Article Title: A Systematic Review of Dissolved Oxygen in Streams and Rivers: Advances, Challenges, and Opportunities

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Authors:

Corresponding author: Jasmine A. Krause, https://orcid.org/0009-0002-2017-0229, Oregon State University, Corvallis, Oregon, USA; krausjas@oregonstate.edu

Cassandra Knutson, Oregon State University, Corvallis, Oregon, USA; knutscas@oregonstate.edu

Erin R. Hotchkiss, https://orcid.org/0000-0001-6132-9107, Virginia Tech, Blacksburg, Virginia, USA; ehotchkiss@vt.edu

Matthew Cohen, https://orcid.org/0000-0001-5674-1850, University of Florida, Gainesville, Florida, USA; mjc@ufl.edu

Adam S. Ward, https://orcid.org/0000-0002-6376-0061, Oregon State University, Corvallis, Oregon, USA; adam.ward@oregonstate.edu

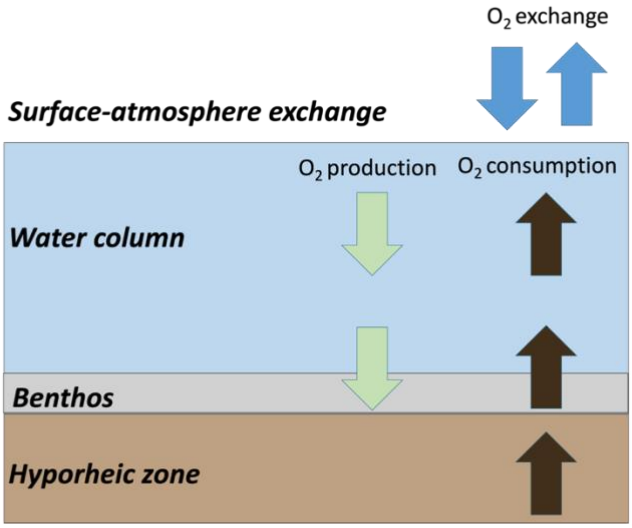
Conflict of Interest

The authors have declared no conflicts of interest for this article.

ABSTRACT

Dissolved oxygen (DO) has been extensively studied in streams and rivers. Despite this breadth of research, the processes governing DO are rarely quantified concurrently with whole-ecosystem measurements. To address this gap, we synthesize 230 empirical studies (1964-2024) to evaluate how, where, and with what methods oxygen exchanges—the processes by which oxygen enters and leaves streams—have been measured. We organize oxygen exchanges into five groupings, treating whole-stream metabolism as an integrative category of four underlying process domains: (1) water column, (2) benthic, (3) the hyporheic zone and sediments, and (4) surface-atmosphere exchange. Across the literature, estimates of whole-stream metabolism and gas exchange dominate, reported in 66% and 18% of studies, respectively, while underlying process domains were collectively reported in fewer than 16% of studies and jointly quantified in less than 7%. Where units permitted comparison, estimates of respiration in benthic, hyporheic, and underlying sediments were among the most variable exchanges yet least frequently measured. Together, these patterns indicate that our current understanding of stream oxygen dynamics relies heavily on integrative, reach-scale metabolism estimates, while the processes that generate these signals remain poorly resolved due to methodological and disciplinary silos. We identify key challenges and opportunities for synthesizing oxygen exchanges, emphasizing standardized reporting, concurrent measurements, and cross-site comparisons to advance integrated assessments of DO exchanges across streams and rivers.

GRAPHICAL ABSTRACT AND CAPTION



Dissolved oxygen in streams reflects the balance between physical exchange with the atmosphere (blue arrows) and biological processes across the water column, streambed (benthos), and hyporheic zone. Green arrows denote oxygen production, while brown arrows indicate oxygen consumption.

1. INTRODUCTION

Dissolved oxygen (DO) is a master variable in aquatic ecosystems as it integrates physical, biological, and chemical processes occurring within a waterbody and the connected river corridor (Hutchinson, 1938). DO serves as a constraint on aquatic life, an indicator of ecosystem processes and their dynamics (e.g., Davis, 1975), and regulates the cycling of both macro- and micronutrients (e.g., Davison, 1993). In well-oxygenated environments, microbial respiration uses oxygen as a terminal electron acceptor, but as DO is depleted processes such as nitrate, iron, and sulfate reduction emerge (Morrice et al., 2000). These redox transitions influence the production of greenhouses gases (McClain et al., 2003; Beaulieu et al., 2011), mobilization of contaminants (Borch et al., 2010; O'Donnell et al., 2024), and determine the net release or retention of nutrients (Hupfer & Lewandowski, 2008). At the same time, DO constrains biological communities, where low oxygen (<5 mg L^{-1}) can impair growth and reproduction in fish and macroinvertebrates (Vaquer-Sunyer & Duarte, 2008; Saari et al., 2018). Moreover, hypoxia (<2 mg L^{-1}) has become increasingly documented in aquatic ecosystems globally driven by a combination of climate warming, nutrient enrichment, and hydrologic alteration (Jane et al., 2021; Blaszczak et al., 2023; Chan et al., 2025). While we have extensive knowledge about DO in lotic systems and its relation to other processes, our overarching hypothesis is that our present understanding of DO in space and time remains limited by methodological heterogeneity, scales of investigation, and divergence between fields and their respective norms.

Oxygen solubility in water is fundamentally controlled by temperature, pressure, and salinity, but the amount of DO and its dynamics in streams result from a complex interplay of physical (e.g., reaeration), biological (e.g., primary production and autotrophic and heterotrophic respiration), and chemical processes (e.g., reduction of iron). In most lotic systems, however, physical (Zhi et al., 2023) and biological (Garvey et al., 2007) controls overwhelmingly dominate oxygen budgets, while chemical processes play a comparatively minor role. Streams themselves are hierarchically organized in both space and time (e.g., Frissell et al., 1986; Ward, 1989), and the dominant controls on DO shift with watershed characteristics (e.g., watershed area, light availability), hydrologic attributes (e.g., discharge, velocity, depth), surface water chemistry (e.g., nutrients, water chemistry), and subsurface conditions (e.g., residence time, soil properties, hyporheic exchange).

Early conceptual and modeling approaches sought to formalize these controls by linking them to the biological and physical components of the oxygen budget. The classic Streeter-Phelps model (Streeter & Phelps, 1925) explicitly coupled organic-matter decomposition via respiration with reaeration. Perhaps the most influential model of oxygen in lotic ecosystems, however, was developed by Odum (1956), who provided a framework to relate and quantify gross primary productivity (GPP), ecosystem respiration (ER), and gas exchange:

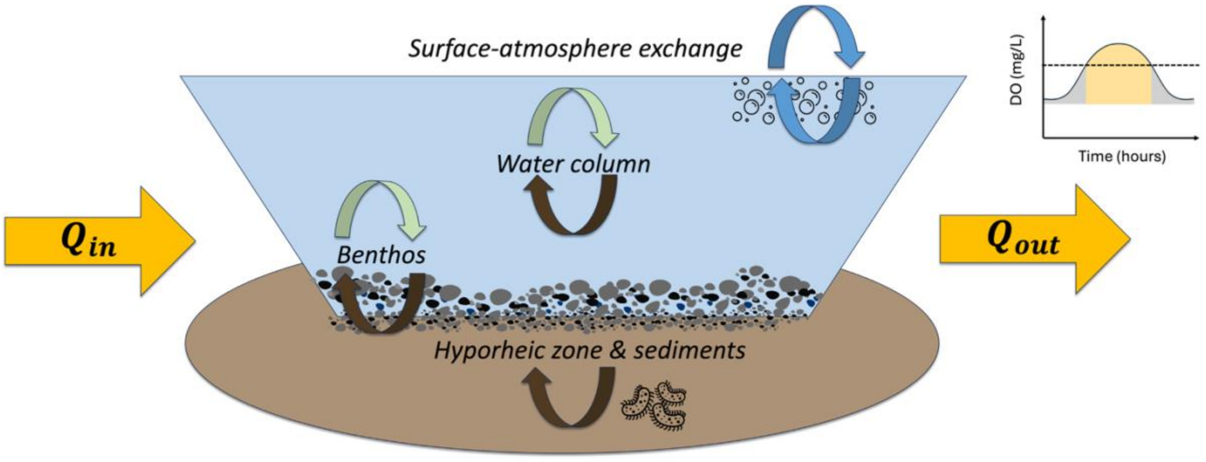
$$\frac{dO_2}{dt} = GPP - ER + k\,(C_s - C)$$

where $\frac{dO_2}{dt}$ is the net areal oxygen flux (g O_2 m^{-2} day^{-1}), *k* is the gas transfer velocity (m day^{-1}), C_s is the dissolved oxygen concentration at saturation (g O_2 m^{-3}), and *C* is the in-stream dissolved oxygen concentration (g O_2 m^{-3}). Building on this early oxygen balance, subsequent models include analytical solutions for estimating diel DO fluctuations (O'Connor, 1967; Gulliver & Stefan, 1984; Chapra & Di Toro, 1991). Concurrently, improved sensor accessibility and reliability (Uehlinger & Naegeli, 1998; Zhang et al., 2024) enabled the application of complementary measurement and modeling approaches, ranging from the two-station method (Marzolf et al., 1994) to eddy covariance (Koopmans & Berg, 2015), and dissolved gas analysis via membrane inlet mass spectrometry (Vautier et al., 2020). The resulting growth in high resolution datasets have enabled new analytical techniques, including network synchrony (Diamond et al., 2023), entropy (Canadell et al., 2021), and frequency-domain approaches (Shin et al., 2024). Lacking, however, is the ability to disaggregate the metabolic processes in streams to better represent oxygen exchanges between ecosystem compartments based on the underlying processes.

Our review defines oxygen exchanges as processes through which oxygen enters or leaves different stream compartments. We organize oxygen exchanges into five distinct categories. First, whole-stream metabolism (GPP and ER) is an integrative measure of stream DO that emerges from the interaction of multiple underlying processes. Next, these underlying processes are grouped by where oxygen is consumed or produced within (1) the water column, (2) the benthos, (3) the hyporheic zone or sediments, and (4) surface-atmosphere exchange (Fig. 1). Together, these four process domain groups represent distinct yet coupled physical and biogeochemical processes that regulate the balance of oxygen, the net aggregation of which are manifest at the whole-stream scale. Different disciplines or research questions may emphasize different groups. For example, physical scientists studying channel hydraulics and gas exchange may focus on surface-atmosphere exchange using empirical tracers (O'Connor & Dobbins, 1958), sound spectral analysis (Klaus et al., 2019), and simulations rooted in fundamental physics (Zappa et al., 2007). Ecosystem ecologists may focus on whole-stream metabolism (Demars et al., 2015) or individual components and their ecological functions (Battin et al., 2016). Still others will emphasize dynamics along particular flowpaths such as those in the hyporheic zone (Zarnetske et al., 2011). Thus, a comprehensive understanding of DO and its dynamics requires bridging disciplines and linking exchanges across a host of spatial and temporal scales, as compartment dominance may vary between stream settings, and even shift seasonally, or under disturbance (Vadeboncoeur et al., 2003; Genzoli & Hall, 2016).

Our objective is to critically review how oxygen exchanges and their controls have been studied in streams and rivers. Here, we evaluate how studies quantify oxygen exchanges and how often these have been measured together to provide an integrated understanding of stream oxygen budgets. We also examine how studies of oxygen have evolved over time, identifying which exchanges and methods have been emphasized, and where persistent gaps remain. We use these patterns to answer the question: *To what extent does existing literature capture interconnected exchanges that comprise a stream oxygen budget, and how have these exchanges been studied?* Our results allow us to highlight biases and limitations in the literature, from which we outline four key challenges to achieving a holistic understanding of DO dynamics in streams, and propose a set of forward-looking goals for the research community.

2. DEFINING OXYGEN EXCHANGES IN STREAMS AND RIVERS



$$\frac{dO}{dt} = \text{Reaeration} + \underbrace{\text{Gross Primary Production}}_{\text{Water column + Benthic}} - \underbrace{\text{Ecosystem Respiration}}_{\text{Water column + Benthic + Hyporheic \& sediments}}$$

Figure 1. Conceptual model of oxygen exchanges into and out of a stream channel. The schematic illustrates the major exchanges governing dissolved oxygen (DO) dynamics in streams organized into water column and benthic production and respiration, hyporheic and sediment respiration, and surface-atmosphere exchange. Arrows depict oxygen production (downward) and consumption (upward), while inflow (Q_{in}) and outflow (Q_{out}) indicate advective transport through the reach. The inset shows a characteristic diel DO signal resulting from the combination of physical and biological exchanges, with daytime (yellow), nighttime (gray), and a dashed line indicating oxygen saturation. The oxygen mass balance equation shown below summarizes whole-stream oxygen dynamics (dO/dt) as the integrated outcome of these interacting fluxes.

2.1 Whole-stream metabolism

Gross primary production (GPP) is inferred from the total oxygen production via photosynthesis, while ecosystem respiration (ER) reflects the total oxygen consumption by autotrophs and heterotrophs; their difference (i.e., GPP - ER) defines net ecosystem production (NEP), capturing the balance between autotrophic energy fixation via photosynthesis and aerobic respiratory demand (Odum, 1956). Although typically evaluated for carbon cycling since DO is easier to measure than CO_2, GPP and ER are fundamentally oxygen exchanges. The primary drivers of GPP are light—particularly biologically available light within the stream channel—and flow variation, whereas ER is more tightly coupled to GPP and flow conditions (Kirk et al., 2021; Bernhardt et al., 2022). Both GPP and ER vary systematically in response to watershed land uses and disturbance regimes (Bernot et al. 2010; Finlay, 2011). For example, in forested headwaters, the combination of shading, low nutrients, and high allochthonous organic matter supply allows ER to exceed GPP, whereas downstream reaches with greater light availability or elevated nutrients from agriculture or urbanization can increase GPP and/or ER and underpin longitudinal patterns in stream ecosystems (e.g., Vannote et al., 1980, Carter et al., 2024). The balance of GPP and ER is increasingly applied as an indicator of land use change and as a tool in stream restoration and management (Young et al., 2008; Arroita et al., 2019; Diamond et al., 2021; Jankowski et al., 2021).

Early diel DO measurements to assess whole-stream GPP and ER were conducted manually using Winkler titrations, a labor-intensive approach that limited temporal resolution and duration. High-frequency *in situ* sensors have revolutionized the estimation of whole-stream GPP and ER by allowing continuous monitoring and reach-scale integration (Marzolf et al., 1994). The most widely used approach for quantifying GPP and ER is the diel oxygen technique, or whole-stream metabolism, where single- and two-station models solve oxygen mass balances to estimate GPP, ER, and gas exchange simultaneously (Riley & Dodds, 2013; Grace et al., 2015). Recent advances in modeling tools, such as streamMetabolizer, have improved parameter estimation by allowing gas exchange to vary with discharge, examining DO residuals, reducing equifinality, and enabling meta-analysis of field studies (Holtgrieve et al., 2010; Appling et al., 2018a; Appling et al., 2018b).

Spatial patterns in river network metabolism are well-established (Vannote et al., 1980; Mulholland et al., 2001; Mejia et al., 2019). Most whole-stream metabolism models and empirical estimates operate at the reach-scale, where accuracy improves with longer time series and well-constrained gas exchange (Appling, et al., 2018a). However, scaling reach-scale metabolism estimates to network or basin scales remains challenging due to equifinality among parameters, site-specific characteristics, and event-driven disturbance that disrupt diel patterns including sediment pulses, storms, and flow intermittence (Hotchkiss & Hall, 2014). In response, a growing body of literature is advancing network-scale modeling frameworks (e.g., Segatto et al., 2023) and synthesizing metabolic patterns that emerge across regions 28/01/2026 22:34:00. Emerging work further integrates stream metabolism with process-based approaches such as hydraulic routing (Payn et al., 2017), partitions autotrophic and heterotrophic production (Hall & Beaulieu, 2013), and links metabolic rates to CO_2 cycling and emissions (Hotchkiss et al., 2015). Despite these advances, challenges remain when interpreting DO signals (e.g., Gomez-Velez et al. 2026). Most metabolism models assume observed DO dynamics reflect in-stream biological processes and surface-atmosphere exchange. In reality, streams lose and gain oxygen from multiple hydrologic processes including hyporheic exchange, groundwater inputs or losses, and overland flow, each likely with potentially different signatures than stream water. Groundwater inputs are known to bias metabolism estimates by altering DO concentrations without corresponding in-stream biological production or consumption (Hall & Tank, 2005).

While whole-stream estimates of ER and GPP have advanced our understanding of DO (and carbon) dynamics at the scale of river segments and networks, improved reach-scale understanding requires quantifying the compartment-specific processes that contribute to integrated whole-stream ER and GPP observations (sections 2.2 and 2.3). Resolving these compartment-specific exchanges is essential because oxygen dynamics arise from the superposition of water column, benthos, hyporheic zone, and groundwater processes, the combination of which can create signals that obscure clear inferences of whole-stream metabolism (Fig. 1).

2.2 Water column production & respiration

Water column metabolism refers to the combination of photosynthesis and respiration occurring within the water column of the stream, often by phytoplankton and microbes on suspended particles and organic matter. Although conceptually distinct from benthic metabolism (section 2.4 below), the two are tightly coupled as they continuously exchange material and energy (Fisher et al., 1998; Battin et al., 2008). Water column contributions to whole-stream metabolism broadly increase with channel size, where greater depth, residence time, and light availability favor planktonic communities (Vannote et al., 1980; Yang et al., 2021). While water column metabolism tends to be minimal in most low-order streams, often an order of magnitude lower than whole-stream estimates (Fisher & Likens, 1973; Bott et al., 2006; Plont et al., 2022), it can represent a substantial fraction of ecosystem metabolism in mid-sized, nutrient enriched rivers (Vink et al., 2005; Oliver & Merrick, 2006). For example, Reisinger et al. (2016) showed that water column contributions to GPP exceeded those to ER in mid-order rivers, with their importance largely dependent on organic matter and nutrients.

Early studies of stream metabolism relied on chamber and incubation techniques, such as light-dark bottle incubations and *in situ* chambers, which isolated water column and benthic processes without the confounding effect of gas exchange (Hargrave, 1972; Bott et al., 1978). While these techniques remain useful, they are labor-intensive and capture only a snapshot in time. Recent advances such as autonomous *in situ* devices that automate light-dark incubations with optode-based oxygen sensors have been applied in marine environments (Collins et al., 2018). These instruments are costly and are not designed for deployment in smaller, more dynamic headwaters, but could be deployed in larger rivers. Remote sensing of phytoplankton via pigment optical effects provides another pathway; while these approaches work well in lakes, they often fail in rivers due to optical complexity (Spyrakos et al., 2018). Beyond sensor technology, integrative approaches that combine metabolic measurements with biogeochemical assays (e.g., nutrient uptake, denitrification) have been used to link water column metabolism to broader biogeochemical cycling, particularly across land use gradients (Reisinger et al., 2021). Long-term monitoring efforts combined with process-based approaches can also track temporal shifts in water column contributions (Van De Bogert et al., 2007), but scaling across sites, seasons, or networks is rare, constraining our ability to generalize rates and controls on water column contributions to whole-ecosystem fluxes.

2.3 Benthic production & respiration

Benthic metabolism, the photosynthesis and respiration occurring on the streambed, is driven by biofilms, periphyton, macrophytes, and sediment microbial communities. Benthic production is regulated by light availability and substrate properties including surface roughness, stability, and disturbance history (scour, burial, or grazing), with algal biomass accrual and disturbance regimes further modulating autotrophic production, particularly in nutrient-limited headwaters (Francoeur et al., 1999; Atkinson et al., 2008). By contrast, benthic respiration is largely driven by organic matter supply, temperature, and oxygen delivery to sediments (Acuña et al., 2004). In most streams and rivers, benthic processes dominate relative to the water column and may be amplified by changes in food web dynamics and external energy sources. For instance, Rutherford (1991) found that benthic metabolism far outweighed water column contributions in a stream receiving paper mill effluent, while Hall et al. (2003) demonstrated how the invasive snail *Potamopyrgus antipodarum* consumed most of the benthic autotrophic biomass produced by GPP and drove nutrient cycling in a highly productive stream.

Benthic metabolism is typically measured using chambers that enclose patches of the streambed (Mulholland et al., 2001; Rüegg et al., 2015; Lopez et al., 2025). Partitioning contributions of different benthic materials has been a research focus with studies targeting macrophyte production (Fisher & Carpenter, 1976; Hensley & Cohen, 2020), algal photosynthesis (Mulholland et al., 1994; Acuña et al., 2011), and microbial respiration in sediments (Hill et al., 2000). Recently, aquatic eddy covariance—a technique widely applied in wetlands and marine systems—has been applied to measure *in situ* benthic oxygen fluxes in streams (Rovelli et al., 2017), though measurements integrate turbulent exchange near the bed and may include water column contributions. Scaling benthic metabolism in space is difficult due to sediment heterogeneity (Lee-Cullin et al., 2018), with fluxes varying up to two orders of magnitude depending on substrate type, catchment land use, and disturbance regime (Fellows et al., 2006), and organic matter quantity (Hill et al., 2017). This variation implies that efforts to quantify these fluxes, especially when estimates are conjoined with open-channel measurements, will improve our understanding of how whole-system fluxes are partitioned.

2.4 Hyporheic respiration and sediment oxygen demand (SOD)

The hyporheic zone is the interface within stream sediments where surface water exchanges with shallow groundwater, encompassing flowpaths where parcels of water temporarily leave the stream channel and return after undergoing biogeochemical transformations within the sediment (White, 1993; Krause et al., 2011). Within this zone, hyporheic respiration—the consumption of oxygen along subsurface flowpaths—can represent a major sink of DO, driven primarily by microbial and faunal respiration (Triska et al., 1989; Findlay, 1995; Boulton et al., 2010). The magnitude and variability of hyporheic respiration are shaped by a combination of hydrologic, biogeochemical, and geomorphic factors. Residence time, hyporheic exchange fluxes, and the reaction rates ultimately control solute transport and transformation within the hyporheic zone, ultimately determining the efficiency with which the hyporheic zone processes oxygen and other constituents (Gomez et al., 2012). Although the hyporheic zone plays a central role in stream oxygen dynamics, much of the literature has focused on carbon and nitrogen transformations, reflecting its function as a biogeochemical reactor (Findlay et al., 1993; Tureţcaia et al., 2023).

Hyporheic respiration has been quantified by vertical oxygen profiles, pore water sampling, and *in situ* or laboratory incubations (Revsbech et al., 1986; Uzarski et al., 2001; Nelson et al., 2019). Experimental flumes have been used under controlled flow and sediment conditions to isolate hyporheic exchange and determine how reaction rates and biogeochemical processes vary across redox conditions (Reeder et al., 2018), while streamside mesocosms packed with bed sediment have been used to replicate *in situ* flow paths to the maximum extent practicable (Serchan et al., 2024; Herzog et al., 2025). High-resolution oxygen sensors have been deployed directly into hyporheic sediment to measure oxygen along hyporheic flowpaths through time (Malcolm et al., 2006; Gooseff et al., 2023), complemented by dissolved gas time series that reveal hyporheic exchange and redox transitions (Mächler et al., 2013).

Sediment oxygen demand (SOD) represents the total biological and chemical consumption of oxygen in the subsurface and is conceptually complementary to hyporheic respiration. While hyporheic research is largely focused on understanding subsurface ecosystem processes (Ward, 2016), SOD emerged as a stream-centric concept to explain oxygen deficits not accounted for by in-stream processes alone, particularly in the context of predicting oxygen sag and organic loading along rivers (Thomann 1972; Lee et al., 1978). SOD has been widely used to assess the biogeochemical consequences of disturbance such as urbanization, logging, and eutrophication that elevate organic matter inputs, alter stream temperature and flow regimes, and change microbial assemblages (Utley et al., 2008). SOD is typically measured using mesocosms or chambers to incubate buried streambed sediment and quantify oxygen consumption (Bowman & Delfino, 1980), while recent reviews have called for standardized *in situ* chamber methods to improve transferability among systems (Coenen et al., 2019). Although rarely measured simultaneously, hyporheic respiration and SOD both quantify net oxygen consumption in the stream-connected subsurface (e.g., the hyporheic zone), yet *ex situ* incubations may not capture the full complexity of *in situ* transport and exchange processes. Because these subsurface fluxes are central to both the oxygen budget of a stream, and to the genesis of open-channel DO signals (Gomez-Velez et al., 2026), renewed attention to quantifying them as part of whole-stream measurements is likely to be critical to improved understanding of metabolic variation in time and space.

2.5 Surface-atmosphere exchange

Reaeration is the flux of oxygen across the stream-atmosphere interface and is a positive flux into the stream if the water is undersaturated relative to the atmosphere (negative if the water is supersaturated). In streams, gas exchange reflects the interaction between flow and channel form. The efficiency of exchange is controlled by turbulent mixing at the air-water interface, which depends on channel hydraulics such as velocity, depth, and slope (Melching & Flores, 1999; Ulseth et al., 2019). The rate of gas exchange depends on both chemical and physical controls, including water temperature (Wanninkhof, 1992; Hall & Ulseth, 2020), gas solubility (Garcia & Gordon, 1992), and the strength of the concentration gradient between the water and atmosphere (Raymond & Cole, 2001; Zappa et al., 2007).

The study of gas exchange in rivers has advanced along three primary methodological pathways. First, empirical tracer injections using a specific gas tracer (e.g., propane, SF_6, Ar) are used to measure degassing and inform empirical (e.g., Schmidt-number) relationships for estimating oxygen exchange (Tsivoglou & Wallace, 1972; Rathbun et al., 1978; Genereux & Hemond, 1992). However, scaling gas transfer across gases can introduce error under bubble-mediated conditions because of differences in gas solubility and diffusivity (Klaus et al., 2022). To reduce this uncertainty, argon has emerged as an ideal tracer due to its similarity in solubility and diffusivity to oxygen, minimizing scaling uncertainty (Hall & Madinger, 2018). Floating dome chambers offer a direct, non-invasive, and easily scalable method for measuring gas exchange, avoiding the logistical challenges of gas tracers but also provide smaller-scale measurements prone to bias when deployments alter stream turbulence (Lorke et al., 2015). Second, analyses of DO timeseries are used to infer gas exchange. The most widely used techniques include night-time regression, which isolates gas exchange from nighttime declines in DO when photosynthesis ceases and requires sufficient daytime oxygen production to generate a resolvable nighttime slope (Hornberger & Kelly, 1975); the solar noon lag, which examines the temporal offset between peak light and peak DO (McBride, 2002); and the delta method, which quantifies fluxes by partitioning observed changes in DO storage during both day and night (Chapra & Di Toro, 1991). Each of these approaches relies on detectable diel signals generated by the dynamics of photosynthesis and performs best in medium to large rivers where turbulence is lower and oxygen dynamics are less spatially heterogenous (Bailey & Ahmadi, 2014). Finally, based on tracer injection and other field studies, empirical relationships to predict gas exchange as a function of river hydraulics have been derived, allowing for gas exchange estimates without direct measurements of DO. Early models related gas exchange rates to velocity and depth (O'Connor & Dobbins, 1958), while later work incorporated turbulence metrics such as the energy dissipation method (Tsivoglou & Neal, 1976; Chu & Jirka, 2003) and used prior tracer experiments to develop physical models of gas exchange for small streams (Raymond et al., 2012; Aho et al., 2025). More recently, these models have been applied in scaling gas exchange across river networks and are widely applied in regional and global syntheses (Raymond et al., 2013; Hotchkiss et al., 2015).

The predictability of gas exchange is scale- and system-dependent regardless of which approach is used. Despite their utility, hydraulic equations are fundamentally reach-averaged estimates and perform poorly in morphologically complex headwaters, where turbulence and bubble entrainments vary over short spatial scales, and are usually generated from log-transformed data, leading to high predictive uncertainty (Rovelli et al., 2018; Vautier et al., 2020). Consequently, site-specific calibration or empirical measurements remain essential for accurate flux estimates in many streams and rivers (Hall & Ulseth, 2020). Methodological advancements including acoustic Doppler velocimetry (Gålfalk et al., 2013), stable isotopes (Tobias et al., 2007; Jamieson et al., 2013), and sensor-equipped floating chambers (Vachon et al., 2010; Arce et al., 2021) have increased our ability to resolve gas fluxes at higher spatial and temporal resolution, yet scaling these approaches across heterogeneous systems remains a significant challenge (Botter et al., 2022). We note that the goal of empirically constraining gas exchange to ensure robust metabolism estimates has been widely recognized, with conjoined measurements of k_{600} and open-channel DO time series new serving as method best practice (Appling et al., 2018a). This recognition highlights our central premise that attention to other compartment-specific fluxes will likely enhance the validity of metabolism measurements.

3. LITERATURE ANALYSIS: METHODS

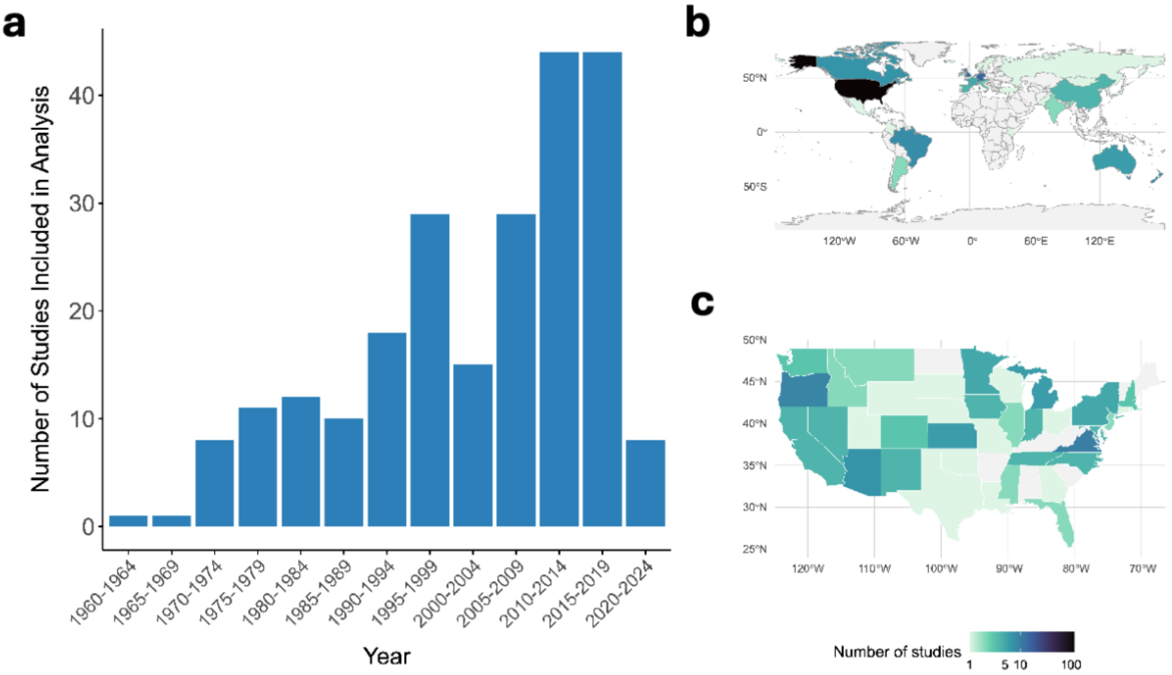


Figure 2. Temporal and geographic distribution of studies included in the synthesis. (a) Number of studies by five-year intervals. (b) Global distribution of study locations, with darker shading representing regions with higher numbers of included studies. (c) Spatial density of studies across the continental United States by state (log-scale color bar).

To assess the extent to which oxygen exchanges and methods have been applied, we conducted a search on Web of Science on August 26th, 2024, with the key words [“stream” OR “river” OR “aquatic”] AND [“dissolved oxygen” OR “O2”] and listed the processes of DO independently (see Table S1 of search strings), yielding a total of 4,086 studies. In Phase 1 of our extraction, we excluded synthesis papers (leaving n = 3,929) and filtered by relevant field of study to focus on streams and rivers (n = 2,832 after excluding studies of lakes, wetlands, marshes, and saltwater systems). The top fields of study represented in the body of literature were environmental sciences (1,487), water resources (622), and environmental engineering (578).

In Phase 2, a total of 2,832 articles were then exported and processed in Covidence, a systematic review management tool (Covidence, 2024). We screened each study by reviewing the title and abstract, retaining papers that met two criteria: (1) papers retained must include the presence of empirical data, excluding literature reviews, remaining syntheses, and modeling-only studies; and (2) papers retained must report an oxygen exchange as a rate or flux. We define oxygen exchanges broadly to encompass all quantified transfers of oxygen into or out of stream compartments, regardless of how rates and fluxes are reported. For consistency, we distinguish a flux as the mass per unit area per unit time and a rate as the mass per unit time (after Stauffer, 2006). A total of 914 studies were retained based on our review of the title and abstract. Next, we reviewed the full text of each study to screen for explicit reporting of a DO rate or flux, finding 321 papers that met our criteria. Studies reporting only carbon metabolism in non-O_2 units (e.g., CO_2 production as a measure of respiration) were excluded, as were studies that reported a flux but did not have a standardized unit such as compartment-specific biofilm studies (e.g., Glud et al., 1992 on cyanobacteria vs. diatoms) or with results standardized to a unit that would not be comparable to other literature (e.g., ash-free dry weight; McIntire, 1966). We excluded 115 studies on this basis, leaving 204 papers. In review of these 204 papers, only 8 included explicit observations of hyporheic processes. Consequently, we relaxed the requirement for hyporheic-centric studies to retain those that included subsurface observations of dissolved oxygen concentration (retaining them even if they did not specifically report a flux or rate), and those for which empirical work in a mesocosm or column was conducted as a proxy for hyporheic conditions. This yielded an additional 26 papers that described hyporheic concentrations of dissolved oxygen. Thus, our searches yielded a total of 230 papers from which data were extracted (Fig. 2a).

For each of the 230 papers, we first recorded background information on the study period and geographic location (Fig. 2b). Over half of studies were conducted in the U.S. (51%), with substantially fewer in Germany (7%) and the United Kingdom (6%; Fig. 2c). Within the U.S., Virginia had the most studies (9%), followed by Oregon (8%), and Alaska and Arizona (6% each). There were few studies in some continents (e.g., n=1 for Africa, n=0 Antarctica) and large countries based on land area (e.g., Russia). Studies were predominantly located in mid-latitude regions (90%), with fewer in tropical (6%) and high-latitude (4%) regions.

Next, we extracted information on stream size, land use, study objectives, watershed attributes, and environmental conditions. Stream size was classified using watershed area when provided: small (<100 km²), mid-sized (100–10,000 km²), and large (>10,000 km²) (after Lyche Solheim et al., 2019). When watershed area was not available, we used stream size binned as small (1-3), mid (4-6), and large (>7) stream orders (after Vannote et al., 1980). If neither metric was provided, we relied on study maps, qualitative descriptors, or conducted additional research on the study location to estimate stream size (n=23 studies). Land use was categorized based on qualitative descriptions in the site or methods sections using indicator terms: “pasture” or “cropland” for agricultural, “dams” or “impervious surfaces” for urban, and “mixed” for sites with multiple influences. Sites described as “pristine” or “forested” were classified as undisturbed. When land use percentages were reported, thresholds of >10% urban and >30% agricultural were used for classification, as these levels have been associated with negative impacts to stream condition (Allan, 2004). Without reported land use, additional research was conducted to characterize that study reach (n=16 studies) or left blank when not readily available from additional research (n=21 studies). Study objectives were categorized as: (1) measurements at the same site or location under varying conditions (e.g., changes between flows or seasons), (2) replicates in different streams, or (3) replicates along a river network. We also documented watershed attributes (canopy cover, elevation, watershed area), hydrologic metrics (gradient, stream size, discharge, and velocity), flow regime (e.g., perennial vs. non-perennial), surface water chemistry and environmental conditions (e.g., turbidity, temperature, nutrient concentrations, light, standing stock) and subsurface characteristics (e.g., hydraulic conductivity, transit time). Nutrient measurements included carbon (TOC, POM, POC, DOC, DIC), nitrogen (NO_3^-, NH_4^+, TN, DON, N_2), and phosphorus (SRP/PO_4^{3-}, TP, TDP). Light was characterized using illuminance (lux), photosynthetically active radiation (PAR), solar radiation, and light-attenuation coefficients. Whenever possible, mean values were taken directly from tables; when unavailable, we extracted ranges from tables or figures.

Because each oxygen exchange is measured and reported using different conventions (e.g., volumetric rates, areal fluxes, mass transfer coefficients), we systematically documented methods used, numerical values and associated units, and standard deviations when reported. We recorded values reported as rates (e.g., day^{-1} or m day^{-1} for gas exchange, and g O_2 L^{-1} day^{-1} for volumetric metabolic rates) and metabolic fluxes (g O_2 m^{-2} day^{-1}). For the comparison of exchange magnitudes in section 4.3, we analyzed only exchanges standardized to areal fluxes, which is the norm for reporting whole-stream metabolism. This requirement omitted 25 studies that did not report an areal flux. Gas exchange was excluded from this conversion because it is conventionally reported as an exchange rate (time^{-1}) or gas transfer velocity (length time^{-1}) that is normalized by depth, rather than a flux. For gas exchange, a host of conventions were used to report raw values (see Fig. S3). Here, we analyzed reported gas exchange as k_{600}, where the k value is normalized to a temperature-dependent Schmidt number (including n=64 studies for which sufficient data were presented for us to compute k_{600} if it was not reported by the authors).

Finally, to evaluate how oxygen exchanges have been measured across studies, we classified methods into eight categories that capture the dominant approaches (Box 1; Fig. 3). Tracer methods include conservative gas additions (e.g., Ar, SF_6, N_2, propane) as well as isotope tracers (e.g., ^{16}O and ^{18}O), which directly quantify gas exchange and transport processes. In-stream DO measurements were used to estimate multiple oxygen exchanges, including discrete *in situ* measurements (e.g., point measurements in wells to quantify hyporheic respiration) and continuous DO observations to estimate GPP, ER, and gas exchange from diel DO dynamics (see Fig. S3). Empirical equations represent velocity-depth or shear stress formulations that predict gas exchange coefficients from hydraulic variables. Interface flux methods incorporate floating probes, eddy covariance, sound velocity, and impermeable surface techniques that directly measure fluxes or turbulence. Standing stock quantifies accumulated biomass or chlorophyll-a as a proxy for metabolic activity. Chamber approaches are divided into field chambers (e.g., *in situ* benthic, mesocosms, light-dark bottles) and lab chambers collected from *in situ* samples (sediment or mesocosm incubations). Lastly, other modeling approaches include coupled biogeochemical (e.g., OTIS, PFLOTRAN) and water quality (e.g., QUAL2K, WASP) models, although these were required to have an empirical component to be retained in our database (i.e., modeling-only studies were excluded).

BOX 1. Oxygen fluxes and their typical methods and scales

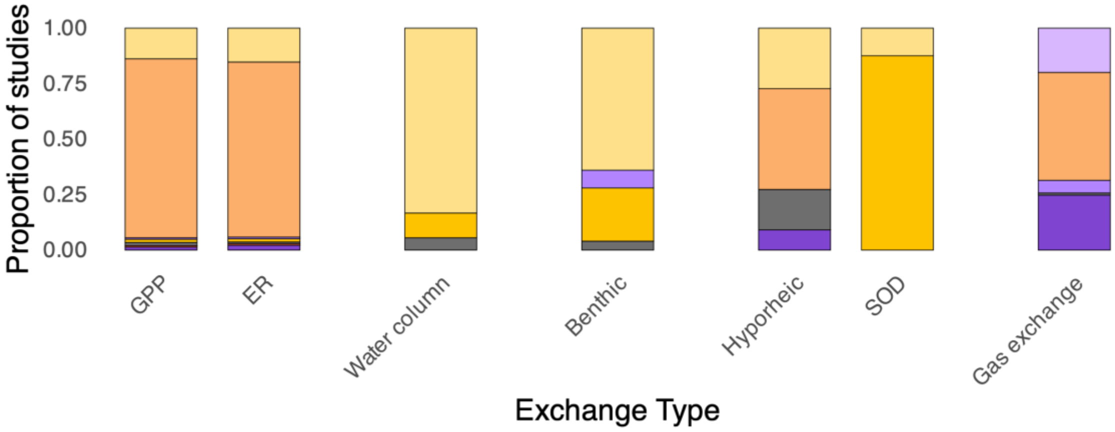


Figure 3. Methods used to quantify oxygen fluxes in streams. Stacked bars show the proportional contribution of different method categories used to estimate each oxygen exchange, while colors denote method categories. See Fig. 5 for temporal breakdown of methods.

Oxygen dynamics in streams emerge from multiple fluxes operating across distinct compartments and spatial scales, each quantified using different measurement approaches (Fig. 3). As summarized below, these fluxes integrate processes over spatial domains, spanning centimeter-scale sediment measurements to reach-scale estimates of metabolism and gas exchange, highlighting the ongoing challenge of integrating oxygen fluxes across compartments.

Sediment oxygen demand: Total oxygen consumption by streambed sediments due to biological respiration and abiotic oxidation of reduced compounds

- *Typical methods:* Quantified using *ex situ* sediment cores or *in situ* chambers
- *Typical spatial scale:* Patch scale (centimeter to meter)

Benthic metabolism: Photosynthesis and respiration occurring on the streambed, often by biofilms, periphyton, macrophytes, and sediment microbial communities

- *Typical methods:* Measured using *in situ* benthic chambers or incubations of rocks or sediments
- *Typical spatial scale:* Patch scale (centimeter to meter)

Water column metabolism: Photosynthesis and respiration occurring within the water column, often by phytoplankton and microbes

- *Typical methods:* Estimated using *in situ* chambers such as light-dark bottles
- *Typical spatial scale:* Patch scale (decimeter to meter)

Hyporheic respiration: Biologically mediated oxygen consumption along subsurface flow paths where surface water exchanges with shallow groundwater

- *Typical methods:* Quantified using *in situ* DO, *in situ* hyporheic chambers, or inferred from residence-time modeling, and tracer- or time-series approaches (e.g., argon, conductivity)
- *Typical spatial scale:* Patch scale (centimeter to meter) to sub-reach (1 to 10 meters)

Gross Primary Production (GPP) and Ecosystem Respiration (ER): Total oxygen produced via photosynthesis and consumed by autotrophs, heterotrophs, sediments, and subsurface pathways

- *Typical methods:* Inferred from diel DO signals using diel metabolism models or *in situ* chambers
- *Typical spatial scale:* Reach-scale (10s of meters to kilometer)

Surface-atmosphere exchange: Physical exchange of oxygen between the stream and the atmosphere

- *Typical methods:* Estimated using *in situ* DO time series, tracer gas injections (e.g., SF_6, propane, argon), empirical equations, or floating probes
- *Typical spatial scale:* Reach-scale (10s of meters to kilometer)

4. LITERATURE ANALYSIS: RESULTS

4.1 Which oxygen exchanges are most frequently reported and co-reported?

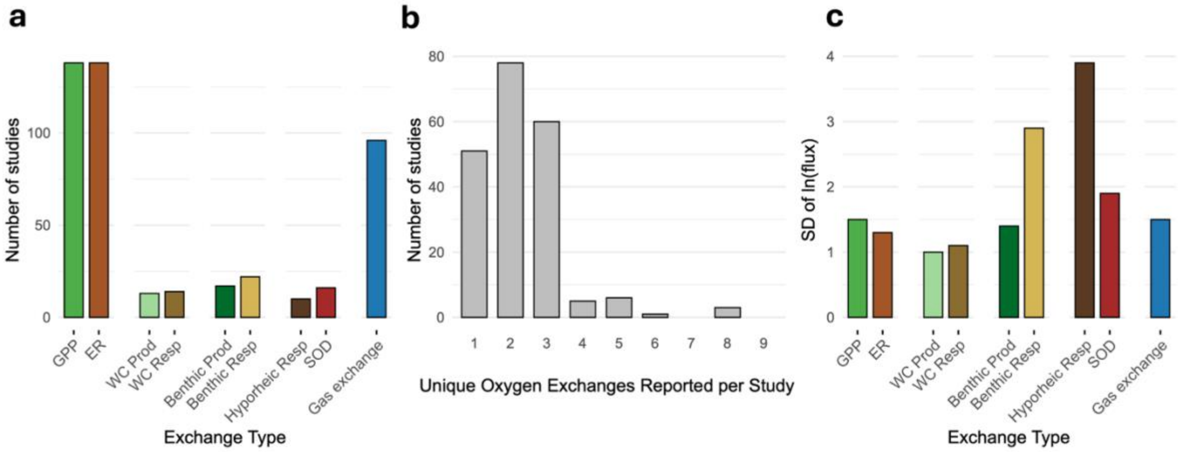


Figure 4. Reporting frequency and variability of oxygen exchange measurements across studies. (a) Number of studies reporting each oxygen exchange type, including GPP and ER, water column and benthic production and respiration, hyporheic respiration and SOD, and gas exchange. (b) Distribution of the number of unique oxygen exchanges reported per study. (c) Variability in reported oxygen exchanges across studies, expressed as the standard deviation of the log-transformed flux values for each exchange type.

Across all studies and exchange groups, reporting effort was highly variable (Fig. 4a). Whole-stream processes overwhelmingly dominated, with GPP and ER each reported in 33% of (66% combined), followed by the surface-atmosphere exchange needed to estimate metabolism (18%). Together, these three exchanges comprise the essential elements of Odum's (1956) whole-stream metabolism model and accounted for roughly 84% of all measurements, underscoring the emphasis on whole-stream metabolism within the literature. In contrast, reporting of underlying process domains was comparatively limited, with benthic exchanges reported in 7% of studies, sediment oxygen demand in 5%, water column processes in 4%, and hyporheic respiration in only 1%.

Co-reported exchanges further illustrate this pattern. GPP and ER were jointly reported in 65% of studies, and gas exchange was commonly paired with one or the other (31% with ER; 30% with GPP; Fig. S5). Beyond whole-stream and surface-atmosphere exchanges, co-reporting declined sharply: benthic production and benthic respiration were the next most frequently paired exchanges at 7%, followed by water column production with gas exchange (5%), and water column production with water column respiration (4%). Notably, hyporheic respiration and SOD were never reported together, and when they were measured, they were typically paired alongside benthic or water column exchanges. The distribution of unique exchanges per study further emphasizes this imbalance, where 94% of studies reported three or fewer oxygen exchanges, indicating that most investigations focus on whole-stream metabolism, often paired with gas exchange, while omitting the water column, benthic, and hyporheic and sediment measurements contributing to whole-stream oxygen signals (Fig. 4b).

Only a handful of studies characterize different oxygen exchanges within streams—Acuña et al. (2011), Hogsett & Goel (2013), and Oliver & Merrick (2006) reported eight exchanges (excluding SOD), and one study (Chessman, 1985) reported six. By measuring multiple oxygen and carbon exchanges simultaneously, these studies gained important information on the spatial and temporal variability of different exchanges, with controls shifting across hydrologic conditions, disturbance, and position along the river continuum. Key insights included the importance of specific processes and compartments, such as the hyporheic zone accounting for a majority of ER and floating macroalgae dominating GPP (Acuña et al., 2011), as well as identifying ecosystems where net water column production exceeded net benthic production (Oliver & Merrick, 2006). Importantly, ecosystems with different metabolic pathways can exhibit similar whole-stream signals, including similar GPP:ER ratios. For example, Oliver & Merrick (2006) showed that sites with different dominant carbon sources (e.g., phytoplankton vs benthic) can have similar NEP values, underscoring the importance of knowing how different zones are contributing to whole-ecosystem productivity and food web energetics.

4.2 How are oxygen exchanges being measured?

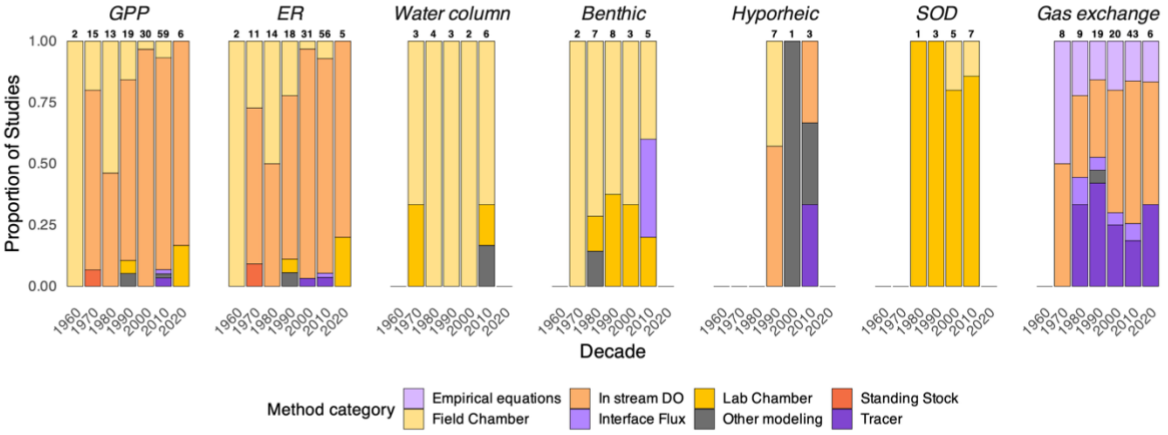


Figure 5. Temporal evolution of methods used to quantify oxygen exchanges across studies. Stacked bar plots show the proportional contribution of different methodological approaches used to estimate oxygen exchanges by decade for each exchange type (GPP, ER, water column, benthic, hyporheic, SOD, and gas exchange). Colors indicate method categories, including empirical equations, field, lab, and flux chambers, standing stock, tracers, in-stream DO, and other modeling approaches. Numbers above bars denote the total number of studies contributing data in each decade. See Fig. 3 for collective methods by exchange type.

Across oxygen exchanges, methodological differences reflected both the spatial scale of measurement and the process of interest (Box 1). In-stream DO was the most common approach for quantifying gas exchange (49% of studies), GPP (81%), ER (79%), and hyporheic respiration (46%), reflecting both discrete and continuous measurements that have evolved through time (Fig. 3). DO-based estimates of hyporheic respiration often relied on the difference between ecosystem and benthic metabolism rather than being directly measured (e.g., Naegeli & Uehlinger, 1997; Acuña et al., 2011; see section 5.2 for limitations). After in-stream DO, gas exchange was most commonly quantified using tracers (25% of studies), encompassing a variety of gases—including argon, propane, helium, xenon, ethylene, nitrogen, sulfur hexafluoride, and krypton (e.g. Young & Huryn, 1999; Roley et al., 2023)—with additional tracers used to link gas exchange and metabolic rates (Piatka et al., 2021; Barbosa et al., 2023), followed by empirical equations (20%). In contrast, water column, benthic, and SOD measurements were dominated by chamber-based approaches, with field chambers accounting for 83%, 64%, 12% of studies and lab chambers comprising 11%, 24%, 88%, respectively.

Beyond in-stream DO, tracers, and chamber-based approaches, a suite of less frequently applied methods has been used to quantify oxygen exchanges. Interface flux approaches have expanded exchange measurements across flow regimes by capturing near-continuous gradients *in situ* such as the soluble floating probe method using oxalic acid as a reactive tracer (De Souza Ferreira et al., 2020), floating probes with O_2 sensors (Hogsett & Goel, 2013), and aquatic eddy covariance (Koopmans & Berg, 2015). The interface flux category was highest for benthic exchanges (8% of studies), then gas exchange (6%), and GPP/ER (1%). Other approaches included the standing stock method—applied exclusively to GPP and ER (1%)—relating photosynthetic or respiratory activity to algal biomass or organic carbon content. Lastly, process-based modeling studies informed by empirical observations, including frameworks such as the PROSE model (Even et al., 2004) or reactive transport models (Diem et al., 2013) accounted for 18% of hyporheic, 6% of water column, 4% of benthic, and less than 1% of GPP, ER, and gas exchange studies.

Methods to quantify exchanges have also shifted through time, both in frequency and diversity (Fig. 5). After relatively few studies in the 1960s, research on most oxygen exchanges increased in the 1970s (except for hyporheic exchange and SOD) and peaked in the 2010s. The apparent decline in the number of studies in 2020 is reflected by limitations of our analysis only considering studies with DOIs assigned before August 2024. Field chambers dominated early studies, comprising all studies in the 1960s and about half in the 1970s, but declining to 8% by the 2010s. In contrast, in-stream DO methods have greatly increased in number and gradually increased by percentage from 46% in the 1970s to 56% in the 2020s, reflecting the transition from discrete sampling to continuous sensor deployments as sensor technology advanced after 2000. Whole-stream metabolism methods have remained relatively stable over time, with single-station approaches predominating, while methodological diversity increased in the 1990s-2000s with greater use of two-station and delta approaches and continues today through use of delta, extreme value, and oxygen-carbon methods (Fig. S4). Tracer techniques were first applied in the 1980s, comprising about 10% of studies, increasing in the 1990s, decreasing in the 2000s-2010s and rebounding to 22% in the 2020s with the emergence of new field methods (e.g., argon; Hall & Madinger, 2018), while empirical equations plateaued during the 1990s at 23% and have remained relatively stable since. Interface flux and modelling approaches only became common after 2010 (10-15%), mainly for benthic and hyporheic studies. Overall, the data methods for GPP, ER, and gas exchange have remained stable since the 1980s, comprised by in-stream DO and tracers (although computational methods have evolved), while longer-term methodological shifts reflect a decline in chamber-based studies and increasing diversification in approaches used to quantify benthic and hyporheic exchanges.

4.3 How variable are the oxygen exchanges in lotic ecosystems?

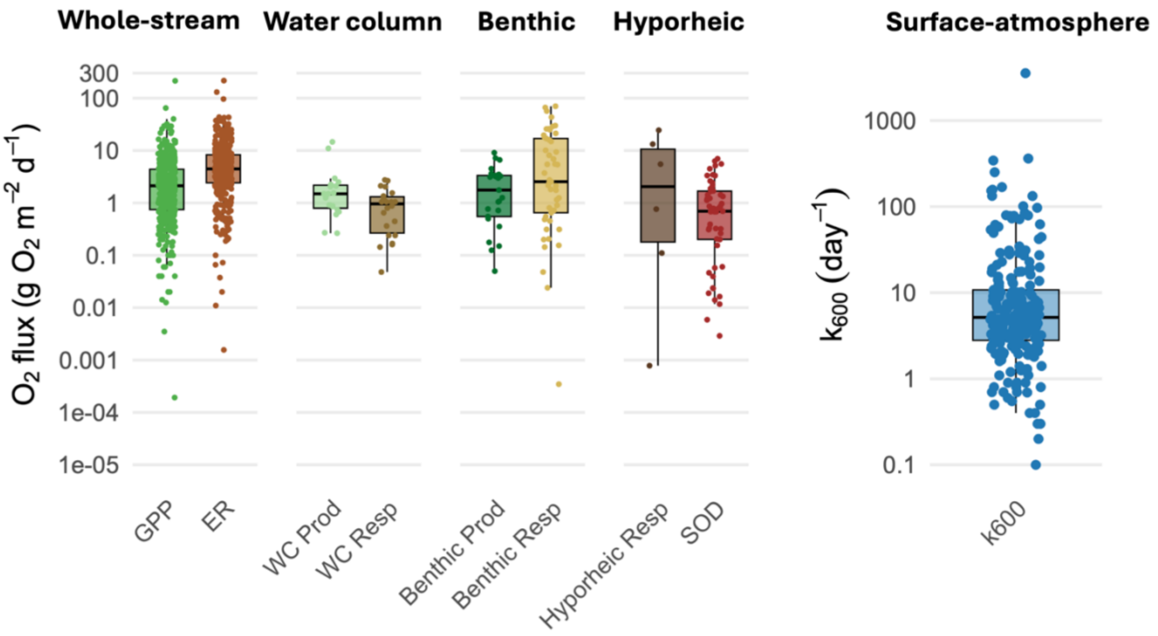


Figure 6. The magnitude of oxygen fluxes reported across all studies. Boxplots summarize the distribution of reported oxygen fluxes for whole-stream metabolism (GPP and ER), water column and benthic production and respiration, hyporheic respiration and sediment oxygen demand, and surface-atmosphere exchange (k_{600}), shown on log-scaled and standardized axes. Boxes represent interquartile ranges with medians, whiskers indicate 1.5× the interquartile range, and points show mean values across individual sites and studies.

Among all oxygen exchanges standardized to fluxes (except gas exchange, which is standardized to k_{600}), site-level mean magnitude varied among groupings (Fig. 6; Table S2). Within whole-stream metabolism, ER exceeded GPP on average (means = 8.0 and 4.4 g O_2 m^{-2} day^{-1}; n = 364 and 371, respectively), meaning most streams were heterotrophic (consistent with Bernhardt et al., 2018). For water column observations, production was higher than respiration on average (means = 2.6 and 1.0 g O_2 m^{-2} day^{-1}; n = 19 and 22, respectively). In contrast, the maximum benthic respiration (range = 3.5 x 10^{-4} to 70 g O_2 m^{-2} day^{-1}; n = 49) was roughly an order of magnitude higher and far more variable than the maximum benthic production (range = 0.05 to 9.1 g O_2 m^{-2} day^{-1}; n = 25). Hyporheic respiration was markedly higher on average than SOD (means = 7.4 and 1.3 g O_2 m^{-2} day^{-1}; n = 6 and 54), implying methodological dissonance in this critical compartment flux.

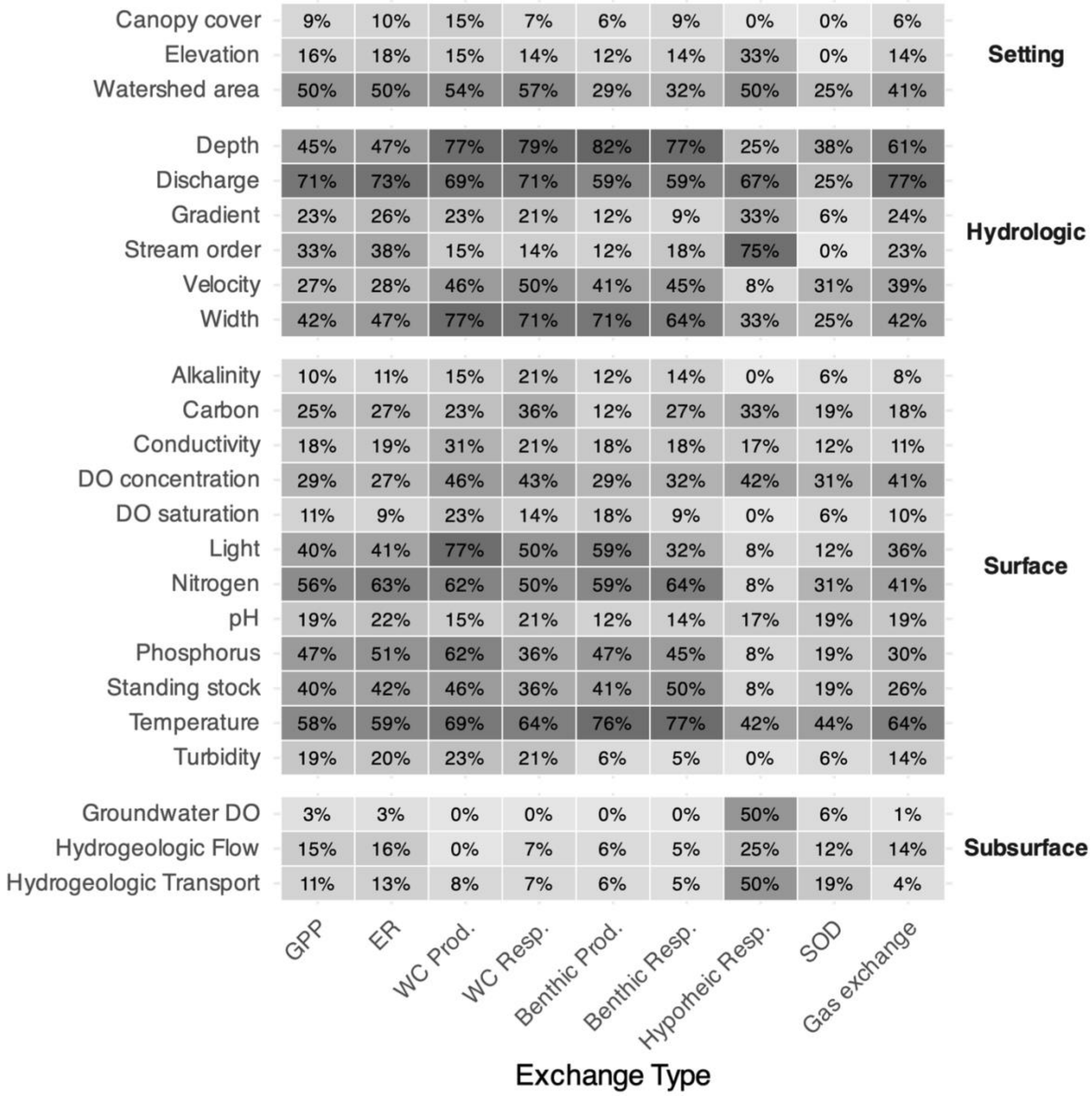
Oxygen exchanges differed markedly in their variability, expressed as the standard deviation of log-transformed fluxes ($\sigma_{\ln}$) to account for strong right skew (Fig. 3c; Table S2). Hyporheic respiration was the most variable ($\sigma_{\ln}$ = 3.9), followed by benthic respiration ($\sigma_{\ln}$ = 2.4), SOD ($\sigma_{\ln}$ = 1.9), and gas exchange (k_{600}; $\sigma_{\ln}$ = 1.8). Whole-stream processes, benthic production, and water column production and respiration were less variable, with $\sigma_{\ln}$ values of 1.5 for GPP, 1.3 for ER, 1.4 for benthic production, and 1.0 and 1.1 for water column production and respiration. This implies that the most variable compartment-specific fluxes are also the least frequently measured.

GPP was lowest in small streams (mean = 2.8 g O_2 m^{-2} day^{-1}), peaked in mid-sized streams (mean = 6.5), and declined in large streams (mean = 5.2; Fig. S1; Table S3). ER followed a similar pattern but had consistently higher magnitudes, averaging 6.8 g O_2 m^{-2} day^{-1} in small streams, 10 g O_2 m^{-2} day^{-1} in mid-sized, and 5.6 g O_2 m^{-2} day^{-1} in large streams. Benthic production was relatively consistent across stream sizes (means = 2.7, 2.6, and 2.3 g O_2 m^{-2} day^{-1} for small, mid, and large streams), whereas average benthic respiration was highest in mid-sized streams (15 g O_2 m^{-2} day^{-1}). SOD was relatively consistent across stream size (means ranging from 0.95 to 1.6 g O_2 m^{-2} day^{-1}). Gas exchange coefficients (k_{600}) generally decreased with stream size, averaging 66 d^{-1} in small streams and 7.0 d^{-1} in both mid-sized and large streams. Limited reporting of water column and hyporheic fluxes across stream size constrained our ability to distinguish trends. Overall, oxygen exchanges tended to peak in mid-sized streams, with higher variability in small streams and lower magnitudes in larger rivers (Fig. S1).

GPP and ER showed similar changes with land use, with the highest values in agricultural streams (means = 7.1 and 10.5 g O_2 m^{-2} day^{-1}) followed by urban (means = 5.4 and 8.8 g O_2 m^{-2} day^{-1}), mixed (means = 4.4 and 9.2 g O_2 m^{-2} day^{-1}), and lowest in undisturbed ecosystems (means = 2.8 and 5.8 g O_2 m^{-2} day^{-1}), although streams in all land use categories were heterotrophic (Fig. S1; Table S3). Water column production was highest in agricultural (mean = 3.4 g O_2 m^{-2} day^{-1}) and urban streams (mean = 3.1 g O_2 m^{-2} day^{-1}), whereas water column respiration was highest in undisturbed (mean = 2.0 g O_2 m^{-2} day^{-1}). Benthic fluxes had a stronger land use response, where benthic respiration was markedly elevated in urban streams averaging 23.6 g O_2 m^{-2} day^{-1}, followed by mixed (mean = 7.9 g O_2 m^{-2} day^{-1}), agricultural (mean = 2.8 g O_2 m^{-2} day^{-1}), and undisturbed ecosystems (mean = 1.1 g O_2 m^{-2} day^{-1}), while benthic production also peaked in urban streams (mean = 4.0) but with smaller contrasts among categories. Hyporheic respiration lacked enough data to infer patterns across land use, whereas SOD was most frequently measured and highest in urban and mixed streams. k_{600} was highest in undisturbed streams (127.9 d^{-1}) and substantially lower in agricultural (16.4 d^{-1}), mixed (8.2 d^{-1}), and urban ecosystems (5.4 d^{-1}). Overall, whole-stream, water column, benthic, and hyporheic and sediment exchanges peaked in agricultural, urban, and mixed land use streams, while surface-atmosphere exchange was highest in undisturbed ecosystems (Fig. S1).

Together, these patterns highlight a shift in the dominant drivers of oxygen fluxes across stream size and land use: while natural gradients predict dominant subsurface metabolism in headwaters and increasing water column activity downstream, elevated respiration in mid-sized and urban streams indicates that human modification can disrupt this expected metabolic hierarchy along the river continuum (Ledford et al., 2021).

4.4 What complementary information & metadata are we reporting alongside oxygen exchange data?



	GPP	ER	WC Prod.	WC Resp.	Benthic Prod.	Benthic Resp.	Hyporheic Resp.	SOD	Gas exchange	
Canopy cover	9%	10%	15%	7%	6%	9%	0%	0%	6%	Setting
Elevation	16%	18%	15%	14%	12%	14%	33%	0%	14%	
Watershed area	50%	50%	54%	57%	29%	32%	50%	25%	41%	
Depth	45%	47%	77%	79%	82%	77%	25%	38%	61%	Hydrologic
Discharge	71%	73%	69%	71%	59%	59%	67%	25%	77%	
Gradient	23%	26%	23%	21%	12%	9%	33%	6%	24%	
Stream order	33%	38%	15%	14%	12%	18%	75%	0%	23%	
Velocity	27%	28%	46%	50%	41%	45%	8%	31%	39%	
Width	42%	47%	77%	71%	71%	64%	33%	25%	42%	
Alkalinity	10%	11%	15%	21%	12%	14%	0%	6%	8%	Surface
Carbon	25%	27%	23%	36%	12%	27%	33%	19%	18%	
Conductivity	18%	19%	31%	21%	18%	18%	17%	12%	11%	
DO concentration	29%	27%	46%	43%	29%	32%	42%	31%	41%	
DO saturation	11%	9%	23%	14%	18%	9%	0%	6%	10%	
Light	40%	41%	77%	50%	59%	32%	8%	12%	36%	
Nitrogen	56%	63%	62%	50%	59%	64%	8%	31%	41%	
pH	19%	22%	15%	21%	12%	14%	17%	19%	19%	
Phosphorus	47%	51%	62%	36%	47%	45%	8%	19%	30%	
Standing stock	40%	42%	46%	36%	41%	50%	8%	19%	26%	
Temperature	58%	59%	69%	64%	76%	77%	42%	44%	64%	
Turbidity	19%	20%	23%	21%	6%	5%	0%	6%	14%	
Groundwater DO	3%	3%	0%	0%	0%	0%	50%	6%	1%	Subsurface
Hydrogeologic Flow	15%	16%	0%	7%	6%	5%	25%	12%	14%	
Hydrogeologic Transport	11%	13%	8%	7%	6%	5%	50%	19%	4%	

Figure 7. Reporting frequency of metadata across oxygen exchange types across studies. The heatmap shows the percentage of studies reporting key metadata for each oxygen exchange type, grouped by setting, hydrologic properties, surface water chemistry and light, and subsurface attributes. Darker cell shading indicates a greater percentage of studies reporting a given covariate. The number of studies reported for each cell, rather than the percent, are presented in Fig. S2.

Oxygen dynamics in streams are shaped by complex interactions among physical, chemical, and biological factors, with dominant controls expected to vary as we consider different exchanges and settings (Fig. 7). Despite this heterogeneity, some variables consistently emerge as more commonly reported regardless of which oxygen exchange(s) were included in a study. Discharge and temperature were the most common covariates, reported in 70% and 56% of all studies, respectively. Among total, particulate, and dissolved nutrient concentrations (see methods in section 3 for the included criteria), nitrogen was most often reported (47% of studies), followed by phosphorus (37%), and carbon (26%). Light-related measurements and standing stock indicators were included in about 30% of studies, while turbidity (13%), alkalinity (10%), and canopy cover (6%), were less frequently reported.

Among surface water variables, temperature, nitrogen, and light were most commonly reported, particularly for whole-stream, water column, and benthic exchanges, aligning with expectations from decades of metabolism literature (Bernhardt et al., 2022). Light was reported in 77% of water column production studies and 59% of benthic production, demonstrating the importance of light in photosynthesis. Standing stocks were also frequently reported in water column, benthic and whole-stream metabolism studies (36-50%), but less reported in gas exchange (26%), SOD (19%), and hyporheic respiration (8%).

By contrast, subsurface variables were rarely reported across all groupings. Groundwater DO – an essential baseline for subsurface oxygen conditions and the impacts of lateral inputs on metabolic estimates – had highest reporting for hyporheic respiration (50%) and SOD (6%), followed by whole-stream (3% for GPP and ER) and surface-atmosphere (1%) measurements, and was not reported at all for water column and benthic exchanges. Hydrogeologic transport metrics which characterize subsurface water fluxes and timescales - such as residence time, hyporheic exchange fluxes, dispersivity, and diffusion coefficients - were reported in about 15% of whole-stream metabolism, 12% of SOD, and 25% of hyporheic respiration studies. Hydrogeologic flow properties, such as hydraulic conductivity and transmissivity, which describe the ease with which water moves through subsurface materials, were included in fewer than 13% of studies, though were highest in hyporheic-focused studies (50%). Organic and inorganic species of carbon were the least reported nutrient across all studies, but most often included with measurements of water column, benthic, and hyporheic respiration, reflecting the coupling between organic carbon consumption and inorganic carbon production during heterotrophic metabolism.

While the influence of the subsurface on in-stream processes is widely acknowledged, our synthesis demonstrates that subsurface variables remain the least reported when studying DO dynamics in flowing waters. This gap is not a result of oversight but rather reflects methodological challenges of measuring processes that are spatially heterogenous, transient, and operate across several orders of magnitude (Strayer et al., 2003). Variables describing subsurface transport and transformation are inherently system-dependent; for example, hyporheic fluxes may be easier to measure and influence in-stream processes more in a steep headwater stream than a low-gradient river (González-Pinzón et al., 2015). Similarly, carbon pools encompass a wide range of forms (DIC, DOC, POC) and the most relevant reporting metric depends on the dominant pathway of heterotrophic metabolism and the research objective.

The heterogenous reporting of metadata across studies is not unique to stream oxygen exchanges but reflects a broader challenge shared across interdisciplinary fields. Understanding oxygen dynamics requires moving beyond single-domain perspectives and instead considering multiple, interacting controls that operate simultaneously (Wohl, 2017; Wymore et al., 2023). Metadata reporting standards that follow from this perspective will enable future synthesis of DO dynamics to be far more inclusive.

5. CURRENT CHALLENGES AND OPPORTUNITIES TO ADVANCE OUR UNDERSTANDING OF LOTIC OXYGEN DYNAMICS

5.1 Ecosystems are not uniformly sampled, biasing our basis for understanding and predicting DO exchanges in streams and rivers

Global research on stream and river DO has been spatially and temporally biased to-date. Most studies have been conducted in North America and Europe with underrepresentation in tropical and high-latitude systems. Study designs are also skewed toward local scales, with a majority quantifying DO within a single stream (51%), then by comparisons among streams (32%), and lastly longitudinally along the river corridor (17%), limiting understanding of how variability scales from reach to watershed and across sites. Temporal bias further compounds these biases as a majority (54%) of the studies included in our synthesis spanned less than one year, 39% lasted two to three years, and 6% extended beyond four years. Although maximum study duration increases substantially in later years, reflecting the emergence of long-term monitoring programs and sensor capability, mean study duration remains persistently low. While short-term studies can provide valuable mechanistic insight under specific conditions, transferring these findings across diel, seasonal, and interannual scales will be key to understanding ecosystem responses across the full flow, light, temperature, and disturbance regimes of river networks.

Expanding and continuing existing work in under-represented regions is therefore critical. Initiatives such as the U.S. Department of Energy's Next-Generation Ecosystem Experiments and field-based programs at high latitudes—such as the McMurdo Dry Valleys LTER and the Arctic LTER—are key to addressing these gaps. Similarly, cross-site comparisons and coordinated efforts like the Lotic Intersite Nitrogen eXperiments (LINX; Mulholland et al., 2008; Bernot et al., 2010; Wymore et al., 2019) demonstrate the value of standardized, collaborative approaches for identifying patterns across diverse hydrologic and geographic gradients. Tools such as streamMetabolizer (Appling et al., 2018a) demonstrate how analytical standardization can enable cross-site synthesis of lotic oxygen dynamics, highlighting a clear opportunity to extend similar coordination to field-based measurements and experimental design.

Hydrologic regime bias remains one of the most significant gaps and opportunities in oxygen research. Although roughly half of global rivers are intermittent (Messager et al., 2021), only 4% of studies in our synthesis include non-perennial rivers. Our current methods used to characterize whole-stream metabolism were primarily developed for perennial waterways and may not accurately represent non-perennial streams. This underrepresentation overlooks stream networks that are both highly vulnerable to climate-driven hydrologic variation (Ward et al., 2020) and disproportionately important for biogeochemical processing (Datry et al., 2014; Stegen et al., 2025). A growing body of evidence indicates that intermittency introduces pronounced spatial and temporal heterogeneity in ecosystem function, particularly through repeated cycles of drying and rewetting that can stimulate organic matter decomposition and respiration. For example, soil research has long documented the "Birch effect," in which rewetting of dry soils triggers large, short-lived respiration pulses (Manzoni et al., 2020), and recent studies indicate that similar dynamics occur in aquatic systems, where respiration from dry stream sediments increases following rewetting (Arce et al., 2021). However, Bretz et al. (2023) found that rewetting can initially suppress observable CO_2 signals via dilution and degassing, with concentrations rebounding as surface water contracts, while Ward et al. (2019) found little variation in biogeochemical function through diurnal wetting and drying cycles. Together, these studies highlight that respiration signals in non-perennial streams are highly variable and can be amplified, delayed, masked by, or insensitive to changes in hydrologic connectivity, indicating a fruitful area for future research.

To address persistent hydrologic regime biases and improve cross-system inference, coordinated initiatives are underway such as the Dry Rivers Research Coordination Network (Datry et al., 2023; Price et al., 2024) and the Aquatic Intermittency effects on Microbiomes in Streams (Open Science Framework, 2025) that integrate cross-biome comparisons, coordinated sampling, the development of new methods and models appropriate for non-perennial ecosystems, and synthesis of ecosystem responses to non-perennial flow.

5.2 Reporting units, methodological silos, and scaling barriers challenge intercomparison

Intercomparison of oxygen exchanges among studies is fundamentally constrained by reporting units. Gas exchange, for example, is typically reported as a rate constant (d^{-1}) or as a velocity ($m\ d^{-1}$), but the literature contains at least 26 distinct gas exchange coefficients (Fig. S3), although recent years have seen a convergence toward using a normalized k_{600} (day^{-1}). Whole-stream metabolism is typically expressed in areal units ($g\ O_2\ m^{-2}\ d^{-1}$), whereas water column, benthic, and hyporheic studies are often reported as volumetric rates ($g\ O_2\ L^{-1}\ d^{-1}$), with some hyporheic and transport-reaction studies additionally expressing respiration as first-order DO uptake or decay coefficients (d^{-1}), further complicating direct comparison across studies and exchange types without appropriate stream attributes.

Oxygen exchanges are typically studied in isolation using methods optimized for specific spatial scales, reinforcing methodological and disciplinary silos that hinder integration. These approaches span patch-scale chambers and incubations for sediment and benthic exchanges to sub-reach water column metabolism assays and reach-scale sensors and associated measurements for GPP, ER, and gas exchange (Box 1). Because these methods differ not only in spatial and temporal resolution, but also in the processes they are designed to resolve, direct comparison and synthesis across exchange types remains challenging.

Scaling isolated measurements to the reach-scale introduces additional uncertainty, particularly related to reach geometry, depth normalization, and underlying spatial variability. Nevertheless, such standardization remains necessary to compare fluxes across sites and systems and understand their sources. In practice, researchers routinely apply scaling assumptions for whole-stream metabolism, accepting a degree of error as a trade-off for interpretability and synthesis. Water column and benthic chambers can be standardized from volumetric rates (e.g., $g\ O_2\ L^{-1}\ d^{-1}$) to an areal basis (e.g., $g\ O_2\ m^{-2}\ d^{-1}$) by normalizing rates to the chamber footprint area. However, hyporheic metabolism is far less frequently scaled to reach-scale fluxes, as doing so requires additional assumptions about metabolically active sediment depth, exchange volume, water residence time, or subsurface connectivity that are rarely constrained empirically. As a result, comparable standardization efforts remain uncommon for hyporheic processes, despite their central role in oxygen dynamics and their potential to dominate whole-stream fluxes. While variation in substrate type, organic matter quantity and quality, and uncertainty in delineating hyporheic boundaries add complexity, these challenges should not preclude systematic attempts at harmonization. Coenen et al. (2019) emphasized the importance of standardizing SOD measurements to enhance comparability – an approach that we call for extending to all oxygen exchanges to foster integration and synthesis.

As a result of methodological fragmentation and scaling uncertainty, studies of whole-stream metabolism, water column, benthic, hyporheic, SOD, and gas exchange have largely advanced in parallel rather than in an integrated fashion. Although some efforts have attempted to bridge these gaps—for example, by comparing patch-scale and whole-stream metabolism estimates despite substantial methodological and scaling challenges (e.g.,Tromboni et al., 2017) or by linking metabolism and nutrient uptake dynamics (e.g., Hoellein et al., 2009)—these integrative approaches remain rare in our review of the literature. This pattern likely reflects both logistical constraints and disciplinary incentives that prioritize measurements directly aligned with specific research questions, rather than coordinated multi-flux designs. Differences in training, terminology, and research questions among hydrologists, biogeochemists, and ecologists have further limited integration across subsurface and whole-ecosystem perspectives, resulting in a lack of “connective tissue” that constrains synthesis across spatial scales and disciplines (Box 1). The integration of pathway-specific fluxes, specifically via local measurements of gas exchange, has already been shown to be enormously valuable for constraining open-channel metabolism methods. We submit that similar improvements in the accuracy of and controls on whole-system metabolism will emerge from routinely connecting benthic and water column fluxes to the common DO concentration inferences.

These methodological and scaling challenges also complicate the application of the Odum (1956) oxygen budget framework, whose simplifying assumptions are increasingly challenged in ecosystems where subsurface processes strongly influence DO dynamics. We caution against differencing whole-stream metabolism estimates with independently measured benthic and water column exchanges, as this approach can introduce statistical uncertainty and process error in systems where hyporheic respiration contributes substantially to DO dynamics and reach-scale GPP and ER partially reflect unresolved subsurface processes (Naegeli & Uehlinger, 1997; Gomez-Velez et al., 2026). Rather than treating methods as interchangeable, complementary approaches should be combined to better constrain which ecosystem components are contributing to whole-stream metabolism. Modified two-station metabolism models, for example, are required to account for groundwater influences on oxygen dynamics that may bias estimates of GPP and ER (Hall and Tank, 2005). Yet, the use of two station models (with or without groundwater corrections) has declined from a peak in the 1990s—when 50% of whole-stream metabolism studies employed a two-station design—to ~25% in the 2000s and 2010s. Re-diversifying beyond single-station models is therefore particularly important for systems that violate the core assumptions underlying those approaches.

5.3 DO should be coupled with other biogeochemical cycles to move from inference to process-based understanding

Explicitly coupling DO with other biogeochemical cycles presents an opportunity to move towards a more integrated understanding of ecosystem processes. While whole-stream metabolism provides valuable insight into aerobic carbon cycling (i.e., presuming oxygen consumption is predominantly related to aerobic respiration), it represents an integrated metric that cannot inform all underlying transformations occurring within streams. Integrating DO with complementary measures such as other naturally occurring dissolved gases (e.g., CO_2, CH_4, Ar), nutrient spiraling, and study of individual fluxes (e.g., water column, benthic, and hyporheic zones) can directly link oxygen dynamics with nutrient and carbon transformations. For example, by coupling DO-derived metabolism with organic carbon and gas exchange, Hall et al. (2016) showed how oxygen dynamics can be used to infer large-scale patterns in carbon metabolism and transport across river networks. Similar cross-scale measurement approaches have illustrated how DO dynamics relate to nitrification, denitrification, and DOC metabolism across land use gradients (Hanrahan et al., 2018; Plont et al., 2022), collectively revealing that oxygen analyses offer enhanced insights into ecosystem processes when considering its tight coupling to carbon and nutrient transformations.

Moving forward, advancing multi-solute and cross-disciplinary frameworks will be critical to link DO-based metabolism with CO_2, nutrient, and redox dynamics. Discrepancies between CO_2- and O_2-based estimates of stream metabolism (Vachon et al., 2020, Shangguan et al., 2024) highlight processes exist that are not captured in DO measurements alone and different spatial scales associated with different gas dynamics. Decoupling may arise from anaerobic respiration that does not impact DO concentration, or hyporheic pathways that induce long lags in water column DO signals (Gomez-Velez et al. 2026). Sources of error are also compounded by the widespread use of a 1:1 O_2-CO_2 stoichiometric ratio when converting DO-based metabolism to carbon units as this ratio is known to vary (Trentman et al., 2023), particularly in ecosystems with strong groundwater influence (Rocher-Ros et al., 2025). Together, these patterns underscore that aerobic and anaerobic respiration reflect distinct redox pathways that together shape organic matter decomposition and nutrient turnover, yet quantifying anaerobic respiration remains challenging due to its spatial heterogeneity. Studies such as Son et al., (2022) demonstrate that hyporheic exchange can drive large-scale variability in anaerobic metabolism, underscoring the need to explicitly represent subsurface pathways in metabolic frameworks. Developing modeling approaches capable of partitioning autotrophic, heterotrophic, and anaerobic signals (Hall & Beaulieu, 2013; Diamond & Bertuzzo, 2025) will be key to linking empirical data and process-based understanding.

5.4 Opportunities for integrating oxygen exchanges across scales through metadata and emerging modeling

Translating process-based insights into cross-study synthesis requires consistent reporting of core metadata that enable integration across spatial scales and datasets. At a minimum, reporting the mean or median oxygen exchange alongside location (latitude and longitude), discharge, water temperature, channel depth, and width for the study period would substantially improve comparability across studies. Where subsurface processes are expected to influence DO dynamics, reporting basic indicators of hyporheic or groundwater exchange (e.g., groundwater DO, sediment depth, residence time, or tracer-based exchange metrics) would further interpretation. Importantly, variables such as discharge and depth are difficult to predict accurately at the reach scale, and gas exchange estimates derived from empirical equations or normalized by depth often require direct measurement for reliable constraint. In contrast, others such as stream order, land cover, and catchment slope can often be estimated reliably from existing geospatial products, including the Stream Catchment Attributes dataset, the National Hydrography Dataset Plus, and the National Land Cover Database (Hill et al., 2016; USGS, 2023; EPA, 2025). Clearly distinguishing between variables that require direct measurement and those that can be inferred would facilitate data reuse, reduce duplication of effort, and strengthen synthesis across spatial scales.

Integrating disciplinary and methodological approaches requires combining complementary methods across spatial and temporal scales, rather than measuring oxygen exchanges in isolation. Advances in time series analysis and the use of naturally occurring tracers (e.g., argon, radon, electrical conductivity) have made it increasingly feasible to quantify hyporheic exchange and respiration without the need for intensive tracer injections or laboratory incubations (e.g., Vieweg et al., 2016). Emerging tools such as low-cost floating chambers can be used to independently constrain gas exchange assumptions in whole-stream oxygen models (Mannich et al., 2019). When combined with synoptic light-dark incubations and benthic chamber measurements and deployed alongside continuous sensor networks (e.g., two-station), these approaches enable process-based attribution of oxygen fluxes across compartments and spatial scales.

Since logistical constraints will always limit direct measurement of all oxygen exchanges, advancing synthesis will increasingly depend on data-driven and modeling approaches that harmonize existing observations across scales. For instance, given the logistical demands of wells, chambers, or mesocosms hyporheic exchange and respiration cannot be quantified ubiquitously, so many studies will focus on a single component of the oxygen budget at a particular location or scale, leaving substantial gaps in cross-scale understanding and assessment of heterogeneity. Looking ahead, data science and modeling tools offer new opportunities to harmonize existing datasets and advance synthesis across exchanges and scales. Large-scale databases and modeling approaches – similar to those developed by Appling et al. (2018b) for whole-stream metabolism – could be expanded to include individual exchanges, while emerging basin-scale models demonstrate growing capacity to infer hyporheic contributions from reach- or network-scale signals (Regier et al., 2025). New time series-based approaches and machine learning frameworks further show promise for resolving overlapping metabolic signals and identifying spatial drivers at network scales that are inaccessible through site-specific studies alone (Segatto et al., 2021; Bertuzzo et al., 2022).

CONCLUSION

Advancing dissolved oxygen science requires moving beyond single-flux measurements toward the concurrent quantification of oxygen exchanges across process domains that collectively give rise to whole-stream signals. Evidence from the relatively few studies that have quantified multiple oxygen exchanges demonstrates that this added complexity yields disproportionate insight. These studies reveal strong spatial and temporal variability in compartment-specific processes, shifts in the relative dominance of individual exchanges (e.g., hyporheic respiration or water column production), and cases where fundamentally different underlying pathways produce similar whole-stream fluxes. Importantly, even partial resolution of multiple exchanges has been shown to improve process attribution by identifying hyporheic exchange as a hidden control on sub-daily oxygen dynamics, explaining apparent variability and bias in GPP, ER, and gas exchange estimates that would otherwise be attributed to noise or equifinality. As a result, whole-stream estimates of GPP, ER, or NEP alone cannot resolve where oxygen and carbon are primarily produced or consumed. Distinguishing whether oxygen dynamics are dominated by water column, benthic, or hyporheic and sediment processes has direct implications for the supply and demand of energy in food webs, aquatic ecosystem health, management decisions, and the interpretation of stream DO signals from which metabolic fluxes are inferred.

At the same time, boundaries between compartments are often diffuse and temporally dynamic, further complicating attribution. Sediments may integrate benthic and hyporheic signals, while under certain hydrologic conditions subsurface flowpaths can dominate metabolic activity influencing in-stream diel oxygen concentrations. Although oxygen dynamics retain distinct process signatures, their effective integration length makes them sensitive to small-scale changes; for instance, more turbulence and mixing can reset oxygen signals and either amplify or dampen hyporheic contributions depending on flow and season. These sensitivities are especially pronounced in intermittent streams, where dynamic suburface flowpaths contribute to streamflow yet remain underrepresented in the literature. While our review highlights the need for compartment-based measurements, we also encourage a shift toward a more integrated perspective, in which oxygen production, consumption, and transport are quantified along hydrologic pathways spanning the water column, benthos, hyporheic zone, sediments, and groundwater. Such an approach better reflects how oxygen moves through and is processed within stream networks, with hydrologic connectivity acting as a master variable that mediates fluxes among compartments and regulates when and where specific exchanges may dominate.

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Data Availability

Data are hosted on HydroShare and are currently discoverable at:

Krause, J., and A. S. Ward (2026). A Systematic Review of Oxygen Exchanges in Streams and Rivers. HydroShare. http://www.hydroshare.org/resource/56ce89df533a4d928f0919b92def79aa

The dataset will be made publicly accessible upon publication, at which time a DOI will be issued.

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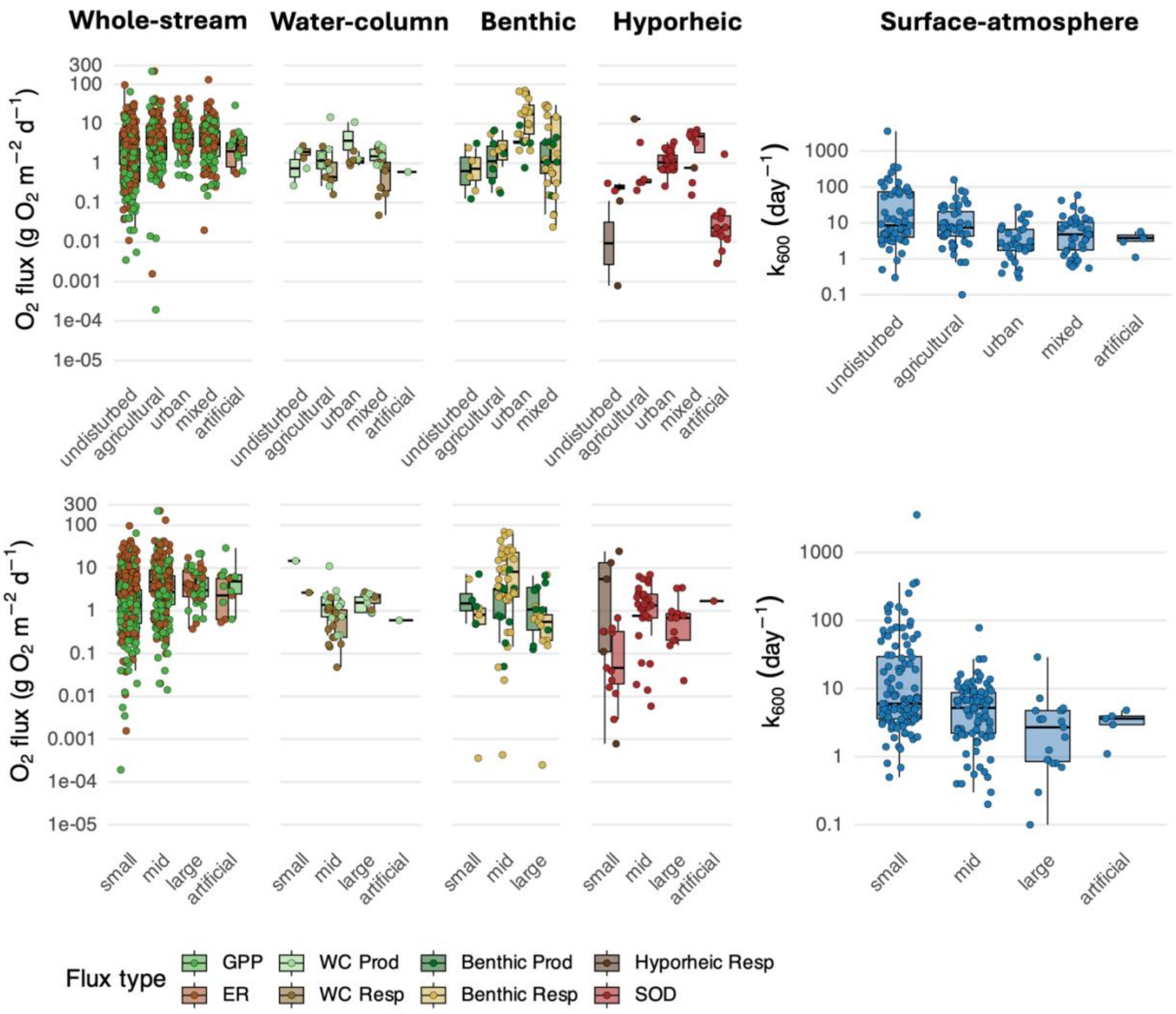
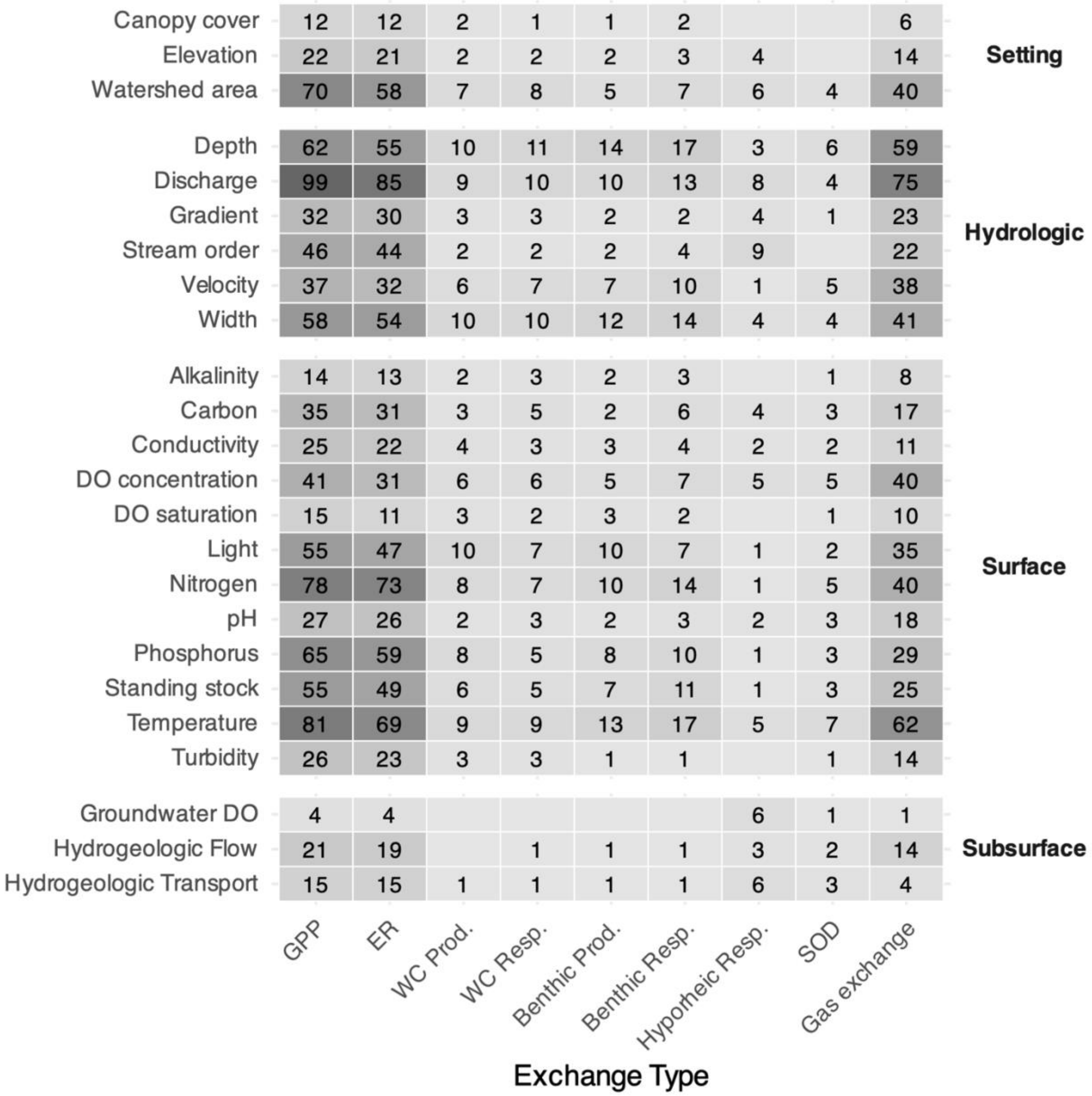


Figure S1. Comparison of flux magnitudes across stream size (top) and land-use (bottom) gradients. Each panel shows oxygen fluxes standardized to units of day^{-1} or g O$_2$ m^{-2} day^{-1} on a log-scaled axis. The top plot shows exchanges by land use (undisturbed, agricultural, urban, mixed, or artificial), while the bottom plot shows exchanges by stream size (small, mid, large, and artificial). Boxes represent the interquartile range with medians, whiskers indicate 1.5× IQR, and points show means across study sites.



	GPP	ER	WC Prod.	WC Resp.	Benthic Prod.	Benthic Resp.	Hyporheic Resp.	SOD	Gas exchange	
Canopy cover	12	12	2	1	1	2			6	Setting
Elevation	22	21	2	2	2	3	4		14	
Watershed area	70	58	7	8	5	7	6	4	40	
Depth	62	55	10	11	14	17	3	6	59	Hydrologic
Discharge	99	85	9	10	10	13	8	4	75	
Gradient	32	30	3	3	2	2	4	1	23	
Stream order	46	44	2	2	2	4	9		22	
Velocity	37	32	6	7	7	10	1	5	38	
Width	58	54	10	10	12	14	4	4	41	
Alkalinity	14	13	2	3	2	3		1	8	Surface
Carbon	35	31	3	5	2	6	4	3	17	
Conductivity	25	22	4	3	3	4	2	2	11	
DO concentration	41	31	6	6	5	7	5	5	40	
DO saturation	15	11	3	2	3	2		1	10	
Light	55	47	10	7	10	7	1	2	35	
Nitrogen	78	73	8	7	10	14	1	5	40	
pH	27	26	2	3	2	3	2	3	18	
Phosphorus	65	59	8	5	8	10	1	3	29	
Standing stock	55	49	6	5	7	11	1	3	25	
Temperature	81	69	9	9	13	17	5	7	62	
Turbidity	26	23	3	3	1	1		1	14	
Groundwater DO	4	4					6	1	1	Subsurface
Hydrogeologic Flow	21	19		1	1	1	3	2	14	
Hydrogeologic Transport	15	15	1	1	1	1	6	3	4	

Figure S2. Heatmap showing the number of studies that reported each metadata variable, grouped into four categories (setting, hydrologic, surface, and subsurface) by measured flux type (gas exchange, GPP, ER, water column production and respiration, benthic production and respiration, sediment oxygen demand, and hyporheic respiration). Darker shading indicates a greater number of studies reporting that covariate.

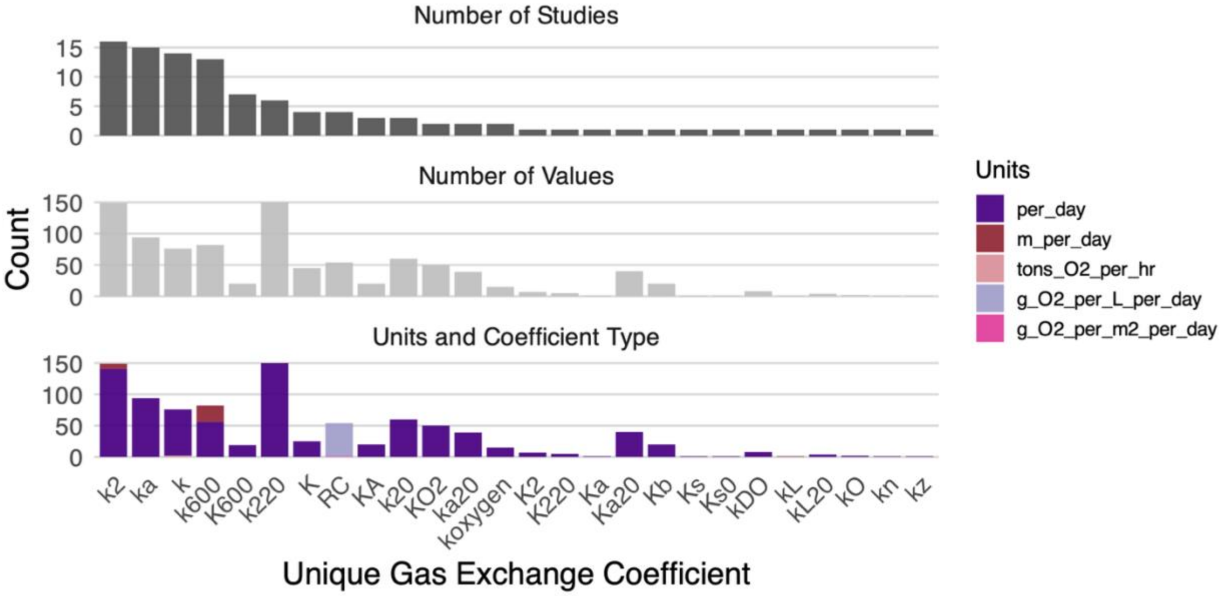


Figure S3. Diversity of gas exchange coefficient reporting. The top panel shows the number of studies reporting each coefficient type, the middle panel shows the total number of reported values, and the bottom panel shows the units associated with each coefficient type.

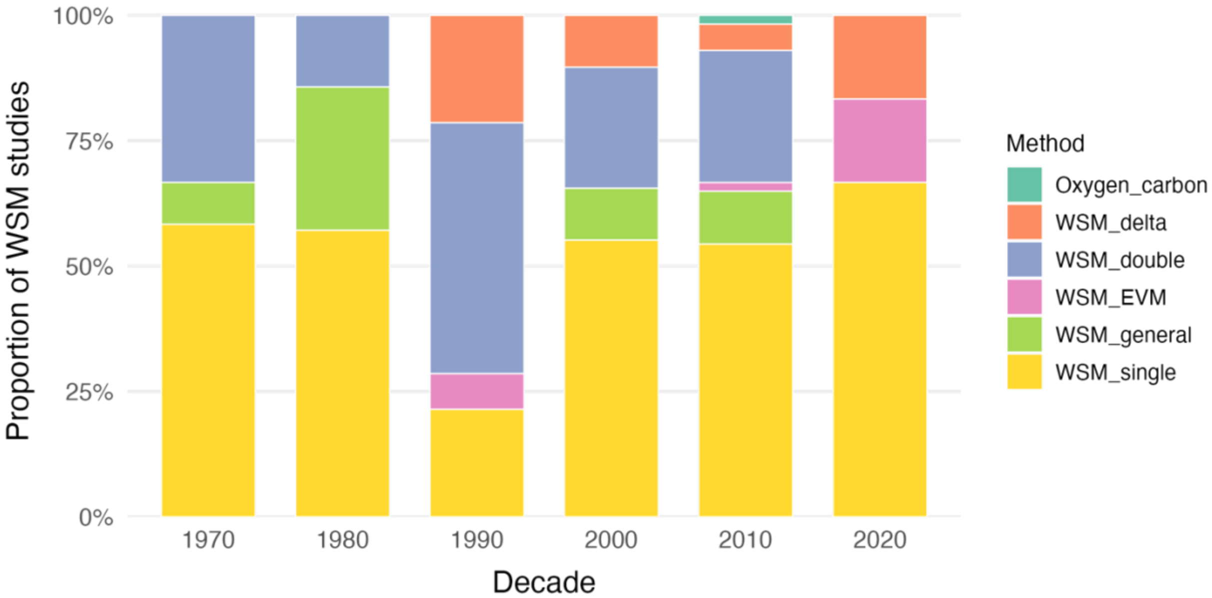


Figure S4. Temporal evolution of whole-stream metabolism (WSM) methods by decade. Stacked bars show the proportional use of single-station, two-station, delta, extreme value method, oxygen-carbon, and other WSM approaches.

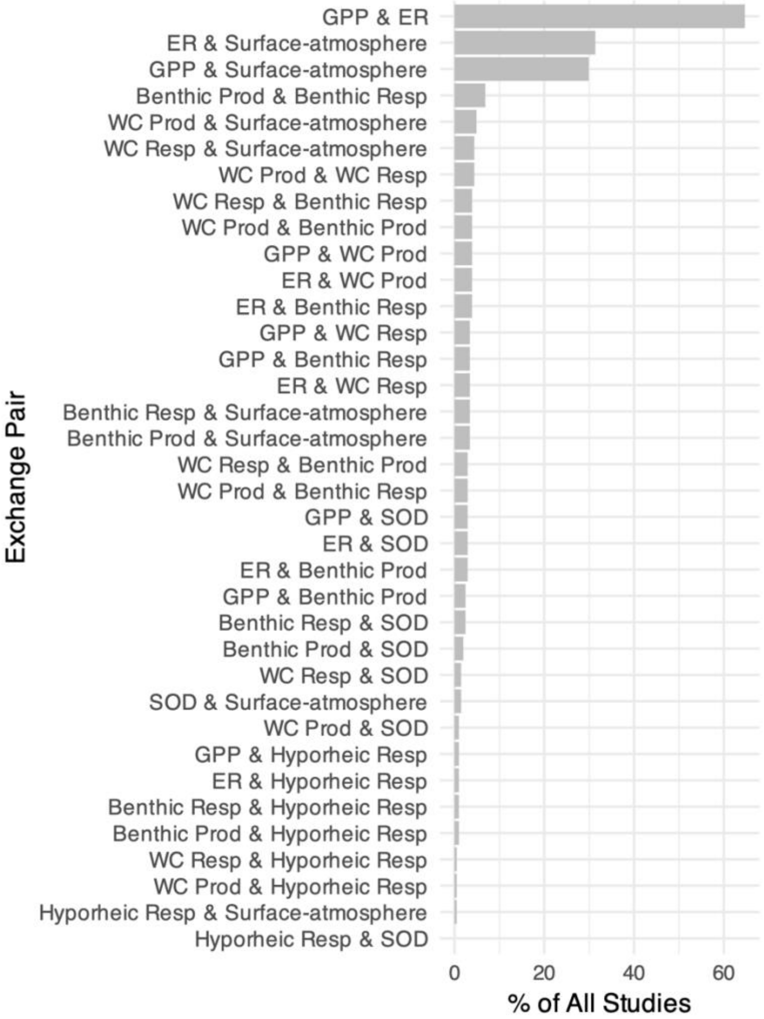


Figure S5. Co-occurrence of oxygen exchange metrics across reviewed across studies. Bars show the number of studies reporting each pair of exchange types, based on unique study-level co-reporting.

Table S1. Web of Science search string used to identify studies included in the oxygen synthesis.

Category	**Search Terms**
Ecosystem terms	stream; river; aquatic
Oxygen terms	dissolved oxygen; O_2
Exchange terms	gas exchange; reaeration; prod*; photo*; metab*; respir*; hyporheic*; benth*
Exclusions	lake; sea; ocean; marine; marsh; wetland; swamp; pond; estuary

Search Field	Web of Science Topic Search (TS)

Table S2. Summary statistics for gas exchange, volumetric metabolic rates, and areal oxygen fluxes standardized across all reviewed studies. Reported values include units, sample size (number of values), number of studies (number of studies), distributional statistics (mean, standard deviation or SD, minimum, and maximum), and log-transformed summaries for skewed metrics (mean$_{ln}$ and SD$_{ln}$).

Exchange	Rate or Flux	Units	# of Values	# of Studies	Mean	SD	Min	Max	Mean (ln)	SD (ln)
Whole-stream GPP	Flux	g O2 / m2 / day	371	113	4.4	12.5	1.9E-04	2.1E+02	0.5	1.5
Whole-stream GPP	Rate	g O2 / L / day	78	27	2.4	5.2	1.9E-04	2.5E+01	-3.0	3.3
Whole-stream ER	Flux	g O2 / m2 / day	364	108	8.0	15.5	1.6E-03	2.2E+02	1.4	1.3
Whole-stream ER	Rate	g O2 / L / day	87	31	1.7	6.1	4E-04	3.1E+01	-4.2	2.4
Water column production	Flux	g O2 / m2 / day	19	10	2.6	3.8	2.6E-01	1.5E+01	0.3	1.0
Water column production	Rate	g O2 / L / day	2	2	0.0	0.0	1.6E-03	2E-03	-6.3	0.1
Water column respiration	Flux	g O2 / m2 / day	22	10	1.0	0.8	4.8E-02	2.8E+00	-0.4	1.1
Water column respiration	Rate	g O2 / L / day	39	4	0.2	0.4	8E-04	1.2E+00	-3.9	2.7
Benthic production	Flux	g O2 / m2 / day	25	14	2.5	2.4	5E-02	9.1E+00	0.3	1.4
Benthic production	Rate	g O2 / L / day	3	3	3.9	4.3	4E-03	8.4E+00	-0.7	4.2
Benthic respiration	Flux	g O2 / m2 / day	49	21	11.4	17.2	3.5E-04	7E+01	0.9	2.4
Benthic respiration	Rate	g O2 / L / day	5	2	0.3	0.7	1.4E-02	1.5E+00	-3.2	2.0
Hyporheic respiration	Flux	g O2 / m2 / day	6	5	7.4	9.8	7.8E-04	2.4E+01	-0.4	3.9
Hyporheic respiration	Rate	g O2 / L / day	8	5	0.4	0.9	2E-03	2.5E+00	-2.6	2.1
Sediment oxygen demand	Flux	g O2 / m2 / day	54	13	1.3	1.7	2.9E-03	7E+00	-0.8	1.9
Sediment oxygen demand	Rate	g O2 / L / day	2	2	0.0	0.0	1.3E-04	1.4E-02	-6.6	3.3
Gas exchange (K600)	Rate	1 / day	300	94	37.9	218.6	2.6E-03	3.6E+03	1.8	1.8

Table S3. Summary statistics for standardized gas exchange (K_{600}) rates (day^{-1}) and areal oxygen fluxes (g O_2 m^{-2} day^{-1}) across stream size (small, mid, large, artificial) and land use (undisturbed, agricultural, urban, and mixed). Reported values include sample size (number of values), number of studies (number of studies), distributional statistics (mean, minimum, maximum), and log-transformed standard deviation (SD$_{ln}$).

Group	Exchange	Units	# of Values	# of Studies	Mean	Min	Max	SD (ln)
small	Whole-stream GPP	g O2 / m2 / day	207	56	3.0	2E-04	7E+01	1.6
small	Whole-stream ER	g O2 / m2 / day	206	56	7.0	2E-03	1E+02	1.4

small	Water column production	g O2 / m2 / day	1	1	14.7	1E+01	1E+01	NA
small	Water column respiration	g O2 / m2 / day	1	1	2.7	3E+00	3E+00	NA
small	Benthic production	g O2 / m2 / day	4	3	2.7	5E-01	7E+00	1.1
small	Benthic respiration	g O2 / m2 / day	6	5	1.3	0E+00	5E+00	NA
small	Hyporheic respiration	g O2 / m2 / day	5	4	8.7	8E-04	2E+01	4.3
small	Sediment oxygen demand	g O2 / m2 / day	11	2	0.2	3E-03	7E-01	1.8
small	Gas exchange (K600)	1 / day	106	28	66.0	0E+00	4E+03	NA
mid	Whole-stream GPP	g O2 / m2 / day	126	51	6.5	1E-02	2E+02	1.5
mid	Whole-stream ER	g O2 / m2 / day	129	50	10.2	2E-02	2E+02	1.3
mid	Water column production	g O2 / m2 / day	14	8	1.8	0E+00	1E+01	NA
mid	Water column respiration	g O2 / m2 / day	18	8	0.7	5E-02	2E+00	1.0
mid	Benthic production	g O2 / m2 / day	12	7	2.6	5E-02	9E+00	1.5
mid	Benthic respiration	g O2 / m2 / day	35	13	15.4	4E-04	7E+01	2.5
mid	Hyporheic respiration	g O2 / m2 / day	1	1	0.8	8E-01	8E-01	NA
mid	Sediment oxygen demand	g O2 / m2 / day	35	6	1.6	0E+00	7E+00	NA
mid	Gas exchange (K600)	1 / day	81	3	7.0	0E+00	8E+01	NA
large	Whole-stream GPP	g O2 / m2 / day	28	16.	5.1	7E-01	2E+01	0.9
large	Whole-stream ER	g O2 / m2 / day	22	14	5.6	4E-01	2E+01	1.0
large	Water column production	g O2 / m2 / day	5	2	1.6	9E-01	2E+00	0.5
large	Water column respiration	g O2 / m2 / day	3	1	2.0	1E+00	3E+00	0.5
large	Benthic production	g O2 / m2 / day	9	4	2.3	1E-01	7E+00	1.5
large	Benthic respiration	g O2 / m2 / day	11	6	1.1	3E-04	7E+00	2.6
large	Sediment oxygen demand	g O2 / m2 / day	13	7	1.0	2E-02	3E+00	1.3
large	Gas exchange (K600)	1 / day	15	7	2.4	1E-01	7E+00	1.2
artificial	Whole-stream GPP	g O2 / m2 / day	9	6	5.9	6E-01	3E+01	1.1
artificial	Whole-stream GPP	g O2 / m2 / day	8	6	7.4	6E-01	3E+01	1.1
artificial	Whole-stream ER	g O2 / m2 / day	6	4	2.4	5E-01	6E+00	0.9
artificial	Whole-stream ER	g O2 / m2 / day	5	4	3.2	5E-01	7E+00	1.2
artificial	Water column production	g O2 / m2 / day	1	1	0.6	6E-01	6E-01	NA
artificial	Sediment oxygen demand	g O2 / m2 / day	13		0.2	3E-03	2E+00	1.5
artificial	Sediment oxygen demand	g O2 / m2 / day	1	1	1.7	2E+00	2E+00	NA
artificial	Gas exchange (K600)	1 / day	6	4	3.7	1E+00	6E+00	0.6
artificial	Gas exchange (K600)	1 / day	5	3	3.3	1E+00	5E+00	0.6
undisturbed	Whole-stream GPP	g O2 / m2 / day	122	47	2.8	4E-03	7E+01	1.7
undisturbed	Whole-stream ER	g O2 / m2 / day	122	47	5.8	1E-02	1E+02	1.5
undisturbed	Water column production	g O2 / m2 / day	3	3	1.0	3E-01	2E+00	1.0

undisturbed	Water column respiration	g O2 / m2 / day	2	2	2.0	1E+00	3E+00	0.5
undisturbed	Benthic production	g O2 / m2 / day	2	2	1.7	1E-01	3E+00	2.3
undisturbed	Benthic respiration	g O2 / m2 / day	4	4	1.1	2E-01	2E+00	1.1
undisturbed	Hyporheic respiration	g O2 / m2 / day	2	2	0.1	8E-04	1E-01	3.5
undisturbed	Sediment oxygen demand	g O2 / m2 / day	2	2	0.3	2E-01	3E-01	0.3
undisturbed	Gas exchange (K600)	1 / day	48	19	127.9	3E-01	4E+03	1.9
agricultural	Whole-stream GPP	g O2 / m2 / day	79	32	7.1	2E-04	2E+02	1.8
agricultural	Whole-stream ER	g O2 / m2 / day	78	32	10.5	2E-03	2E+02	1.4
agricultural	Water column production	g O2 / m2 / day	6	4	3.4	3E-01	1E+01	1.4
agricultural	Water column respiration	g O2 / m2 / day	5	3	0.9	2E-01	3E+00	1.1
agricultural	Benthic production	g O2 / m2 / day	6	4	2.1	2E-01	7E+00	1.4
agricultural	Benthic respiration	g O2 / m2 / day	7	5	2.8	2E-01	7E+00	1.2
agricultural	Hyporheic respiration	g O2 / m2 / day	1	1	13.3	1E+01	1E+01	NA
agricultural	Sediment oxygen demand	g O2 / m2 / day	5	3	0.9	2E-01	3E+00	1.1
agricultural	Gas exchange (K600)	1 / day	50	17	16.4	0E+00	2E+02	NA
urban	Whole-stream GPP	g O2 / m2 / day	54	22	5.4	4E-01	3E+01	0.9
urban	Whole-stream ER	g O2 / m2 / day	53	21	8.8	1E+00	4E+01	0.8
urban	Water column production	g O2 / m2 / day	4	3	3.1	0E+00	1E+01	NA
urban	Water column respiration	g O2 / m2 / day	4.0	3	1.3	9E-01	2E+00	0.4
urban	Benthic production	g O2 / m2 / day	5	3	4.0	8E-01	9E+00	0.9
urban	Benthic respiration	g O2 / m2 / day	16	5	23.6	2E+00	7E+01	1.2
urban	Sediment oxygen demand	g O2 / m2 / day	26	7	1.3	3E-01	3E+00	0.6
urban	Gas exchange (K600)	1 / day	29	14	5.4	3E-01	3E+01	1.2
mixed	Whole-stream GPP	g O2 / m2 / day	73	34	4.4	1E-01	2E+01	1.1
mixed	Whole-stream ER	g O2 / m2 / day	73	33	9.2	2E-02	1E+02	1.3
mixed	Water column production	g O2 / m2 / day	7	4	1.8	9E-01	3E+00	0.5
mixed	Water column respiration	g O2 / m2 / day	11	4	0.7	5E-02	2E+00	1.2
mixed	Benthic production	g O2 / m2 / day		5	1.9	5E-02	4E+00	1.6
mixed	Benthic respiration	g O2 / m2 / day	20	8	7.9	2E-02	3E+01	2.2
mixed	Hyporheic respiration	g O2 / m2 / day	1	1	0.8	8E-01	8E-01	NA
mixed	Sediment oxygen demand	g O2 / m2 / day	14	4	2.3	0E+00	7E+00	NA
mixed	Gas exchange (K600)	1 / day	41	15	8.2	6E-01	6E+01	1.2