

# Time is of the essence: A general framework for uncovering temporal structures of communities

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## Funding information

National Science Foundation Graduate Research Fellowship Program, Grant/Award Number: 1842494

Editor: Adrian Craig Stier

## Abstract

Ecological communities are inherently dynamic: species constantly turn over within years, months, weeks or even days. These temporal shifts in community composition determine essential aspects of species interactions and how energy, nutrients, information, diseases and perturbations ‘flow’ through systems. Yet, our understanding of community structure has relied heavily on static analyses not designed to capture critical features of this dynamic temporal dimension of communities. Here, we propose a conceptual and methodological framework for quantifying and analysing this temporal dimension. Conceptually, we split the temporal structure into two definitive features, sequence and duration, and review how they are linked to key concepts in ecology. We then outline how we can capture these definitive features using perspectives and tools from temporal graph theory. We demonstrate how we can easily integrate ongoing research on phenology into this framework and highlight what new opportunities arise from this approach to answer fundamental questions in community ecology. As climate change reshuffles ecological communities worldwide, quantifying the temporal organization of communities is imperative to resolve the fundamental processes that shape natural ecosystems and predict how these systems may change in the future.

## KEYWORDS

biodiversity, community metrics, networks, phenological shifts, temporal ecology, time series

## THE TEMPORAL DIMENSION OF COMMUNITY STRUCTURE

Communities are organized across two fundamental dimensions: time and space. Research on spatial patterns has increased rapidly in the past decades and transformed how we think about natural communities by emphasizing the importance of spatial organization (structure) of species (Brown, 1995; Kareiva, 1994; Leibold & Chase, 2017; Tilman & Kareiva, 2018). In comparison, we still know surprisingly little about how communities are organized in time, which has only recently gained renewed attention as a line of research (Post, 2019; Wolkovich et al., 2014; Yang, 2020). The ongoing and projected impacts of climate change on ecological communities, as well as calls for their short- and long-term mitigation and adaptation plans (IPCC, 2023), create an urgency to develop frameworks explicitly focusing on the temporal dimension of community structure to fill this conceptual

gap (CaraDonna et al., 2021; Rudolf, 2019; Takimoto & Sato, 2020; Wolkovich et al., 2014; Yang, 2020; Yang & Rudolf, 2010).

Ecologists have long recognized that the temporal patterns and shifts in community composition are a hallmark of any natural community (Elton, 1927). Their importance manifests in several critical ecological concepts, like the temporal niche (Carothers & Jaksic, 1984; Jensen et al., 2019; Loreau, 1989a; Schoener, 1974), succession (Ha 1927; Connell & Slatyer, 1977; Poorter et al., 2023), the window of opportunity (Yang et al., 2008; Yang & Censer, 2020) and the seasonal timing of life history events (phenology; Cohen et al., 2018; Miller-Rushing et al., 2010; Parmesan & Yohe, 2003; Post, 2019; Roslin et al., 2021). Yet, despite the widespread appreciation of the dynamic nature of community structure, community ecology has traditionally taken a largely static approach. For instance, the structure of ecological networks is typically assumed to be fixed and time-invariant such

that only the abundance of species may change over time (CaraDonna et al., 2021; Ings et al., 2009; Montoya et al., 2006). When analysing empirical patterns, studies of community structure predominantly use a single data ‘snapshot’ in time or aggregate time points to calculate key biodiversity metrics, thereby potentially overlooking transient states and critical ecological processes present at the community level, such as seasonality (McMeans et al., 2015). Consequently, our current understanding of the temporal structure of natural communities remains limited concerning its variations across ecosystems, space and time and the factors that drive such variations. Yet, answering these and many related questions about the temporal structure of communities is fundamental to our ability to understand and predict the dynamics of natural communities and how they will respond to environmental change (CaraDonna et al., 2021; Rudolf, 2019; Wolkovich et al., 2014; Yang, 2020).

Given that ecologists have long appreciated the dynamic structure of communities, what has prevented us from answering these questions already? In large part, progress has been hampered by the lack of a unified conceptual and methodological framework for analysing the temporal patterns and the logistical challenges in obtaining the fine-scaled temporal data required, which can require a lot of resources or new technologies. To move towards filling these gaps, we propose a general framework to quantify and analyse temporal structure in natural communities. First, we define the concept of temporal community structure and discuss its potential role in both well-studied and understudied ecological concepts. We then briefly introduce temporal-ordered networks and suggest how and why these networks can theoretically capture the definitive features of temporal structure in natural communities by applying perspectives from temporal graph theory. We end by applying this framework to publicly available phenological data and highlight some promising research directions and outstanding questions that this approach helps address.

## What is the temporal structure of communities?

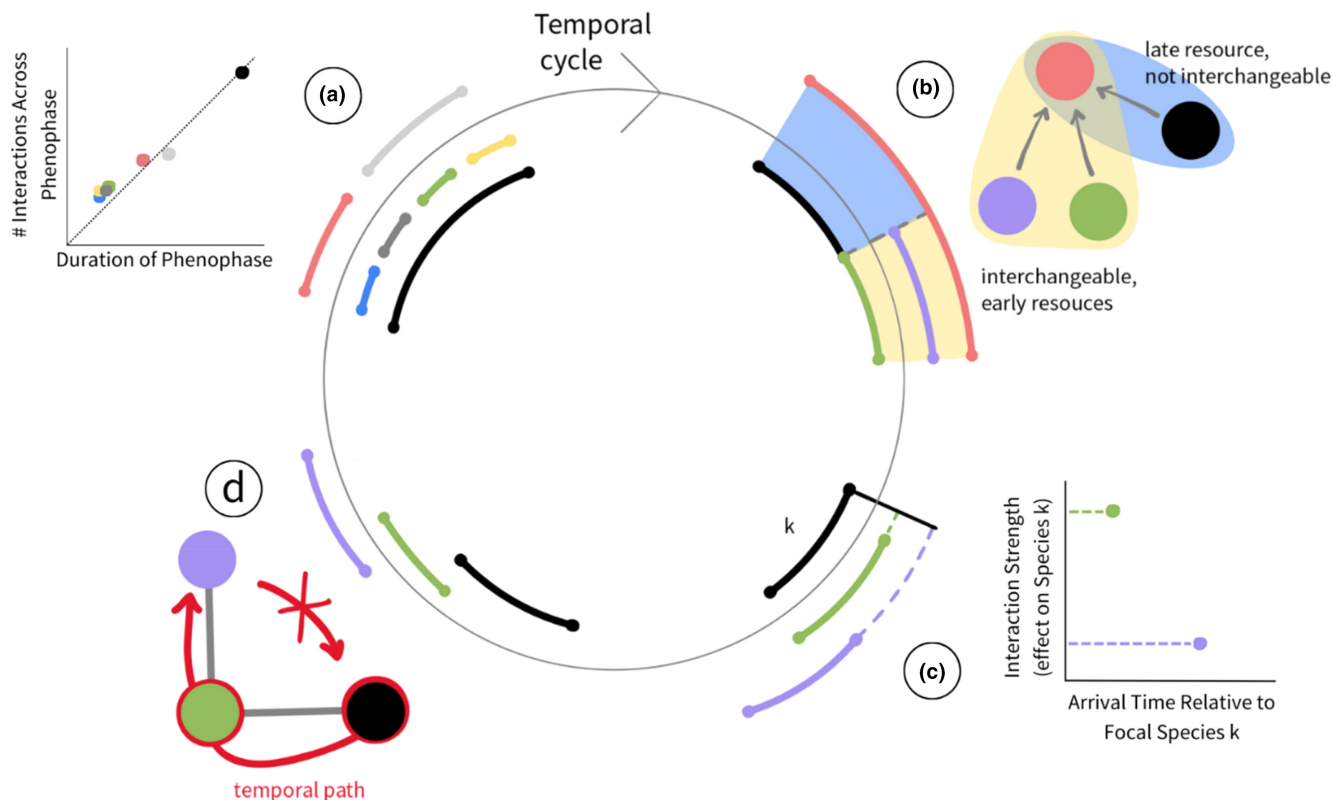
Just like ‘spatial structure’ generally denotes how species are organized in space, ‘temporal structure’ refers to the organization of species in time. However, unlike space, time is unidirectional: It always moves forward, never stops and we cannot go back. This directionality means that events and processes from the past can affect events and processes that happen in the future, but not the other way around. Temporal structure is thus fundamentally about the *sequence* (chronological order) and *duration* of and between events (Wolkovich et al., 2014). Take a piece of music, for example. Knowing all the notes played in a melody does not tell you how it sounds. What makes any melody unique is the sequence of notes (relative timing), how long each note is, and the pauses

between them. Similarly, knowing what species exist in a community (aggregated over time) does not reveal much about how the community looks at any given point in time or the ‘pace’ or ‘rhythm’ of key ecological processes and change. Instead, if we are to truly understand the ecological and evolutionary processes that shape the dynamics of natural communities and how communities will respond to environmental change, we need to study their temporal structure: We need to analyse the duration and sequence of when certain groups (e.g. species) are active and their intervening times (gaps).

## Why are the sequence and duration of events so important?

The critical aspects of temporal structure—sequence and duration of and between events—play essential roles in structuring species interactions and ecosystem processes. The sequence and duration of species’ phenophases determine which species co-occur and, thus, what interactions are possible. A predator cannot consume prey, and a bee cannot pollinate a flower if neither is present at the right stage at the right time(s). Understanding what interactions are possible through temporal co-occurrences can thus help predict and capture species interactions, even though co-occurrence does not necessarily imply a direct interaction between species (Blanchet et al., 2020; Thurman et al., 2019). For instance, the loss of temporal overlap of phenologies can explain the loss of plant–pollinator interactions over a century (Burkle et al., 2013). Similarly, species with longer phenophases tend to co-occur with more species and thus have more species interactions (Resasco et al., 2021; Figure 1a). However, in this case, interactions also typically occurred in sequence with only one or a few interactions at any given point in time. Thus, species that might have seemed like generalists were often ‘sequential specialists’ (Figure 1b). These examples highlight that the sequence and duration of species’ activities can help identify the possible interactions and reveal the forces that structured life histories and community composition.

The sequence of species arrival times and duration between arrivals can also determine the outcome and strength (i.e. per-capita effect) of species interactions (Rudolf, 2019; Zou & Rudolf, 2023; Figure 1c). For instance, reducing the overlap of flowering times can either increase or decrease the reproduction of plant species in a community via recruitment or competition for pollinators respectively (Faust & Iler, 2022; Mitchell et al., 2009). Early arrivers often have a competitive advantage over species that arrive later, and this advantage typically depends on the difference in relative arrival times (Alexander & Levine, 2019; Blackford et al., 2020; Rasmussen et al., 2014; Rudolf, 2018). Similarly, predation rates decline with



**FIGURE 1** Temporal structure, as defined by the sequence and duration of and between events, influences many aspects of species interactions. Our four examples (a–d) may happen simultaneously or in different orders and were arranged arbitrarily along a cyclical rather than linear timeline to emphasize that many natural events reoccur periodically. Line segments indicate the presence of a species for a temporal (e.g. annual) cycle. Colours represent different species. (a) How long species are present (length of phenophases) typically correlates positively with the number of interactions per species (e.g. the black species has more interaction than the green or the grey species). (b) Consumers who appear as generalists in static networks (coral) often feed on resources that occur during different periods (purple, green, black) and thus are not interchangeable. (c) The sequence of species' arrival times and duration between arrivals can determine the strength of species' interactions. (d) The order of phenologies determines what direct and indirect interactions are possible in a community: Early-arriving species (black) can affect later-arriving species, even after the early arrivers leave (e.g. via resource depletion, habitat modification or other community members), but not vice versa.

a delay in salamander and dragonfly predator arrival relative to its tadpole prey (Rudolf, 2022). Such timing effects (also called priority effects or historical contingencies) are well documented in animal, plant and microbial systems and determine the dynamics and composition of natural communities (Fukami, 2015; Zou & Rudolf, 2023).

Furthermore, the sequence and spacing in which species are arranged along a temporal axis also determine the causal chain of possible events (Blonder et al., 2012). In the absence of temporal overlap, species present earlier in a community can still affect those that appear later but not vice versa (Figure 1d). For instance, experiments in pond communities found that *Bufo* tadpoles that breed early in the season can negatively affect later arriving *Hyla* tadpoles, even though the two species never co-occurred in time (Wilbur & Alford, 1985). Such 'legacy effects' are common in natural communities and can arise through a range of different mechanisms (Fukami, 2015), for example, by altering the environment (Kostenko et al., 2012), consuming a competitor of a later arriving species, or by changing the community

composition that later arriving species experience (Rudolf & Van Allen, 2017). However, the potential to affect other community members naturally declines towards the end of a season; for example, species that arrive at the end of a season tend to have fewer interactions (i.e. are more specialized; Seifert et al., 2021). The species that arrive last can only affect a limited number of species with which they co-occur. The relative temporal position of species is, therefore, inherently linked to its potential impact on the community and how it can be affected by other community members.

At the community and ecosystem level, the duration and sequence of temporal co-occurrences limit the possible pathways through which diseases, energy, water, organic and inorganic elements and perturbations cascade through the ecosystem. Perturbations (e.g. fire, drought, heatwave, chemical spill or disease outbreak) that happen in the middle of a season can only affect species that are already present or arrive later in the season, while species that arrived and left before the perturbation will not be affected. Thus, explicitly accounting for the sequence and duration of events is imperative to capture

the mechanisms that drive community dynamics and composition, ecosystem processes and how they will respond to environmental change.

### What can we learn from the temporal structure of communities?

The presence of species along the temporal axis is not random but rather an emergent property that reflects its ecological and evolutionary responses to constantly changing environmental conditions and interactions. Therefore, the temporal positions of species can tell us a lot about the ecology of species and the processes that structure natural communities. For example, specific patterns of temporal spacing between species presences can suggest functional relationships of species, competition and coexistence mechanisms, or predict the invasion success of species (Table 1). Anomalies in temporal spacing may reveal when environmental conditions create windows of opportunities or constraints (Yang, 2020; Yang & Censer, 2020; Yang & Rudolf, 2010) and indicate facilitative interactions or co-dependence (Dante et al., 2013). As mentioned earlier, temporal co-occurrence indicates, at minimum, what interactions are possible and is, therefore, a crucial driver of the structure of ecological networks (CaraDonna et al., 2021; Morente-López et al., 2018; Yang et al., 2013). Temporal structure also helps us to predict the potential pathways and even speed of transmission of energy, infectious diseases, and perturbations (Blonder, 2015). These examples and studies highlight how temporal structure has contributed to our understanding of community processes.

Nevertheless, we still have significant gaps in our current understanding of temporal community structure. Ecology still lacks a general framework to predict what temporal structure should look like and how it is shaped by and interacts with various processes. For instance, how do changes in season length, productivity and biodiversity alter the duration and sequence of species presences and how species partition time? What patterns of the temporal structure of communities are typically robust and shared across most ecosystems and which tend to vary? We can start to answer these and many related questions by analysing and comparing temporal structure across taxa, systems, environments, space and timescales to help us identify and understand many biological processes that shape natural communities. However, because the past can shape the future, a mechanistic and comprehensive understanding of temporal patterns must account for the sequence of events to capture causality. Importantly, this exploration encourages the development of more well-rounded and nuanced frameworks for the roles both space and time play in communities and more testable and accurate predictions of how they will respond to environmental change (Wolkovich et al., 2014; Yang, 2020).

Finally, studying the temporal structure of communities also provides new quantitative approaches to detect phenological shifts (e.g. due to climate change) and put them in a community context. Current metrics typically do not capture concurrent changes in the temporal structure of entire communities. Yet, as we will explain in more detail below, quantifying changes in the temporal structure of communities can increase the power to detect phenological shifts and help us learn more about their ecological consequences.

## THE NEED FOR A GENERAL FRAMEWORK TO QUANTIFY TEMPORAL COMMUNITY STRUCTURE

Because various studies and related ecological concepts use the sequence and duration of (or between) events to understand community dynamics (Table 1), we believe in the merits of establishing a general quantitative framework designed to capture the critical features of temporal community structure. Current approaches to analysing the temporal structure of communities fall mainly into a few research areas: phenology, species turnover (including succession) and interaction networks. Each approach has strengths and limitations in capturing the complexity and essential features of the temporal structure of communities.

To date, phenology studies have predominantly focused on metrics for the onset (timing) or duration of phenological events at the single species level (CaraDonna et al., 2014; Cohen et al., 2018; Forchhammer et al., 1998), pairwise correlations of these events (Ovaskainen et al., 2013; Thackeray et al., 2016) and the temporal overlap of interacting pairs of species (CaraDonna et al., 2014; Carter et al., 2018; Renner & Zohner, 2018; Theobald et al., 2017; Visser & Both, 2005; Visser & Gienapp, 2019). While these and other studies have been fundamental in documenting the temporal coordination and variability of interactions over time, many aspects of the temporal community structure only emerge from the community context. For instance, the dynamic structure of communities could show periods of high activity separated by periods of inactivity. We can only identify such bursts of activity by analysing the distribution of ‘gaps’ between phenologies of all species. Furthermore, distributions of multiple species’ phenologies and gaps between them could characterize distinct temporal modules, for example, subsets of interacting species that always co-occur or a set of species in a module to consistently appear in the same chronological order. Of course, while co-occurrence does not necessarily mean the realization of their direct interactions, co-occurrence is a necessary condition. Such modules may thus help predict the presence/absence and strength of interactions,

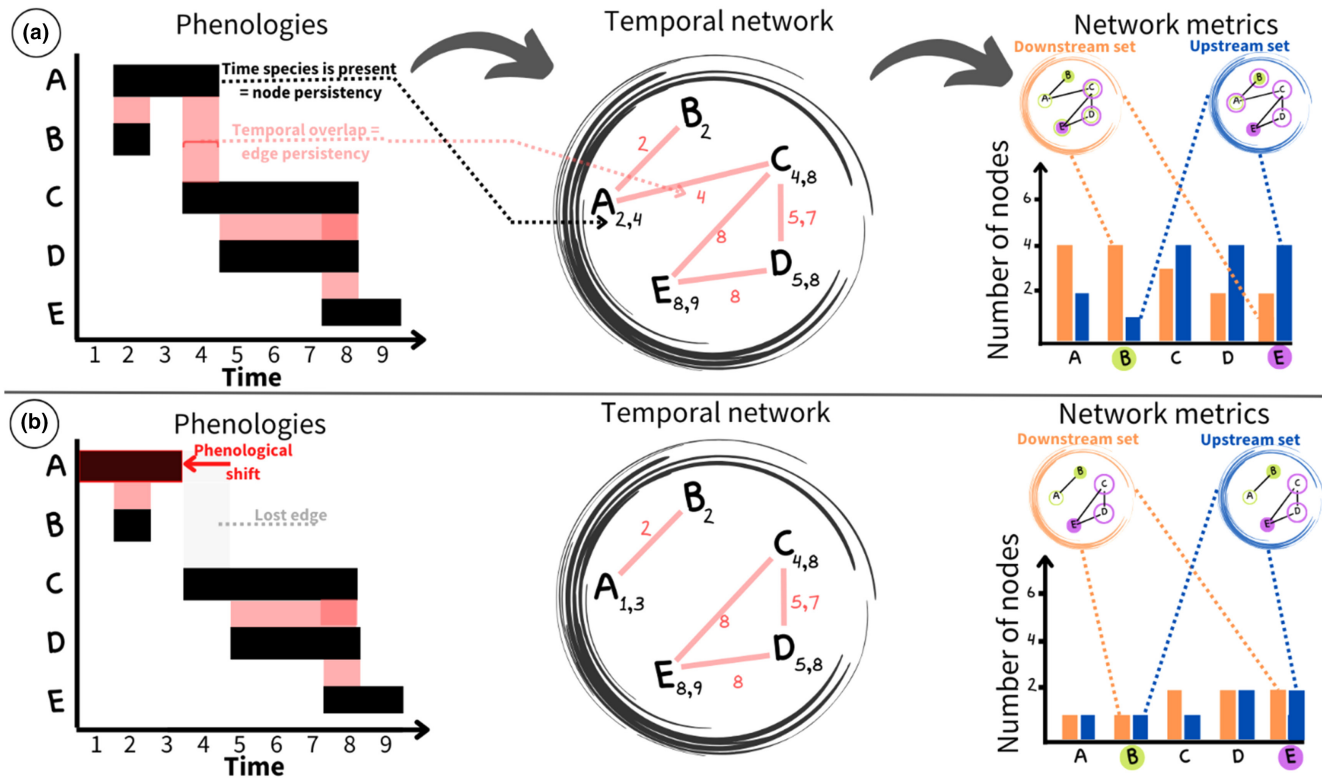
**TABLE 1** Examples of questions in community ecology linked to temporal patterns.

Ecological concept	Temporal pattern used to infer concepts	Example references
What are the potential mechanisms of community assembly?	Reduced temporal variation and non-random temporal patterns (over time, e.g. years or habitats) were used to infer the strength of stochastic versus deterministic processes, historical contingencies and priority effects	(Neale & Rudolf, 2023; Puschke et al., 2013; Van Allen et al., 2017)
	Slope of species time relationship (STR) can be used to infer processes that determine biodiversity, like dispersal/migration and extinction rates, succession and speciation, or to differentiate neutral from niche-based processes	(Adler, 2004; McKinney & Frederick, 1999; Rivett et al., 2021; Rosenzweig, 2010; White et al., 2006)
What are potential coexistence mechanisms?	The sequence of species' arrivals and the time between them determines the potential for coexistence (via correlated changes in fitness and niche differences)	(Alexander & Levine, 2019; Blackford et al., 2020; Godoy & Levine, 2014; Rudolf, 2019)
Do species compete for and partition time?	Lower temporal overlap than expected from a null model was used to infer temporal niche partitioning and competition	(Jensen et al., 2019; Koide et al., 2007; Loreau, 1989b; Schamp & Jensen, 2019)
	Altered phenologies after species removal suggested reduced competition, via temporal niche separation	(Dumandan et al., 2023)
What is the functional relationship between species?	Temporal covariances of occurrences helped infer species interactions	(Deutschmann et al., 2023; Steele et al., 2011; Ushio et al., 2018)
	Temporal clustering was used to infer facilitation/positive indirect interactions between species	(Dante et al., 2013)
	Phenological tracking can indicate strong inter-dependency of species (e.g. predator–prey, plant–pollinator)	(Visser & Gienapp, 2019)
	Competitive dominance depends on the relative time between and order of species arrivals	(Faust & Iler, 2022; Rudolf, 2018; Rudolf & McCrory, 2018)
What factors determine network structure?	Phenological timing determines predator–prey and host–parasitoid interactions and community structure	(Alford, 1989; Pardikes et al., 2022; Rudolf, 2022)
	Loss of temporal overlap results in loss of interactions	(Burkle et al., 2013)
	Phenological attributes determine network robustness and persistence of species	(Guzman et al., 2021; Ramos-Jiliberto et al., 2018)
What determines invasion success?	Phenology drives modularity	(Morente-López et al., 2018)
	Invasion success/growth rates dependent on the relative timing of arrival (e.g. phenology of germination or flowering)	(Godoy & Levine, 2014; Wolkovich & Cleland, 2011; Zettlemoyer et al., 2019)
How do traits determine specialization?	Species with narrow time windows (short presence) are more likely to specialize in temporary resources and certain environmental conditions (e.g. seasonal specialist vs. generalist)	(Humphries et al., 2017)
What determines transmissions of pathogens, nutrients and energy?	Temporal structure predicts the possible pathways and speed of transmission through a community (e.g. faster with higher average overlap, less time between arrival)	(Blonder et al., 2012)
How can we predict the effects of perturbations?	The effects of perturbations on species and communities depend on the specific timing of perturbation and temporal organization of species	(Craine et al., 2012; Crawley, 2004; Li & Pennings, 2017; Shepherd et al., 2012)
How can we identify windows of opportunity?	Temporal clustering and gaps in species presence can indicate favourable (and unfavourable) environmental conditions	(Martínez-Falcón et al., 2010)

symbiotic relationships, temporal guilds, temporal niche partitioning or identify temporal windows of opportunity and species that exploit similar resources or abiotic conditions (Table 1). Similarly, the ecological consequences of phenological shifts may only become fully apparent in a community context (e.g. when shifts create temporal partitioning, Figure 2). In short, the temporal features characteristic of species' phenologies may suggest important community dynamics, but

identifying these temporal features requires a holistic approach that moves beyond analyses of single species or pairwise metrics that we traditionally use in phenological studies.

On the other hand, studies on temporal succession focus on turnover in species composition (e.g. Connell & Slatyer, 1977; Dornelas et al., 2014; Penny et al., 2023; Poorter et al., 2023; Van Allen et al., 2017) and interactions (e.g. CaraDonna et al., 2021; Díaz-Castelazo



**FIGURE 2** Steps to build, analyse and compare time-ordered networks using phenology data. The start and end date of a phenophase quantifies when species are present and active in a community (black bars in left column). We can then calculate the species' temporal overlap/co-occurrence (red bars). From a network perspective, the length of the phenophase (black bar) and overlap (red bar) indicate the persistency of nodes and links, respectively. We use this phenology data to build time-ordered networks of communities (middle column), where nodes are species with corresponding timestamps that indicate when a species is present. Timestamps can be a single time point, a time interval with start and end date, or multiple points or intervals if species re-enter a community. The temporal co-occurrence of species gives links that connect nodes (species) with their corresponding timestamps (red bars). Once these time-ordered networks are constructed, we can calculate a range of time-ordered network metrics that explicitly account for the temporal sequence of events (see Table 2). For instance, we can find the 'downstream set' and 'upstream set' for each species (bar graphs on the right) to determine how species influence each other given the temporal sequence of species occurrences/phenologies (see Table 2 for complete definitions). Circular insets show a graphical example of how those two metrics are calculated for focal species B and E, with a solid circle indicating a focal species and an open circle indicating a corresponding (by colour) source or set of influence species. These metrics are sensitive to the relative temporal position of a species and the sequence of temporal overlap. They provide new insights into the basic temporal structure of communities and can also be used to gain a deeper understanding of the functional role of species. For instance, species that appear earlier often have a more extensive downstream set of nodes but a smaller upstream set than species that appear late (e.g. B vs. E in the top right panel). However, this can change when temporal gaps (no species present) are present, which create 'subsets' of networks (top vs. bottom bar graph). (a) versus (b) shows how a phenological shift in a single species can lead to dramatic changes in network structure and metrics, especially when this results in the loss of a link that connects temporally separated groups of species (e.g. a shift of species A in top scenario (a) vs scenario (b)), highlighting the utility of this approach for comparing temporal structure of communities across space and time and quantifying phenological shifts in a community context.

et al., 2010; Kantsa et al., 2018; Suzuki et al., 2023; Ushio et al., 2018) and thus prioritize a multi-species perspective to capture how communities change over time. These studies revealed that species compositions and interactions are highly dynamic and can rapidly turn over across years, seasons, weeks and even days, while some structural patterns at the network level (e.g. nestedness or connectivity) may change comparatively little (Bramon Mora et al., 2020; Kaartinen & Roslin, 2012; Petanidou et al., 2008; Schwarz et al., 2020). These studies also highlight how we can infer important ecological and evolutionary processes that drive community dynamics (e.g. the concept of 'succession' or 'community drift') from the temporal organization of species. However, they still mainly rely

on static metrics (either based on snapshots or time-aggregated data) that, at best, only contain indirect information on the sequence and duration of events. For instance, metrics for temporal turnover in species composition indicate that species come and go (e.g. Dornelas et al., 2014; Penny et al., 2023), but these metrics do not provide information on the duration and sequence of events, for example, how long species are present, which ones might return, how the current composition relates to previous events and if community states differed in how long they last. To use the music analogy again, temporal turnover, for example, helps quantify the tempo of a song but not the melody itself. Consequently, turnover can only capture a subset of patterns of the temporal structure itself. Of course, it

would be unrealistic to assume that any single metric can comprehensively describe the complex temporal organization of communities. Accomplishing this requires a comprehensive toolset: a set of temporally explicit metrics, with each metric specialized to capture a different aspect of the dynamic temporal organization of communities.

Thus, despite significant recent advances that helped develop a more temporally explicit view of community ecology, we still have much to learn from the temporal structure of communities. A general framework accounting for the pros and cons of existing approaches would bring together different research areas in community ecology for a more comprehensive understanding of temporal community structure. Especially in this age of unprecedented environmental change, doing so should help the field better understand communities and anticipate how they will respond.

## A GENERAL APPROACH TO STUDYING THE TEMPORAL STRUCTURE OF NATURAL COMMUNITIES: TIME-ORDERED CO-OCCURRENCE NETWORKS

Here, we propose that time-ordered co-occurrence networks provide a powerful unifying framework to study the temporal structure of natural communities. Over the past decades, spatial ecology has proven that we can learn a lot from studying the (co-) occurrence patterns of species (Araújo et al., 2011; Borthagaray et al., 2014; Freilich et al., 2018; Galiana et al., 2023; Gao et al., 2022). The proposed framework takes a similar comparative approach for analysing the temporal organization or species co-occurrences, except that it accounts for the directionality of time and keeps track of the possible causal chains of events.

### Time-ordered networks

Time-ordered networks (also called time-varying, temporal or dynamic networks) differ from traditional static networks because they are inherently dynamic and provide a complete record of the sequence and duration of events (Holme & Saramäki, 2012; Masuda & Lambiotte, 2020). In these networks, each node (vertex) and link (edge) is only active during specific time points (shown explicitly in Figure 2). The unidirectionality of time (time always moves forward) means that the relationships between nodes have to follow a 'time-respecting walk' of adjacent nodes and links. Importantly, these time-respecting walks have to follow the natural temporal sequence of events and thus lay out the possible causal chains contributing to community dynamics. For instance, if the path between nodes *A* to

*B* ends before the link between *A* to *C* becomes active (Figure 2 scenario (a)), then node *B* could potentially indirectly affect node *C* (via *A*), but nothing from *C* can propagate to *B*, since signals cannot travel back in time. Thus, analysing the structure of temporally ordered networks helps us to better visualize and quantify the organization of events in time.

The study of time-ordered networks is ongoing, but it is a rapidly growing interdisciplinary field (Holme & Saramäki, 2019; Masuda & Lambiotte, 2020). Time-ordered networks, in general, have been used to describe temporal patterns for a range of systems, from public transportation and neurons in the brain to social networks (Holme & Saramäki, 2019), but these networks have received surprisingly little attention in community ecology. Yet, as we will show below, they are ideally suited to study the temporal organization of natural communities, and recent advances and development of analytical tools not only help overcome the limitations of previous approaches discussed above but also provide unique opportunities for new temporally explicit analyses.

### Building time-ordered co-occurrence networks from phenology data

We will focus here on phenology data to demonstrate how we can apply this approach to quantify the temporal organization of species occurrences (but see 'Future directions' for how this can be applied to other types of data). We already have a rich body of phenology data for various animal and plant communities in marine, freshwater and terrestrial systems that are typically publicly available (e.g. USA National Phenology Network, Pan European Phenology project, Environmental Data Initiative). These data sets often have a fine temporal resolution and span decades, and they are rapidly growing with help from researchers, community-driven science initiatives and government-funded observation networks (e.g. NEON, GBIF). Even with the taxonomic resolution varying by group (e.g. most vertebrates are resolved at species levels while some invertebrate groups are often only resolved at the genus or family level), collecting this data is being increasingly facilitated by recent technological advances. For instance, deploying cameras and machine learning to identify flowers and even pollinators at very fine temporal scales (Besson et al., 2022) can significantly help reduce the workload needed to collect this type of data. Similarly, DNA approaches can quantify phenologies and even interactions at similar or even finer temporal scales than direct observation (e.g. metabarcoding of airborne pollen DNA, pollinator DNA in flowers or eDNA analysis in freshwater and marine systems; Besson et al., 2022; Jensen et al., 2022; Jönsson et al., 2023). Importantly, phenology data provide essential information about the temporal structure of

communities by documenting when species are present and active in a given community.

Building time-ordered networks from phenology data (phenology networks) is relatively intuitive and generally straightforward in practice (see [Figure 2](#) for a worked example). Following traditional approaches, we can build a network where a species represents a node, and its phenology determines the node's timestamps (interval). Depending on the system, a node may thus have a single timestamp (e.g. present/active for a single day), a time interval (e.g. present from day  $x$ - $y$ ) or multiple timestamps if there is a temporal gap (pause) between activity periods (e.g. multiple distinct breeding events in a year). Links show relationships between nodes to represent when two species are active simultaneously in a given community. The timestamps for links would be similar to those of nodes (e.g. single or multiple timestamps), except that they represent the duration of the temporal overlap. In time-ordered networks, these links are sometimes called 'contacts' to emphasize a time-limited information exchange ([Holme, 2015](#)). Constructed in this way, these phenology networks capture co-occurrences and, thus, the complete temporal structure of communities.

Of course, if additional information on species interactions is available, it is straightforward to incorporate them into the network representation. Namely, we can restrict the topology of these co-occurrence networks further to focus only on direct interactions. Note that this would shift the focus from analysing temporal co-occurrence patterns of species to analysing temporal patterns of direct interactions. Furthermore, species or individuals could be grouped in other ways, for example, by taxonomic group, traits, functional roles or life stages. The taxonomic grouping may be necessary to standardize the data and facilitate interpretation when data are not fully resolved at the species level. Lastly, a particularly intriguing approach is to use this time-ordered network approach to track transitions in community states, with nodes representing community states and timestamped links signalling transitions between these states (see [Box 1](#) and [Figure 3](#) for an example). This approach is particularly promising in more complex systems and can help identify cycles, critical transitions in community states, and which species drive them. In general, the overall time-ordered network approach is very flexible, and the type of structure used to define nodes and links ultimately depends on the specific questions of interest and available information.

## Quantifying time-ordered networks to understand natural communities

Converting species' phenologies into time-ordered networks opens the door to calculating a range of informative metrics that could provide new and more profound insights into species' biology, their

temporal relationships and the organization of natural communities. Some of these metrics for time-ordered networks are unique to temporal analyses, while others build on static network metrics to account for the unidirectionality of time. Here, we highlight and discuss a subset of previously developed time-ordered network metrics ([Table 2](#)) that we believe are among the most conceptually straightforward and biologically meaningful for analysing phenology network data. Existing software can already calculate most of these metrics (e.g. *tsna* package ([Bender-deMoll & Morris, 2021](#)), *timeordered* ([Blonder, 2015](#)) and *networkDynamic* ([Butts et al., 2023](#)) in R, and *Straph* in Python). Several metrics like burstiness and memory have applications beyond network analysis and do not necessarily rely on network-specific software. Altogether, these metrics for phenological data capture important network properties such as connectivity, transmissibility and persistence and the sequence and duration of events, the key features of temporal structure.

To better understand these metrics' biological meaning and utility, it helps to think about what information they capture. Metrics like 'upstream set' and 'downstream set' ([Table 2](#); also called 'backward reachable set' and 'forward reachable set') quantify how species are connected in time to other community members that appear either before or after them in time. For instance, we can compare the *downstream set* across species to identify which species have the highest potential to influence other members within a given community or how infections might spread (see [Figure 2](#) for worked-out example). Note that these metrics depend on the community context and temporal position of species in the community; species that appear earlier will always have smaller upstream sets since few species appear before them (e.g. upstream set for species B vs. species D in [Figure 2](#), panel a), and if there are temporal gaps in overlap, these sets will be interrupted and thus smaller (e.g. upstream set for species E, panel a vs. b).

Connectivity also depends on transmissibility—how easily and fast a signal or substance can travel across a community. In static networks, we typically measure this with the 'shortest path', that is, the smallest number of nodes we must traverse to connect one node to another. In time-ordered networks, this is sometimes called 'flow' ([Blonder et al., 2012](#)), but distances between nodes can be measured in two ways in time-ordered networks: the number of nodes that need to be traversed (*distance*) or the actual time required to travel from one node to another (*latency*). Comparing these metrics across species gives us a better idea of species' relative temporal position in a given community. They could also help identify the potential for indirect effects between species ([Figure 1](#)), differences in the sensitivity of communities to environmental perturbations (e.g. how fast perturbations or infectious diseases could spread in communities and how many species may be affected), or at what point in time

### BOX 1 Applying the temporal framework: temporal patterns of anuran calling community versus plant fruiting community

To highlight some of the utility of our framework, we show an example of how we can use it to compare the temporal structure of communities using publicly available data sets on two very different systems: one on anuran calling in Texas (Carter et al., 2018) and the other on fruiting phenology in Thoreau's Concord (Ellwood et al., 2022; Figure 3). Due to the complexity of the communities and to highlight the flexibility of our approach, we focused here on changes in community states. The approach to building time-ordered networks is still the same (see Figure 2), except that here, nodes represent a unique combination of co-occurring species (community state), and links (relationships between nodes) show the transition between the different community states. These links have timestamps for when transitions occur, while nodes have time intervals for the duration of community states.

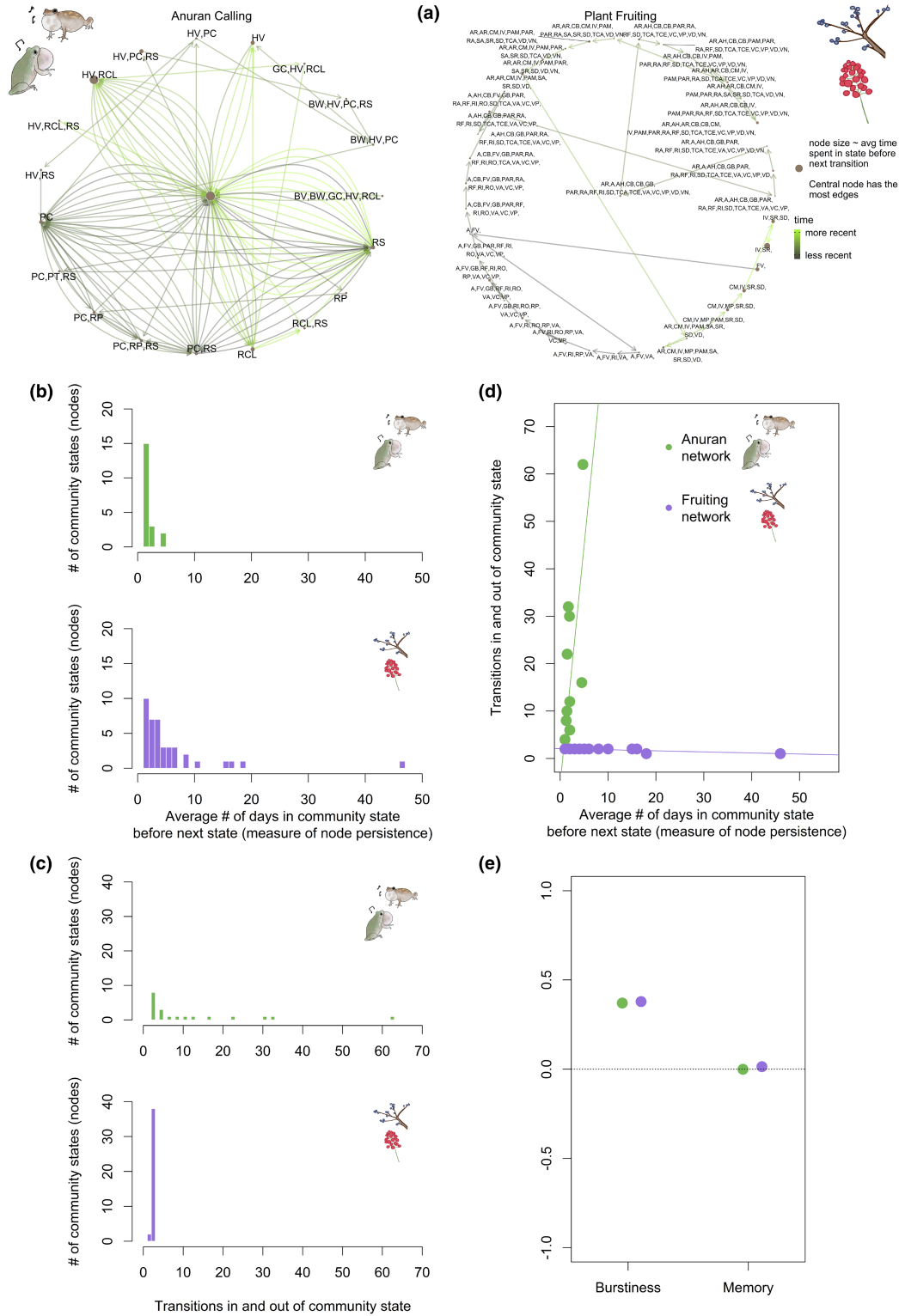
We can immediately see striking differences in the temporal structure of both networks (Figure 3a). The anuran-calling time-ordered network shows many recurring community states but with considerable variation in how long each state lasts and how often it reappears (green histograms in Figure 3b,c, respectively). This pattern arises because most species have more than a single time interval during which they are active and can vary in the length of their phenophases (i.e. few species with long vs. many with short phenophases). Together, this creates a complex and highly dynamic network with many possible causal chains and where species with long phenophases (which form the long tail in the histogram in Figure 3b) act as 'hubs' connecting different community states. In contrast, the fruiting network suggests a sequential turnover of community states because species typically only fruit during a single period. Consequently, there is a much more explicit temporal hierarchy with a simpler causal structure (who comes first and could influence later arrivers). Each community state typically occurs only once (note that because in and out transitions count each separately, this pattern is indicated by the step peak at 2 in Figure 3b). In both networks, most states (nodes) do not last long before transitioning to another state, but a minority of states in the plant fruiting network last much longer and form a right-skewed distribution. When plotting the distributions of how long each community state lasts on average (node persistence) and recurring community states in the same plot (Figure 3d), we see the networks follow very different relationships reflective of differences in time-ordered network structure (i.e. strongly positive relationship in frog network vs. weak to no relationship in plant network). Yet, despite these differences, both communities show similar temporal distribution of events at the community level, that is, a moderate signal of temporal clustering of community shifts (burstiness in Figure 3e) and no clear autocorrelation in times between community shifts (memory in Figure 3e). This moderate clustering suggests some periods when multiple species tend to enter/leave in quick succession (e.g. due to windows of opportunities or species belonging to similar functional guilds). These examples illustrate just some of the various analyses that can be performed with our approach to comprehend better the common and unique temporal structures and functions of natural communities.

communities are most vulnerable to perturbations. For instance, in communities with long average *distances*, perturbations will take a much longer time to reach all species and will have to go through a long temporal sequence of species which could dampen the effect of perturbation over time. Similarly, indirect interactions are less likely between community members that are separated by long distances. Note that these connectance metrics depend on the sequence and duration of and between events. Thus, they can give important insights into the functional role of species and their relationships in time (Table 2).

Other metrics, such as *burstiness*, *memory*, *node* and *link* persistency (Table 2), focus on the duration of or between events to quantify the permanence/transience of time-ordered network structures, including temporal turnover of interactions. A high level of burstiness indicates temporal 'clustering' (i.e. species tend to appear

in groups during certain periods) and can help identify windows of opportunity (e.g. favourable environmental conditions, resource pulses) or temporal guilds. In contrast, a low level of *burstiness* indicates that the appearances (or presences) of species are more evenly spaced out over time and could indicate temporal niche partitioning (Table 1). Species with higher link persistency encounter more species over time and thus could indicate their interaction potential (Castro-Arellano et al., 2010; Resasco et al., 2021), while node persistency could help identify different life history strategies among species (e.g. seasonal specialists with short-node persistency vs. generalists with long persistency).

We want to emphasize that time-ordered networks have not been widely applied to phenological data, so there is much room to grow and develop new metrics and tools. The metrics presented here are just a starting



point, and we hope that they inspire the development of complementary approaches for analysing temporal communities. For instance, how can time-ordered networks incorporate count data from phenological data sets as weights to better predict ecological consequences

of co-occurrences? How can we implement sequence in metrics of overlap or account for differences in proportional overlap? Developing these and other metrics is a promising new research area that will grow as we learn about temporal structure.

**FIGURE 3** Changes in community structure over a 1-year time window in two different communities. (a) Transition networks, where nodes represent unique community states (species combinations, with each list of two-letter codes for a different species combination or an underscore for all species absent). The node's size indicates its average duration (scaled to the respective community) and is scaled on a power function to improve visualization. Directed edges or links (arrows) indicate transitions between states. Note that we could have shown the same networks in a more condensed form by having a list of timestamps per arrow (like in Figure 2). This would reduce the number of arrows drawn repeatedly between the same two community states, but we decided against this to visually emphasize the difference between the networks. The colours of links indicate the relative order of transitions (light green = near the end of the calendar year, dark brown = near the start of the calendar year). The anuran network (left) is based on daily calling data throughout an annual breeding season at one pond in Texas, USA, in the early 2000s (Carter et al., 2018), while the plant fruiting network (right) comes from Massachusetts, USA with single first and last date estimates based on observations made during 1850–1860 (Ellwood et al., 2022). Frequency plots show the distribution of (b) the duration (node persistence) of community states and (c) the number of transitions in and out of a given community state in the respective network (note that incoming and outgoing links count as two separate transitions), and (d) indicates how both metrics are correlated with each other within a network. (e) Two metrics that quantify different aspects of the temporal distribution of events at the community level for each network: burstiness and memory (see Table 2 for metric details).

## Practical considerations

The size of any time-ordered network scales with the length of the period analysed. Results of several temporally explicit metrics can differ based on the length of time over which network structures get quantified. This difference is particularly important for metrics that rely on time-respecting path lengths since they typically correlate positively with the period length (e.g. upstream and downstream set, distance, betweenness centrality in Table 2). Therefore, as best practice, any analyses of temporal community structure should have a clearly defined time window  $t$ . Fortunately, when analysing phenology data, the calendar year or seasonal constraints (e.g. start and end of snow cover) often set the temporal window. However, these boundaries are sometimes blurred for some systems, for example, when individuals or life stages stay active all year round. In this case, researchers must identify other biologically meaningful time windows (e.g. does the system show a cyclical pattern reflecting the timing of El Nino Southern Oscillation events?) or stick with widely used time windows like the calendar year. In both cases, researchers must clearly communicate the time windows used in their analyses and standardize network metrics by the length of time windows when comparing time-ordered networks with variable time windows.

Visual representation of time-ordered networks can become cumbersome when exceeding a certain complexity. However, for metrics or network visualizations like those in Figure 3, we can adapt existing core, open-source software packages developed for static networks (R packages: ggraph, igraph, network; Python packages: NetworkX). Given the increasing popularity of time-ordered networks and the development of new comprehensive guides (Masuda & Lambiotte, 2020), we anticipate that more user-friendly options that work more directly with time-ordered networks will emerge over the next decade.

Finally, we must consider potential data limitations and caveats to help decide when this approach will be most helpful. Like all network approaches, it becomes

more powerful when more nodes (species) are included. Similarly, very short or sparse time series may not contain enough information to reveal specific temporal patterns. Some metrics, like memory, require a minimum number of time points (Table 2). While phenology data are becoming increasingly available, the data recorded varies across studies, which determines the types of possible analyses. For instance, phenology data sets may only have start dates once per species per year (e.g. first flowering, first emergence). Without a biological notion of start and end times, a time-ordered network reduces to a temporal path or chronological sequence of events. This limits the amount of information we can extract from the temporal pattern. However, we can still extract some helpful information on temporal structure that can help put phenological shifts in a community context (see Figures S1, S2) for an example of an empirical application using a data set on the leafout of woody plants.

## APPLICATIONS AND FUTURE DIRECTIONS

The acceleration of climate change has created a need for a more temporally explicit approach to ecology in the Anthropocene to understand and predict how these changes will affect natural ecosystems (Wolkovich et al., 2014; Yang, 2020; Yang & Rudolf, 2010). To predict how systems will change, we first need to understand the temporal structure of communities and the mechanisms that drive this structure. To date, progress in answering these questions has been hampered by a lack of a unified framework and limited available methods.

Our framework aims explicitly to overcome some of these limitations by offering comprehensive quantitative approaches that could scale across communities. With multiple metrics in hand, researchers can visually and quantitatively assess and compare the temporal structures of communities across timescales, space and ecosystems (see Box 1 and Figure 3 for a worked example) and help identify the underlying mechanisms. We have already mentioned some applications above but would like to highlight some additional exciting new research

**TABLE 2** Metrics to quantify different aspects of the temporal structure of natural communities.

Temporal structure	Metric	Definition of metric	Biological interpretation(s) and potential applications
Sequence of events	Time-respecting traversal/path	Indicates sequences of links (edges) that can be traversed in a time-ordered network under the constraint that the following link to be traversed is activated at some point in time after the current one.	This concept is a foundation for many time-ordered network metrics and establishes a potential <i>causal relationship</i> . It assures that the connection between nodes (e.g. species) and time-ordered network metrics account for the temporal sequence/order of events and their durations. It reflects that time always moves forward.
	Downstream set	The collection of all nodes that can be reached from a node $i$ via time-respecting paths.	Indicates <i>which and how many species could be influenced by a focal species</i> . This includes species (nodes) that do not have direct temporal overlap with the focal species. The distribution of downstream sets across all species identifies species that play a central role in connecting the network or could exert a disproportionate influence on others (see <a href="#">Figure 2</a> for a worked-out example)
	Upstream set	Number of nodes that can reach a given node $i$ via temporal paths	Indicates <i>which and how many species could affect a focal species</i> . Like a stream where water flows downhill and not uphill, nodes in the downstream set cannot affect nodes in the upstream set, due to the unidirectionality of time. Note that since this definition relies on temporal paths, the upstream set strings together a series of co-occurrences with no temporal gaps between co-occurrences from back in time up to the specified present time. The resulting downside is that the upstream set will not count species creating gaps in time between co-occurrences, even though the species and co-occurrences happened before the focal species. (see <a href="#">Figure 2</a> for a worked-out example) Combined with the downstream set, the upstream set helps determine how well-connected a species is. This information could be used to infer the temporal position of species relative to other community members or how likely it is to be influenced by events that happen before it even appears.
	Distance	The smallest number of nodes between node $x$ and $y$ following time respective traversal	Indicates <i>how many indirect contacts are needed to reach another species</i> . It provides new insights into the <i>functional roles of species (or other groups) in a community</i> by resolving relationships between species in a temporal context. The <i>average distance</i> at the community level tells us <i>how spread out a network is</i> (related to temporal overlap but goes beyond pairwise overlap) and <i>how easily perturbations, energy or infections spread between members in a community</i> .
	Time-dependent-betweenness centrality	Measures the fraction of shortest paths that go through a node	Measures how well connected a species is to others. More specifically, this metric quantifies how much a species is a temporal ‘bottleneck’ versus a mediator in connecting species from the past to species in the future. ‘Shortest paths’ connecting these species here refer to paths connecting the least number of species (nodes) to reach species of interest following their chronological sequence (or in other words via their time-respecting paths). This meaning of ‘shortest path’ differs from the one for latency specified later in this table.
Duration of events	Node persistency	Period a node is present	Indicates <i>how long species are present/active</i> . It is likely to be correlated with connectivity metrics. (see <a href="#">Figure 3</a> for a worked-out example)
	Edge persistency	Period a link is present	Measures <i>how long species co-occur</i> , which indicates their <i>interaction potential</i> . Applies only to networks where edges can represent durations (e.g. networks in <a href="#">Figure 2</a> )

TABLE 2 (Continued)

Temporal structure	Metric	Definition of metric	Biological interpretation(s) and potential applications
Duration between events	Latency	The shortest time interval between node $x$ and $y$ following time respective traversal	Time-specific equivalent to distance. Essentially tells us <i>how fast a signal (like energy, perturbation or infection) could travel between two species, including species without temporal overlap</i> . The average latency tells us <i>how long</i> (e.g. number of days) <i>it takes on average for a signal to travel between species in the community</i> . Unlike distance, this metric just depends on the total absolute time and thus temporal spacing between species.
	Time-dependent centrality—closeness	The inverse of average latency	Measures how quickly a node reaches all others Temporal metric of the centrality of a node, that is, <i>how close in time is a node connected to all other nodes in a network</i> .
	Burstiness	Temporal distribution of consecutive inter-event times over a given time	Measures <i>how evenly events</i> (e.g. <i>contact or overlap</i> ) <i>are spread out over time</i> . Requires at least three time points. A time-ordered network with a high degree of <i>burstiness</i> indicates temporal clustering of events, for example, when phenologies are highly synchronized across species. Emphasizes events themselves (see <a href="#">Figure 3</a> for a worked-out example)
	Memory	Correlation between consecutive inter-event times	Determines whether short (long) inter-event intervals are usually followed by short (long) inter-event intervals. A measure of ‘predictability’ of gaps. Requires at least four time points (see <a href="#">Figure 3</a> for a worked-out example)

*Note:* For consistency, the meaning and applications column assumes the structure is a time-ordered species co-occurrence (e.g. phenology) network. Although definitions vary among studies, these are all previously developed metrics and can be calculated with current software packages (see main text for details). Here, we largely follow the notations from Holme and Saramäki (2019).

avenues and applications ([Box 2](#)). Of course, these areas serve as starting points and do not represent a complete list of potential applications.

## Functional roles and relationships among species

One novel aspect that emerges from this framework is that it can provide new ways to quantify and compare species' ‘temporal niche’ and functional roles by putting them in a temporally explicit community context. This analysis can reveal previously hidden functional differences between species within and across communities. For example, species that co-occur with the same number of species but differ in how long they are present in the community, when they are present, or how their interactions are distributed over time could show different responses to species extinctions and other environmental perturbations. To better understand species' roles at the community level, we can perform robustness and sensitivity analyses (e.g. randomly removing species or species at risk of extinction; Dunne & Williams, 2009; Rudolf & Lafferty, 2011) on these time-ordered networks to identify keystone species (e.g. those that result in most significant changes in time-ordered network metrics) or those species and ecosystems at greatest risk (i.e. species that experience the largest or more frequent changes in node-specific network metrics). These findings could complement existing knowledge to help guide management and conservation efforts in a rapidly changing world.

## General patterns and environmental drivers of temporal community structure

Since temporal structure is non-random and reflects a community's ecological and evolutionary processes, we can expect to learn much from studying temporal patterns. For instance, perhaps weak burstiness and memory of fruiting plant communities ([Figure 3e](#)) could arise from plant species starting but not ending their fruiting phenophases in the same month. Such a pattern suggests a potential shared underlying driver that might be linked to changes in environmental conditions or species' life histories. However, weak burstiness could also arise from a temporal niche partitioning, for example, to avoid competition for frugivores. These examples highlight how our framework can help identify new patterns and potential mechanisms and guide future research directions.

When we applied our approach to compare two very different communities (anuran calling vs. a plant fruiting community), we found striking differences in the temporal network structure and some surprising similarities. These differences suggest corresponding patterns in the mechanisms regulating the temporal assembly of communities (see [Box 1](#) and [Figure 3](#) for a complete example). This comparison highlights the power of having a set of metrics at hand to detect generalities and essential differences in the temporal structure across communities and environments that do not necessarily share the same abiotic drivers. At the same time, our worked examples also highlight significant gaps in our current

**BOX 2** Some of the many outstanding questions (in no particular order) can be addressed with the framework proposed here (see ‘Applications and Future Directions’ for worked examples)

- What are the general, non-random features of temporal community structure that are shared across most ecosystems?
- How do environmental conditions and patterns in human land use influence different aspects of the temporal structure of communities?
- How do ecological and evolutionary processes shape the temporal structure of communities?
- What effects do seasonal constraints (like the length of the growing season) have on the temporal structure of communities?
- How does the temporal structure of communities change across time and space?
- How will climate change (including phenological shifts) alter the temporal structure of communities?
- How are species' traits linked to the temporal structure of communities?
- Which causal relationships or pathways of flow (or spread) are plausible in a community?
- How does species, functional or trophic diversity influence the temporal structure of communities?
- How is the temporal structure of communities linked to their stability?
- What new metrics and tools are missing to better capture the temporal structure of communities?

knowledge of temporal community structure: ecology currently lacks a general framework to predict what these structures should look like or why and how they should vary across systems. Are those differences representative of the respective ecosystems or different environments? Do the similarities indicate shared drivers and biological constraints, or do they arise by chance? How will the patterns for a given type of ecosystem vary across different environments or with different species combinations? What will other types of communities look like? Answering these and many other related questions will significantly advance our understanding of the ecological and evolutionary processes shaping natural communities.

A crucial step towards answering these questions can involve comparing network metrics (Table 2) across systems, time and space to identify potential drivers that shape the temporal structure of communities. For instance, our approach allows us to compare network metrics across latitudinal or altitudinal gradients to test how differences in seasonality influence the temporal organization of communities. Growing and reproductive seasons are often shorter in colder climates, but we don't know how consistently this abiotic constraint shapes the temporal structure of communities. Do communities with shorter breeding/growing seasons show higher temporal overlap but shorter co-occurrences or the opposite? Does a shorter season alter the connectivity of time-ordered networks and their temporal relationships (e.g. *upstream set* vs. *downstream set*, Table 2)? Are changes uniform across species, or do they depend on their temporal position (e.g. early vs. late in the season)?

We can also see great potential in using our framework with temporally explicit null modelling approaches to narrow down potential mechanisms driving temporal structure. One of the challenges of working with any

observational data, including temporal patterns, is that similar patterns can be created by different mechanisms. However, null models can often help us differentiate between mechanisms. For instance, we can randomize timestamps of nodes within a given community to break up sequence and temporal correlations or randomize the duration of phenophases to decouple the sequence and duration of events. The high degree of flexibility offered by these null or random network models allows for ensembles of increasingly randomized time-ordered networks useful for disentangling and identifying nested temporal patterns (Holme, 2015). Comparing metrics from reference null models to empirical patterns within or across ecosystems helps identify non-random patterns in different aspects of temporal structure and better understand the processes that control temporal network structure. Say the latency between a set of species is much shorter than expected by chance. Then, there are processes causing temporal correlations between these species (Blonder et al., 2012). Ultimately, just like with spatial patterns (Gotelli et al., 2010; Gotelli & Graves, 1996), we believe that confronting different null models with empirical data of time-ordered networks offers a particularly powerful approach for detecting general patterns in temporal community structure and for testing hypothesis to identify the underlying mechanisms of community assembly.

### Quantifying phenological shifts in a community context

Time-ordered networks also provide new tools to study the ecological consequences of phenological shifts. We want to reiterate that while past studies have primarily focused on metrics at the species level (i.e. first or mean arrival) or pairs of species (e.g. differences in

first arrival), some effects may only become apparent in a community context. Small changes in the phenology of a species may have significant consequences at the community level depending on the temporal position of the species relative to other community members. For instance, the advancing phenology of species A in [Figure 2](#) fundamentally alters the network structure and thereby affects the metrics (upstream and downstream set) of all species. In contrast, a similar shift in species D would have little consequence. Our approach represents a step toward identifying these species (e.g. species' phenologies most important for maintaining the temporal structure and functioning of the existing ecosystem) and the groups likely to be the most affected by phenological shifts. These predicted differences in relative consequences following phenological shifts could then be used as *a priori* hypotheses and tested empirically.

## Paleo and bacterial data

Finally, we can also integrate time-ordered networks with other data types. For instance, recent advances in genetic methods have improved Quaternary paleo-records (Fordham et al., 2020), which have emerged as an important way to explore the long-term dynamics of communities and how they are linked to climate change (Blois et al., 2010; Jackson & Blois, 2015). Our approach could easily be used with this type of data by simply using the presence of species in the archaeological record instead of phenologies to build time-ordered networks that study how communities have changed in the distant past. Since both types of data document co-occurrences, time-ordered networks could help bridge gaps between community ecology of the present and distant past, thereby improving our ability to understand the potential consequences of climate change (Fordham et al., 2020). Similarly, next-generation sequencing is increasingly providing us with data on the temporal changes in the composition of bacterial communities (Espinoza et al., 2020). Combining this data with our time-ordered network approach could yield valuable new insights into the temporal structure of these communities, like their seasonal and annual dynamics, and how it is linked to their functioning (Deutschmann et al., 2023). Both paleo-records and sequencing data raise the importance of considering data types beyond those we have emphasized in the bulk of this paper to further strengthen our understanding of temporal community structure.

## CONCLUSIONS

Like spatial ecology, integrating temporal structure into community ecology has the potential to fundamentally alter our understanding of the critical forces

and processes that shape natural communities. To date, we still lack a general understanding of how temporal structures of communities vary, what general patterns might exist in nature, and what the underlying drivers are. We know even less about their consequences. Nevertheless, answering these questions is fundamental to understanding the maintenance of ecological communities (Ushio et al., 2018) and predicting how they will respond to future perturbations and climate change. Our framework outlines how to take the next important steps towards building a temporally explicit framework for community ecology and suggests new and exciting opportunities to help overcome some previous limitations. Building this framework is particularly important to understand and predict how natural ecosystems will change as climate change reshuffles the temporal structure of natural communities worldwide. The next challenges include collecting, accessing and analysing this temporal data to shed new light on this understudied dimension of natural systems.

## AUTHOR CONTRIBUTIONS

VHWR conceived the general idea. VHWR developed the framework and analogies together with HY. VHWR and HY wrote the manuscript, and HY collected and analysed the data.

## ACKNOWLEDGEMENTS

We would like to thank A.E. Dunham, J. HilleRisLambers, A. Silva and A. Simha for feedback on the ideas, methods and manuscript. This work was supported by NSF DEB-1655626 to V.H.W. Rudolf and by the NSF Graduate Research Fellowship Program under Grant No. 1842494. Any opinions, findings and conclusions or recommendations expressed in this material are those of the author(s) and do not necessarily reflect the views of the National Science Foundation.

## PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.14481>.

## DATA AVAILABILITY STATEMENT

All codes and dates are freely available at <https://doi.org/10.6084/m9.figshare.23629203.v1>.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**How to cite this article:** Yin, H. & Rudolf, V.H.W. (2024) Time is of the essence: A general framework for uncovering temporal structures of communities. *Ecology Letters*, 27, e14481. Available from: <https://doi.org/10.1111/ele.14481>