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Temporal Coherence Between Lake and Landscape Primary Productivity

Jonathan A. Walter,[1]* Rachel Fleck,[2] Jude H. Kastens,[3] Michael L. Pace,[1] and Grace M. Wilkinson[2]

[1]*Department of Environmental Sciences, University of Virginia, 291 McCormick Rd, Box 400123, Charlottesville, Virginia 22904, USA;* [2]*Department of Ecology, Evolution, and Organismal Biology, Iowa State University, 2200 Osborne Dr., Ames, Iowa 50011, USA;* [3]*Kansas Applied Remote Sensing Program, Kansas Biological Survey, University of Kansas, 2101 Constant Ave, Lawrence, Kansas 66047, USA*

ABSTRACT

Understanding the patterns and drivers of primary productivity is a major goal of ecology, but little is known about whether the primary productivities of different types of ecosystems—here, lakes and the landscapes in which they are embedded—fluctuate in related ways through time. Due to shared climatic variation and well-known connections between lake and terrestrial ecosystems, such as nutrient and resource subsidies, we hypothesized that interannual fluctuations in aquatic and terrestrial primary productivity indices could be coherent. We also expected that lake and watershed characteristics could modify the strength and nature of primary productivity relationships. We applied wavelet coherence analyses to time series of lake chlorophyll-a and satellite-derived NDVI to examine coherence between lakes and land, and used random forest regression and generalized additive models to evaluate why coherence varies among lakes. There can be substantial coherence between lake and terrestrial primary productivity, but the strength and phase (direction and time lag) of this relationship vary widely, and there were marked differences between short (2–4-year periods of oscillation) and long ($>$ 4-year periods of oscillation) timescales. Across all timescales, variables associated with the connectedness of lakes to their watersheds were consistently the important explanatory variables of the strength and phase of coherence. The patterns observed in this study suggest the importance of cross-ecosystem flows, as opposed to shared climatic variation, in determining temporal coherence between lakes and the landscape.

Key words: Synchrony; Compensation; Chlorophyll-a; NDVI; Resource subsidies; Hydrologic connectivity.

HIGHLIGHTS

- Lake and watershed primary production can vary coherently.
- The magnitude, direction, and time lag of coherence relationships vary widely.
- Hydrologic connectedness is a key feature mediating the lake–landscape coherence relationship.

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Author Contributions JAW, MLP, and GMW conceived the study. RF prepared lake datasets and JHK produced NDVI datasets. JAW performed analyses and drafted the manuscript. All authors contributed to manuscript edits.

Corresponding author; e-mail: jaw3es@virginia.edu

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INTRODUCTION

Quantifying the primary productivity of ecosystems, and how and by what mechanisms this process varies spatiotemporally, is a fundamental goal of ecology, especially in light of global climate change (Schlesinger and Bernhardt 2013). There are rich, but separate, bodies of literature on the rates and patterns of primary productivity in lakes (Carpenter and others 1985; Dodson and others 2000; Downing 2009; Seekell and others 2018) and in terrestrial landscapes (Melillo and others 1993; Running and others 2000; Schimel and others 2001; Anav and others 2015). Less is known about the relatedness of temporal fluctuations in primary productivity between lakes and the landscape. Aquatic and terrestrial ecosystems are linked through substantial and temporally variable fluxes of matter and energy (Cole and others 2007; Harison and others 2009; Butman and others 2016), which plays an important role in regional and global carbon cycles (Tranvik and others 2009; Buffam and others 2011). Given these factors, whether there are persistent relationships in temporal fluctuations (that is, coherence) in primary productivity between lakes and the landscape has substantial implications for understanding the dynamic linkages between these systems. Coupling of temporal patterns in primary productivity across different ecosystem types has received little attention with the exception of studies focused on synchronization of terrestrial and coastal marine ecosystems (Ong and others 2016; Black and others 2018; Lara and others 2019).

Temporally coherent fluctuations in terrestrial and aquatic primary productivity might plausibly arise from two general mechanisms. The systems might both be influenced, directly and independently, by the same exogenous environmental drivers (for example, climate and weather), bringing them into coherence. This mechanism is analogous to the Moran effect, in which a shared environmental driver synchronizes spatially disjunct populations (Moran 1953). While spatial synchrony among lakes has been observed for variables like surface water temperature (Magnuson and others 1990), it is unclear if exogenous environmental drivers also result in coherence between different ecosystem types. Coherence could also arise from flows of carbon and nutrients across ecosystem boundaries. One possible scenario is that terrestrially fixed carbon enters a lake as dissolved organic matter, reducing light availability and therefore photosynthesis (Karlsson and others 2009; Solomon and others 2015). Alternatively, nutrients entering a lake along with organic matter can stimulate primary productivity (Thrane and others 2014; Corman and others 2018; Kelly and others 2018), or terrestrially fixed carbon could affect aquatic primary productivity by providing subsidies to consumers (Tanentzap and others 2017).

These two mechanisms (Moran-like effects and cross-ecosystem flows) may not be mutually exclusive, as climate and weather may be important drivers of temporal variability in the magnitude of cross-ecosystem flows. For example, anthropogenic nutrient enrichment of terrestrial ecosystems enhances terrestrial primary production and could also drive variability in aquatic primary production through episodic nutrient loading from the watershed, for example in runoff from precipitation events (Kelly and others 2019; Stockwell and others 2020). Although nutrient loading is an exogenous forcing that may be shaped by weather (for example, precipitation), we distinguish between this and the pure Moran-like effect because of the likelihood of vegetation and watershed processes determining the magnitude and timing of inputs to the lake and creating time lags between nutrients' stimulating effects on primary productivity on the landscape and in lakes. Although the Moran-like independent effects of weather could be positive in one system and negative in the other, we do not expect them to be time-lagged given the short response times of plant photosynthetic rates and high turnover rates of phytoplankton.

Properties of lakes and watersheds likely shape the strength and direction of relationships between aquatic and terrestrial primary productivity, and time lags between these variables. Lakes are differentially affected by catchment processes based on their position in the watershed, with lower lakes tending to be more strongly influenced (Kratz and others 1997; Martin and Soranno 2006). Lake morphology could also play an important role, with shallower lakes (Qin and others 2020) or those with greater shoreline development indices (Scheuerell and Schindler 2004) potentially experiencing stronger influences of the adjacent terrestrial ecosystem. What dominates cross-ecosystem flows could also help determine whether lakes and the landscape tend to be positively or negatively related. If the dominant mechanism is nutrient inputs from land to lake, then the two systems may be positively related, whereas if inputs of dissolved organic carbon (DOC) from land to lake dominate, then reductions in water clarity could inhibit lake primary productivity (Karlsson and others 2009; Solomon and others 2015), resulting in a negative relationship. Time lags between lake and landscape primary productivity could reflect time differences between carbon fixation and release (Kuzyakov and Gavrichkova 2010), and lags associated with processing and transport through the watershed (Harman 2015). Thus, temporal relationships in primary productivity between the lake and the landscape provide insight into the drivers of those dynamics and the strength of the linkages among these ecosystems.

Temporal relationships have often been studied using correlation, but approaches based on the wavelet transform (Torrence and Compo 1998) have grown in popularity because of their ability to resolve common patterns that confound standard correlation (Vasseur and Gaedke 2007; Downing and others 2008; Sheppard and others 2016; Walter and others 2017). Ecology is multi-causal and mechanisms often have specific timescales of variation, so timescale-specific relationships can reflect specific drivers (Defriez and Reuman 2017; Sheppard and others 2019; Wilkinson and others 2020). Standard correlation can fail to resolve timescale-specific and temporally lagged effects (Sheppard and others 2016; Walter and others 2019). Time lags result from common processes including transport times between observation points, intervals between generations, and certain predator–prey relationships. Wavelet coherence overcomes both problems by indicating the strength of relatedness between two variables, and the time lag (phase difference) between them, as a function of timescale (Grinsted and others 2004; Sheppard and others 2017). Figure 1 illustrates a timescale-specific relationship and examples of phase differences between two variables.

To investigate patterns of temporal coherence in primary productivity between lakes and the landscapes in which they are embedded, we analyzed 135 long-term (≥ 20 years) paired lake and land time series in the northeastern USA. We focus specifically on the following questions. (Q1) To what extent are multi-annual [sensu Wilkinson and others (2020)] patterns of lake primary productivity coherent with primary productivity in the surrounding landscape? (Q2) What are the phase differences between them, and what does this imply about the predominant mechanisms coupling primary productivity in lakes and the landscape? (Q3) What factors explain variability in the magnitude and phase of coherence between lake and landscape primary productivity? (Q4) Do the answers to questions Q1 through Q3 depend on timescale? We found that on multi-annual timescales landscape and lake productivity vary widely in their coherence and the phase differences between landscape and lake. The coupling relationships appear to mainly reflect flows of carbon and nutrients between the ecosystem types.

METHODS

Data Acquisition and Processing

We obtained time series data on chlorophyll-a, an indicator of primary production, from the LAGOS-NE LIMNO database, version 1.087.3 (Soranno and others 2017; Soranno and Cheruvelil 2019). The LAGOS-NE database contains time series of physical, chemical, and biological parameters from lakes located in seventeen states of the northeastern and mid-western portions of the conterminous United States. Data were aggregated to annual intervals by averaging measurements from May–September, the period of most active growth. If a lake had fewer than three observations during a growing season, data for that year were discarded. Lake time series selected for analysis spanned a minimum of 20 years, could have a maximum of two years with missing data, and years with missing data were non-consecutive. Because our analyses require complete time series, missing data were filled with the median of the time series. A number of lakes in LAGOS-NE narrowly missed satisfying these criteria, but because this version of LAGOS-NE contains data through the year 2013, we augmented the dataset by obtaining additional, freely available data on a total of 38 lakes from the Wisconsin Department of Natural Resources (14 lakes) and Minnesota Pollution Control Agency lake monitoring programs (24 lakes). These data were processed to match the format of the LAGOS-NE data. In total, 135 lake time series were analyzed. A map of lakes and selected examples of coherent and non-coherent time series is provided in Figure S1.

We also obtained from LAGOS-NE, or derived from data contained therein, a suite of 53 variables describing lake morphometry, watershed land cover, hydrologic connections, landscape position, atmospheric deposition, glaciation history, and climate for each lake (Soranno and Cheruvelil 2017). Surficial geology was also considered but could not be adequately addressed due to the lack of data for most variables in this category. A complete list and a criterion for culling the list of potential variables are given in Supplementary Material S1. These variables reflect conditions either of the lake itself, in the watershed as delineated in LAGOS-NE (Soranno and others 2017), or within the Hydrologic Unit Code (HUC) Level-12 unit. Hydrologic Unit

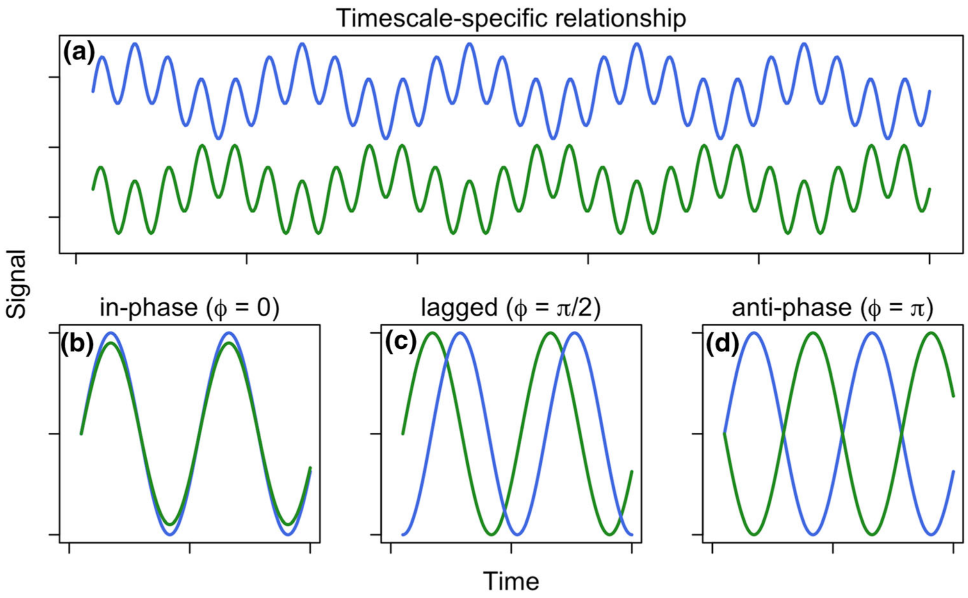

Figure 1. Illustration of timescale-specific relationships between two variables (**A**) and different phase relationships (**B**–**D**). In (**A**), the blue and green signals are perfectly positively correlated on short timescales and perfectly negatively correlated at long timescales; this relationship would be confounded by standard correlation. In (**B**), fluctuations are in-phase (ϕ = 0), corresponding to positive correlation; in (**C**), fluctuations are temporally lagged, with the green signal peaking ahead of the blue signal (ϕ = π/2); in (**D**), fluctuations are anti-phase (ϕ = π), corresponding to negative correlation.

Codes are a hierarchical system for identifying watersheds, of which level-12 (that is, a 12-digit identifying code) is the finest. In our dataset, there was only one lake in 101 of 114 HUC-12 units, and at most 5 lakes. LAGOS-NE was accessed through the LAGOSNE R package (Stachelek and Oliver 2019).

We used growing season accumulated normalized difference vegetation index (NDVI) data as a proxy for annual primary productivity in the terrestrial landscape surrounding each lake. To develop this dataset, start-of-season (SOS) and end-of-season (EOS) dates were estimated annually using the 30-year (1989–2018) Advanced Very High-Resolution Radiometer (AVHRR) NDVI time series dataset available for the conterminous U.S. (United States Geologic Survey). These raster image data, which have 1-km spatial resolution, consist of weekly issued, biweekly maximum value composite NDVI scores (Eidenshink 1992, 2006). Source imagery was collected almost daily, so that the biweekly maximum value composite NDVI scenes are largely cloud free (clouds, ice, and snow tend to suppress NDVI values). AVHRR sensors on multiple satellite platforms have been utilized over the years to provide a gapless time series.

For each pixel and each year, SOS was determined using the midpoint of the methods described in Zhang and others (2003) and Yu and others (2004). Considering the temporal uncertainties associated with the NDVI time series (for example, the precise date of acquisition for each pixel's value in a composite image is not known), time steps were assigned to integers in [1:52] representing calendar week of issue. Both SOS approaches are somewhat sensitive to high-frequency noise, so to facilitate consistent SOS estimation, NDVI time series were initially smoothed using time series tail and minima treatment methods adapted from Wardlow and others (2006). To obtain EOS, NDVI time series were reversed prior to processing, with the result subtracted from 53 to obtain the correct temporal position. Growing season accumulated NDVI was then determined by summing NDVI values from SOS to EOS. Some years for some pixels representing water or barren lands did not satisfy NDVI threshold-based criteria for vegetation presence, and in those cases no growing season accumulated NDVI was assigned.

Using only AVHRR pixels consisting of less than 5% water based on the National Land Cover Database (NLCD 2011; Homer and others 2015), we averaged annual terrestrial NDVI within a radius dependent on the surface area of the lake. Prior research established that there is a power-law relationship between lake surface area and watershed area, and that the intercept (but not the scaling parameter) differs between lakes and reservoirs (Walter and others 2020). We set a minimum radius of 2.5 km to ensure an adequate sample of terrestrial pixels. Otherwise, we used the simplifying assumption that lakes are circular to derive the following equation to scale the search radius to the surface area of the lake:

$$r = \sqrt{\frac{10^{\beta_0 + \beta_1 \log_{10} A_l}}{\pi}}.$$

Here, β_0 and β_1 are empirically estimated regression coefficients that differed between lakes and reservoirs, and A_l is the surface area of the lake. For reservoirs, $\beta_0 = 1.8$ and $\beta_1 = 1.05$, and for lakes, $\beta_0 = 1.4$ and $\beta_1 = 1.05$ (Walter and others 2020). We also considered using watershed boundaries as spatial units for NDVI time series; however, a number of small lakes had too few suitable AVHRR pixels within their watersheds and so were discarded. For the remaining lake–landscape pairs, wavelet coherence test results (see *Analyses*) were entirely consistent whether NDVI time series were determined from circular buffers or from watershed boundaries, and so we present results using circular buffers.

Analyses

We tested for wavelet coherence (Grinsted and others 2004; Sheppard and others 2017) between time series of lake chlorophyll and terrestrial NDVI to determine the strength and phase of temporally persistent relationships between lake and land primary productivity. Wavelet coherence quantifies the degree to which two time series have correlated magnitudes of oscillation and consistent phase differences through time, as a function of timescale. Its magnitude ranges from 0 (no relationship) to 1 (perfect coherence). As we focus on consistent, as opposed to transient or episodic, relationships, we considered coherence over the full time series. Significance testing was performed by comparing the empirical coherence to a distribution of surrogate coherences generated under a null hypothesis of no coherence that retained the spectral (that is, temporal autocorrelation) properties of the empirical time series (Sheppard and others 2017). This test is conservative because in the procedure by which surrogates are generated only the phase of oscillations varies, while the power spectrum of each time series is entirely preserved. In reality, if one variable drives fluctuations in a second variable, the power spectrum of the second variable is influenced by the first. However, incorporating such effects is difficult, and failure to do so appropriately would result in potentially identifying false relationships.

To determine to what extent interannual patterns of lake and terrestrial primary productivity are coherent (Q1), we examined the distribution of coherence magnitudes at short (2- to 4-year periods of oscillation) and long (> 4-year periods of oscillation) timescale bands and compared the number of statistically significant coherences to the number expected under a false-positive error rate of $\alpha = 0.05$, assuming independent tests. The period length of 4 years was chosen to demarcate short from long timescales because it separates anti-persistent patterns (that is, successive observations tend to be negatively correlated) from persistent patterns (that is, successive observations tend to be positively correlated) (Sheppard and others 2016). Choosing focal timescale bands a priori facilitates significance testing (Sheppard and others 2016).

To assess the prevalence of different phase relationships between lake and terrestrial primary productivity (Q2), we examined the distribution of coherence phases for coherence relationships exceeding the 70th percentile of a distribution of surrogate coherences generated under a null hypothesis of no coherence but preserving the spectral properties of each time series. Only relatively strong coherences were used because for incoherent variables the phase difference is essentially a random variable uniformly distributed between $-\pi$ and π, and hence is not meaningful. Short and long timescales were again considered separately.

To assess what factors explain variability in the magnitude and phase of coherence between lake and landscape primary productivity (Q3), we combined "feature selection" using conditional random forest regression (Hothorn and others 2006) with generalized additive models (Wood 2006). Because phases are angular measurements, we performed analyses on the sine- or cosine-transformed phase difference between lake and landscape primary productivity indices. Taking the cosine assigns in-phase relationships ($\phi = 0$) to a value of 1, anti-phase relationships ($\phi = \pm\pi$) to a value of -1, and quarter-phase relationships ($\phi = \pm\pi/2$) to a value of 0. Consequently, analysis of $\cos(\phi)$ focuses on how close the relationship is to being in-phase. Taking the sine transforms to a value of 0 for both in-phase and anti-phase relationships; to -1 for a relationship in which peaks in chlorophyll-a lag NDVI by ½ a cycle length, or in other words a time-lagged positive relationship; and to 1 for a relationship in which peaks in chlorophyll-a lead NDVI by ½ a cycle length, or in other words a time-lagged negative relationship, assuming that the dominant direction of flows is from land to lake. Consequently, analysis of sin(ϕ) focuses on whether the time-lagged relationship between NDVI and chlorophyll-a tends to be positive or negative. Whether to apply the sine or cosine transformation depended on the dominant mode of variability in ϕ for a timescale band.

Conditional random forests were used to select the most important predictors from the suite of 53 predictor variables described above and in Supplementary Material S1. Conditional random forests are an ensemble machine learning technique based on classification and regression trees (Hothorn and others 2006). We fit conditional random forests consisting of 50,000 trees for each predictor variable and quantified variable importance values for each predictor. Variable importance values and the Pearson correlation between empirical values and model predictions were stable at this forest size.

We used generalized additive models (GAMs) to investigate statistical effects and overall explanatory power of selected predictors on the timescale-specific coherence and phase between chlorophyll-a and NDVI. GAMs replace regression coefficients with penalized regression splines, thereby identifying nonlinear relationships while balancing parsimony and model complexity (Wood 2006). We built GAMs with 3 predictors for the response variables short-timescale coherence magnitude (n = 135), long-timescale coherence magnitude (n = 135), short-timescale phase (n = 39) and long-timescale phase (n = 45). Predictors were chosen for inclusion in rank order of variable importance, skipping variables with strong concurvity with a higher-ranked predictor. Concurvity is a generalization of collinearity used with GAMs. We deemed estimated concurvity values less than 0.6 to be acceptable; GAMs are highly robust to concurvity (Wood 2008). Observations were weighted by time series length to give greater weight to longer time series, for which we have greater certainty in the nature of lake–landscape coherence. Since coherence magnitudes are bounded between 0 and 1, we used a beta distribution with the GAM models for these variables. Some predictors were $\log_{10}$ or square-root transformed to reduce the influence of extreme values. Because our goal for this analysis was to explore relationships explaining variability in temporal coherence between lake and land primary productivity indices, as opposed to testing a priori hypotheses about these potential drivers, we did not apply significance testing or further model selection/model parsimony methods to our GAMs.

The timescale specificity of the magnitude, phase, and predictors of coherence (Q4) was determined by comparing results from short timescales (2- to 4-year periods of oscillation) versus from long timescales (> 4-year periods). Analyses were carried out in R version 3.5.1 (R Core Team 2018) using the ''wsyn'' (Reuman and others 2019), ''party'' (Hothorn and others 2019), and ''mgcv'' (Wood 2006) packages.

RESULTS

Coherences between lakes and landscape primary productivity varied widely, spanning nearly 0 to 1, the entire range of the statistic (Q1). Example time series from a particularly coherent lake–landscape pair and a particularly non-coherent lake–landscape pair are shown in Figure S1. At short timescales, coherence ranged 0.06 to 0.92 with a median of 0.37 (Figure 2A). Nine lake–landscape pairs were significantly coherent at short timescales using $\alpha = 0.05$ significance level. At long timescales, coherence magnitudes ranged 0.08 to 0.95, with a median of 0.53, and fifteen lake–landscape pairs were significantly coherent using $\alpha = 0.05$ significance level (Figure 2B). In each case, the number of significant coherences is greater than the number expected by chance given the selected type-1 error rate (that is, 135*0.05 = 6.75) assuming independent tests. This result highlights that there is robust evidence that *some* lake–landscape pairs are strongly coherent, but we emphasize that it is also meaningful that there is a wide range of observed coherences. The spatial distribution of coherences at short (Figure 3) and long (Figure S2) timescales indicates no apparent regional patterns in lake–landscape coherence. Lake–landscape coherences were substantially timescale specific (Q4). Although coherence magnitudes were somewhat greater at long timescales than short, wavelet coherence suffers from a bias wherein greater values tend to be returned at long timescales, so care should be taken in comparing coherence magnitudes across timescales. Our significance tests do not suffer the same bias, however. There was no correlation between coherence magnitudes at short timescales and coherence at long timescales (Pearson correlation = 0.03), and only three lakes were significantly coherent at both short and long timescales.

Phase relationships between lakes and the landscape also spanned the range of possible values (0 to ± π), but certain phase relationships were more common than others (Q2). At short timescales, most coherence relationships were approximately

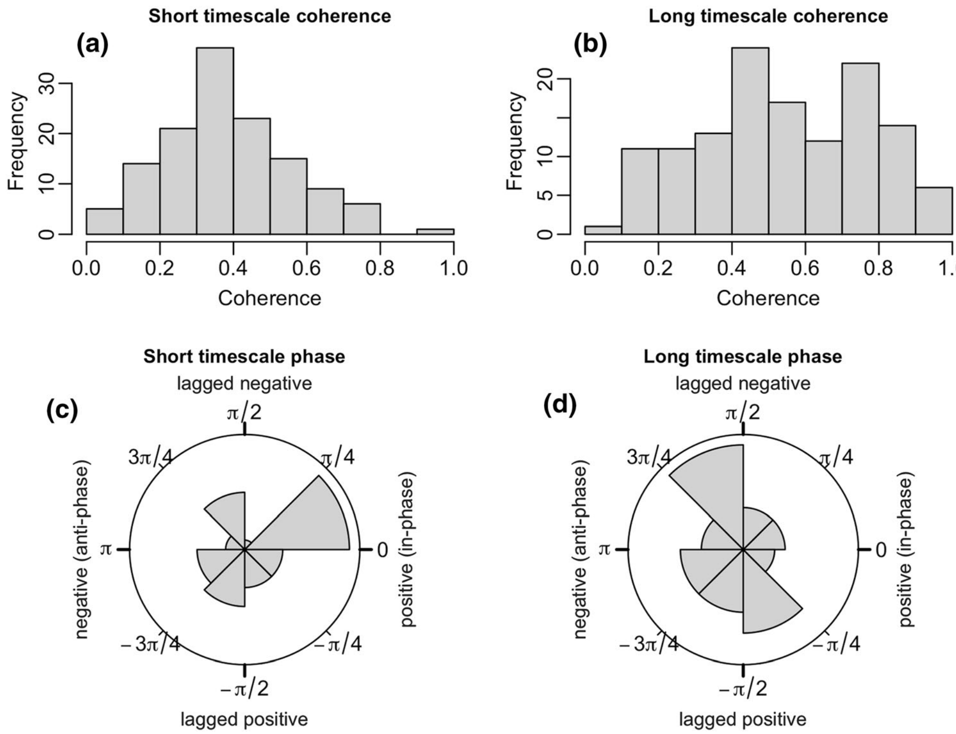

Figure 2. Distributions of coherence magnitudes (**A**, **B**) and phase differences (**C**, **D**) at short timescales (2–4 years; panels **A**, **C**) and at long timescales (> 4 years; panels **B**, **D**). In (**C**, **D**), frequency is proportional to radius length.

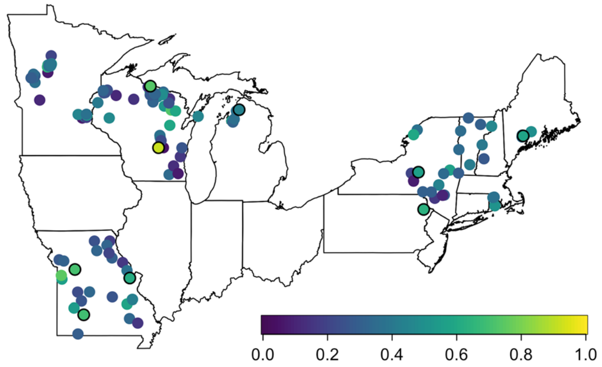

Figure 3. Map of lakes included in this study by short-timescale coherence between chlorophyll-a and NDVI. Black outlines indicate statistically significant coherence. See Figure S2 for long timescales.

in-phase (Figure 2C). At long timescales, coherence relationships were bimodally distributed with most coherent lakes exhibiting either phase-lagged positive ($-\pi/4 < \phi < -3\pi/4$) or negative ($\pi/4 < \phi > 3\pi/4$) relationships with terrestrial NDVI (Figure 2D).

The coefficient of variation in NDVI and variables associated with modulation of flows between lake and the landscape (herein termed ‘‘hydrologic connectedness’’) tended to be the best predictors of lake–landscape coherence and phase relationships (Q3). Such variables included wetland cover and shoreline, precipitation and runoff, and groundwater recharge. Variation in the magnitude of coherence at short timescales was best explained by total nitrogen deposition, the temporal coefficient of variation in terrestrial NDVI [cv(NDVI)], and several variables related to wetland cover in the watershed and adjacent to the lake (Figure 4A). A GAM model including the top 3 predictors explained 14.6% of deviance in short-timescale coherence, and featured a negative effect of total N deposition, and positive effects of cv(NDVI) and herbaceous wetland cover (Figure 5A–C). Among lakes exhibiting substantial coherence with the landscape, for which computed phase relationships are reliable, lakes with more open water wetlands on their shoreline and with higher average chlorophyll-a concentrations (that is, more eutrophic lakes) were more likely to be in-phase with the landscape, but those with a high percentage of shrub/scrub land cover were less likely to be in-phase with the landscape (Figure 5D–F). A GAM model with these predictors explained 20.9% of deviance in cos (ϕ).

At long timescales, coherence was best explained by the percentage of shrub/scrub land cover in the watershed, cv(NDVI), annual precipitation, and the percentage of watershed area composed of semi-

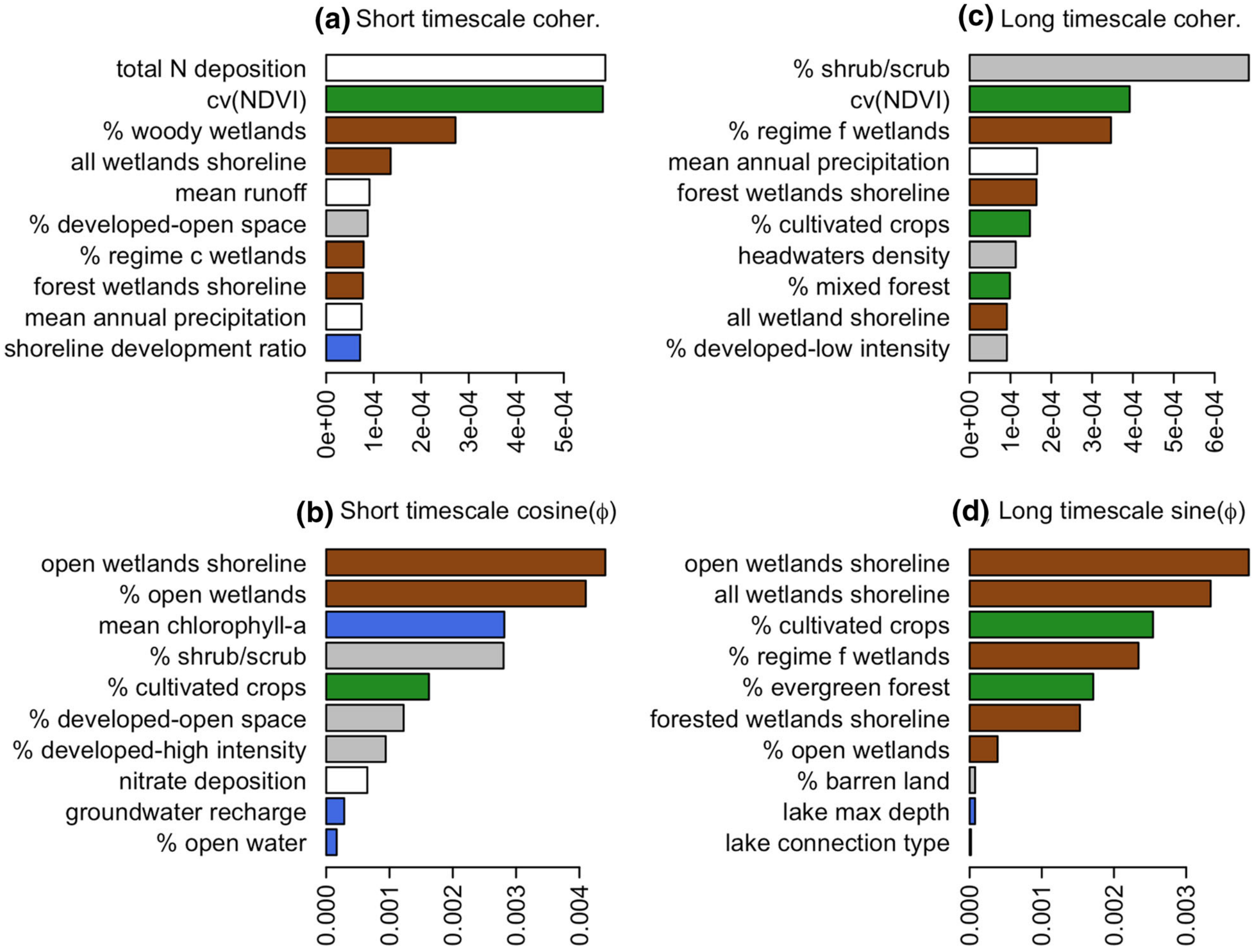

Figure 4. Variable importance values (in descending order) from conditional random forest analyses of among-lake variability in the coherence magnitude (**A**, **C**) and phase difference (**B**, **D**) between primary productivity in lakes and the landscape. Results for short timescales (2–4 years) are shown in panels **A**, **B**; those for long timescales (> 4 years) in panels **C**, **D**. Wetland variables are drawn in brown; lake variables are in blue; terrestrial vegetation variables are colored in blue; climate and atmospheric deposition variables are in white; and variables not fitting these categories are in gray.

permanently flooded (regime f) wetlands (Figure 4C). Regime f wetlands are semi-permanently flooded where surface water persists throughout the growing season in most years. Long-timescale coherence decreased with increasing percentages of shrub/scrub land cover in the watershed and with the percentage of watershed area covered by semi-permanently flooded wetlands, and increased with increasing cv(NDVI) (Figure 5G–I). This combination of predictors explained 13.5% of deviance in coherence. Phase relationships at long timescales were most strongly influenced by wetland shoreline and area, and other land cover types (Figure 4D). Sin(ϕ) tended to decline with increasing open-wetland shoreline, notwithstanding a few outliers, indicating a tendency toward time-lagged negative effects of NDVI on chlorophyll-a fluctuations (Figure 5J). Increases in the areal percentage of semi-permanently flooded wetlands in the watershed were also associated with time-lagged negative effects, and the percentage of cultivated crops was associated with time-lagged positive effects (Figure 5I, L). These predictors explained 31.9% of deviance in sin(ϕ).

DISCUSSION

There is wide variability in the coherence of indices of primary productivity between lakes and the surrounding landscape, from complete incoherence to near-perfect coupling across interannual timescales. Although the presence of links between terrestrial and aquatic systems is well known (Wilkinson and others 2013; Tanentzap and others 2017; Tranvik and others 2018), our findings underscore the importance of temporally dynamic

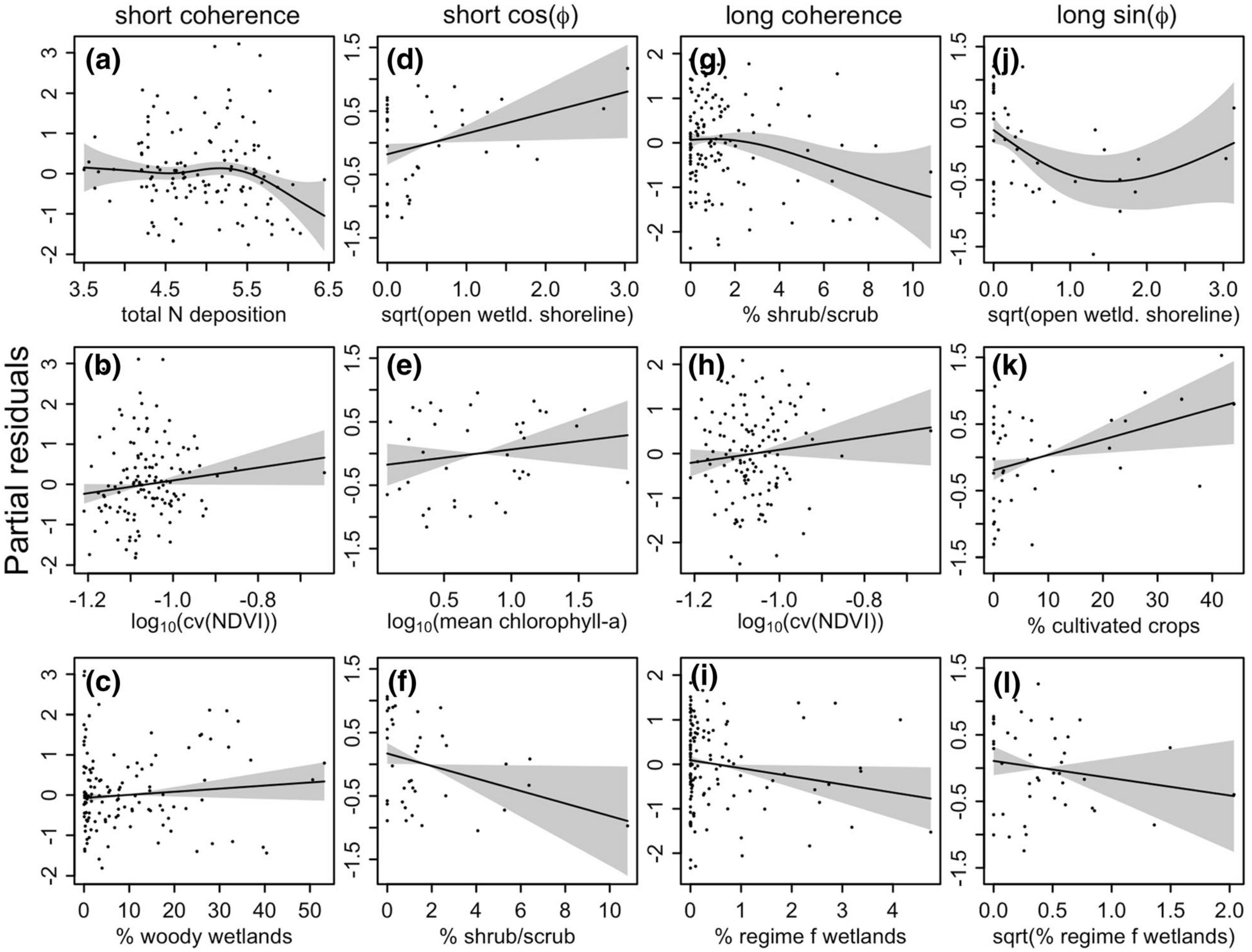

Figure 5. GAM partial effect plots depicting effects of top predictors on (**A**–**C**) short-timescale coherence; (**D**–**F**) cosine-transformed short-timescale phase difference; (**G**–**I**) long-timescale coherence; (**J**–**L**); sine-transformed long-timescale phase difference. Models explained, respectively, 14.6%, 20.9%, 13.5%, and 31.9% of deviance in the response variable. Gray regions indicate ± 2 standard errors.

links between aquatic and terrestrial ecosystems. Although lakes typically make proportionally small contributions to regional primary productivity, except in particularly lake-rich regions, aquatic ecosystems process large amounts of terrestrially derived nutrients and organic matter (Cole and others 2007; Downing 2009). Understanding whether these inputs stimulate or inhibit lake primary productivity, and the mechanisms that couple these systems, is important especially on timescales from a few years to decades [that is, multi-annual timescales sensu Wilkinson and others (2020)]. For example, episodic nutrient inputs may stimulate algal blooms, while precipitation-driven dissolved organic matter inputs may have longer-term effects on lake primary producers.

We proposed that coherence between lakes and the landscape could be driven by shared responses to weather, potentially mediated by flows of carbon and nutrients across ecosystem boundaries, and by lake characteristics (Figure 6). Our results provide some inference into the importance of these mechanisms in the lakes we studied, specifically that lake–landscape coherence largely arises through cross-ecosystem flows of carbon and nutrients, with wetlands playing a key mediating role. If coherence was driven predominantly by shared, independent Moran-like effects of exogenous drivers like weather, we should expect strong coherences to mainly be in-phase or anti-phase; instead, we see many time-lagged relationships, although short-timescale coherences were more often in-phase or anti-phase. Further evidence for this interpretation is that variables associated with hydrologic connections between lakes and the landscape—for example, wetlands area and shoreline, runoff, groundwater recharge, and headwater stream density—were among the most important

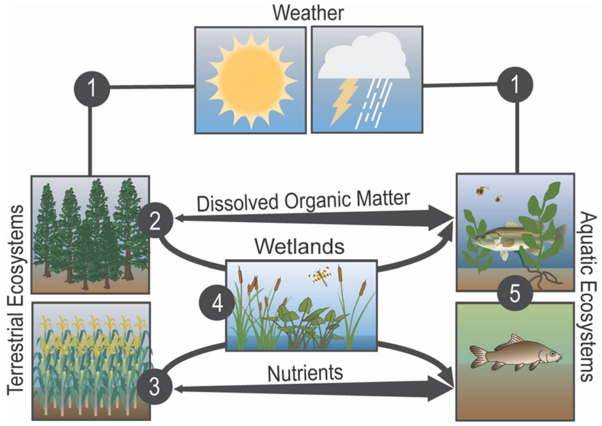

Figure 6. Diagram of hypothesized mechanisms underpinning lake–landscape coherence results. (1) Weather may cause shared, independent effects on terrestrial and aquatic primary production leading to in-phase or anti-phase coherence. (2) Dissolved organic matter from terrestrial primary production may carry nutrients that stimulate aquatic primary production or decrease light availability in lakes. Land cover shapes the quantity and quality of terrestrial dissolved organic matter delivered to lakes; flow paths and terrestrial decomposition contribute to time (phase) lagged effects. (3) The form and magnitude of nutrient loading from the watershed into lakes are influenced by land use. Nutrients that stimulate production in the watershed can also stimulate primary production in the lake at a phase lag based on the bioavailability of the exogenous inputs and the timing of delivery to the receiving aquatic ecosystem. (4) Wetlands modify the coherence between lakes and the landscape by altering flow paths. Wetlands retain water that would otherwise be immediately delivered downstream and process nutrients and dissolved organic matter, altering the quality and quantity of material delivered downstream. (5) Lake characteristics such as the size, depth, and food web structure potentially modify these influences. Artwork attribution: graphics from Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/imagelibrary/); pine tree by Tracey Saxby, corn stalk by Jane Thomas, pondweed by Dieter Tracy, carp by Kate Moore, and largemouth bass and *Daphnia* by Kim Kraeer and Lucy Van Essen-Fishman.

predictors of the magnitude and phase of lake–landscape coherence. Hydrologic connectivity, via both surface waters and sub-surface flows, has a fundamental role in the spatiotemporal dynamics of lake ecosystems (Canham and others 2004; Martin and Soranno 2006; Fergus and others 2017). Wetlands are an important component of these connections, processing and exporting large amounts of carbon and nutrients (Detenbeck and others 1993; Gergel and others 1999; Martin and Soranno 2006). Many of these variables are also correlates of lake–landscape position (Kratz and others 1997; Martin and Soranno 2006). The area of wetlands around the lake tends to increase moving from high in the watershed to low; these lakes also tend to accumulate inputs from larger areas, and also are more likely to have inflowing streams. However, other correlates of lake–landscape position including stream density, lake connection, and upstream lake area were also candidate predictor variables but were less influential.

Interestingly, the dominant mode of variability in phase differences among lakes that were coherent with the landscape on long timescales was between a time-lagged positive and a time-lagged negative effect. Negative effects of terrestrial primary productivity on aquatic primary productivity could reflect dissolved organic carbon (DOC) loading; DOC may inhibit photosynthesis by decreasing water clarity (Karlsson and others 2009; Solomon and others 2015). In our analyses, time-lagged negative relationships were associated with increasing amounts of wetlands in the watershed and on the shoreline, and time-lagged positive relationships were associated with the more agricultural watersheds. DOC export to aquatic systems is associated with forests and wetlands (Gergel and others 1999; Canham and others 2004), while agriculture can be a considerable source of nutrient runoff. The time lags between terrestrial and aquatic primary productivity may reflect both transport time, for example, through slow pathways like groundwater, and the timing of biogeochemical transformations (Cardille and others 2007). For example, a typical pathway for DOC originating on land is for carbon to be fixed into leaves during the growing season, fall during autumn senescence, and decompose before entering the DOC pool.

Surprisingly, we found little evidence that lake–landscape coherence depended on characteristics of lakes themselves. We considered a number of predictors characterizing lake morphometry (maximum depth, shoreline development ratio) and biogeochemistry (mean chlorophyll-a), but only mean chlorophyll-a was a relatively important predictor of any response variable. Taken together with our results on the importance of hydrologic connectedness and cv(NDVI) for lake–landscape coherence, it seems that lake–landscape coherence is largely imposed by the terrestrial landscape and mediated through flows of carbon and nutrients across the terrestrial-aquatic interface (Carpenter and others 1998; Buffam and others 2011).

Insights from the study of spatial synchrony in population dynamics (Liebhold and others 2004; Walter and others 2017) suggest that weather variation and climate oscillations should be important in coupling these dynamics, in a sort of cross-ecosystem ''Moran effect'' (Moran 1953). Indeed, spatially synchronous weather has been inferred to synchronize dynamics across lakes (Magnuson and others 1990; Baines and others 2000; Pace and Cole 2002; Pham and others 2008; Rusak and others 2008) and drive spatial synchrony in terrestrial primary production (Koenig and Knops 1998; Wettstein and others 2011; Shestakova and others 2016; Defriez and Reuman 2017). However, weather may not synchronize lakes at the regional spatial extent of our study (Soranno and others 2019), and weather does not seem commonly to directly synchronize lakes with the landscape, at least on multi-annual timescales. Although we did not explicitly test for weather drivers of coherence, the relative predominance of phase-lagged coherences—particularly at long timescales—and the relatedness of hydrologic connectedness to spatial variation in coherence between lakes and the landscape suggest that the proximal mechanisms of lake–landscape coherence likely have more to do with nutrient and organic matter subsidies from the landscape to the lake, than shared environmental forcing operating similarly, but separately and simultaneously on the lake and the landscape. This is in contrast to spatial synchrony in population dynamics, where climate can synchronize populations over large areas, even with little or no dispersal between them (Liebhold and others 2004). Other studies of cross-ecosystem synchrony between terrestrial and marine ecosystems have found climate to be an important driver (Ong and others 2016; Black and others 2018), but the relative magnitude of inputs from the land to lakes is likely larger than from the land to the ocean.

The magnitude of lake–landscape coherence was entirely uncorrelated across timescales, affirming the power of our timescale-specific approach. Standard approaches based on correlation or regression would not have uncovered this pattern and would have been confounded by the strong differences between short and long timescales. Importantly, this also suggests that different underlying mechanisms are responsible for short- versus long-timescale coherence between lakes and the landscape. Particular mechanisms have characteristic timescales of variation and tend manifest on those same timescales, as has been shown in studies of population spatial synchrony (Sheppard and others 2016; Anderson and others 2019) and inferred for some studies of synchrony in lakes (Baines and others 2000; Pace and Cole 2002). Although variables associated with hydrologic connectedness tended to explain among-lake variation in lake–landscape coherence, specifically what mechanisms are at play are not yet known. For example, the role of ''flashy'' events, such as storms resulting in overland flows and relatively high flow rates through riverine systems, versus slow-but-consistent processes like groundwater recharge, is unclear, but could be resolved by studying time series with sub-annual intervals between observations.

Our conclusions are limited by data drawn from a biased set of lakes (Stanley and others 2019) with relatively short time series of error-prone indicator variables. Despite these limitations, we believe it would be inappropriate to dismiss evidence for lake–landscape coherence on these grounds. We chose NDVI and lake chlorophyll-a as indices of primary productivity because of their relative availability. Other measures, such as from eddy covariance for terrestrial ecosystems (Vesala and others 2006; Aubinet and others 2012) and in situ measurements of oxygen dynamics and carbon fixation for lakes provide more direct measurements of primary productivity. However, their limited availability made them ill-suited to the goals of this study. Satellite remote sensing of lake water quality can enable study of additional lakes, but the need for calibration data (Ross and others 2019) and cloud cover mean that remotely sensed time series would have similar limitations to our dataset. Additionally, while our time series are near the lower length limits where wavelet analyses can be reasonably applied, our data are among the longest records that currently exist, and requiring longer time series would have substantially reduced the number of lakes in the study, hindering our goals. Considering the limited statistical power afforded by our short time series and potential for observation error, the detection of strong relationships is meaningful.

This study provides evidence of wide variation in the coupling of temporal ecosystem dynamics between lakes and the landscapes they are embedded in, and provides a springboard for future work leveraging temporal pattern to understand causes and consequences of coupling between lakes and the landscape. Although further research is needed to clarify the specific mechanisms of temporal coherence between lakes and the landscape, variables associated with hydrologic connectedness explained substantial spatial variation in lake–

landscape coherence, suggesting that cross-ecosystem flows may commonly be a proximal mechanism. Based on analogs with synchrony in populations and communities, and observations of coastal systems (Ong and others 2016; Black and others 2018; Lara and others 2019), we expected that shared climatic fluctuations could induce synchrony between lakes and the landscapes, but this does not seem prevalent. Finally, this study affirms that multi-annual dynamics, which particularly in aquatic ecosystems are less well understood compared to seasonal and short-term trends (Wilkinson and others 2020), exhibit rich patterns, and that their investigation can lead to new insights into ecosystem dynamics.

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DATA AVAILABILITY

Derived datasets and code for reproducing the analyses have been archived on Zenodo. The DOI is https://doi.org/10.5281/zenodo.3937417.

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