ESSAY

Paired O_2–CO_2 measurements provide emergent insights into aquatic ecosystem function

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Scientific Significance Statement

Metabolic stoichiometry predicts that dissolved oxygen (O_2) and carbon dioxide (CO_2) in aquatic ecosystems should covary inversely; however, field observations often diverge from theoretical expectations. Here, we propose a suite of metrics describing this O_2 and CO_2 decoupling and introduce a conceptual framework for interpreting these metrics within aquatic ecosystems. Within this framework, we interpret cross-system patterns of high-frequency O_2 and CO_2 measurements in 11 northern lakes and extract emergent insights into the metabolic behavior and the simultaneous roles of chemical and physical forcing in shaping ecosystem processes. This approach leverages the power of high-frequency paired O_2–CO_2 measurements, and yields a novel, integrative aquatic system typology which can also be applicable more broadly to streams and rivers, wetlands and marine systems.

Dissolved oxygen (O_2) remains one of the most studied attributes of aquatic ecosystems since the beginning of modern ecology. In 1957, G. E. Hutchinson famously wrote "A skillful limnologist can probably learn more about the nature of a lake from a series of oxygen determinations than from any other kind of chemical data" (Hutchinson 1957). The value of oxygen as an indicator of ecosystem function stems from its role in biogeochemical reactions, where it regulates

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and is regulated by a broad range of biotic and abiotic ecosystem processes. In the case of metabolic activity, dissolved O_2 is generated via anabolic assimilation of carbon dioxide (CO_2) and consumed through catabolic processes that produce CO_2; thus, variation in both gases is driven by complementary biological processes that occur simultaneously. Coupling between O_2 and CO_2 has been previously demonstrated in freshwater systems (e.g., Cole and Caraco 2001; Hanson et al. 2006), which has, in part, fueled the widespread assumption that the two gases can be used interchangeably in studies of ecosystem metabolism.

More recent paired O_2–CO_2 high-frequency measurements in surface waters challenge some of our assumptions concerning the coupling between these gases. Measurements of O_2 and CO_2 concentration often show decoupling over diel and longer time scales (Torgersen and Branco 2008; Crawford et al. 2014; Stets et al. 2017). Here, we build on a previous study highlighting fundamental metabolic insights that can be obtained from paired O_2–CO_2 measurements (Torgersen and Branco 2007) and propose a quantitative framework based on our own observations. This framework will enable scientists to use high frequency O_2 and CO_2 measurements to track and study integrative ecosystem properties that cannot be easily inferred from standard measurements. First, we provide an overview of underlying processes controlling both gases, then explore the temporal patterns of decoupling of O_2 and CO_2 in surface waters of 11 northern lakes as an empirical example. We propose a series of metrics to characterize the relationship between both gases and show how they link to key lake and catchment properties.

Drivers of dissolved O₂ and CO₂ concentrations in aquatic ecosystems

To simultaneously study O_2 and CO_2 in aquatic systems, it is useful to express their concentrations in terms of departure from atmospheric equilibrium (Fig. 1a). Within this "departure space," ecosystem processes can move gases either away from or towards atmospheric equilibrium (i.e., the origin), either in tandem or independently (Fig. 1a). The most common tandem processes are biochemical reactions that link the consumption or production of O_2 and CO_2 (e.g., photosynthesis, respiration). Viewed in terms of departure concentrations, aquatic ecosystems dominated by aerobic metabolism should display a relationship between O_2 and CO_2 that falls roughly on a 1:–1 line (Fig. 1a). Deviation from this theoretical metabolic 1:–1 line (stoichiometry of glucose production and respiration) is caused by combinations of biological, chemical, and physical processes that affect one of the two gases disproportionately or independently (Fig. 1a).

Most bio- and photo-chemical reactions generate or release O_2 and CO_2 in different stoichiometric proportions, and several biological processes produce CO_2 without consuming O_2

(e.g., anaerobic processes) (Torgersen and Branco 2007). The respiratory quotient (RQ), or moles of CO_2 biologically produced per mole of O_2 consumed, depends on the degree of oxidation of the substrate respired, but is usually slightly above 1 (Berggren et al. 2012). In aquatic ecosystems where RQ > 1, CO_2 is produced in excess of O_2 consumed, and would cause the respiration vector to shift upward, while in the opposite direction for RQ < 1 (Fig. 1a). The photosynthetic quotient (PQ; moles of O_2 biologically produced per mole of CO_2 used) in natural systems often deviates from the theoretical value of 1 based on the production of glucose (Lefèvre and Merlivat 2012), which would cause O_2 enrichment when PQ > 1 and O_2 depletion relative to CO_2 when PQ < 1 (photosynthesis vector shifting away from the 1:–1 line in Fig. 1a). Photochemical degradation of dissolved organic matter typically results in greater O_2 consumption relative to CO_2 production (downward shift in Fig. 1a) (Cory et al. 2014). Chemoautotrophic processes, such as nitrification and sulfide oxidation, simultaneously consume O_2 and CO_2 (Enrich-Prast et al. 2009) (downward-left shift in Fig. 1a) and can be an important CO_2 fixation process in lakes (Squires et al. 2006). Finally, a wide array of microbe-mediated anaerobic pathways, which typically occur in sediments and bottom layers of deeper aquatic systems (Torgersen and Branco 2007), produce CO_2 without concomitant consumption of O_2 (e.g., denitrification and acetoclastic methanogenesis). Such anaerobic processes cause CO_2 enrichment without affecting O_2 (rightward shift in Fig. 1a).

Several abiotic processes may further alter the ambient O_2 and CO_2 stoichiometry of an aquatic ecosystem. First, changes in water temperature affect the departure of both gases according to their respective saturation potentials, but affect O_2 departure more due to its lower solubility (Carrillo et al. 2004) (Fig. 1a). Chemistry can affect CO_2 without affecting O_2, since CO_2 interacts with bicarbonate within the carbonate system (Millero 2007; Stets et al. 2017). Dissolved bicarbonate (HCO_3^-) can dissociate to CO_2 and water if excess carbonate precipitates (rightward shift in Fig. 1a). Likewise, CO_2 reacts with water to form dissolved HCO_3^- when solid carbonate dissolves (leftward shift in Fig. 1a). Catchment inputs of CO_2-rich water can also sustain an excess of CO_2 relative to O_2 concentrations in surface waters (Crawford et al. 2014; Wilkinson et al. 2016). Finally, atmospheric gas exchange forces gas departures toward equilibrium (toward the origin of Fig. 1a), and systems with relatively high atmospheric gas exchange rates tend to force O_2 and CO_2 departures closer to the origin.

Extracting the information underlying patterns in paired O₂–CO₂ measurements

Any single paired O_2–CO_2 measurements in the departure space provides useful information regarding the net metabolic balance at a particular point in time (Bogard and Giorgio 2016). However, the processes shaping O_2 and CO_2 coupling are
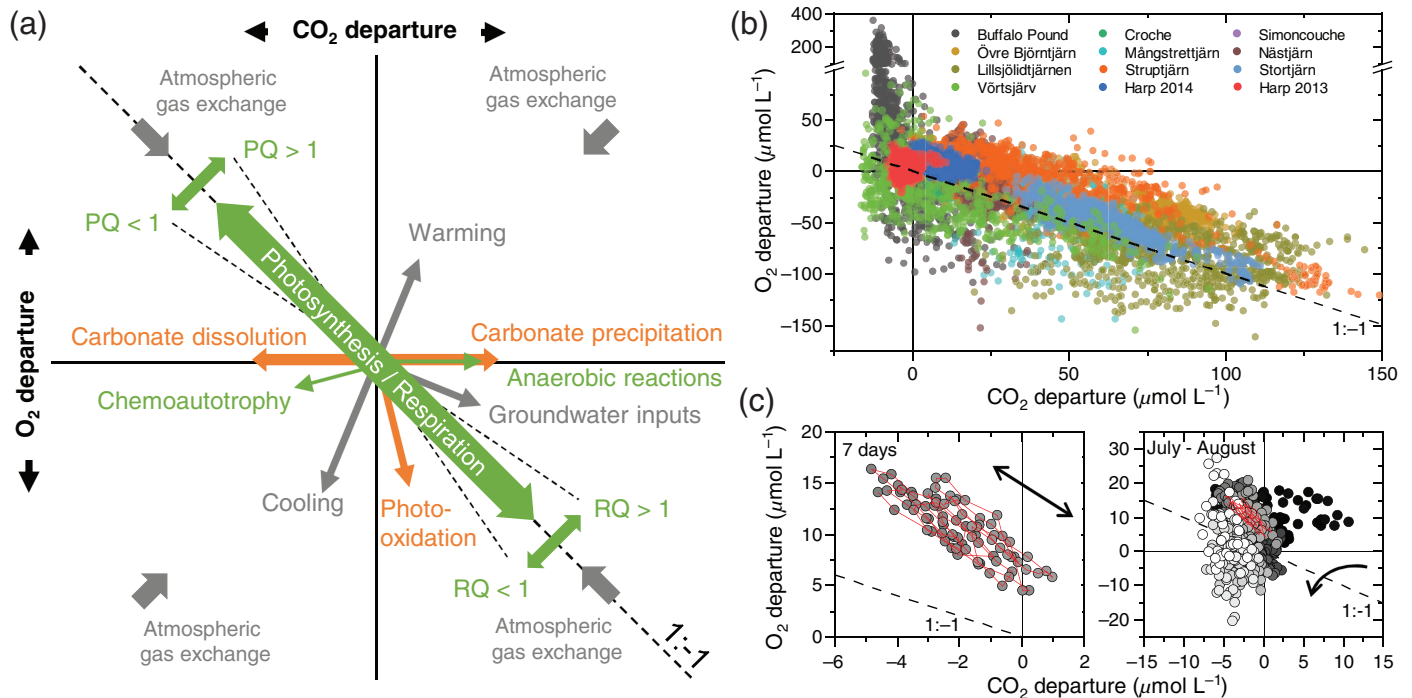
Fig. 1. (**a**) Conceptual figure showing the O_2 and CO_2 departures from atmospheric equilibrium and the potential role of the different drivers. Biochemical processes involving organic matter (green arrows) are respiration and photosynthesis, PQ and RQ, chemoautotrophy and anaerobic reactions. Chemical processes (orange arrows) are carbonate dissolution and precipitation, and photo-oxidation of organic matter. Physical and hydrological processes (light gray) are change in temperature (i.e., warming and cooling of surface waters), groundwater inputs, and atmospheric gas exchange. Note that each arrow lengths and widths were set to ensure visual clarity and do not scale with the relative importance of each process. The angle of each arrow was set to represent the approximate direction to which each process will affect gas departure. (**b**) O_2 and CO_2 departures from atmospheric equilibrium dynamics (2-h measurements) for July and August in 11 northern lakes. (**c**) Temporal evolution of O_2 and CO_2 departures during summer 2013 in Harp Lake showing 7 d with day–night patterns (left plots) and summer monthly dynamics (from July in black to end of August in white: right plot). Solid black arrows indicate the general direction of temporal change in paired O_2–CO_2 dynamics. Red lines show the temporal path during the 7 d pattern. The 1:–1 lines are shown in dashed lines.
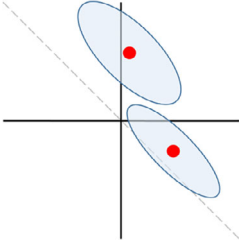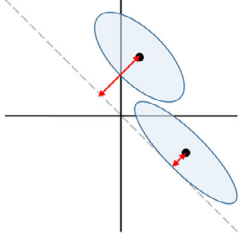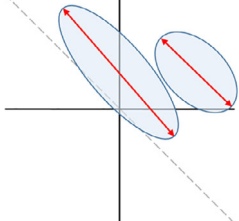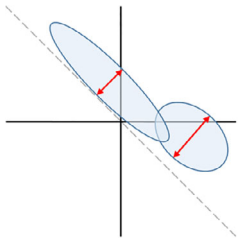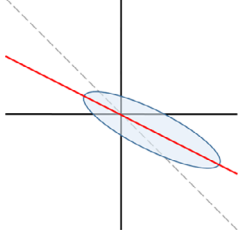
dynamic and are best interpreted within a temporal context. High-frequency measurements generate time series of points that ultimately form "clouds" in the paired O_2–CO_2 departure space. Figure 1b shows summer (July–August) measurements of surface-water O_2 and CO_2 concentrations taken every 2 h from 11 northern lakes, expressed in terms of departure from saturation. Point clouds vary in size, orientation, and shape as a result of simultaneous biological, chemical, and physical drivers uniquely regulating each gas through time (Fig. 1a).

The relative importance of O_2 and CO_2 drivers may vary seasonally, and with the temporal scale of data collection. We exemplify this with data from oligotrophic, boreal Harp Lake, Canada (Fig. 1c). As surface O_2 and CO_2 are recorded through time at a central location of the lake, the signal not only integrates the shifts in temporal drivers operating on diel timeframes (e.g., temperature, light), but progressively integrates spatial patterns dictated by the timescales of physical mixing processes. For example, for 1 week in mid-July, points oscillate diagonally, roughly along the −1:1 line, suggesting photosynthesis and aerobic respiration are the dominant drivers of both gases. At this scale, the cloud remains relatively compact, and

the small range of change is linked to day/night elliptical shifts. Increasing the time frame to 2 months expands the dispersion of the cloud (Fig. 1c), with greater opportunity for the paired O_2–CO_2 departure cloud to change shape in response to surface-water temperature changes, and longer-term shifts in inputs from the catchment (Fig. 1c). Furthermore, longer measurement timescales also reflect the effects of advection of water masses from adjacent littoral habitats and vertical mixing with bottom waters, resulting in a larger spatial footprint beyond local metabolic processes (MacIntyre and Melack 1995). For the information contained in these clouds to be useful, however, it is necessary to formalize their analysis and to develop quantifiable metrics.

Here, we define a set of cloud metrics (Table 1) that provide a quantitative framework to assess paired O_2–CO_2 dynamics within and across ecosystems. The simplest metric is the *centroid* coordinates of the cloud in departure space, representing an average of all processes operating through a given period of time. Systematic shifts of the cloud away from the 1:–1 axis are termed *offset*. A common offset generally occurs toward more CO_2 oversaturation, reflecting a systematic and sustained CO_2

Table 1. Cloud metrics to describe and quantify O_2 and CO_2 departures. The ellipses represent the paired O_2–CO_2 departure clouds relative to the CO_2 departure axis (x) and the O_2 departure axis (y). The dotted gray line is the 1:−1 reference line.

Metric	How it is computed*	Ecosystem process represented[†]	Conceptual examples
Centroid	Time averages of O_2 and CO_2 departure values	The quadrant in which a cloud is located provides information about the average net effect of different environmental processes influencing O_2 and CO_2 dynamics	
Offset	Sum of CO_2 and O_2 departures averages	Characterizes extent or relative role of external inputs, anaerobic respiration, carbonate precipitation and/or increase in water temperature	
Stretch	Major axis length of 95% covariance error ellipse	Characterizes the strength of the dominant process (usually metabolism) driving O_2 and CO_2 departures	
Width	Minor axis length of 95% covariance error ellipse	Characterizes the variability around the dominant process (major axis)	
1/[*slope*]	Inverse of the absolute slope of type II linear regression	The inverse of the cloud absolute slope (i.e., 1/[*slope*]) is the EQ, reflecting the integrated stoichiometry of the ecosystem.	

*See Section S2 in Supporting Information for further details.
[†]Refer Fig. 1a for description.

input (e.g., groundwater inputs). Metrics that characterize the size and shape of point clouds provide additional information. For example, the *width* and *stretch* of the cloud may reflect the dominance of the metabolic signal relative to other processes (Fig. 1a). Cloud *stretch* should generally reflect the temporal variability in rates of photosynthesis and respiration (where these rates exceed those of gas exchange), with longer clouds reflecting larger oscillations in the balance between the two processes. Cloud *width* may reflect additional processes, operating in tandem to and superimposed on the metabolic signal, which increase the dispersion of the cloud (Fig. 1a). Finally, the *slope* of a linear model fit to the cloud yields important integrated information at the ecosystem level. The inverse of the absolute slope (1/[*slope*]) can be interpreted as the ecosystem quotient (EQ), that is, the ratio of moles of CO_2 produced to moles of O_2 consumed at the ecosystem level.

Exploring patterns in paired O₂–CO₂ cloud metrics in 11 northern lakes

We applied these cloud metrics to high frequency summertime O_2 and CO_2 measurements from the surface of 11 Northern Hemisphere lakes (Fig. 1b), and explored the potential insights that such metrics may provide on their functioning (Fig. 2). As these are merely examples based on a limited

number of lakes that share a certain geographic location, the generality of these patterns remains to be tested, and should be interpreted with caution. Below we present the most relevant relationships, with a more complete correlation matrix between metrics and potential drivers presented in Supporting Information Table S1.

We found a strong positive correlation between cloud *stretch* and total phosphorus (TP) concentrations (Fig. 2a). Increasing nutrient availability in lakes is known to enhance the rates of respiration and photosynthesis (Staehr and Sand-Jensen 2006). Therefore, enhanced *stretch* likely reflects wider diurnal oscillations in primary production during the day (toward upper left quadrant) and respiration at night (lower right quadrant), thus elongation of the cloud of points along the 1:–1 line (Fig. 1a). Interestingly, TP was not clearly correlated with the average O_2 or CO_2 departures (Supporting Information Table S1), suggesting that TP concentration does not itself necessarily determine the summer net metabolic balance or whether primary production exceeds respiration (i.e., the quadrant in which the centroid is located).

The *width* of paired O_2–CO_2 point clouds increases with decreasing lake depth (Fig. 2b). Shallower systems may be more influenced by benthic metabolism, where a wide range of organic substrates are oxidized. Lakes with large *width* also tended to have higher dissolved organic carbon (DOC) concentrations and
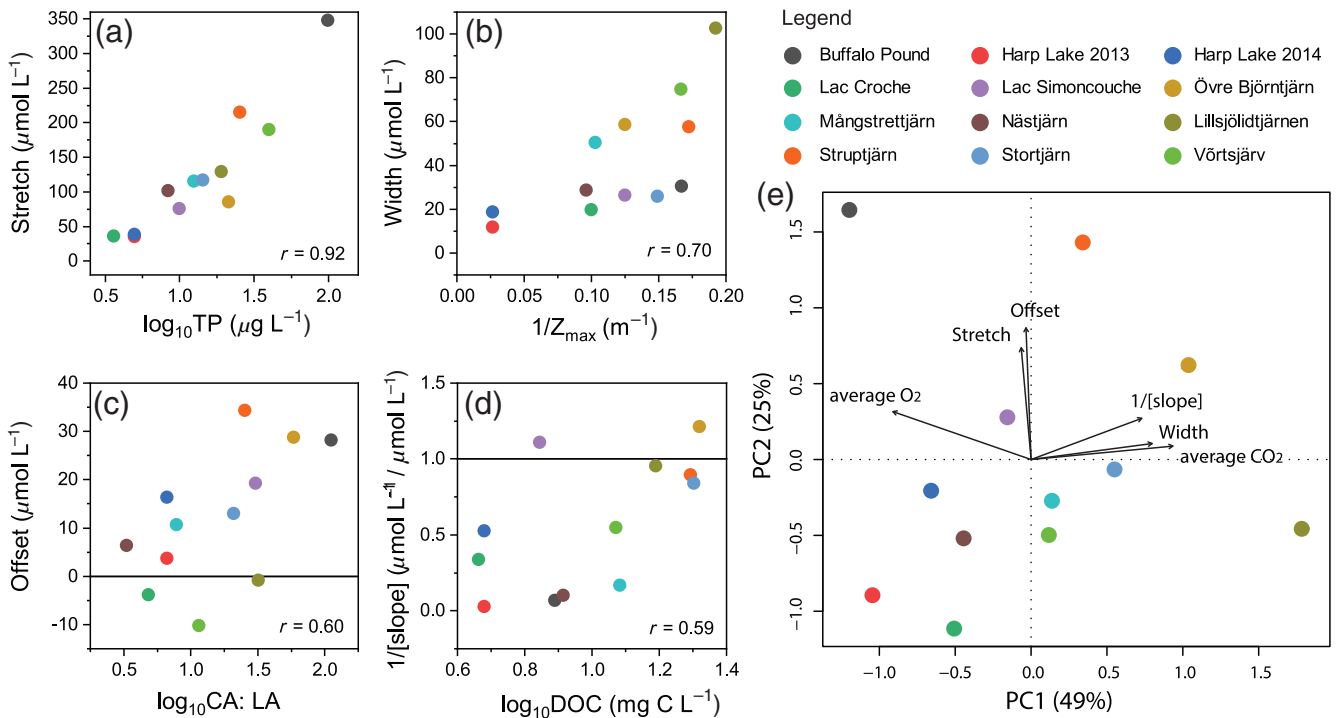

Fig. 2. Correlations (showing *r* coefficient) between cloud metric (*stretch*, *width*, *offset*, and 1/[*slope*]) and limnological and morphometric parameters for each lake: (**a**) *stretch* and log₁₀TP, (**b**) *width* and 1/Z_{max}, (**c**) *offset* and log₁₀ of the catchment area to lake area ratio (log₁₀ CA:LA), and (**d**) 1/[*slope*] and log₁₀ DOC. Note that in (**a**) Harp Lake 2013 is under Harp Lake 2014. (**e**) PCA of all the metrics. See Section S2 in Supporting Information for further details.

lower mean water temperature (Supporting Information Fig. S1). Higher DOC may also reflect a wider range of organic substrate oxidation, while lower temperatures reduce the metabolic signal (along the 1:–1 line), all of which would increase the noise, and thus the cloud *width*. We observed an increase in the magnitude of cloud *offsets* as a function of the ratio of watershed to lake area (Fig. 2c). This suggests that the relative contribution of external inputs of terrestrially derived CO_2 to lake oversaturation increases as a function of increasing relative watershed area to lake area (Vachon and del Giorgio 2014).

The 1/[*slope*] of the cloud (i.e., EQ calculated as the inverse of the absolute slope) increases with DOC content (Fig. 2d). In DOC-rich lakes, 1/[*slope*] approaches and exceeds 1, suggesting an ecosystem stoichiometry that increasingly favors the production of CO_2 relative to O_2 consumption. This may reflect the increasing importance of anaerobic respiration, which aligns with observed increases in cloud *width* as discussed above. In low DOC lakes (which also tend to be deeper), the consumption of O_2 exceeds CO_2 production. This could imply one or a combination of effects arising from limited bottom layer contact, increased importance of carbonate re-equilibration during periods of intense photosynthesis producing CO_2 (e.g., Buffalo Pound, a high pH lake, in Fig. 1b) or the presence of chemoautotrophy, probably at the thermocline (Squires et al. 2006). Clearly, many factors can influence 1/[*slope*], making it less straightforward to extract information from this metric, as the correlations are typically weaker than for other metrics (Supporting Information Table S1).

Further insights into ecosystem functioning can be gained by defining how these metrics relate to each other across systems and how they covary through time. We exemplify this using a principal component analysis (PCA) that combines the six metrics from all 11 lakes (Fig. 2e). The lakes are differentiated along two main axes, with axis 1 largely representing the average departures of each gas, together with cloud *widths*, while axis 2 captures the shape and position of clouds (i.e., *stretch* and *offset* metrics). Interestingly, 1/[*slope*] and *width* tend to covary along the same axis as the *centroids* (Fig. 2e, Supporting Information Table S1). This indicates that ecosystem heterotrophy may be associated with an increasing diversity of metabolic pathways and organic matter substrate availability. These in turn may be linked to systematic shifts in ecosystem stoichiometry. Likewise, that *offset* and *stretch* tend to covary across lakes suggests that coupled inputs of catchment-derived nutrients and carbon may be more important in lakes displaying greater *offset* and *stretch* of data clouds. Importantly, *stretch* and *offset* appear to be essentially orthogonal to 1/[*slope*], *width*, and *centroids* (Fig. 2e). This relationship implies that the degree of CO_2 oversaturation and amplitude of ecosystem metabolism are essentially independent from the average metabolic balance and average gas stoichiometry. None of these potential links are evident or predictable from existing data or from first principles, but rather emerge

through the combined analysis of the metrics derived from the high-frequency paired O_2–CO_2 dynamics. Importantly, the cloud metrics appear to illustrate a novel lake typology not available from conventional limnological metrics. This inference is supported by differences in clustering of lakes based on traditional limnological metrics (e.g., TP, DOC, lake area, etc.; Supporting Information Fig. S2) and the cloud metrics we quantified (Fig. 2e).

Integrative insights and new perspectives on aquatic ecosystem function

Here, we showed that paired O_2–CO_2 departure data clouds can be explored to obtain an integrative perspective of ecosystem functioning. While the use and interpretation of cloud metrics remains speculative and requires further empirical and conceptual exploration, we have demonstrated that these metrics have consistent, cross-lake relationships that scale with key environmental properties. Combined, these metrics yield an integrative "fingerprint" of individual aquatic ecosystems (Bernhardt et al. 2018), and when placed into a comparative, cross-system or temporal context, result in a typology of aquatic ecosystems that is distinct from that obtained from conventional limnological variables.

Although we used northern lakes as a model system to develop the framework, this paired O_2–CO_2 departure cloud framework can be implemented in streams and rivers (Crawford et al. 2014; Rocher-Ros et al. 2019), as well as wetlands and marine systems, albeit with the interpretation nuances specific for each system type. Furthermore, the examples provided above are based on a particular window of time. When diverse aquatic ecosystems or time scales are considered, new or different patterns will likely emerge, especially if different mixing regimes type are included (e.g., polymictic lakes). Nonetheless, the basic conceptual framework that we propose here will remain.

In summary, although there is great value in measuring high-frequency O_2 or CO_2 patterns individually, there is underexploited value in combining these variables. The instrumentation needed to conduct these measurements is improving and becoming widely accessible. This will enable a broader comparison of paired O_2–CO_2 departure clouds, which could lead to novel aquatic system typologies that provide new information not available from traditional typologies based, for example, on trophic status. While O_2 (or CO_2) alone can provide two insightful metrics (e.g., respiration and photosynthesis), the monitoring of both gases enables the computation of at least six additional metrics that, taken together, may provide simple, yet powerful integrative tools for lake diagnostics and management. Hutchinson (1957) followed his famous quote on the importance of oxygen by stating that: "If these oxygen determinations are accompanied by observations on Secchi disk transparency, lake color and

some morphometric data, a very great deal is known about the lake." We suggest that the simple coupling of high frequency CO_2 and O_2 measurements may result in the next breakthrough in aquatic ecosystem science.

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