trigger wildfires (Littell, Peterson, Riley, Liu, & Luce, 2016), which in turn can have deleterious effects on amphibians (Zylstra et al., 2019), fishes (Turner, Osborne, McPhee, & Kruse, 2015) and invertebrates (Robson, Chester, Matthews, & Johnston, 2018; Verkaik et al., 2015) populations and communities. For example, Zilsta et al. (2019) showed that Leopard frog populations declined during drought years and downstream of sites exposed to wildfires due to increased post-fire erosion. Robson et al. (2018) also found that fires and droughts could have antagonistic effects on the invertebrate communities of Australian streams. For example, the abundance of filter-feeder invertebrates increased with fire, which counterbalanced the negative effect of drought on this trophic guild.

Combined alterations in flow and thermal regimes caused by drought can also favour establishment and dominance of non-native species of riparian plants (Glenn & Nagler, 2005; Scott, Reynolds, Shafroth, & Spence, 2018), fish (Bêche et al., 2009; Bernardo, Ilhéu, Matono, & Costa, 2003; Hopper, Gido, Pennock, Hedden, Frenette, et al., 2020; Jaeger et al., 2014; Rogosch et al., 2019; Whiterod, Hammer, & Vilizzi, 2015) and invertebrates (Kouba et al., 2016; Larson, Magoulick, Turner, & Laycock, 2009) in IRES. Such invasions are facilitated if invasive species are more resilient and resistant to drought than native species. For example, Kouba et al. (2016) found that non-native crayfish were able to survive longer than native European species during drought because of their capacity to burrow deeper into the sediment. Drought can also benefit non-native predators at the expense of small-bodied native species (Propst, Gido, & Stefferud, 2008), presumably owing to habitat contraction and increased biotic interactions (Magoulick & Kobza, 2003). Conversely, drought can limit the progression of invasive species by increasing their mortality or decreasing their dispersal through increasing fragmentation, the same way natural intermittence may prevent the establishment of non-native species (Bogan et al., 2019; Coleman et al., 2017). However, evidence of drought-induced stalling of non-native species establishment in IRES is lacking. Anecdotal observation of Asian clam (*Corbicula fluminea*) mortality due to hypoxia in drought-stricken stream reaches of southwestern Georgia (U.S.; Golladay et al., 2004), range expansion limitations of Brown trout (*Salmo trutta*) in the upper reaches of the Lerderderg River (Australia; Closs & Lake, 1996) and the extirpation of exotic common carp (*Cyprinus carpio L.*) populations from Granite Creeks in Victoria (Australia; Lake, 2003) are the only examples in IRES known to the authors. Therefore, it is likely that recurrent drought tends to accelerate rather than slow the progression of invasive species within IRES networks.

Anthropogenic activities in IRES catchments, including agriculture or wastewater treatment, can induce increased concentrations of water pollutants or eutrophication, whose effects on IRES can be amplified when combined with drought. For example, as water recedes during drought, anoxia and the concentration of chemical compounds may increase to unsafe levels for aquatic biota taking refuge in pools (Palma et al., 2020). Overall, however, we know little about the interactions between droughts and human induced pollution, particularly in IRES.

Finally, fragmentation caused by dams and weirs is likely to compound the effect of droughts by limiting recolonization capacity post-drought. Under non-drought conditions, biodiversity dynamics in an IRES networks were shown to be overwhelmingly driven by permanent fragmentation, including weirs and small retention ponds, rather than by temporary fragmentation from drying (Gauthier et al. 2021), suggesting that anthropogenic barriers can be a strong determinant of diversity patterns in drying river networks. Recently, Marshall, Lobegeiger & Starkey (2020) showed that instream barriers such as weirs reduced fish movement opportunities by more than 70% during and following a two-year drought in south Australia, compromising fish access to refugess and post-disturbance recovery.

5. Conclusion and perspectives

Although a rich body of literature exists on the effects of droughts on flowing waters, research on their impacts on IRES ecosystems remains limited. Confusion in terminology and the lack of tools and data to assess the hydrological responses of IRES to drought may have hindered development of drought research in IRES. We found that 43% of studies confused the term drought with seasonal drying and that a minority of studies measure droughts in a transferable way. Studies on ecological responses to drought in IRES networks are still rare and limited to a few climatic zones, countries, organisms, and mainly explored in perennial sections, most probably because disentangling responses between natural flow intermittence and drought remains a challenge. By accentuating the severity, duration, and extent of drying across IRES networks, droughts may cause irreversible ecohydrological changes if tipping points are crossed and resilience is compromised. Network-scale perspectives encompassing a gradient of flow intermittence are needed to explore the drivers of ecological responses to droughts in IRES.

We identified interdisciplinary research directions (Table 2) whose pursuit should improve our understanding of the hydrological, ecological and socio-economical responses of IRES to drought. These research directions are non-exhaustive but represent gaps that should be addressed as priorities to develop further drought-research in IRES. In this review, we strictly focused on ecological responses to drought at the scale of populations and communities yet we also lack a synthesis of the effects of droughts on the biogeochemistry and ecosystem services of IRES (Arce et al., 2019; Datry et al., 2018; Table 2). As droughts are unpredictable and their legacy on hydrological and ecological processes may last for years, additional long-term monitoring of IRES networks is needed to capture the effects of extreme events on these ecosystems and measure their resilience (Kovach et al., 2019; Table 2). Research involving ecologists and hydrologists could help develop metrics for identifying tipping points beyond which the hydro-ecological resilience capacity of IRES is compromised (Table 2). More generally, increased collaboration between hydrologists, ecologists, social scientists and managers is needed to explore the impacts of droughts on IRES and the adverse effects of shifts from perennial to intermittent regimes from a socio-ecological perspective (Table 2). Such interdisciplinary research could help designing nature-based solutions (Maes & Jacobs, 2017) to ensure the resilience of IRES hydro-ecosystems and dependent socio-economical systems in a changing and uncertain climatic future.

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Data availability statement

The data used in this review will be deposited on an open repository such as figshare.

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Tables

Table 1: Definition of the different attributes of flow regime and hydrological drought

Phenomenon	Attribute	Definition
Flow regime (adapted from Poff et al. 1997[1])	Magnitude	The amount of water moving past a fixed location per unit of time (e.g. mean minimum monthly discharge)
	Frequency	How often a flow above a given magnitude recurs over some specified time interval (e.g., annual number of no-flow events)
	Duration	The period of time associated with a specific flow condition (e.g., mean monthly number of days having zero daily flow)
	Timing (or predictability)	The period and the regularity with which flows of defined magnitude occur (e.g., mean date of the first no-flow occurrence)
	Rate of change	How quickly flow changes from one magnitude to another (e.g., dry-down duration, the number of days from a local streamflow peak to the first occurrence of no-flow)
Hydrological drought (adapted from Dracup et al. 1980[2] and Mishra and Singh 2010[3])	Timing	Initiation and termination dates of a streamflow deficit
	Duration	The number of consecutive time periods (e.g., months, years) for which the streamflow is below the long-term mean or another defined threshold reflecting a critical level
	Severity	The cumulative deficit of streamflow below the critical level for that duration
	Intensity (or magnitude)	The average deficit of streamflow for that duration (severity/duration)

	Spatial extent	The areas, river sections, basins, or regions affected by streamflow deficit (e.g. the cumulative dry river length)

(1) Poff, N. L. R., Allan, J. D., Bain, M. B., Karr, J. R., Prestegaard, K. L., Richter, B. D., Sparks, R. E., & Stromberg, J. C. (1997). The natural flow regime: A paradigm for river conservation and restoration. *BioScience*, *47*(11), 769–784. https://doi.org/10.2307/1313099; (2) Dracup J.A., Lee K.S., Paulson E.G., (1980). On the definition of droughts. *Water Resource Research*, 16, 297–302; (3) Mishra, A. K., & Singh, V. P. (2010). A review of drought concepts. *Journal of Hydrology*, *391*, 202-216. https://doi.org/10.1016/j.jhydrol.2010.07.012

Table 2: Research questions and perspectives to improve our understanding of IRES responses to droughts.

Research question	**Scientific breakthrough examples**	**Disciplines**
What drives the propagation from meteorological drought to hydrological drought in IRES?	Identify river reaches whose hydrology is most severely affected by meteorological droughts.	Hydrology, hydrogeology, modelling
How do the delayed onset and recovery of groundwater drought affect IRES ecosystem resilience?	Understand the role of groundwater in mediating the short and long-term effects of hydrological drought.	Hydrology, hydrogeology, modelling
To which extent are drought impacts amplified by increased human withdrawals of water during droughts?	Understand how surface and groundwater abstraction dynamics interact during drought episodes in IRES.	Hydrology, hydrogeology, modelling
Where and under which conditions are IRES ecosystems, including organisms, populations and communities are most sensitive to drought?	Determine the tipping points in drying patterns after which the resilience of individual species and communities in IRES river networks is compromised.	Hydrology, ecology

What are the long-term hydrological and ecological trajectories in IRES after droughts?	Understand the legacy of droughts on IRES resilience.	Hydrology, hydrogeology, ecology
How do floods and droughts interact in IRES?	Quantify the relative roles of extreme hydrological events on IRES resilience.	Hydrology, hydrogeology, ecology
What is the impact of drought compared to seasonal intermittence on biotic interactions?	Disentangle the relative role of abiotic and biotic factors in determining community trajectories in IRES after droughts.	Ecology
How do droughts in IRES networks affect nearby terrestrial ecosystems?	Identify the ripple effects of droughts in terrestrial food webs during and after the event.	Ecology, biogeochemistry
What are the effects of drought on local to network-scale ecosystem processes (e.g., decomposition, CO_2 emissions)?	Understand how droughts can disrupt ecosystem-wide processes.	Hydrology, ecology, biogeochemistry
How do IRES ecosystems respond to different suites of interacting stressors?	Quantify the interactive effects of multiple stressors in a context of flow intermittence.	Hydrology, ecology, ecotoxicology
What are the differences in ecological responses between natural and human-induced IRES?	Predict socio-ecological consequences of shifts from perennial to intermittent flow regimes and vice-versa.	Hydrology, hydrogeology, ecology, ecotoxicology, social sciences

How do droughts affect the provision of ecosystem services in IRES river networks?	Translate the changes in biophysical templates due to drying into socio-economical responses.	Hydrology, hydrogeology, ecology, social sciences, economy, modelling
How can societies mitigate and adapt to drought-induced changes in flow regimes?	Test and develop management strategies, including Nature-Based Solutions to mitigate the effects of droughts in IRES.	Hydrology, hydrogeology, ecology, social sciences, economy, modelling

Figures

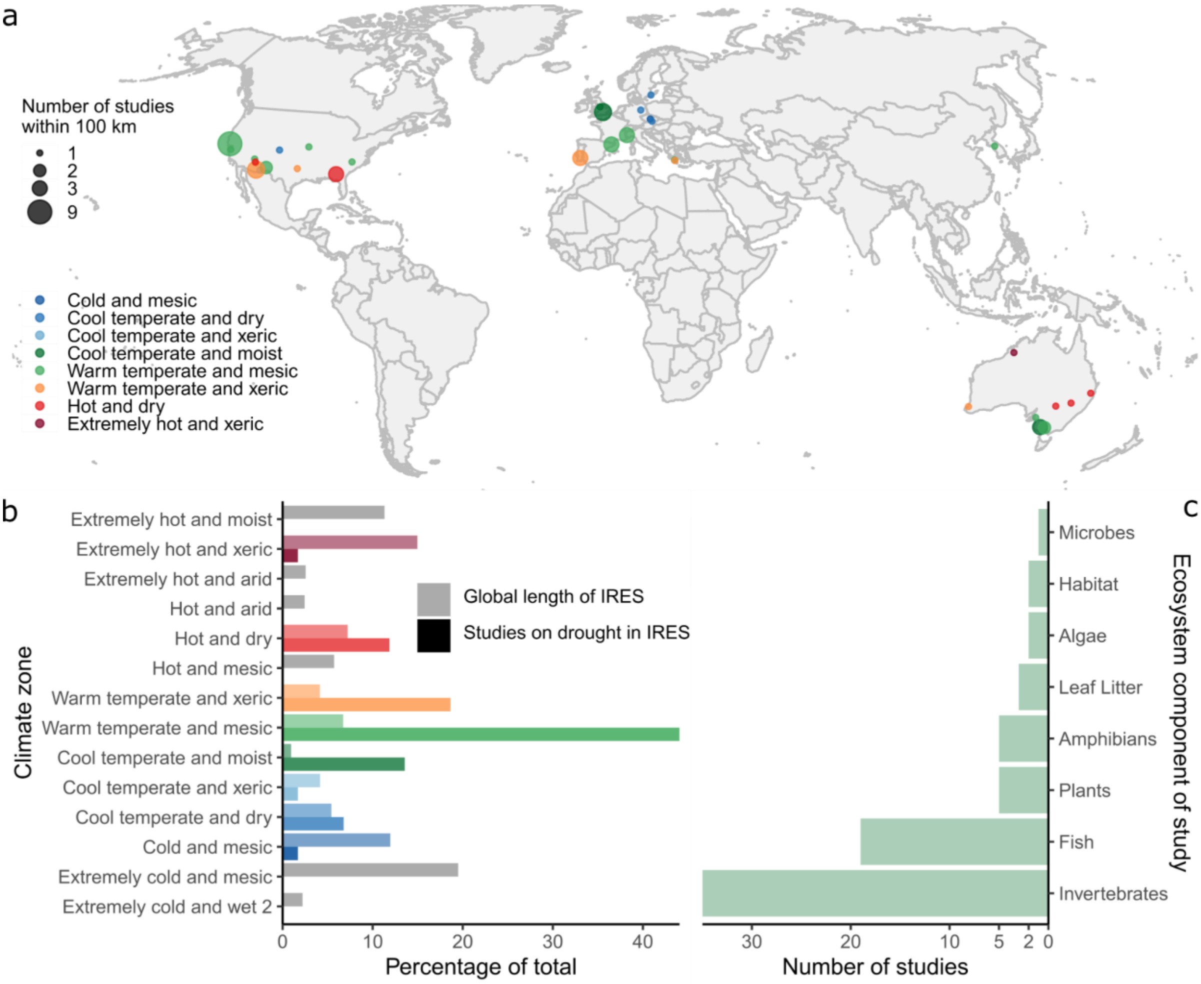

Figure 1: Global distribution of studies on the ecohydrological responses of intermittent rivers and ephemeral streams (IRES) to droughts. Studies were clustered by geographic location and climate (a), larger points show locations with more studies. Comparing the distribution of studies (darker-colored bars) to that of IRES (lighter-colored bars; Messager et al. 2021) across climate zones (b) reveal climates for which there are currently no studies (grey bars) and climates that are disproportionately studied (e.g., warm temperate and mesic, cool temperate and moist). Most research on IRES responses to drought have focused on invertebrates and fish (c). See Appendix 1, Figure S1 for the full distribution of climate zones (Global Environmental Stratification; Metzger et al., 2013; zones that include less than 1% of the world's IRES length and were not studied are not included in panel B).

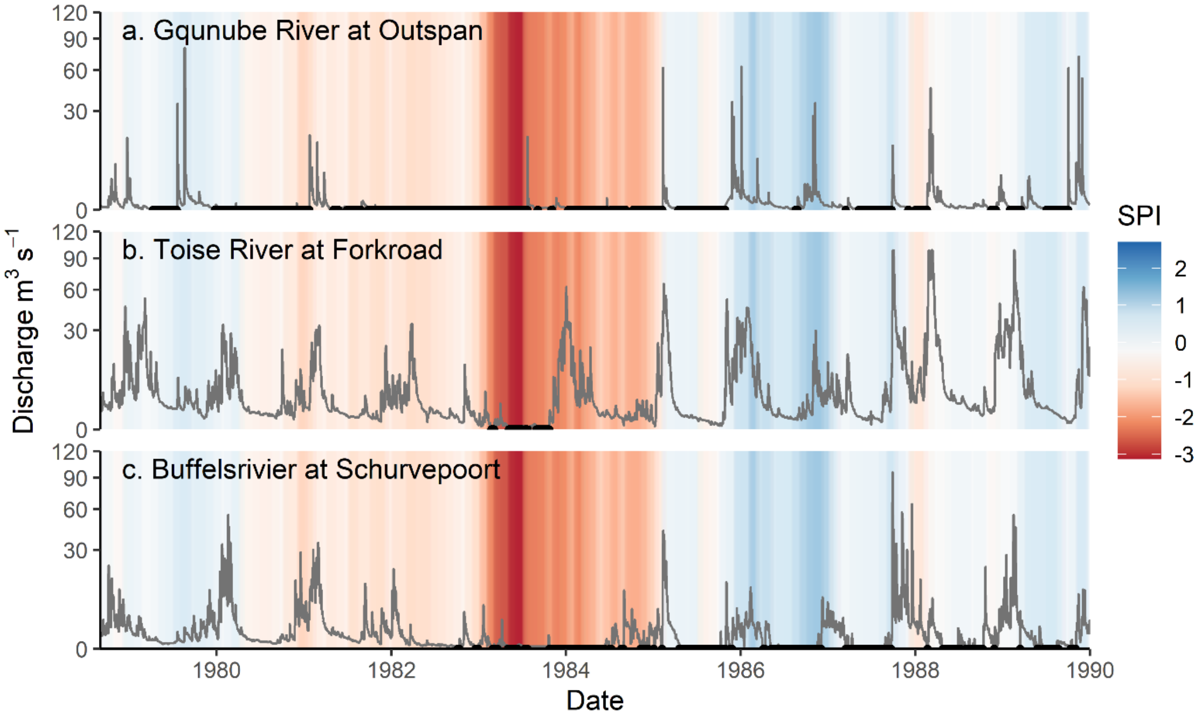

Figure 2: The hydrological consequences of meteorological droughts vary among rivers with different flow regimes. The responses of three rivers of eastern South Africa to a drought in the early 1980s differ. In a naturally intermittent river (a), flow cessation is a natural process, but droughts can result in more prolonged and severe drying; in naturally perennial rivers (b-c), severe droughts can cause temporary flow cessation (b), and in exceptional cases, permanently shift the flow regime of a river from perennial to non-perennial (c). Thicker, black sections of the hydrograph line identify days of zero flow. The shading reflects daily Standardized Precipitation Index (SPI) values calculated over the previous 24 months (see Section 2.3 for more details on this index).

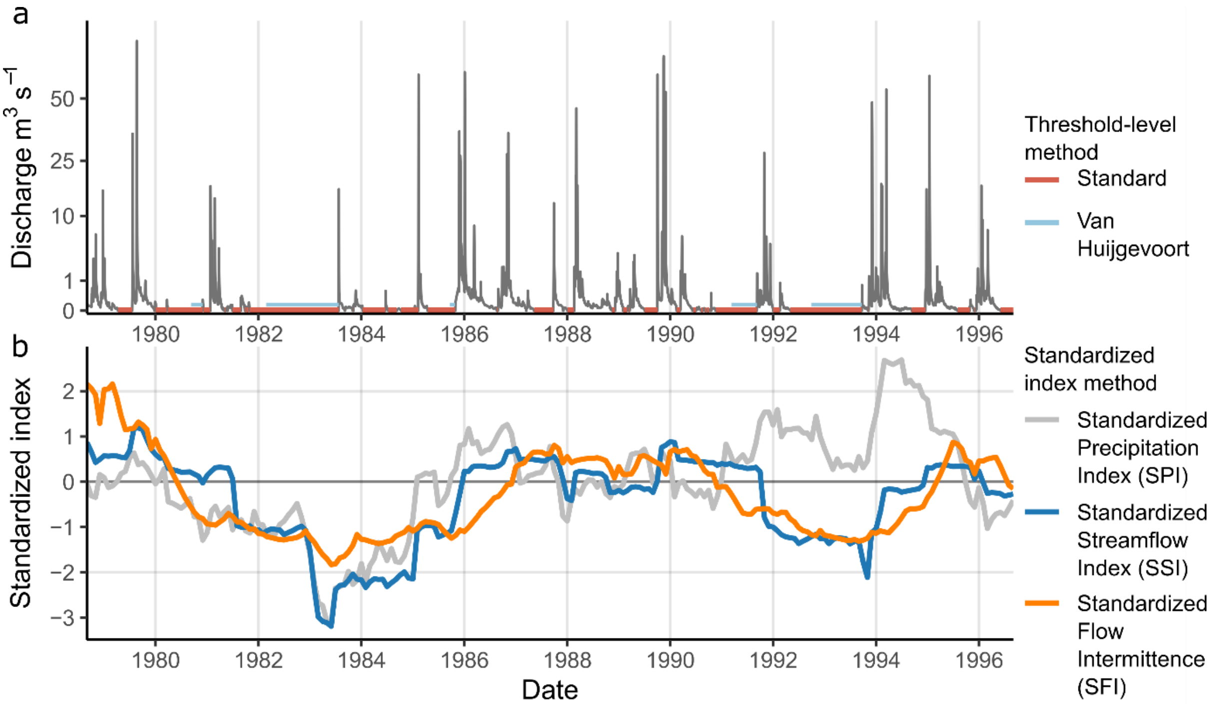

Figure 3: Commonly-used drought indices imperfectly reflect hydrological droughts in the naturally intermittent Gqunube River at Outspan in South Africa. (a) a standard threshold-level drought index that flags every discharge value at or under Q90 classifies all instances of flow cessation as drought days (red highlight). The drought index developed by Van Huijgevoort, by contrast, only flags abnormally long periods of zero discharge as drought events (blue highlight). Of the standardized drought indices (b), the Standardized Precipitation Index (SPI; grey line) is the most commonly used but only reflects the meteorological character of a drought. In this case, the SPI calculated based on a weather station near the Gqunube River (< 70 km) does not reflect a hydrological drought in 1993 identified with the Standardized Streamflow Index (SSI; blue line) and Standardized Flow Intermittence (SFI; orange line). All three standardized indices were computed at the monthly time scale based on records over the previous 24 months.

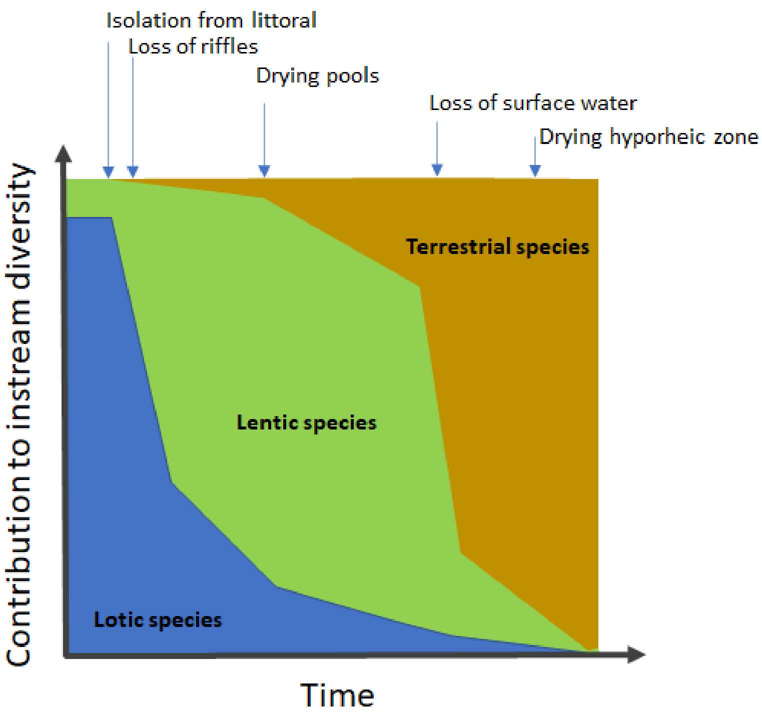

Figure 4: Stepped changes in instream community composition as drying progresses and aquatic habitats are lost in IRES. Figure inspired by Boulton (2003).

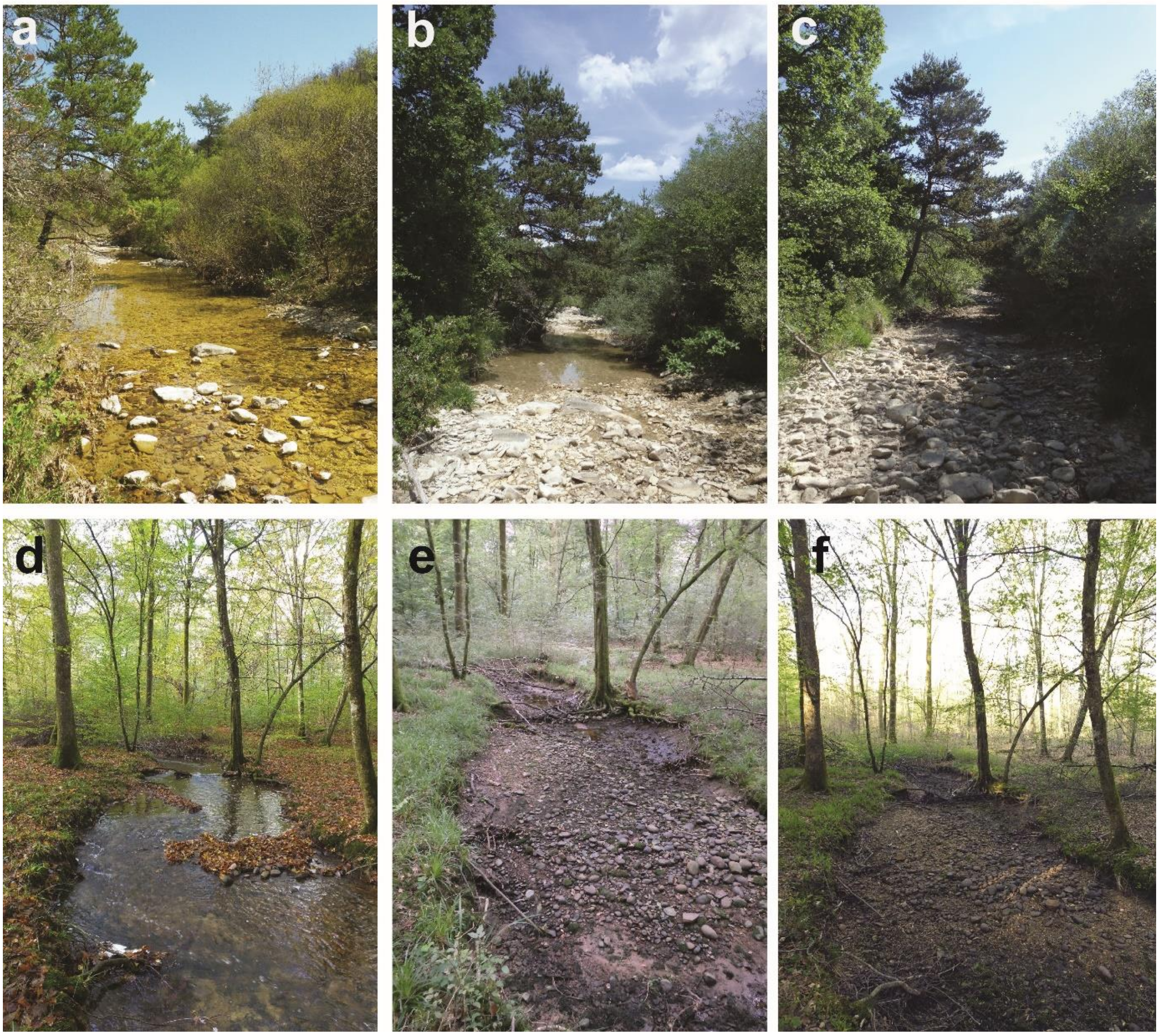

Figure 5: Two IRES in different hydrological stages, including one during a drought. The Calavon River, Southeastern France, during flowing (a), non-flowing (b) phases and with an extremely dry streambed during a drought in 2017 (c). The Clauge River, Eastern France, for the same hydrological phases: flowing (d), non-flowing (e) phases and during a drought in 2017 (f). Photos: Bertrand Launay.

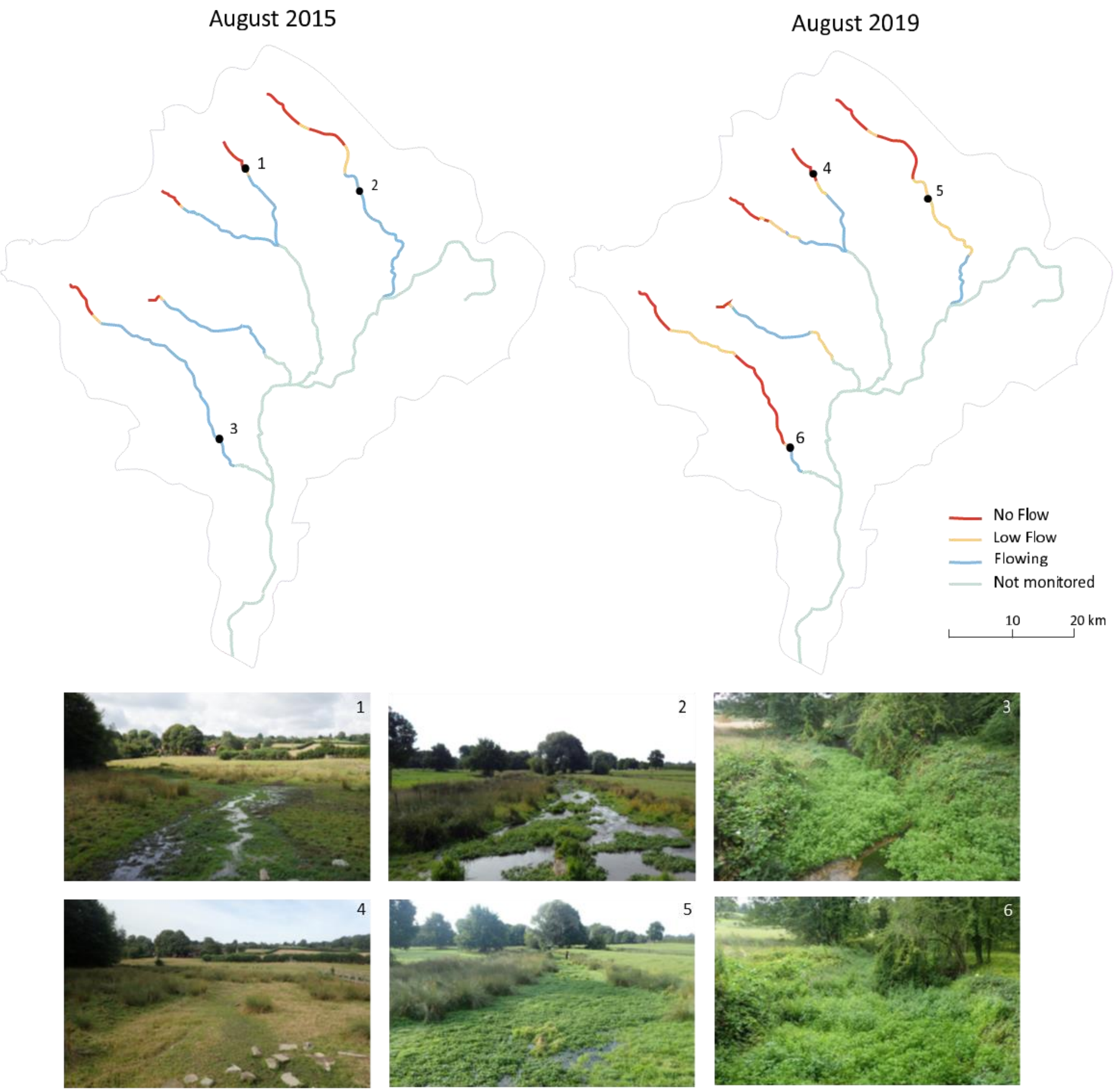

Figure 6: Changes in the configuration of flow conditions and habitat within an IRES river network (The Colne river, England) between an average (1-3) and a drought (4-6) year.

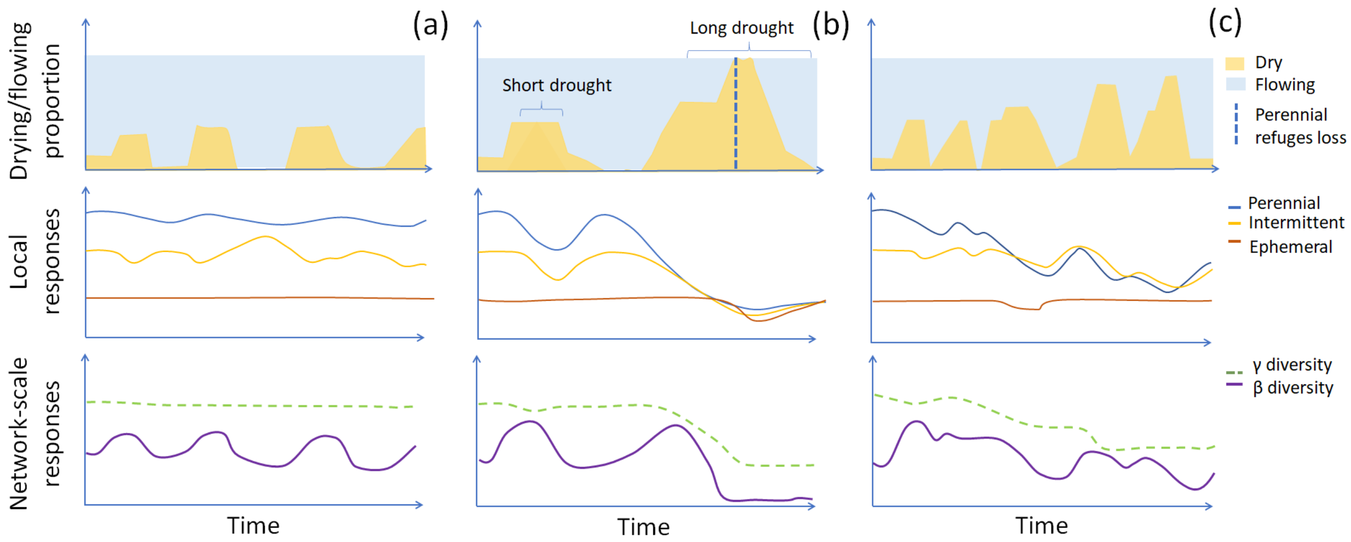

Figure 7: Effects of intermittent drying (a) and droughts duration (b) and frequency (c) on the extent of drying reaches at the network scale (upper panel) and hypothesized responses of local (i.e., diversity and abundances; middle panels) and regional (i.e. β and γ diversity; lower panels) biodiversity. In IRES where drying is cyclic and an inherent part of the natural flow regime, local and regional diversity may fluctuate between the dry and wet season. However, droughts can induce decreases in local diversity and population density beyond those observed during seasonal drying, with likely stronger initial responses in perennial and intermittent streams as habitats contract than in ephemeral streams mainly composed of resistant taxa. Short droughts may induce increases in community variability if network scale environmental conditions become more variable and if refuges prevent regional extinctions. Spatially and temporally extended drought may however lead to synchronous declines in diversity across streams with different permanence regimes as resistance capacities of species are exceeded. Such events can lead to decrease in regional diversity and a homogenization of communities at the regional scale if only a subset of resistant species remain everywhere. Drought periods interrupted by short periods of rainfall may allow the persistence of diversity by avoiding complete loss of refuges. However, increases in drought frequencies may lead to a selection of a set of taxa with short life cycle able to recover quickly between droughts, leading to a homogenization of the communities at the network scale.