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A Classification Framework to Assess Ecological, Biogeochemical, and Hydrologic Synchrony and Asynchrony

Erin C. Seybold¹, Megan L. Fork², Anna E. Braswell³, Joanna R. Blaszczyk⁴, Matthew R. Fuller⁵, Kendra E. Kaiser⁶, John M. Mallard⁷, Margaret A. Zimmer⁸

¹Kansas Geological Survey, University of Kansas, 1930 Constant Ave, Lawrence, KS, USA.

²Cary Institute of Ecosystem Studies, 2801 Sharon Turnpike, Millbrook, NY, USA.

³School of Forest, Fisheries, and Geomatics Sciences, Fisheries and Aquatic Sciences Program, University of Florida, 7922 NW 71st Street, Gainesville, FL, U.S.A.

⁴Department of Natural Resources and Environmental Science, 1664 N. Virginia St., University of Nevada, Reno, NV, USA.

⁵Currently ORISE postdoc at Atlantic Coastal Environmental Science Division, US Environmental Protection Agency, 27 Tarzwell Drive, Narragansett, RI, USA.

⁶Department of Geosciences, Boise State University, 1295 University Drive, Boise, ID, USA.

⁷Department of Earth, Marine, and Environmental Sciences, University of North Carolina, 104 South Road, Chapel Hill, NC, USA.

⁸Department of Earth and Planetary Sciences, University of California, Santa Cruz, 1156 High St, Santa Cruz, California, USA.

Abstract

Ecosystems in the Anthropocene face pressures from multiple, interacting forms of environmental change. These pressures, resulting from land use change, altered hydrologic regimes, and climate change, will likely change the synchrony of ecosystem processes as distinct components of ecosystems are impacted in different ways. However, discipline-specific definitions and *ad hoc* methods for identifying synchrony and asynchrony have limited broader synthesis of this concept among studies and across disciplines. Drawing on concepts from ecology, hydrology, geomorphology, and biogeochemistry, we offer a unifying definition of synchrony for ecosystem science and propose a classification framework for synchrony and asynchrony of ecosystem processes. This framework classifies the relationships among ecosystem processes according to five key aspects: 1) the focal variables or relationships representative of the ecosystem processes of interest, 2) the spatial and temporal domain of interest, 3) the structural attributes of drivers and focal processes, 4) consistency in the relationships over time, and 5) the degree of causality among focal processes. Using this classification framework, we identify and differentiate types

Corresponding author: Erin C. Seybold; erinseybold@ku.edu; phone: 785-864-1544.

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of synchrony and asynchrony, thereby providing the basis for comparing among studies and across disciplines. We apply this classification framework to existing studies in the ecological, hydrologic, geomorphic, and biogeochemical literature, and discuss potential analytical tools that can be used to quantify synchronous and asynchronous processes. Furthermore, we seek to promote understanding of how different types of synchrony or asynchrony may shift in response to ongoing environmental change by providing a universal definition and explicit types and drivers with this framework.

Keywords

synchrony; asynchrony; ecosystems; biogeochemistry; hydrology; environmental change; classification

Introduction

Ecosystems are comprised of abiotic and biotic components that interact and function as tightly coupled dynamic systems through space and time. The timing of interactions is vital for ecosystem function (e.g., transport and/or transformation of water, nutrients, and energy) and the continued provision of services upon which humans and other organisms depend (Costanza and others 1997). In the Anthropocene, ecosystems face pressure from broad-scale social-environmental changes such as land use modification, altered hydrologic regimes, and climate change (Steffen and others 2011; Kueffer 2015; Tarolli and Sofia 2016). These pressures disturb ecosystems at multiple spatial and temporal (hereafter “spatiotemporal”) scales by altering the timing, spatial extent, and degree of interaction between ecosystem processes (Box 1). Differences in the nature of relationships among ecosystem processes and the type of synchrony or asynchrony they exhibit could lead to complex and divergent responses to ongoing environmental change. Therefore, understanding future ecosystem change is contingent on an accurate and clear description and differentiation between key aspects of synchrony and asynchrony (hereafter “(a)synchrony”). The acceleration of climatic and other anthropogenic perturbations to ecosystems is driving a correspondingly accelerated need for synthesized knowledge of interactions among ecosystem processes across studies and disciplines.

Climate change directly influences both biotic (e.g., plant growth) and abiotic (e.g. precipitation) ecosystem processes. Changes in climate stationarity may disrupt relationships between previously synchronous ecosystem processes. For example, biotic processes like plant growth that occur in synchrony with abiotic drivers, such as precipitation or temperature, are likely to decouple as a result of deviations in the timing or magnitude of these abiotic drivers (Mahoney and Rood 1998; Tonkin and others 2018). Further, the degree of synchrony among biotic processes may decrease as a result of divergent reactions to climate change between species, altering ecosystem function and species persistence. Such alterations may be particularly pronounced between species that react to long-term climatic averages versus those triggered by short-term climatic cues (Ovaskainen and others 2013).

These changes in the (a)synchrony of ecosystem processes in response to changing climate are only exacerbated by their interaction with anthropogenic alterations to landscapes, such

as hydrologic modifications and land use and land cover change. For example, changes in the timing and magnitude of streamflow that result from dam construction and operation have pervasive downstream consequences for populations and ecosystems (Kennedy and others 2016; Grill and others 2019; Weston 2014; Walling 2012). Additionally, urbanization and agricultural expansion have altered hydrologic flowpaths (Guan and others 2011; Kaushal and Belt 2012), changed the heterogeneity and permeability of landscapes (Boland-Brien and others 2014; Kelleher and others 2020), and altered pools and fluxes of solutes (Kaushal and others 2014; David and others 2016), all of which change the timing and magnitude of water and material movement through the landscape. These changes may have cascading impacts on the (a)synchrony of ecosystem processes from landscape to continental scales (Grimm and others 2008; Heffernan and others 2014).

The concept of (a)synchrony is used in ecology to evaluate and interpret ecosystem attributes and processes including trophic interactions (Bjørnstad and others 1999), metapopulation dynamics (Hanski 1998; Yeakel and others 2013), life history strategies (Moore and others 2014), and community composition (Micheli and others 1999). For example, synchrony between individual predator and prey populations is observed (or modeled theoretically *sensu* Lotka-Volterra) to determine the level of control a predator population may have on the prey population and vice versa (Bulmer 1975). Scaling up, researchers evaluate whether numerous predator and prey subpopulations fluctuate synchronously or asynchronously and hypothesize why this occurs (Moran 1953; Bjørnstad and others 1999). Population and community ecologists developed a rich body of literature and theory that analyzes how asynchrony in population and community dynamics, in particular functional complementarity amongst species, may stabilize communities (Micheli and others 1999; Blüthgen and others 2016; Wilcox and others 2017). Ecologists have also described how (a)synchrony in growth among plant species within a community controls key ecosystem processes, such as net primary production through time (Micheli and others 1999). The diversity of examples of (a)synchrony in ecology reflects its broad conceptual appeal to ecologists seeking to describe how patterns in the timing of biotic and abiotic processes impact stability, productivity, and interactions in ecosystems.

Beyond ecology, the concept (but not necessarily the terminology) of (a)synchrony is pervasive and important in the related ecosystem science fields of hydrology and biogeochemistry. In biogeochemistry, the “hot spot hot moment” concept posited that the convergence of reactants in space and time would give rise to the heterogeneity in reaction rates across a landscape that is key to understanding ecosystem function at scale (McClain and others 2003). Within the hydrologic literature, many studies have explored how the synchronous interaction of multiple ecosystem processes give rise to key hydrologic processes. For example, studies have identified the synchrony of antecedent soil moisture with rainfall as a crucial driver of streamflow generation (Detty and McGuire 2010). Yet, when compared to the ecological examples, the biogeochemical and hydrologic literature has generally used definitions of (a)synchrony that are less consistent among studies and often described the concept using other terms (e.g., “decoupled”, “cyclical”, “interacting”, “in phase”, “lagged behavior”). While these terms are intuitive and well-defined in the context of individual studies, subtle differences in application complicate our ability to generalize findings.

We suggest that diverse terminology for identifying (a)synchrony has limited the potential for broader synthesis both among and within fields. While clearly defined within some subdisciplines of ecology, what is missing is a common classification framework for identifying and differentiating aspects of (a)synchrony that draws on and synthesizes similar concepts and ideas from numerous fields. Such a framework would allow scientists to use similar, precise definitions and methodological approaches across related disciplines such as ecology, hydrology, geomorphology, and biogeochemistry. Particularly within the context of climate change and human landscape modification, a synthesized approach for understanding and describing how the (a)synchrony of ecosystem processes will respond to changing environments will be paramount to predicting and managing ecosystems.

Defining (a)synchrony

Before classifying types of (a)synchrony, we propose that a synthetic definition of what synchrony and asynchrony are (and are not) is needed to unify their diverse use among ecosystem sciences. In defining (a)synchrony, it is essential to first define the spatial and temporal scale (grain and extent) and the processes of interest. The focal temporal scale can have a profound influence on conclusions made about the processes under scrutiny. For example, two processes may appear to be unrelated at the daily time scale, but be highly correlated at the annual time scale (e.g., daily vs. annual patterns in streamflow across a large river basin). Defining the spatial scale of inquiry, or extent, is similarly important. The dynamics of a process may appear to be uncorrelated at finer spatial scales, but show stronger patterns at broader scales (or vice versa; e.g., local air temperature patterns vs. latitudinal gradients in temperature). Thus, similar to the concept of resilience, it is necessary to specify “[*(a)synchrony*] of what [*with*] what?” (Carpenter and others 2001) by identifying the processes among which we will study (a)synchrony. We define “synchrony” as *one or more ecosystem processes within a designated system that have high spatiotemporal coherence or consistent lagged behavior over the time scale of interest*. In contrast, *one or more processes are considered “asynchronous” when they exhibit low spatiotemporal coherence within a designated system, and where the relative timing of interactions is not structured or consistent*.

We offer two important clarifications to this general definition. First, we propose that ecosystem *processes* (*sensu* Box 1; e.g., disturbance regimes, circadian rhythms, annual phenology), but not individual *events* (e.g., individual fires, single rainfall events, leaf-out date(s) for an individual year), can exhibit synchrony or asynchrony. While individual events may be coincident with other events or fluctuations in an ecosystem process, without repeated observations it is challenging to assess synchrony because these single phenomena lack context and information about the mechanisms driving their fluctuations. Second, a key aspect of this definition is that processes with a consistent lag between their peaks (i.e., periodic processes that are out-of-phase) are considered synchronous. This contrasts with many studies that characterize out-of-phase relationships as asynchrony, which may obscure shared drivers or lagged interactions (Feng and others 2019; Van Meter and others 2019). We think it is critical to identify out-of-phase processes as synchronous if they are responding to the same shared driver or trigger. This language allows us to describe situations where despite the fact that two processes respond in different directions or with

a lag relative to each other, they are not independent and are correlated in a predictable manner. In fact, processes that are out-of-phase may be strongly correlated from a statistical standpoint, but may have negative correlation coefficients. To reflect the relationship between these types of processes, we define them as synchronous, but crucially provide additional modifiers to describe lagged or out-of-phase dynamics.

Our classification framework creates a common language to categorize types of (a)synchronous relationships between ecosystem processes and identify the drivers of changes in (a)synchrony. This classification framework is needed for several reasons. First, conflating different types of (a)synchrony may hinder our understanding of the processes that control them and prevent accurate comparisons across ecosystems. Second, quantifying different types of (a)synchronous processes may require different approaches, tools, and metrics. Categorization can provide guidance for selecting the best methodological approach. And third, this explicit categorization of relationships and identification of drivers provides a point of reference from which predictions can be made for how current processes and the relationships among them may respond to environmental change. With these definitions and this context in mind, the goals of this synthesis are three-fold:

1. Discuss and characterize current uses of the concept of (a)synchrony across hydrology, biogeochemistry, geomorphology, and ecology.
2. Provide an integrative classification framework for identifying and characterizing (a)synchrony of ecosystem processes.
3. Apply our classification framework to published studies to highlight how differentiating types/mechanisms of (a)synchrony facilitates comparison and synthesis among studies and across fields.

Current insights & motivation for classification framework

To provide insight into how the concept of (a)synchrony is currently being used and discussed across the hydrologic, biogeochemical, and ecological literature, we searched for publications that discussed (a)synchrony in ecosystem processes. Although an exhaustive review was precluded by a lack of consistent terminology across disciplines, we sampled the literature using a broad variety of terms including: “asynchrony”, “synchrony”, “phase mismatch”, “temporal mismatch”, “coupled processes” and “decoupled processes” in combination with the three discipline areas (hydrology, biogeochemistry, ecology). For each study that we examined as part of this exploration (n=63, Table S1), we evaluated a set of common metrics to understand how the concept of (a)synchrony was used in that particular study. This included identifying: the focal process of the study and whether they were biotic (e.g., plant growth) or abiotic (e.g., dissolved inorganic nitrogen export); the key drivers of (a)synchrony and whether they were biotic (e.g., life history traits) or abiotic (e.g., temperature); whether the focal processes were (a)synchronous (per the authors’ definition); whether a change in the (a)synchrony between processes was described; and the causes of changing (a)synchrony, if relevant and known. This exercise helped shape our understanding of how these concepts were used within and across disciplines, and allowed us to identify

what different aspects of (a)synchrony were important and thus needed to be included in a classification framework.

The subdisciplines of population and community ecology are especially rich with examples of (a)synchronous processes, including organismal phenology and life history mismatch (Thackeray and others 2010), the Moran effect (Moran 1953, Hansen and others 2020) habitat connectivity (LeCraw and others 2014), and metapopulation/metacommunity stability (Wilcox and others 2017), among others. Furthermore, reviews and theoretical evaluations (e.g., Micheli and others 1999) of these processes have defined specific classes and/or types of synchronous processes that arise as a function of differences in aggregate and compositional variability due to community and population dynamics. Many of these studies have focused on the relationship between spatial or temporal (a)synchrony in population dynamics and community stability. However, despite the frequent use of (a)synchrony, there remained differences among studies in how (a)synchrony was defined and/or quantified, particularly with respect to the spatial and temporal dimension of (a)synchrony. For example, the term (a)synchrony was used to refer to both the temporal dynamics of changing phenology (e.g., “trophic level asynchrony”, Thackeray and others 2010) and the spatial relationships in regional population dynamics (“regional synchronization”, LeCraw and others 2014). A precise classification of (a)synchrony would enable comparisons of drivers of relationships among processes and studies, especially for meta-analysis projects or comparative works.

The terminology and treatment of the concept of (a)synchrony is less consistent in biogeochemistry and hydrology than in ecology. Broadly, we observed that studies tended to invoke the concept of synchrony to describe the relationship between two processes with similar temporal patterns and trends (Diawara and others 2016; Huryn and others 2014), or dissimilar patterns/trends, in the case of asynchrony (Kaye and others 2003; Lajtha and Jones 2013). However, beyond this, there were few rigorous definitions of (a)synchrony or detailed descriptions of the attributes of (a)synchronous relationships. More often than not, we found the term (a)synchrony used *post-hoc* in a descriptive rather than quantitative manner. For example, many studies used the term (a)synchronous to describe their results without specifying *a priori* a definition of (a)synchrony or quantifying the magnitude of fluctuations in (a)synchronous processes or the degree of (a)synchrony, which limits the ability for comparisons of (a)synchronous processes across ecosystems or watersheds.

We found numerous analytical approaches for quantifying (a)synchrony across the ecological, hydrologic, and biogeochemical literature, which we discuss in more detail below (“Analytical tools for quantifying (a)synchrony”). The diversity in methods for quantifying (a)synchrony within and across disciplines, as well as the lack of strong quantitative tests, highlights the opportunity both for improved definition and classification of (a)synchrony among ecosystem processes as well as identification and application of appropriate analytical approaches. We will discuss more quantitative methods that enable hypothesis testing relative to our proposed classification framework below.

(A)synchrony Classification Framework

Here, we propose a framework that classifies (a)synchrony among ecosystem processes according to five key aspects: 1) the focal ecosystem processes or interactions, 2) the spatial and temporal domain of interest, 3) the consistency in the relationships over time, 4) the structural attributes of ecosystem processes, and 5) the degree of causality among focal processes. In the following sections, we present a series of questions that guide researchers through these five aspects.

1. (A)synchrony focus: what is the focus of the research question?

First, researchers should explicitly identify the *focus* of the research, specifically whether the focus is on understanding the *drivers* or *triggers* of events or the *outcomes* of interacting processes (Box 1, Figure 1). As shown in Figure 1, two ecosystem processes (A and B) can co-occur in space and their fluctuations interact temporally to produce a third ecosystem process that is the outcome of their interactions. For example, ecosystem processes A and B could represent soil moisture and microbial respiration, respectively, and the outcome of their interaction is CO₂ flux, which is strongly influenced by soil physicochemical conditions like temperature and moisture (Curiel Yuste and others 2007). In order to describe the synchronous dynamics at work here, first we must be clear about whether our focus is how ecosystem processes A and B are *triggered* (i.e., what elicits fluctuations in ecosystem processes A and B? Do they have common or different drivers? Does ecosystem process A trigger a response in ecosystem process B?), or if the ultimate focus is describing the *outcome* of their interactions (i.e., what new ecosystem process arises as the result of interactions between other ecosystem processes?). Clearly articulating the focus of the research is relevant for how we describe the patterns of (a)synchrony in subsequent questions.

2. (A)synchrony domain: are the main comparisons of ecosystem processes among locations in space or fluctuations in time?

Second, researchers identify the spatiotemporal *domain* appropriate to the research question, specifically whether the question is primarily focused on comparing a single ecosystem process among numerous locations in space (pattern synchrony; Figure 2) or on fluctuations and interactions of multiple ecosystem processes through time within a given spatial context (process synchrony; Figure 2).

For example, pattern synchrony can be used to describe the relative timing of variations in chlorophyll concentrations among lakes within a region in response to regional climatic forcing (*sensu* Baines and others 2000) or the synchrony in leaf-out dates across a climatic region (Zohner and others 2017), where the primary focus is on how aquatic or terrestrial productivity at multiple locations responds simultaneously to a single climatic forcing or trigger (Figure 2a). This is a fundamentally different focus than process synchrony, which describes the fluctuations and interactions among multiple ecosystem processes over time (Figure 2b). For example, process synchrony could be applied to the temporal fluctuations and potential interactions of predator and prey populations in response to seasonal food availability (Krebs and others 2001). We note that while these examples highlighting pattern

versus process synchrony differ in scale, the concept and definitions themselves are scale independent and can be applied from local to global scales. As such, it is essential to define the spatial and temporal grain or resolution of the processes of interest to identify the frequency and spatial detail of data needed to determine (a)synchrony between processes.

We also highlight that the distinction between pattern and process synchrony is not purely about spatial vs. temporal relationships. All ecosystem processes have both a spatial and temporal grain and extent, and teleconnections can mean that processes occurring in distinct places can share drivers. However, differentiating between pattern and process synchrony can help highlight whether the *primary focus of the study* is on a single process across space or multiple processes over time, and can be useful in helping identify shared drivers and responses across studies and identifying potential quantitative methods.

3. Degree of synchrony: how consistent is the relationship between ecosystem processes?

The next aspect of the classification framework describes the *degree* of synchrony, or how consistent the relationship among ecosystem processes is over time (Figure 3). Some ecosystem processes may exhibit a high degree of synchrony, where the structural attributes and relationships among processes are very consistent through time (Figure 3a). Examples of ecosystem processes with high degrees of synchrony include annual solar radiation and air temperature (Ahas and others 2005), sub-daily fluctuations in soil temperature and soil CO₂ concentrations (Jones and Mulholland 1998), and diel patterns in streamwater temperature, bacterial activity, and stream water dissolved organic carbon concentrations (Kaplan and Bott 1989). In contrast, some ecosystem processes may exhibit a lower degree of synchrony, where the temporal relationship between two ecosystem processes is less consistent or regular (Figure 3b). Temporally irregular processes, like precipitation, can exhibit synchrony with other processes, provided the relationship between them is coherent over the temporal scale of interest. An example of this case is the synchrony between precipitation and in-lake ecosystem respiration rates. Zwart and others (2017) found that when large storms occurred, ecosystem respiration rates increased due to elevated availability of terrestrial dissolved organic carbon, particularly in lakes with short hydrologic residence times. However, elevated ecosystem respiration rates did not necessarily follow smaller, less intense rainstorms. Because of this, we may characterize the relationship between these two ecosystem processes (precipitation and ecosystem respiration) as having a low degree of synchrony. While some individual storms are coincident with elevated rates of ecosystem respiration, precipitation as a process does not consistently co-occur with high respiration. Researchers focused on synchrony could redefine the focal process to be precipitation above a relevant threshold, in which case there may be a high degree of synchrony between this stochastic process and ecosystem respiration.

4. (A)synchrony structure: what are the structural attributes of the focal ecosystem processes?

This aspect of the classification framework describes the *structural* attributes of the focal ecosystem processes. We have identified three key structural attributes of (a)synchronous

processes that should be differentiated and described: 1) the characteristic lag, 2) the magnitude of fluctuations, and 3) the additive outcomes of the focal ecosystem processes.

The characteristic lag describes the relative alignment of events/peaks of more than one ecosystem process in time, and characterizes either the phase relationship of periodic processes or the repeated lags in non-periodic processes through time (Figure 4a). For example, this can consist of characterizing two ecosystem processes as in-phase with one another or out-of-phase with a quantifiable lag between peaks for some period of time (e.g., the out-of-phase behavior between aquatic dissolved oxygen concentrations and diel nitrate patterns; Heffernan and Cohen 2010; Figure 4a), or for non-periodic variables quantifying the characteristic lag between process fluctuations. Importantly, we highlight that out-of-phase ecosystem processes are considered synchronous within this framework, in part because they may have shared drivers but different response times. Classifying two out-of-phase processes as asynchronous misses the opportunity to more fully understand and quantify the relationship between these two processes. In the case of diel dissolved oxygen and nitrate concentrations, these two ecosystem processes share a driver, thus characterizing them as asynchronous would limit our understanding of how gross primary production and nitrate uptake are related. Identifying these out-of-phase ecosystem processes as synchronous enhances our ability to understand shared drivers or predict how they may change in response to anthropogenic change.

The second structural attribute to characterize is the magnitude of fluctuations in two ecosystem processes relative to each other. Do we observe fluctuations of a similar relative size in both ecosystem processes A and B in response to their shared or individual drivers, or is one ecosystem process more sensitive with a larger relative response?

The third attribute to characterize, if relevant, is whether the *outcome(s)* of focal ecosystem processes are constructive or destructive (Figure 4b). To illustrate these three attributes, we use the example of annual diatom biomass (process B in Figure 4b) and zooplankton biomass (process A in Figure 4b) in a lake (*sensu* Winder and Schindler 2004). These two processes are nearly in-phase with each other, but have a consistent, characteristic lag where zooplankton biomass lags behind diatom biomass, and the annual fluctuations in diatom biomass and zooplankton density are similar or nearly equal in magnitude. Finally, when combined, diatom and zooplankton biomass contribute to the total organic carbon stock in the ecosystem, and the effect of these two ecosystem processes (diatom and zooplankton biomass) on the total organic carbon stock is constructive (Figure 4b).

5. Nature of synchronous relationships: are ecosystem processes related in a correlated or causal manner?

Last, the classification framework identifies whether the *relationship* between the focal processes is correlative or causal. This differentiates between scenarios in which the processes are driving each other (causal) vs. co-occurring and/or initiated by a shared trigger or driver (correlated). Revisiting the example of diatom and zooplankton abundance, we characterize the relationship between these two ecosystem processes as causal - zooplankton abundance is driven, in part, by the availability of diatoms as a food source (Winder and Schindler 2004). In contrast, we would characterize the relationship between zooplankton

biomass and dissolved silica concentrations as correlated, because ultimately these patterns are controlled by a third ecosystem process (diatom growth and production).

Flexibility in application of the framework

While essential for studies of ecosystem (a)synchrony, the first two components of the framework are broadly applicable for studies across environmental science. It is beneficial for all researchers to clearly identify the focal processes, as well as the grain and extent of data needed, for a given study. However, we emphasize that not all of the components of the framework may be relevant for a given study. For example, identifying the additive direction (constructive/destructive) of two processes is only relevant if they can be summed or multiplied in a meaningful way and if the outcome of their interaction is focal to the research. Magnitude may not apply to the characterization of binary processes such as the frequency of freeze-thaw cycles. We further note that questions regarding characterization of structural attributes and the nature of synchrony relationships may have either continuous or categorical answers depending on the research focus, approach, and data availability. In some applications, the descriptions of structural attributes and relationships are of less interest than their changes in response to shifting environmental drivers.

This framework helps to disambiguate the responses of environmental processes to global change by distinguishing among commonly conflated types of (a)synchrony (e.g., differences or shifts in phase vs. asynchrony). In addition, the framework can harmonize future research of ecosystem (a)synchrony while promoting comparison and common vocabulary across sub-disciplines of ecology and environmental science.

Analytical tools for quantifying (a)synchrony

Methodological approaches for quantifying (a)synchrony between one or more ecosystem processes are largely dependent on the question of interest, the timescale of variability in the ecosystem process relative to the resolution and length of the available data set, and the continuity of the time series data. We have summarized a few central analytical approaches in Table 1, and indicated how these quantitative methods can be used to characterize various aspects of this (a)synchrony framework.

In our assessment of (a)synchrony studies, two common approaches were used across the pattern and process domain to quantify synchronous ecosystem processes. Several studies used the coefficient of variation or cross-correlation coefficients to assess the similarity of time series of a single ecosystem process across multiple spatial locations (Abbott and others 2018) or between two or more time series through time (Blüthgen and others 2016; Zwart and others 2017). This approach parallels the use of the variance ratio in population and community ecology, which compares the variance of an aggregate community to the variances of individual species population as a metric of the temporal synchronicity in population dynamics (Gonzalez and Loreau 2009). One promising extension of the variance ratio is the development of a timescale-specific variance ratio, which assesses the variance ratio over distinct timescales to identify how synchrony of ecosystem processes may change depending on the focal timescale of interest (Zhao et al. 2020).

Another common approach was to use generalized linear models (GLMs), including analysis of variance (ANOVA) and ordinary linear regressions, to quantify the strength of the relationship between two processes or to quantify changes in the *degree* of synchrony over time (Hua and others 2016; Van Meter and others 2019). These approaches can be useful with data of lower temporal resolution if a quantifiable definition of synchrony is determined *a priori* (e.g., Arismendi and others 2013; Zhang and others 2019), and the variation in the ecosystem process occurs on a sufficiently longer timescale than the data interval. While “high frequency” time series that capture variability in ecosystem processes over the timescales of minutes to hours are becoming more common in environmental sciences, data of this frequency are not necessary to capture the variability in all types of processes. Capturing variation in most animal and plant populations and communities, for example, requires only monthly or annual observations whereas hydrologic and biogeochemical studies may require data on the timescale of hours to days. Ultimately these approaches require sufficiently frequent observations and long enough time series to capture variation in the ecosystem process of interest as determined for each individual study.

There are some statistical considerations that may limit the applicability of these simple approaches for quantifying pattern and process (a)synchrony. Temporal autocorrelation in time series data can violate the assumption inherent to many classic statistical tests that observations are independent (i.e., no autocorrelation among the residuals of the model). Therefore, explicitly addressing autocorrelation (e.g., including an autocorrelation function in a model) is particularly important when considering mixed-effects models as a statistical approach to evaluate process (a)synchrony in high-frequency time series data. Trends in individual time series might also bias evaluations of synchrony if ecosystem processes become more correlated through time, not due to increasing synchrony or a common driver, but because of underlying trends caused by unrelated/different drivers. This consideration is particularly important when testing for correlated ecosystem processes. While not always necessary, detrending approaches such as differencing methods (Holmes and others 2020), windowed approaches (Zimmer and others 2019), or time series decomposition (Lambert and others 2013) can be helpful when looking at shorter focal timescales or when there is not evidence for a shared driver that may be driving trends.

Non-parametric methods were commonly used to evaluate (a)synchrony in data that were not normally distributed (Arismendi and others 2013; Feng and others 2019; Leach and others 2019). One approach to quantifying changes in process (a)synchrony over time, and identifying potential *drivers* of these changes, is combining analysis of long-term trends with correlation of interannual variability metrics among processes (Leach and others 2019). Non-parametric approaches can also be used to quantify key *structural* attributes of synchronous ecosystem processes. Specifically, use of information theory-based metrics, which quantify the relative entropy of variables or mutual information shared among variables (i.e., the asynchrony index based on the Jensen-Shannon divergence (Endres and Schindelin 2003) in Feng and others 2019), when combined with comparisons of probability distributions can be used to quantify the key *structural attributes* of synchronous ecosystem processes, including characteristic lags and the magnitude of fluctuations, as well as the *degree* of synchrony between multiple ecosystem processes (Feng and others 2019).

Additional methods for assessing (a)synchrony are available with high frequency data or long-term data. A cross-correlation function (CCF) approach can be used to evaluate the characteristic lag distance between periods of correlation among time series (Paradis and others 2000). Fourier transforms can be used to gain more understanding about the frequencies of the patterns and drivers while quantifying characteristic lag times (Pandey and others 1998). While Fourier transforms characterize the general frequency of time series data, they do not characterize variation in the frequency characteristics over time. Thus, any episodic events or variations are poorly resolved with this method. Wavelet coherence analysis is a comprehensive method for assessing how processes and their drivers are related to each other over time, allowing for the quantification of the *degree* of synchrony, patterns and scales of importance, and characteristic time lags (Carey and others 2013; Wallace and others 2019). Given adequate data frequency and extent, wavelet analysis is able to resolve temporal variations at any desired frequency, allowing users to resolve patterns or variations from individual events to annual or longer time periods.

Statistical advances in time series analysis provide an exciting opportunity to use data-driven causal discovery to investigate whether observations of (a)synchrony among processes are causal or correlated (Detto and others 2012; Sugihara and others 2012; Goodwell and Kumar 2017; Runge and others 2019a). Methods such as the partial correlation momentary conditional independence are at the forefront of estimating linear and nonlinear, time-delayed dependencies. These methods also address challenges related to high dimensionality and strong interdependencies (Runge and others 2019b). The proliferation of high-frequency time series data from environmental sensors has opened a frontier in ecosystem (a)synchrony research in ecosystem and earth sciences to move beyond descriptive analyses and harness the power of data-driven models.

Outside of time series analysis and statistical modeling, numerical models and experiments can be useful tools for exploring pattern and process (a)synchrony, understanding *triggers* of (a)synchronous processes, or predicting changes in the *degree* of synchrony in response to changing environmental drivers. Numerical models often serve as prediction tools or experimental frameworks to determine how changes in processes or driving forces affect the (a)synchrony of specific ecosystem processes (Ranta and others 1997; Nardin and Edmonds 2014). Nardin and Edmonds (2014) use a hydrodynamic numerical model to simulate differences in the relative timing of fluctuations in vegetation biomass and sediment delivery. With these models, they determine the *degree* of synchrony between focal processes that enhances their *outcome*, sedimentation. In addition to models, experimental manipulations are often used to simulate changes in (a)synchrony. In particular, many studies use warming or precipitation experiments to determine how these environmental drivers will affect ecosystem processes, such as plant phenology under future climate (Sherry and others 2007). Through the simulation of current and future conditions, models and experiments are useful tools to understand the mechanisms driving (a)synchrony and how the (a)synchrony of ecosystem processes may change in the future.

The quantitative approaches and methods highlighted in this section and Table 1 are a starting point for quantifying and characterizing ecosystem (a)synchrony, but are not an exhaustive summary. In fact, these methods are changing and evolving rapidly as

computational power expands and cross-disciplinary work accelerates, thus the potential for new methods to be used to quantify (a)synchronous dynamics is an exciting avenue for future research.

(A)synchrony case studies

As an interdisciplinary group of ecosystem scientists and hydrologists, we have found that the development of a framework and common, synthetic vocabulary for describing synchronous ecosystem processes has helped us better discuss them with our colleagues and recognize commonalities across studies. To demonstrate the utility and value of the classification framework, we applied it to existing studies in the biogeochemical, hydrologic, and geomorphic literature. While our author group's expertise, and the examples in the case studies below, focus on aquatic ecosystems, this framework is also broadly applicable to terrestrial systems. We welcome new application, testing, and strengthening of these ideas among ecosystems in an effort to more broadly characterize and understand (a)synchrony across earth and environmental sciences.

Biogeochemical case study: spatial and temporal patterns of streamwater chemistry

A central challenge in aquatic ecology and biogeochemistry is predicting the spatial and temporal patterns in streamwater chemistry and identifying what controls them. Across a landscape with multiple streams and sub-watersheds, both broad-scale drivers and local environmental conditions interact to produce (a)synchronous spatiotemporal patterns in solute concentrations among streams. While solute concentrations across headwater streams may vary by orders of magnitude and are challenging to predict at a given location, synchronous patterns can emerge when examining the timing of relative concentration change. Abbott and others (2018) describe an example of pattern synchrony in streamwater chemistry of networked tributaries, where fluctuations across network locations had very little characteristic lag (i.e., fluctuations were in-phase) and had a high degree of synchrony. They observed water chemistry fluctuations were of smaller relative magnitude in streams draining larger watersheds (or with more tributaries contributing to their flow) as compared to smaller streams. Using a metric of temporal variance in solute chemistry among sub-watersheds, they found decreasing temporal variance as a function of increasing watershed area; in larger watersheds, the synchrony of signals from sub-watersheds with varying solute concentrations over time dampened variability in signals relative to headwaters. By clearly identifying the key aspects of synchrony researched in this paper, we can identify the appropriate methods (temporal covariance) to understand landscape scale variability in synchronous streamwater chemistry.

(A)synchrony between stream discharge and solute concentrations also reveals differences in the dynamics of sources and transport among watersheds. For example, Van Meter and others (2019) described how watershed context affects the process synchrony of the correlative relationship between nitrate concentration and stream discharge. In this study, the authors used stream nitrate concentration and discharge data to determine whether seasonal discharge and nitrate concentration regimes were predominantly in- or out-of-phase with each other, and what watershed characteristics controlled this relationship. They found that

land use was the primary determinant of whether nitrate concentration and stream discharge are in- or out-of-phase. In forested and agricultural landscapes, they observed that nitrate concentration was generally in-phase with stream discharge (e.g., nitrate concentrations were high when stream discharge was high, with little to no lag between their peaks). With increasing urbanization (specifically percentage of urban land cover and population density), there was a greater tendency for out-of-phase behavior between the seasonal nitrate concentration and stream discharge (e.g., nitrate concentrations were high when stream discharge was low, with lags of several months between their peaks). Although the study refers to this out-of-phase behavior as “asynchronous,” based on our definitions of (a)synchrony, both the in- and out-of-phase dynamics described by Van Meter and others are examples of *synchrony* because they exhibit structured relationships with a consistent characteristic lag over time.

This work by Van Meter and others highlights an example of correlated ecosystem processes. The temporal fluctuations and phasing of the concentration regime and discharge were both driven by other watershed drivers (% agriculture land cover, tile drain density, % urban land cover, population density), rather than one directly controlling the other. Further, the authors used a flexible set of methods for quantifying in-phase process synchrony and how it changes as a result of watershed-scale changes like urbanization. This approach could be implemented broadly with other datasets to characterize (a)synchrony in two or more processes, and to determine how it is changing over time or space. Characterizing the key aspects of (a)synchrony allows us to more thoroughly understand the driver of synchronous dynamics, and facilitates better comparison across studies of land use change and anthropogenic alteration.

Hydrologic case study: (a)synchrony of precipitation and evapotranspiration in Mediterranean climates

While the balance between hydrologic inputs and outputs (e.g., precipitation, evapotranspiration, and streamflow) are the primary drivers of ecosystem water availability (Whittaker 1970), it is often strongly modified by the relative timing of these water balance components. Mediterranean climates, for example, are characterized by warm, dry summers (high evapotranspiration and low precipitation) and mild, wet winters (low evapotranspiration and high precipitation). This strong phase difference between precipitation and potential evapotranspiration rates makes these systems especially vulnerable to climate change-induced water deficits and shifting vegetation phenology (Diffenbaugh and Giorgi 2012). Feng and others (2019) describe the process synchrony between evapotranspiration and precipitation in Mediterranean climates and propose an index to identify where this synchrony is changing. This ‘asynchronicity index’ quantifies both the characteristic lag and the relative magnitudes of precipitation and potential evapotranspiration rates. Such an approach could be implemented broadly with other datasets to characterize the lag between two processes, and to determine the relationship between the relative magnitudes of their fluctuations. As above, we consider these lagged, out-of-phase dynamics between precipitation and evapotranspiration to be synchronous when the lag duration is consistent over time. This distinction is particularly relevant for this paper, as the authors assess how the synchrony of precipitation and evapotranspiration has

shifted in recent decades, thus altering the distribution of Mediterranean climates globally. By identifying the types of synchrony tested in this case study, other studies could leverage this approach more broadly.

Ecogeomorphic case study: flooding, vegetation phenology, and sedimentation

In an ecogeomorphic framework, vegetation and geomorphic processes interact to shape landforms (Corenbilt and Steiger 2007; Corenbilt and others 2011). These interactions are often influenced by plant characteristics, density, or life history traits (Schwarz and others 2018). The interaction between vegetation and sediment-mobilizing flood events is critical to maintaining intertidal landforms, such as freshwater and salt marshes. Nardin and Edmonds (2014) describe an example of process synchrony in which sedimentation in the Mississippi River delta is the outcome of interactions between two processes (vegetation phenology and sediment delivery) that have a low degree of synchrony. The magnitude of the outcome (delta sedimentation) depends on the characteristic lag between peak vegetation biomass and sediment delivery by high flows, in part because their outcome is destructive. When the peaks of sediment delivery and vegetation biomass are aligned, wetland sedimentation decreases due to vegetation blocking sediment delivery to the interior of the wetland. When there is some lag between the peaks (i.e., high sediment delivery at intermediate vegetation biomass), there is an optimum sedimentation rate on the marsh surface due to slowing of water and subsequent deposition (Nardin and Edmonds 2014; Nardin and others 2016). Therefore, the relative timing of storms or hurricanes and plant phenology control sediment deposition on the marsh surface and affect the persistence of the deltaic wetland.

Understanding these relationships is critical for delta and wetland persistence. The timing and frequency of sediment delivery is affected by both climate and land use drivers, including hurricanes and dams (Nardin and Edmonds 2014; Twilley and others 2016). With the future alterations to the timing and size of flood events in freshwater deltaic systems, we may see changes in the synchrony between sediment delivery and peak vegetation phenology. Models such as those used by Nardin and Edmonds (2014) can be particularly useful tools in exploring how changes in the synchrony of sediment delivery and vegetation phenology may affect the ability of coastal and deltaic wetlands to persist into the future. In detailing and classifying these complex relationships, we can better identify similar relationships across ecosystems or landforms.

Across these case studies, we identify several key benefits to utilizing the (a)synchrony classification framework. First, accurately classifying types and aspects of (a)synchrony allows for better description and comparison of (a)synchrony within and across studies. Across these case studies, we saw that characteristic lags (Van Meter and others 2019, Feng and others 2019, Nardin and Edmonds 2014) and degree of synchrony (Abbott et al. 2018, Nardin and Edmonds 2014) were both central concepts for describing interactions among ecosystem processes with consequences for water quality and variability in nutrient fluxes. Using a unified language across these studies thus provides the opportunity to compare drivers of (a)synchrony and identify similarities and differences in how disturbances like land use change (Van Meter et al. 2019) or climate change (Feng et al. 2019, Nardin and Edmonds 2014) may alter the (a)synchrony of ecosystem processes, and thus ecosystem

function and services, in the future. Further, identifying types of synchrony and using common language opens up opportunities for applying novel methodological approaches across disciplines, thus advancing quantitative approaches for characterizing ecosystem asynchrony and responses to environmental change.

Conclusions and Future Directions

A common classification framework for characterizing and describing (a)synchronous processes will be a useful tool across earth and environmental sciences. Our proposed framework provides language that distinguishes between different types and aspects of (a)synchronous relationships and identifies drivers of (a)synchrony, and by doing so allows for predictions of how they may respond to environmental change. We hope that in doing so, this framework avoids conflation between different types of (a)synchrony, provides a more comprehensive understanding of the drivers that control (a)synchronous processes, fosters accurate comparisons across ecosystems, and informs research on how (a)synchrony in biogeochemical and hydrologic processes may respond to future environmental change.

One objective for the framework presented here is to serve as a platform for discussion and development of future research directions. Environmental sciences include processes with cycles spanning a wide range of temporal scales (milliseconds to millennia). Historically, (a)synchrony research was more common in fields such as population ecology where cycles occur across longer time scales and are readily observed without technological advances. This previous bias could have been due to labor-intensive data collection limiting the frequency at which observations could be made, or because key cycles of interest within sub-disciplines like population and community ecology occur over longer time periods. The rapid adoption of high-frequency sensors in both terrestrial and aquatic sciences enables the creation of high frequency time series data that can characterize temporal trends in previously unattainable ways. High-frequency data presents an excellent opportunity to combine our framework with emerging computational tools to gain a new understanding of ecosystem functions and reframe many hydrologic and biogeochemical processes around (a)synchrony.

We have presented a flexible classification framework in which we provide definitions and a lexicon to describe and quantify a broad range of (a)synchronous process and pattern relationships in environmental systems. This will enable researchers interested in ecosystem (a)synchrony to more efficiently identify analogous studies and appropriate methods for their question of interest, and will serve as a mechanism to frame and contextualize their own work. Although our case studies focus on hydrologic, biogeochemical, and ecogeomorphic examples, this framework has broad application across ecosystem and earth sciences, including topics in terrestrial ecology such as plant phenology, pest outbreaks, and trophic mismatches. In designing future research, we envision using this classification framework to determine testable hypotheses about the types and attributes of (a)synchrony among ecosystem processes, and to design tests to discriminate among possible responses to ongoing global change.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Box 1:**Key terms**

- *Ecosystem process*: A temporal sequence of abiotic or biotic events occurring in a discrete spatial domain. Examples: precipitation, streamflow, gross primary production, secondary production/biomass accumulation, CO₂ flux.
- *Events*: Individual occurrences of a biotic or abiotic phenomena that, when aggregated, compose an ecosystem process. Examples: an storm (event) vs. a precipitation regime (ecosystem process).
- *Driver*: A force outside of the system of interest that influences the (a)synchrony of ecosystem processes. Examples: climate, human land use
- *Trigger*: A discrete event or change in an ecosystem process that causes subsequent changes in other processes. Triggers are often within the system of interest, but can be influenced by external drivers, such as climate.
- *Outcome*: an ecosystem process that emerges as a result of the interactions of other ecosystem processes.
- *Synchrony*: Condition when one or more ecosystem processes within a designated system have high spatial and/or temporal coherence or consistent lagged behavior.
- *Asynchrony*: Condition when ecosystem process(es) exhibit low spatial and/or temporal coherence, and where the relative timing of interactions is not structured or consistent.

Box 2:**Key aspects of (a)synchrony**

- *Focus* - what is the focus of the research question?
 - Drivers or triggers
 - Focal outcomes
- *Domain* - are comparisons being made among locations in space or time?
 - Pattern (space) vs. process (time) synchrony
- *Structure* - what are the structural attributes of the focal ecosystem processes?
 - Characteristic lag
 - Magnitude
 - Constructive vs. destructive interactions
- *Degree* - how consistent is the temporal or spatial relationship among variables?
 - High vs. low degree of synchrony
- *Relationship* - are variables driving each other or co-occurring?
 - Correlated vs. causal behavior

Manuscript Highlights:

- Environmental change has the potential to alter the synchrony and asynchrony of ecosystem processes.
- Despite cross-disciplinary appeal, synchrony and asynchrony are defined and quantified differently across fields.
- The classification framework presented here synthesizes and characterizes different attributes of synchrony and asynchrony in ecosystems.

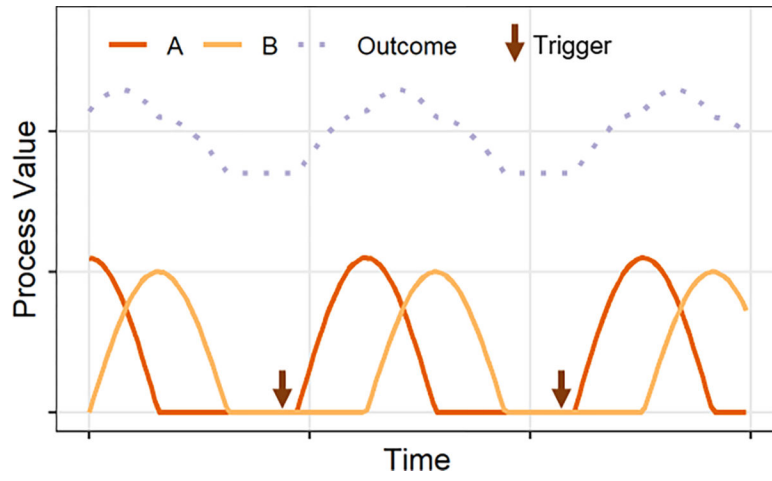


Figure 1. Ecosystem process A and B interact to produce a third ecosystem process that is the outcome of their interactions (shown in dotted purple).

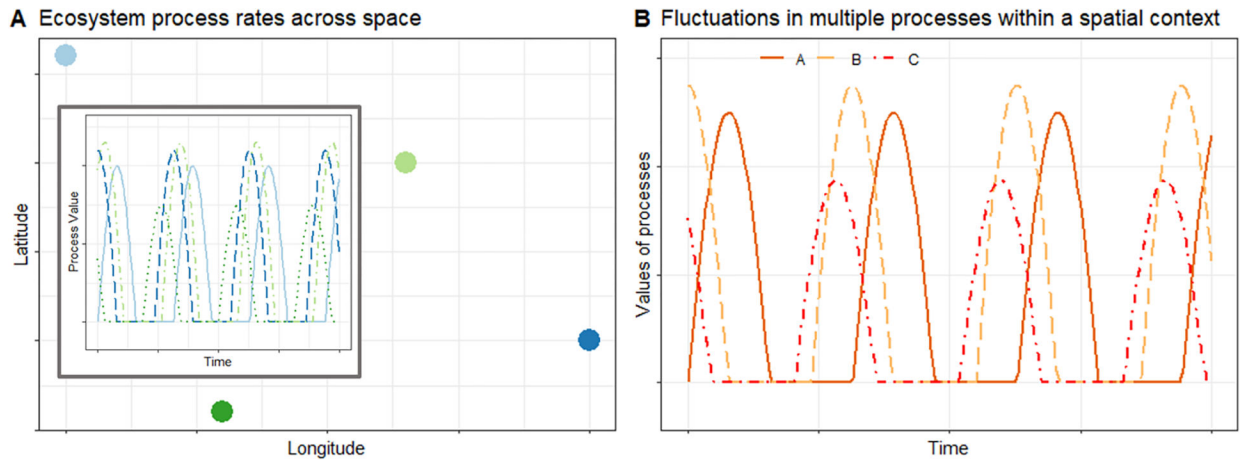


Figure 2.

(A) Four sites across a landscape exhibit pattern synchrony. Inset: process rates at each of those sites. (B) The timing and interaction of multiple ecosystem processes within a given spatial context exhibit process synchrony.

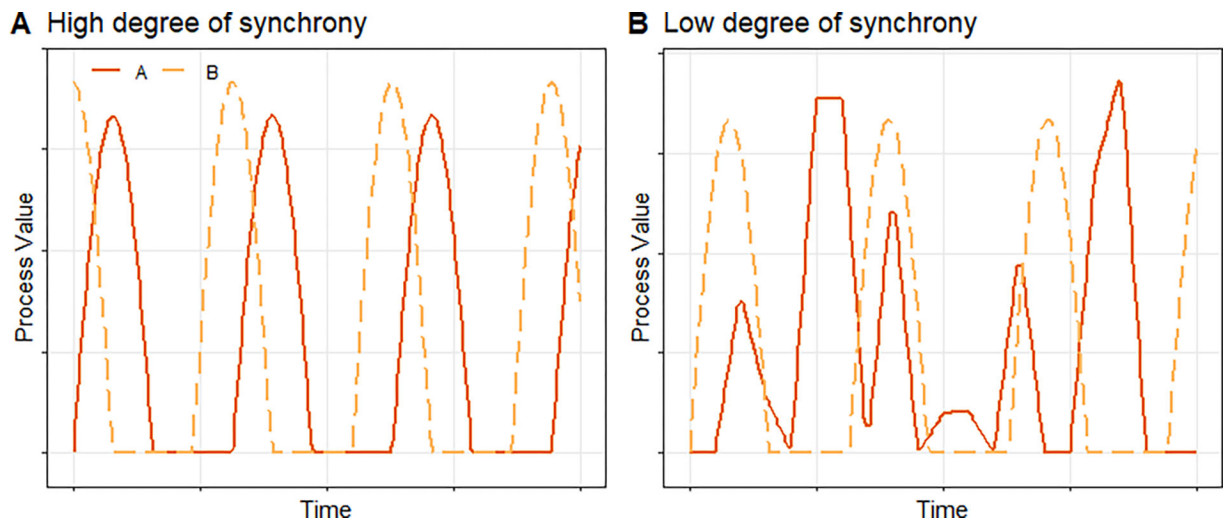


Figure 3.
The degree of synchrony can vary from (A) consistent/high to (B) irregular/low.

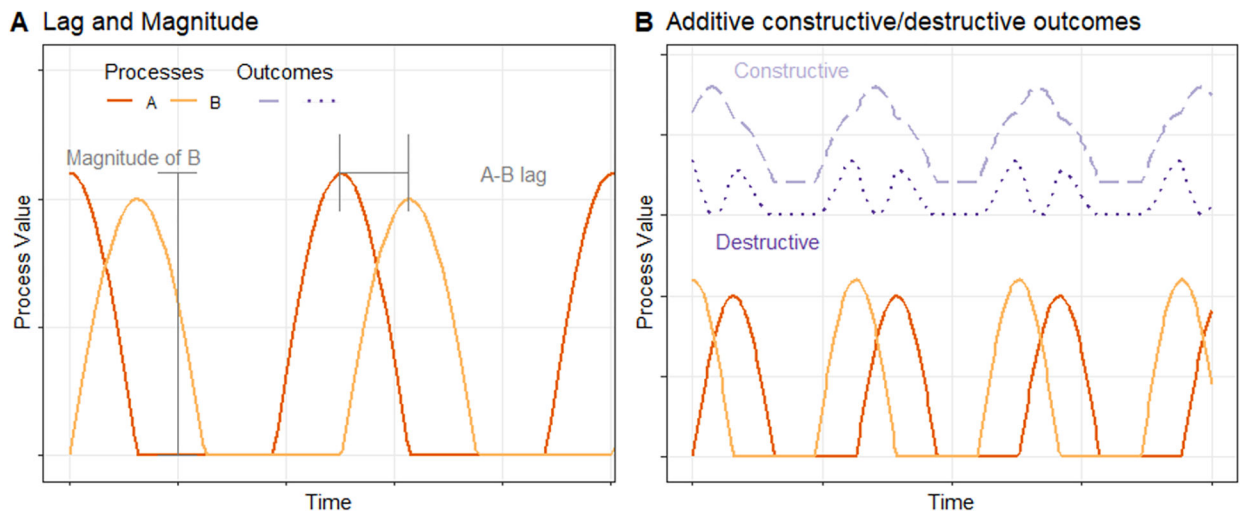


Figure 4. Structural descriptors to characterize ecosystem process time series relevant to (a) synchrony research include (A) the characteristic lag and the magnitude of process, and (B) type of additive outcome (constructive or destructive) between ecosystem processes.

Table 1.

Analytical tools to test components of (a)synchrony and example citations

What is the test assessing?	Analytical Tools	Citation
<i>Degree of (a)synchrony</i>	GLMs and LMMs	Hua and others 2016; Van Meter and others 2019
	ANOVA	Austin and Sala 2002
	Wavelet Analysis	Carey and others 2013; Wallace and others 2019
<i>Driver of (a)synchrony</i>	Correlation analysis	Leach and others 2019
	Experiments	Sherry and others 2007
<i>Structural attributes of synchronous processes</i>	Asynchrony index	Feng and other 2019
<i>Characteristic lags</i>	Cross-Correlation Functions	Paradis and others 2000
	Wavelet Analysis	Carey and others 2013; Wallace and others 2019
<i>Frequency of patterns and drivers</i>	Fourier transforms	Pandey and others 1998
<i>Interdependencies</i>	Causal inference frameworks	Runge and others 2019a, b
<i>Triggers of (a)synchronous extents</i>	Numerical Models	Ranta and others 1997
<i>Predicting changes in (a)synchrony in response to changing drivers</i>	Numerical Models	Nardin and Edmonds 2014