**INTRODUCTION**

Rivers were long considered as passive pipes for carbon (C) transport between the land and ocean in early conceptual models of the C cycle (Wohl et al., 2017). Now, we know that physical, chemical and biological processes in river networks have an important influence on C dynamics (Benstead & Leigh, 2012; Cole et al., 2007; Wohl et al., 2017). River networks are areas of disproportionate biogeochemical exchange compared to their spatial extent in the landscape (Allen & Pavelsky, 2018). The river continuum concept describes the longitudinal gradient of physical conditions in unaltered rivers (Vannote et al., 1980). It details the fate of organic matter along a river network, with high allochthonous inputs in headwater reaches, and increasing importance of autochthonous primary production.
and organic matter transport from upstream as stream size increases (Vannote et al., 1980). However, river networks do not always follow this conceptual model, for example, owing to alterations as a result of the increasing pressure of fragmentation of river networks in the Anthropocene era (Fuller et al., 2015). In this review, we define fragmentation at the landscape scale as the temporary (drying) or permanent (damming) change in hydrological connectivity, disrupting the spatial flows of energy, materials and organisms within a river network (Fahrig, 2003; Fuller et al., 2015; Loreau et al., 2003). River networks are fragmented by both natural (e.g., drying, waterfalls, beaver dams) and anthropogenic agents (e.g., damming, water withdrawal, pollution; Fuller et al., 2015). In this review, we will focus on drying and damming (referring to artificial in-stream barriers of all sizes), as they are two of the most widespread causes of fragmentation in river networks (Bellettì et al., 2020; Messager et al., 2021).

The occurrence of drying in river networks is increasing as a result of climate change, damming and water abstraction (Datry et al., 2023). These waterways that periodically cease to flow, can be defined as intermittent rivers and ephemeral streams (hereafter, IRES; Datry, Larned, & Tockner, 2014). Recent estimates have quantified the extent of IRES which dry for at least one day of the year, as comprising 51–60% of the total global stream network (Messager et al., 2021). Fragmentation by drying can create different states in space and time: dry river beds, isolated pools and lotic waters. These flow regime states, and the transitions between them (i.e., rewetting and drying), create unique environments that may promote the production and consumption of GHGs.

In parallel, a large majority of the earth’s river systems are impacted by damming. A global analysis found that only 37% of rivers longer than 1,000 km are free-flowing without barriers over their entire length (Grill et al., 2019). Dams are a disruption to the river continuum, as defined in the serial discontinuity concept (Stanford, 1983), causing alterations in abiotic and biotic processes and patterns through the fragmentation of longitudinal, lateral and vertical pathways (Wang et al., 2018). Dams also alter river hydrology, sedimentation and nutrient biogeochemical cycling, reducing the connectivity of water, organisms, sediments, organic matter, nutrients and energy (Grill et al., 2019). Dams can promote greenhouse gas (GHG) emissions from both the reservoir surface, as well as degassing emissions at the reservoir outlet (i.e., dam spillways and turbines), downstream river emissions, and drawdown emissions from reservoir sediments that are periodically inundated and exposed to the atmosphere (Deemer et al., 2016; Maavara et al., 2020).

Fragmentation by drying and damming occur both separately and in interaction, and they may have certain comparable effects, as well as interactive effects, on GHG fluxes from river networks. Reservoirs increase water residence time in rivers and transform lotic reaches into lentic waters (Abril et al., 2015; Sabater, 2008). Below impoundments, flow rates may be reduced or the flow regime may change from perennial to temporary, leading to an increase in dry riverbed surface and modifications in ecosystem processes (Abril et al., 2015; Bianchi et al., 2017; Datry et al., 2023). In many cases, natural and anthropogenic drivers interact to cause intermittence (Datry et al., 2023). Alternatively, baseflow augmentation by reservoirs can create artificial permanent flow regimes downstream of reservoirs in reaches that previously may have been intermittent in nature (Acuña et al., 2017). These impacts are in many ways parallel to those posed by drying, where we observe a spatial and temporal mosaic of dry, lentic and lotic reaches (Datry, Larned, & Tockner, 2014). Global dry inland waters represent a significant source of CO₂ and methane (CH₄) emissions (Keller et al., 2020; Marce et al., 2019; Paranaiba et al., 2021). Additionally, enhanced CO₂ emissions have been observed upon the rewetting of riverbed sediments and leaf litter accumulated in dry reaches (Datry et al., 2018; Gallo et al., 2014; von Schiller et al., 2019). In lentic pools and impoundments, organic matter and sediment also can accumulate (Wang et al., 2018). This accumulation coupled with increased water retention time, allows for an augmentation in water temperature and the creation of anaerobic conditions, which promote denitrification and methanogenesis, and the generation of GHGs (Wang et al., 2018). Both drying (Döll & Schmied, 2012) and damming (Zarfl et al., 2015) are occurring with increasing frequencies, and therefore it is important to quantify their impacts on GHG fluxes in order to inform management decisions and improve global GHG budgets.

Our objective was to review the literature of the effects of fragmentation by drying and damming on GHG fluxes in river networks. We discuss the factors and processes affecting GHG fluxes at different hydrological states of flow regimes in IRES and dammed rivers: exposed sediments, lentic waters and lotic waters. Flow regime states are described along a continuum of scale, from the reach, to the network, to the global scale. We then discuss the individual and interactive effects of drying and damming at the network scale. Finally, we propose four actionable future research directions.

2 | METHODS

We conducted a systematic search of studies addressing the effects of drying and damming on GHG fluxes from river networks. The search was primarily conducted using the Web of Science for studies published from 1900 to January 2021, in addition to personal literature databases and reference lists of the identified primary studies and review papers. Relevant papers published after our literature search were not included in the figures, but mentioned in-text where pertinent. We used a comprehensive combination of keywords to describe intermittent rivers, reservoirs, and GHGs (Table S1). For practicality, when the search returned over 1,000 entries, we only considered the first 1,000 entries, sorted in order of relevance. Articles were excluded from analysis if they were identified as aquatic but not a stream or river environment (e.g., wetland, pond).

We considered three of the principle GHGs responsible for the greenhouse effect: carbon dioxide (CO₂), methane (CH₄) and nitrous oxide (N₂O). Although they do not measure GHG fluxes directly, we considered studies of potential denitrification providing a proxy of N₂O fluxes, and studies that indirectly estimated GHG fluxes from dissolved GHG concentrations in stream water. Given the vast body of literature addressing the effects of drying and damming on GHG fluxes in river networks, we propose four actionable future research directions.
of research regarding GHG fluxes in reservoirs, we only considered studies that took measurements from the river upstream and/or downstream of the reservoir in addition to the reservoir itself. We additionally considered studies that compared GHG fluxes at the reservoir surface to nearby free-flowing rivers or lakes. Studies that did not report GHG fluxes clearly, included only a single day of data, or did not report fluxes on a per areal basis were not included in our final selection of studies reported in the figures and tables. In a few cases, mean GHG fluxes were not reported in text and, thus, they were extracted from the article figures using visual inspection. When the gas flux was reported in grams per area, we converted the value to a per molar basis (e.g., CO$_2$-C, CH$_4$-C and N$_2$O-N). For the 43 studies about rivers impacted by drying, 49 about damming and six about their interactive effects, we collected a suite of qualitative and quantitative information. This included basic information about the study type and location, as well as information about the GHG measurements including which gases were measured, their fluxes and drivers (see Table S2 for the full list of information extracted from each study). Direct comparisons of GHG fluxes between studies are done with caution, appreciating the impacts of differences in spatial and/or temporal scales, and sampling methodologies between studies.

3 | GREENHOUSE GAS FLUXES IN INTERMITTENT RIVERS

Recent advances in our knowledge of controls of GHG fluxes along with updated maps of inland waters have allowed for more well-informed estimates of GHG fluxes in fresh waters (Drake et al., 2018; Raymond et al., 2013). Streams and rivers in particular have been identified as global hotspots of CO$_2$ evasion, with recent global CO$_2$ estimates of 2.0 ± 0.2 Pg C/year (Liu et al., 2022), with an additional 1.02 Pg CO$_2$ eq./year from CH$_4$ and N$_2$O (Zheng et al., 2022). However, research in the field of IRES has historically fallen behind that of perennial systems, particularly with respect to studies examining biogeochemical cycling (Leigh et al., 2016). This lag in research may be a consequence of the unique nature of intermittent ecosystems – not terrestrial, but not always aquatic – making them difficult to fit into the domain of aquatic or terrestrial ecology (Arce et al., 2019; Steward et al., 2012). We found 43 studies examining GHG fluxes in IRES, with a peak of studies published within the last decade (Figure S1). Most of the studies were conducted in arid regions, where IRES are prevalent such as the Mediterranean, Australia, and Arizona, USA (Figure 1). The majority of studies that we identified were metabolism studies, which measure diel oxygen curves as a proxy for metabolism (Hall & Hotchkiss, 2017). These metabolism studies were primarily reach-scale field studies during lotic and dry states, just in isolated pools, or lotic reaches within an intermittent river network. For those studies measuring in situ GHG efflux, most studies measured CO$_2$ alone, some measured N$_2$O alone, and a few measured several or all three major GHGs (Figure 2a). Studies most frequently examined all three of the major hydrological states: dry, isolated pools and lentic waters. Some studies just looked at drying and rewetting, and others just measured fluxes in isolated pools or just sediment rewetting. We found four global efforts examining GHG fluxes in IRES; however, the large majority of identified studies were at the reach scale, with only a few at the network scale (Figure 2b).

3.1 | Greenhouse gas fluxes associated with river damming

There is a large body of literature about GHG fluxes from reservoirs, so we restricted our review to studies which included measurements upstream and/or downstream of the reservoir, in addition to the reservoir itself. Forty-nine studies investigated GHG flux dynamics in river networks impacted by reservoirs. The vast majority of the studies were conducted in China, with studies also frequently occurring in Brazil, French Guiana and the USA, with some global efforts (Figure 1). Most of the identified studies were conducted on what could be considered a large reservoir, with an average volume of 15.6 ± 18.0 km$^3$ and an average surface area of 769.9 ± 654.2 km$^2$. The median catchment area for studies examining damming was 58,000 km$^2$, compared to 505 km$^2$ for the studies examining drying (Figure S2). Over half of the identified studies were field studies, but there also were several review studies, and some studies used modelling or laboratory incubations. There is more abundant research, and more even distribution of research on each gas for studies we identified pertaining to reservoirs than to IRES, indicating that the field of research about damming is at a more advanced stage (Figure 2a). With the exception of one study on floodplain sediments, all of the studies on damming measured GHG fluxes at the air–water interface. Considering the limited number of studies addressing GHG fluxes from exposed reservoir sediments identified in our literature review, we do not extensively discuss them. Additionally, a few studies compared GHG fluxes during low and high water levels.
3.2 | Greenhouse gas fluxes from dry sediments can exceed those of inundated ones

3.2.1 | Carbon dioxide fluxes

The CO₂ flux from exposed, dry sediments in IRES was consistently higher than fluxes from lotic waters in the same study; on average dry fluxes were nearly double the flux from lotic waters (Figure 3a; Table S3). This suggests a positive effect of drying on CO₂ fluxes, possibly caused by an increase of oxygen (O₂) in the sediments promoting organic matter degradation when water is no longer limiting diffusion (Kosten et al., 2018). In a synthesis of CO₂ fluxes from dry inland waters, dry sediment fluxes were higher than those from lentic waters, and more similar to fluxes reported from lotic waters (Marcé et al., 2019). In some cases, the CO₂ flux from IRES dry sediments is comparable to riparian soil fluxes (Bretz et al., 2021; Gómez-Gener et al., 2016; von Schiller et al., 2014). Similar to observations in dry riverbeds, CO₂ fluxes from reservoir drawdown areas
are on average higher than those from the reservoir surface (Keller et al., 2020), resulting in a 50% increase in the current global CO₂ emission estimate from reservoirs when accounting for drawdown areas (Keller et al., 2021).

The factors that most influenced CO₂ fluxes in IRES were sediment moisture, temperature, organic matter content, and texture (Figure 4). Sediment moisture strongly influences CO₂ fluxes, as water stress can inhibit microbial activity (Manzoni et al., 2012). In a global analysis of CO₂ fluxes in dry inland waters, soil moisture was the strongest predictor of CO₂, followed by the interaction of organic matter content and moisture (Keller et al., 2020). Thus, under moisture-limiting conditions, increasing the organic matter content or temperature of the sediments will not increase the CO₂ flux, as the microbial activity is inhibited by the water stress (Keller et al., 2020). However, the relationship of CO₂ flux with sediment moisture is not always linear, as significantly higher microbial activity was observed between 20% and 40% water-filled pore space at an Australian IRES (McIntyre et al., 2009). One study even reported a negative relationship between CO₂ flux and sediment moisture in a Mediterranean IRES (Gómez-Gener et al., 2015). They noted that although higher water content may promote CO₂ production by facilitating contact between microorganisms and the available substrate, it may at the same time act as a physical barrier to restrict the evasion of CO₂ (Gómez-Gener et al., 2015). High sediment moisture content also may lead to anaerobic conditions, which inhibit the production of CO₂ by aerobic respiration due to O₂ limitation (Kosten et al., 2018). Temperature stimulates the microbial activity of autotrophic and heterotrophic respiration in soils (Raich et al., 2002), with a similar effect in inland water sediments (Lü et al., 2023). A diurnal pattern was observed in high-frequency CO₂ measurements from exposed riverine sediments, suggesting that warming during the day exponentially increased fluxes (Koschorreck et al., 2022). Sediment organic matter content influences CO₂ fluxes as organic matter provides a substrate for decomposition. However, the quantity of organic matter may not explain the whole story, since the quality of organic matter can vary widely, with a rapidly decomposable fraction with a turnover rate in days, to a more slowly decomposable fraction with a turnover rate in days to years (Qiu et al., 2015). Sediment texture also plays an important role in CO₂ fluxes, as soils with a finer texture can have higher organic matter content and moisture retention, as well as greater surface area for microbial colonisation, creating more favourable conditions for respiration (Gallo et al., 2014). For example, higher CO₂ fluxes were reported in loam and sandy loam (490 and 333 mmol m⁻² day⁻¹, respectively) than in sandy (77 mmol m⁻² day⁻¹) channels (Gallo et al., 2014).

**Figure 4** Principal factors influencing greenhouse gas (GHG; CO₂, CH₄, N₂O) fluxes at all scales in river networks impacted by damming (top), and intermittent rivers and ephemeral streams (IRES; including all phases; bottom) as identified in our review of the literature. The number in the circle and circle size denote the number of studies identifying the factor. Factors identified by at least two studies were included for IRES, and at least three studies for damming. Insufficient data for N₂O (n=1) in IRES.
There has been some research examining the fluxes of CO₂ from both sediments and organic matter in IRES upon rehydration due to a rain event, with rewetting fluxes at least an order of magnitude higher than dry sediment fluxes in the same study (Table S4). In soils, pulses of CO₂ after rehydration have been termed the "Birch effect", wherein the decomposition of labile soil organic matter, nitrogen mineralisation, as well as CO₂ flux are enhanced upon rewetting (Birch, 1958). Sediment texture can play an important role in rewetting fluxes; CO₂ fluxes were significantly higher and more variable in sites with fine sediment texture than more coarse textures (Gallo et al., 2014). Carbon dioxide flux had a significant positive correlation with percentage clay content, soil nitrogen, ammonium and nitrate content (Gallo et al., 2014). The rewetting of leaf litter also may contribute to rewetting CO₂ pulses, yet sediments emitted CO₂ an order of magnitude higher than leaf litter, considering an equivalent surface area (Datry et al., 2018; von Schiller et al., 2019). Only one study measured CO₂ fluxes from dry riverbeds at the network scale, two studies were conducted at the global scale, and the majority of studies conducted at the reach scale. The study conducted at the network scale measured in situ CO₂ and CH₄ fluxes across two IRES networks impacted by drying and damming in Spain during the summer drought period (Gómez-Gener et al., 2015). The CO₂ flux from dry riverbeds (209 nmol CO₂ m⁻² day⁻¹) was similar to that from lotic waters (120 nmol CO₂ m⁻² day⁻¹), but significantly higher than from impounded waters (36.6 nmol CO₂ m⁻² day⁻¹) and isolated pools (17.2 nmol CO₂ m⁻² day⁻¹). They were not able to observe spatial variations along a longitudinal gradient from the headwaters to the river mouth for dry riverbed CO₂ efflux, since the dry sites were all located in the headwaters (Gómez-Gener et al., 2015). The magnitude of CO₂ fluxes from lotic waters has been found to be higher in headwaters than the mainstem as a result of greater inputs of terrestrially derived CO₂ and organic C (Hotchkiss et al., 2015). However, it remains unknown whether or not this phenomenon also would hold true for dry rivers at the network scale.

3.2.2 | Methane fluxes

Few studies measured CH₄ fluxes, all of which reported relatively low rates of CH₄ emission from dry riverbeds, <0.6 nmol m⁻² day⁻¹ (Table S3; Figure 3a). The small number of studies limits our ability to draw conclusions, and demonstrates the need for more measurements of CH₄ fluxes in IRES. A recent study of forest drainage ditches found similarly low dry condition CH₄ fluxes (on average a mean flux of 0), which were significantly lower than lotic fluxes (Peacock et al., 2021). Likewise, CH₄ fluxes from reservoir drawdown areas are presently considered of minor importance compared to total aquatic CO₂ and CH₄ fluxes from reservoirs (Keller et al., 2021; Paranaiba et al., 2021). However, some studies have demonstrated the potential for sediment in drawdown areas to be CH₄ sources (Amorim et al., 2019; Kosten et al., 2018; Paranaiba et al., 2021; Serça et al., 2016). The observed CH₄ fluxes are likely to be a result of the stimulation of the microbial community upon rewetting (Conrad et al., 2014). Methane fluxes from exposed sediments in both reservoirs and IRES should not be ignored in global GHG budgets for inland waters.

Several factors control CH₄ fluxes in IRES: sediment temperature, moisture and organic matter content (Figure 4). As discussed in Section 3.2.1 for CO₂ fluxes, sediment temperature is associated with the stimulation of many biogeochemical processes. In soils, for example, temperature has a positive relationship with CH₄ production (Dalal & Allen, 2008). In a similar way to CO₂, sediment moisture controls CH₄ fluxes through a balance between the stimulation of microbial metabolism and the limitation of gas diffusivity (Gómez-Gener et al., 2015; Paranaiba et al., 2021). Methane production occurs primarily through methanogenesis under anaerobic conditions as a consequence of submergence or water-logging (Dalal & Allen, 2008). We expect sediment organic matter content to drive C fluxes, as it provides substrate for decomposition (Dalal & Allen, 2008). Surprisingly, a global study of CH₄ fluxes from dry inland waters found a negative relationship between CH₄ fluxes and organic matter content (Paranaiba et al., 2021). However, they noted that this relationship may be more complex than it seems, with the quality of the organic matter playing an important role in particular in dry sediments, since the more frequently a sediment is exposed to the atmosphere, the less labile its organic matter tends to be (Serrano-Silva et al., 2014).

3.2.3 | Nitrous oxide fluxes

There is limited research about N₂O fluxes from dry riverbeds of IRES (Table S3). We found a singular in situ reach-scale study measuring N₂O fluxes from dry riverbeds, which reported relatively low fluxes, driven primarily by sediment texture (Gallo et al., 2014). Several other studies were conducted in the laboratory using sediment and/or water incubation assays to measure denitrification. To our knowledge there are no network- or global-scale studies of N₂O fluxes from dry riverbeds. Likewise for reservoir drawdown areas, the few studies suggest that reservoir sediments can be sources of N₂O upon drying (Jin et al., 2016). Nitrous oxide production was found to be highest in the recently exposed reservoir sediments, and was associated with a temporary increased in organic matter processing caused by increased O₂ availability upon drying (Jin et al., 2016).

Based on the few field and laboratory studies, sediment texture and moisture may be important influences on N₂O fluxes. Finer sediment texture was associated with higher N₂O fluxes, likely resulting from the higher nutrient and moisture content creating more favourable conditions for denitrification and/or nitrification, when compared to coarser-textured sediments (Gallo et al., 2014). Additionally, sediment moisture had a significant positive relationship with N₂O fluxes, but only at the sandy sites (Gallo et al., 2014). Likewise, in a laboratory study, N₂O production was inhibited as soil moisture decreased (Gómez et al., 2012). In soils, N₂O is produced mainly through the processes of nitrification and denitrification, which are
considered to be at their optimum at 50%–60%, and above 60% water-filled pore space, respectively (Dalal & Allen, 2008).

Following the rewetting of sediments in an IRES, the N$_2$O flux was two orders of magnitude greater than from dry sediments (Gallo et al., 2014). Similar to CO$_2$, N$_2$O rewetting fluxes were significantly higher for finer sediment texture, indicating that higher soil nutrient concentration and enhanced moisture retention are likely to have allowed for conditions favourable for denitrification and nitrification (Gallo et al., 2014). In wet– dry cycles in sediments of aquatic ecosystems, N$_2$O pulses are observed following sediment drying and rewetting, with peak fluxes observed when nitrification and denitrification are coupled under conditions with intermediate oxygen availability (Koschorreck, 2005; Pinto et al., 2021). There is a clear need for more measurements of CH$_4$ and N$_2$O fluxes upon sediment rewetting, particularly given the high global warming potential of these two gases (Myhre et al., 2013).

### 3.3 Lentic waters can promote greenhouse gas fluxes from IRES and reservoirs

#### 3.3.1 Carbon dioxide fluxes

The research on CO$_2$ fluxes from isolated pools in IRES is limited, with no clear trend in fluxes when compared to lotic states (Table S5). While increasing attention is being paid to IRES by researchers, the research on isolated pools in IRES still remains limited (Bonada et al., 2020). Temporary, isolated pools are transitional environments between lotic and dry states, characterised by low dissolved oxygen (DO) concentrations, high temperature and an accumulation of organic matter (Bonada et al., 2020). The abundance of organic matter within isolated pools tends to be high as a result of evaporation and accumulation of riparian vegetation inputs, fuelling microbial respiration and leading to high production and, thus, concentration of CO$_2$ (Granados et al., 2020). Despite the high CO$_2$ production, there may be relatively low emission owing to limited gas exchange in the stagnant waters (Gómez-Gener et al., 2015; Granados et al., 2020). As isolated pools can be present for only short periods of time in IRES, during the transition between lotic and dry states, they are methodologically difficult to measure, and the amount of available data is limited.

By contrast, there is a larger body of knowledge about CO$_2$ fluxes from reservoirs. Carbon dioxide flux from the downstream river were on average three times higher than from the reservoir surface and 3.8 times higher than from the upstream river (Figure 3b; Table S6). This trend may indicate relatively high production of CO$_2$ in reservoirs, but low diffusion rates because of (1) lower concentration in the surface water layer and/or (2) minimal turbulence, which tends to increase going downstream, thereby releasing the CO$_2$ accumulated in the deepest part of the reservoir to the atmosphere.

Water temperature, retention time, DO and phytoplankton Chlorophyll-a concentration were key factors influencing CO$_2$ flux in reservoirs and their associated rivers (Figure 4). Carbon dioxide fluxes increase with warmer water temperature; for example, tropical reservoirs typically emit GHGs at greater rates than high latitude temperate and boreal reservoirs, which is likely to the result of higher rates of biological activity stimulated by warm water temperature and higher flooded biomass in tropical regions (Wang et al., 2018). Increased water residence time is associated with increased interaction between organic substrates and microorganisms, allowing for decomposition of organic matter and CO$_2$ production (Gómez-Gener et al., 2018). Carbon dioxide fluxes from reservoirs typically had a negative relationship with DO and Chl-a concentrations. This is likely to be caused by the increased water residence time and nutrient accumulation characteristic of reservoirs being associated with increased photosynthetic activity of the phytoplankton, Chl-a concentrations increase as CO$_2$ in the water is fixed, reducing dissolved CO$_2$ concentrations, and producing more DO (Qin et al., 2019).

#### 3.3.2 Methane fluxes

Research about CH$_4$ fluxes from isolated pools in IRES is limited (Gómez-Gener et al., 2015), in contrast to the large body of research on reservoirs. Mean CH$_4$ efflux was not significantly different between isolated pools, lotic waters and dry riverbeds, across two intermittent river networks in Spain, with nearly negligible average fluxes (mean <0.3 mmol CH$_4$ m$^{-2}$ day$^{-1}$) recorded (Gómez-Gener et al., 2015). Impounded waters in the same river networks had notable CH$_4$ efflux (mean 13.8 mmol CH$_4$ m$^{-3}$ day$^{-1}$). The global GHG flux from reservoirs was recently estimated at 1.076 Tg CO$_2$ eq./year, with CH$_4$ as the dominant contributor (748 Tg CO$_2$ eq./year) (Harrison et al., 2021). Ebullitive (bubbling) CH$_4$ emissions, can make up a large proportion of total CH$_4$ emissions from reservoirs (Deemer et al., 2016). Reservoirs increase water residence time, trapping sediments and organic matter (Crawford et al., 2016; Wang et al., 2018). The resulting bottom anoxia can lead to conditions favourable for methanogenesis in reservoir sediments, generating CH$_4$ (Wang et al., 2018). On average, CH$_4$ fluxes were an order of magnitude higher from the downstream reaches than from the reservoir surface and upstream reaches (Figure 3b). However, in individual studies the results were variable (Table S6), with observed CH$_4$ fluxes at the reservoir surface that were greater or lower than upstream (Yang, 2019; Yang et al., 2013) and downstream waters (Guérin et al., 2006; Zhao et al., 2013). Methane production may not translate directly to CH$_4$ efflux, as the upwardly diffusing CH$_4$ can be converted to CO$_2$ by methanotrophic bacteria (Wang et al., 2018). However, when water is released from the bottom of the dam, CH$_4$ emissions can be very high (Wang et al., 2018). As such, CH$_4$ emission rates can be high directly after the dam outflow, and decline further downstream (Guérin et al., 2006).

Water temperature, air temperature, Chl-a, dissolved organic C and DO controlled CH$_4$ fluxes from reservoirs and their associated rivers (Figure 4). Water and air temperature control biological activity, in the case of CH$_4$ production, the activity of methanogenic bacteria. 

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*Note: The provided text is a continuation of the research on greenhouse gas fluxes from isolated reservoirs (IRES) and reservoirs in aquatic ecosystems.*
As such, in temperate Northern Hemisphere climates, maximum CH₄ flux can be observed in the summer when the water and air temperatures are at their highest (Basstien et al., 2011). Methane fluxes are positively correlated to phytoplankton Chl-α concentrations (Descloux et al., 2017), which can reflect the trophic status of a reservoir. A global review found an order of magnitude higher CH₄ flux from eutrophic than oligotrophic reservoirs (Deemer et al., 2016), where the high nutrient concentrations, low DO concentrations and high water temperatures are likely to stimulate CH₄ production. When other environmental conditions are favourable, increased C content in the sediment can provide substrate to stimulate microbial activity and promote the release of CH₄ in reservoirs (Yang et al., 2020). The influence of allochthonous C inputs on CH₄ production may be especially important in small, temperate reservoirs with lower water residence times (Chanudet et al., 2020). Dissolved oxygen concentrations have a negative relationship with CH₄ fluxes, as anaerobic conditions in sediments promote methanogenesis. Moreover, lower DO concentrations can prevent the oxidation of CH₄ during its transport through the water column from the sediments (Yang et al., 2020). The large number of studies focusing on reservoirs have allowed researchers to identify the key factors influencing CH₄ fluxes; however, to reach this level of knowledge with IRES, more data are needed.

### 3.3.3 Nitrous oxide fluxes

We did not identify a single study of N₂O fluxes from isolated pools of IRES, whereas several studies examined N₂O fluxes from reservoirs and their associated rivers (Figure 3: Tables S5 and S6). Global N₂O fluxes from reservoirs was estimated at 31.7 Tg CO₂ eq./year (Deemer et al., 2016), which is notable, but a smaller contribution than CO₂ (328) and CH₄ (748) (Harrison et al., 2021). There was no clear trend in the spatial variation of N₂O fluxes (Figure 3b; Table S6) with some studies reporting the highest average fluxes at the upstream river (Cheng et al., 2019), downstream river (Yang, 2019) and reservoir surface (Yang et al., 2020). Anoxic conditions in reservoir sediments can lead to conditions favourable for denitrification, generating N₂O emissions (Wang et al., 2018). Thus, in theory, if water is then released from the bottom of the reservoir to the downstream river, it can result in a large release of N₂O downstream.

Nitrate concentrations, DO and water temperature were cited as influencing N₂O fluxes from reservoirs and their associated rivers (Figure 4). Nitrous oxide fluxes are a function of both nitrification and denitrification rates, which are controlled by N and O availability (Liang et al., 2019). Denitrification in particular is limited by nitrate availability (Bauuch et al., 2011), explaining why nitrate concentrations had a positive relationship with reservoir N₂O fluxes. Dissolved oxygen concentrations are particularly important in controlling N₂O production in reservoirs and their associated rivers. However, the relationship varies depending on whether nitrification or denitrification dominate N₂O production, as nitrification is an aerobic process while denitrification is an anaerobic process (Liang et al., 2019). A DO concentration that optimises the co-occurrence of nitrification and denitrification will result in the highest yield of N₂O, for example in the oxycline (Liang et al., 2019). When nutrient availability is not limiting, warmer water temperatures can stimulate the microbial activity contributing to the production of N₂O (Beaulieu et al., 2010).

### 4 SPATIAL AND TEMPORAL PATTERNS OF DRYING AND DAMMING AT THE NETWORK SCALE

River networks are meta-ecosystems made up of an aquatic continuum embedded within a terrestrial matrix (Battin et al., 2008). A meta-ecosystem is defined as a set of ecosystems connected by spatial flows of energy, materials and organisms across ecosystem boundaries (Loreau et al., 2003). Meta-ecosystem theory, an extension of metapopulation and metacommunity theories, is useful in conceptualising the effects of river network fragmentation on biogeochemical and ecological processes (Loreau et al., 2003), such as those leading to the production and consumption of GHGs. In river networks, energy, materials and organisms flow by-way-of hydrological connectivity in three spatial dimensions: longitudinal, lateral and vertical (Cid et al., 2021). In fragmentation by drying and damming, the interruption of surface flow disrupts hydrological connectivity in one or more of the three dimensions, creating heterogeneous mosaics of habitat patches with varying conditions (Boulton et al., 2017; Cid et al., 2021; Datry et al., 2017). This spatial variability also varies temporally within and among years (Costigan et al., 2015), further contributing to the high habitat heterogeneity in IRES. Compared to the temporary nature of fragmentation by drying, reservoirs typically represent a permanent discontinuity feature within the network altering the fluxes of water, sediment, materials (including organic matter) and organisms (Grill et al., 2019). We propose that the spatial distribution of fragmentation at the network scale is a major factor influencing the magnitude and dynamics of GHG fluxes. More specifically, the network location of the fragmentation (i.e., upstream, downstream) and the type of fragmentation (i.e., drying, damming), and their interaction play an important role in GHG dynamics at the river-network scale.

The location of fragmentation along a river network is an important consideration for determining its ecological impacts (Jacquet et al., 2022; Schmida et al., 2018). Intermittent reaches can occur anywhere in a river network, from headwaters to the mainstem (Datry, Larned, Fritz, et al., 2014). Network scale drying patterns vary as a result of differences in climate, geology, vegetation and human interference (Shanafield et al., 2021). For example, in temperate regions intermittent reaches are often in headwaters (Kampf et al., 2021), although central and downstream drying reaches also are common (Arscott et al., 2010; Datry, 2012). In arid regions, intermittent reaches can occur anywhere and often entire river networks are intermittent (Welter & Fisher, 2016). Network-scale patterns of drying can have important implications on biogeochemical cycling owing to the disparate conditions observed along a river network from the headwaters to the estuarine zone (Allen et al., 2020; Larned et al., 2010).
Within a river network, we expect high GHG fluxes from dry sediments at upstream reaches (Figure 5a), where allochthonous organic matter inputs to the stream bed tend to be greater as a result of a higher edge-to-area ratio of riparian tree cover (Richardson & Danehy, 2007). For example, the greatest amount of terrestrial organic matter input in dry channels was reported from first-order, forested, temperate IRES when sampling 212 streams across nearly all continents (Datry et al., 2018). Moreover, the relatively stronger land-water connectivity in headwaters compared to the mainstem can supply terrestrially derived C inputs to stream under lotic conditions (Hotchkiss et al., 2015), and it may be an important source of C during drying events (Gómez-Gener et al., 2020). The shading effects of riparian cover in headwaters also can buffer against the negative impacts of sediment desiccation on decomposer communities and associated GHG production (Schreckinger et al., 2021). However, the lower sediment temperature near the headwaters and coarser sediment texture may conversely limit CO2 fluxes. We could expect the highest CH4 and N2O fluxes from dry river reaches in the mainstem, where finer sediments tend to accumulate, retaining moisture and nutrients (Saxton & Rawls, 2006), along with the diminished effect of riparian shading creating warmer sediment temperatures stimulating microbial activity (Raich et al., 2002). Nevertheless, these proposed network-scale patterns in dry sediment GHG fluxes still need to be tested.

As with drying, the spatial position of a reservoir is important for determining GHG flux magnitudes at the river-network scale (Figure 5b). We expect reservoirs located in downstream reaches to have higher CO2 and N2O fluxes associated with their larger size and the warmer water temperatures when compared to shaded and higher elevation upstream reaches. We expect higher biological activity and Chl-a levels in warmer waters (Sarkar et al., 2021), leading to potentially high production and emission of CO2. However, if there are significant reservoirs upstream, this may reduce the amount of organic matter transported downstream (Stanford & Ward, 2001), thereby diminishing the emission potential despite the more favourable environmental conditions for GHG production. At the network scale, CO2 evasion from lakes was controlled by residence time and size, with CO2 fluxes increasing with the stream order of their network position, suggesting that larger lakes downstream are more efficient emitters of terrestrial CO2 (Brinkerhoff et al., 2021). We expect to observe a similar trend in reservoirs, where a reservoir on a large-order river, with no upstream reservoirs, might have a higher magnitude of GHG fluxes than a reservoir located in the headwaters, considering two reservoirs with similar physical characteristics.

We may expect to see higher N2O fluxes at reservoirs in downstream reaches compared to upstream ones. Point sources of N entering the river may accumulate in downstream reaches, where the often sparse riparian cover has a reduced capacity of nitrate removal when compared to upstream reaches (Wherry et al., 2021). Application of the nutrient spiralling concept at the network scale found that nitrate was recycled more intensively in higher order streams where mass flux was greater (Ensign & Doyle, 2006). In addition, the generally warmer water temperatures in downstream reaches may further promote N2O production (Beaulieu et al., 2010). Thus, although complex and understudied, we propose that the network position of reservoirs has an important influence on the magnitude of GHG fluxes.

5 | INTERACTIVE EFFECTS OF DRYING AND DAMMING AT THE NETWORK SCALE

Drying and damming present complex and interactive fragmentation effects on a river network. The interactive effect of drying
and damming at the network scale, may result in more organic matter processed in dry reaches and reservoirs than in lotic reaches (Acuña & Tockner, 2010). According to our review, dry reaches and reaches downstream of reservoirs have a higher on average GHG flux potential than lotic reaches (Figure 3). Only six studies examining the interactive effects of drying and damming to different degrees were found in our search. The importance of the spatial distribution of drying and damming together along a river network is an important, but heavily understudied research area. In a Mediterranean river network impacted by drying and damming, there was both an increase and a decrease in the frequency of low-flow events at two different reaches downstream of reservoirs, but an overall decrease in the frequency of high-flow events (Aristi et al., 2014). They further found a consistent increase in all organic matter variables below reservoirs, which was possibly related to materials originating from the reservoir (e.g., re-suspended organic matter or outflow plankton) (Aristi et al., 2014). Likewise, an investigation of small reservoirs along an intermittent Mediterranean river network, found that reservoirs had higher microbial community processing of organic C, and they subsidised downstream lotic reaches, thereby increasing production and transformation of organic C along the river network (Proia et al., 2016). In disagreement with the aforementioned studies, a simulation of organic C dynamics in a Mediterranean river network found lower sediment C and respiration rates downstream of reservoirs, resulting from the accumulation of C in reservoirs via sedimentation as a result of high water-residence times (Acuña & Tockner, 2010). They further found that increasing flow variability increased the amount of C processed within a river network, whereas reservoirs had a counteractive effect on extreme flow events owing to their flow regulation capacity (e.g., reservoir water retention was not markedly reduced during droughts) (Acuña & Tockner, 2010). These differences may be attributed to context-dependent reservoir (e.g., age, depth, water residence time) or river network (e.g., geology) characteristics (Poff & Hart, 2002). For example, if the water is released from the top or the bottom of the reservoir, where the latter is more likely to be enriched in nutrients and organic matter (Nürnberg, 2007).

With the interactive effect of drying and damming at the network scale, we expect more organic matter to be processed in dry reaches and reservoirs than in lotic reaches. The potential additive effect would therefore result in more GHGs emitted to the atmosphere compared to an equivalent, unfragmented, river network (Figure 5c). However, upstream drying and reservoirs also may hold back organic matter from downstream reaches (Stanford & Ward, 2001), resulting in lower downstream GHG fluxes. We also could expect the temporal nature of GHG fluxes to be more variable in fragmented river networks, as upon the rewetting of previously dry reaches, the accumulated organic matter can be transported downstream (Datry et al., 2018), where it would then be stored and processed in a reservoir. In addition, there may be a potential synergistic effect as the presence of a reservoir can reduce flow rates, or, particularly if water is abstracted from the reservoir, create new intermittent reaches downstream (Bianchi et al., 2017; Zhou et al., 2020). As a result, organic matter processing rates and associated GHG fluxes in the river network are augmented as a consequence of the creation of these new dry and lentic states. However, in other cases, the reservoir baseflow may turn previously intermittent reaches perennial (Acuña et al., 2017), resulting in a compensatory effect on GHG fluxes caused by the replacement of dry reaches with lotic ones. The interactive effects of drying and damming are complex and context dependent. With much of the current literature on this topic focused on the Mediterranean, we need an increased geographical diversity in studies to test our conceptual models of drying and damming interactive effects.

6 | Future Research Directions

We uncovered several research gaps in geography, spatial scale, type of gas measured and hydrological state measured. We additionally identified a major knowledge gap on the interactive effects of drying and damming. Here, we propose four actionable future research directions as identified in our review of the literature on the effects of fragmentation by drying and damming on GHG fluxes.

1. Firstly, we identified an information gap in terms of the geographical distribution, spatial sampling scale, and GHG measured by studies. Most of the studies about IRES were conducted in the Mediterranean, Australia and southern United States. This narrow spatial focus omits the world’s temperate regions, which also include IRES (Messager et al., 2021), as well as many other arid landscapes, such as those found in Central and South America, Africa and Asia. The majority of studies about river systems impacted by damming were from China, with some studies in Brazil, French Guiana and the USA. Moreover, most of the studies done on IRES systems were conducted at the reach scale, with few studies at the global or network scale. These scales are important for understanding the ramifications of the highly variable spatial patterns in IRES. Likewise, very few studies examined the impacts of damming on GHG fluxes in rivers at a network scale. The magnitudes and drivers of fluxes may vary across the longitudinal gradient from headwaters to the mainstem. Furthermore, studies that measured GHG fluxes from dry and rewetting IRES most commonly measured CO₂, with few studies measuring CH₄ and N₂O. A similar tendency was observed in studies of river networks fragmented by damming, where fewer studies included measurements of N₂O when compared to CH₄ and CO₂.

2. Since our literature review, several notable studies examining GHG fluxes from dry inland waters have been published (e.g., Arce et al., 2023; Bretz et al., 2021; DelVecchia et al., 2021; Koschorreck et al., 2022; Paranaíba et al., 2021; Pinto et al., 2021; Schreckinger et al., 2022). However, there is still a marked
shortage of studies on GHG fluxes from isolated pools in IRES, with most studies focused on dry sediments (Bonada et al., 2020). For example, we did not find a single study about N₂O fluxes from isolated pools. Although isolated pools may occur at a lower frequency and over a smaller area than dry states, they may have a high GHG production potential (Bonada et al., 2020). Isolated pools have lentic waters, warm water temperatures and high organic matter accumulation, which may result in anoxic conditions which can promote methanogenesis and denitrification (Bonada et al., 2020; Day et al., 2019). Thus, isolated pools represent a potential source for CH₄ and N₂O, particularly under future predictions of increasing freshwater temperatures (van Vliet et al., 2013) and augmented terrestrial subsidies to inland waters (Regnier et al., 2022).

3. We found that most studies focused on large reservoirs, while small reservoirs (e.g., hydropower plants with <10 megawatts) were studied to a lesser extent, even though there are significantly more of them (Chanudet et al., 2020; Couto & Olden, 2018). There is currently a boom in small hydropower plants as the hydropower potential of larger rivers has already been exploited, public support for new large reservoirs has diminished, and small reservoirs are perceived to have a lesser ecological impact (Couto & Olden, 2018; Lange et al., 2018). Although their surface area and therefore total local GHG flux potential may be smaller, small reservoirs may have important cumulative fragmentation effects on GHG fluxes at the network scale which warrant further investigation.

4. Fragmentation by drying and damming do not occur independently. Therefore, it is important to understand how drying and damming interact to influence the dynamics of GHG fluxes. We found six studies that covered this topic in our review of the literature, predominantly conducted in the Mediterranean, with mixed results. Reservoirs may support downstream flow during drought periods, or may exacerbate drying downstream. Given the increasing occurrences of drying and damming (Döll & Schmied, 2012; Zarfl et al., 2015), it is imperative to examine their interactive effects on GHG fluxes in river networks, thereby better integrating global GHG budgets over space and time.

In summary, there has been a recent increase in studies examining GHG fluxes in river networks fragmented by drying and damming. We propose that the location and type of fragmentation within a river network are important factors influencing GHG dynamics. There are still many unexplored gaps in the research, which, if addressed, can improve our understanding of these complex and globally important systems and help to inform local management of fragmented river networks as well as climate change mitigation strategies.

AUTHOR CONTRIBUTIONS
Conceptualisation, data interpretation, and writing: Teresa Silverthorn, Thibault Datry, Vincent Chanudet, Arnaud Foulquier, and Naïara López-Rojo. Preparation of figures and tables: Teresa Silverthorn and Naïara López-Rojo. Preparation of figures and tables: Teresa Silverthorn. All authors read and approved the final manuscript. All authors agree to be accountable for the accuracy and integrity of the work.

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CONFLICT OF INTEREST STATEMENT
The authors have no conflicts of interest to declare that are relevant to the content of this article.

DATA AVAILABILITY STATEMENT
The dataset collected from our literature review as well as the code used to analyse the data and create the figures for this study are openly available in Zenodo at https://doi.org/10.5281/zenodo.7431750.

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