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

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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 analyzing 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.

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 & Jaksić 1984; Jensen *et al.* 2019; Loreau 1989a; Schoener 1974), succession (Connell & Slatyer 1977; HA 1927; Poorter *et al.* 2023), the window of opportunity (Yang *et al.* 2008; Yang & Cenzer 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, with few notable exceptions (e.g., Kantsa *et al.* 2018; Ushio *et al.* 2018), 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 analyzing 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 analyzing 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 toward filling these gaps, we propose a general framework to quantify and analyze 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 can't 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* (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) doesn't 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 analyze the duration and sequence of when certain groups (e.g., species) are active and their intervening times (gaps).

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 could provide insights into prior and ongoing competition and coexistence mechanisms (Anten & Hirose 1999; Blackford *et al.*

2020; Jensen *et al.* 2019; Schamp & Jensen 2019; Tan *et al.* 2013), or predict the invasion success of species (Alexander & Levine 2019; Godoy & Levine 2014; Wolkovich & Cleland 2011; Zettlemoyer *et al.* 2019). Anomalies in temporal spacing may reveal when environmental conditions create windows of opportunities or constraints (Yang 2020; Yang & Cenzer 2020; Yang & Rudolf 2010) and indicate facilitative interactions or co-dependence (Dante *et al.* 2013).

The distribution of species in time also structures species interactions. For instance, many interactions are only possible when species stay synchronized enough to overlap in time; a bee can only pollinate a flower and a predator can only consume a prey when both are present simultaneously (see **Box 1**). Temporal co-occurrence thus indicates, at minimum, what interactions are possible and is a crucial driver of the structure of ecological networks (CaraDonna *et al.* 2021; Morente-López *et al.* 2018; Yang *et al.* 2013). Furthermore, the sequence of species arrivals in a community and the time interval between arrivals typically determines the per-capita strength and outcome of interactions (see **Box 1**, **Fig. 1**) (Rudolf 2019).

Finally, how species are arranged along the temporal axis also determines the causal chain of possible events (like the potential for indirect interactions between species, **Box 1**, **Fig. 1**) and limits the pathways through which perturbations, infectious diseases, energy, nutrients, and information can spread through an ecosystem (Blonder *et al.* 2012). Thus, temporal structure simultaneously acts as an integrative response variable for communities and constrains possible ecological outcomes.

Analyzing and comparing temporal structure across taxa, systems, environments, space, and timescales helps us identify and understand many biological processes that shape natural communities (**Table 1**). This understanding allows for more testable predictions on how communities respond to environmental change and unlocks more well-rounded and nuanced

perspectives on the roles both space and time play in communities (Wolkovich *et al.* 2014; Yang 2020). 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. As we will explain in more detail below, studying the temporal structure of communities also provides new quantitative approaches to detecting phenological shifts (e.g., due to climate change) and putting them in a community context.

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 analyzing 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 the onset (timing) or duration of phenological events of single species (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 (Carter *et al.* 2018; Renner & Zohner 2018; 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 analyzing the

distribution of "gaps" between phenologies of all species. Distributions of multiple species' phenologies and gaps between them could characterize distinct temporal modules, e.g., subsets of interacting species that always co-occur or a set of species in a module to consistently appear in the same chronological order. Such modules may help predict the presence/absence and strength of interactions, 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, **Fig. 1**). 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 (CaraDonna *et al.* 2021; e.g. Díaz-Castelazo *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 (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 don't provide information on the duration and sequence of events, e.g., 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. Spatial ecology has proven over the past decades 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 analyzing 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 **Fig. 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 (**Fig. 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, analyzing 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). 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 workforce 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., meta-barcoding of airborne pollen DNA, pollinator DNA in flowers, or eDNA analysis in freshwater and marine systems) (Besson *et al.* 2022; Jensen *et al.* 2022; Jønsson *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 straight forward in practice (see **Fig. 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 time stamps (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 time stamps 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 time stamps for links would be similar to those of nodes (e.g., single or multiple time stamps), 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 (or inferred from the time series itself (e.g., Ushio *et al.* 2018)), it is straight forward to further restrict the topology of these co-occurrence networks to focus only on the direct interactions. However, this would shift the focus from analyzing temporal co-occurrence patterns of species to analyzing temporal patterns of direct interactions. Furthermore, species or individuals could be grouped in other ways, e.g., by traits, functional roles, or life stages. 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 signaling transitions between these states

(see **Box 2 and Fig. 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, this 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 analyzing 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. Connectance metrics like the "*upstream set"* and "*downstream set"* (**Table 2**) (also called backward reachable set and forward reachable set) show the

relationships of species to other community members that appeared before or after them, respectively (see **Fig. 2** for worked-out example). 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.

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*", i.e., 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 (Box 2), 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 communities are most vulnerable to perturbations. 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 can help identify windows of opportunity (e.g., favorable environmental conditions, resource pulses) or temporal guilds. In contrast, a low level of *burstiness* could indicate temporal niche partitioning

(Table 1). Link persistency can indicate the interaction potential of species (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 they inspire the development of complementary approaches for analyzing temporal communities. For instance, how can time-ordered networks incorporate count data from phenological datasets as weights to predict ecological consequences of co-occurrences better? 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.

Practical considerations

The size of any time-ordered network scales with the length of the period analyzed. 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 analyzing 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, e.g., 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 **Fig. 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 is becoming increasingly available, the data recorded varies across studies, which determines the types of possible analyses. For instance, phenology datasets 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 **Supplement, Fig. 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 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 **Fig. 3** for a worked example) and help identify the underlying mechanisms. We already mentioned some applications above but would like to highlight some additional exciting new research avenues and applications. 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 help guide management and conservation efforts in a rapidly changing world.

General patterns and environmental drivers of temporal community structure

Given that temporal structure is non-random and reflects a community's ecological and evolutionary processes, we can expect to learn a lot from studying temporal patterns. For instance, perhaps weak burstiness and memory of fruiting plant communities (**Fig. 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, e.g., to avoid competition for frugivores.

When we applied our approach to compare two very different communities (anuran calling versus a plant fruiting community), we found striking differences in the temporal network structure and some surprising similarities (see Box 1 and Fig. 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 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 toward 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 modeling approaches to narrow down potential mechanisms driving temporal structure. For instance, we can randomize time stamps 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 single species or pairs, 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 **Fig. 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. The relative consequences of phenological shifts predicted from these networks generate *apriori* hypotheses that researchers could test experimentally.

Paleo data

Finally, we can also use time-ordered networks to analyze 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).

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 toward 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 analyzing this temporal data to shed new light on this understudied dimension of natural systems.

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Box 1: ***Why is 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) (**Fig. 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" (**Fig. 1b**). These examples highlight that the sequence and duration of species' activities 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) (**Fig. 1c**). For instance, reducing the overlap of flowering times can either increase or decrease the fitness 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 a delay in salamander and dragonfly predator arrival relative to its tadpole prey (Rudolf 2022a). 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 of species' arrivals in a community and the time interval between arrivals determines the chain of causal events. In the absence of temporal overlap, species present earlier in a community can affect those that appear later but not vice versa (**Fig. 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), e.g., 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, this potential to affect other community members naturally declines towards the end of a season; e.g., 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.

Box 2: ***Applying the temporal framework: temporal patterns of anuran calling community vs. 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*. 2022a) (**Fig. 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 **Fig. 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 time stamps for when transitions occur, while nodes have time intervals for the duration of community states.

Just comparing the network visually, we can immediately see striking differences in their temporal structure (**Fig. 3a**). The anuran-calling time-ordered network shows many recurring community states (combination of species) but with considerable variation in how long each community composition lasts and how often it reappears (green histograms in **Fig. 3b** and 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, where species with long phenophases (which form the long tail in the histogram in **Fig. 3b**) are more central and 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 **Fig. 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 (**Fig. 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, i.e., a weak signal of temporal clustering of community shifts (burstiness in **Fig. 3e**) and no clear autocorrelation in times between community shifts (memory in **Fig. 3e**). 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.

578 **Table 1**: Examples of ecological concepts and how they are related to temporal patterns

Ecological concept	**Temporal pattern used to infer concepts**	**Example references**
Mechanisms of community assembly	Reduced temporal variation & non-random temporal patterns (over time, e.g., years or habitats) were used to infer the strength of stochastic vs. deterministic processes, historical contingencies, & priority effects.	(Neale & Rudolf 2023; Purschke *et al.* 2013; Van Allen *et al.* 2017)
Niche partitioning	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)
	Temporal restructuring (change in phenologies) after species removal as an indicator for temporal niche separation to avoid competition	(Dumandan *et al.* 2023)
Coexistence mechanisms	The sequence of arrivals and 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)
Functional relationships	Temporal covariances of occurrences used to infer species	(Deutschmann *et al.* 2023; Steele *et al.*

of species	interactions	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)
	Phenology timing determines predator-prey and host-parasitoid interactions and community structure.	(Alford 1989; Pardikes *et al.* 2022; Rudolf 2022b)
Network structure and stability	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)
	Phenology drives modularity	(Morente-López *et al.* 2018)
Invasion success	Invasion success/growth rates dependent on the relative timing of arrival (germination or flowering)	(Godoy & Levine 2014; Wolkovich & Cleland 2011; Zettlemoyer *et al.*

		2019)
Specialist vs. generalist	Species with narrow time windows (short presence) are more likely to specialize on temporary resources and certain environmental conditions (e.g., seasonal specialist vs. generalist)	(Humphries *et al.* 2017)
Potential pathways for and speed of disease, information, and energy transmission	Temporal structure predicts the possible pathways and transmission speed through a community (e.g., faster with higher average overlap, less time between arrival, etc.)	(Blonder *et al.* 2012)
Effect 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)
Windows of opportunity	Temporal clustering and gaps in species presences can indicate favorable (& unfavorable) environmental conditions.	(Martinez Falcon et al 2010)

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Table 2: Metrics to quantify different aspects of the temporal structure of natural communities. 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 & Saramäki 2019).

Temporal structure	**Metric**	**Definition of metric**	**Suggested biological meaning & 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 **causal relationship**. 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	Indicates *which* and *how many species could be "influenced" by a focal species*. This includes species (nodes) that do not have direct temporal

		time-respecting paths.	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 **Fig. 2** for a worked-out example)
	Upstream set	Number of nodes that can reach a given node *i* via temporal paths	Indicates *which* and *how many species could affect a focal species*. 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 **Fig. 2** 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 *how many indirect contacts are needed to reach another species*. The **average distance** tells us *how spread out a network is* (related to temporal overlap but goes beyond pairwise overlap). It provides new insights into *the functional roles of species (or other groups) in a community* by resolving relationships between species in a temporal context. At the community and ecosystem level, the pace of phenological shifts this metric identifies suggests *how perturbations, energy, or infections "flow" through a community and at what time scale*.
	Time-dependent –	Measures the fraction of shortest	Measures how well connected a node is to others. It can *identify a node's relative level of importance in terms of its ability to act as an*

	betweenness centrality	paths that go through a node	*intermediary to other nodes in a network*.
Duration of events	**Node persistency**	Period a node is present	Essentially, it indicates *how long species are present/active*. It is likely to be correlated with connectivity metrics. (see **Fig. 3** for a worked-out example)
	Edge persistency	Period a link is present	Measures *how long species co-occur*, which indicates their **interaction potential**. Applies only to networks where edges can represent durations (e.g., networks in **Fig. 2**)
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 *how fast a signal could travel between two species, including species without temporal overlap*. **Average latency** (across all combinations) tells us *how long it takes on average for a signal to travel in a network*.

	Time-dependent centrality - closeness	The inverse of average latency	Measures how quickly a node reaches all others Essentially metric of the centrality of a node, i.e. *how closely is a node connected to all other nodes in a network*.
	Burstiness	Temporal distribution of consecutive inter-event times over a given time	Measures *how evenly events (e.g. contact, or overlap) are spread out over* time. Requires at least three time points. A time-ordered network with a high degree of *burstiness* indicates temporal clustering of events, e.g. when phenologies are highly synchronized across species. Emphasizes events themselves. (see **Fig. 3** 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 **Fig. 3** for a worked-out example)

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. Colors 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.

Figure 2. Steps to build, analyze, 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 time stamps that indicate when a species is present. Time stamps 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 time stamps (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 inserts 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 color) 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**) vs. (**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.

Figure 3: Changes in community structure over time 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 time stamps per arrow (like in **Fig. 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 colors 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 a ~1-year 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 based on estimates during 1850-1860 (Ellwood *et al.* 2022a). Frequency plots show the distribution of **(b)** the duration (node persistency) 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)** show two metrics that quantify different aspect of temporal distribution of events at the community level for each network: burstiness and memory (see **Table 2** for metric details).

Figure 1

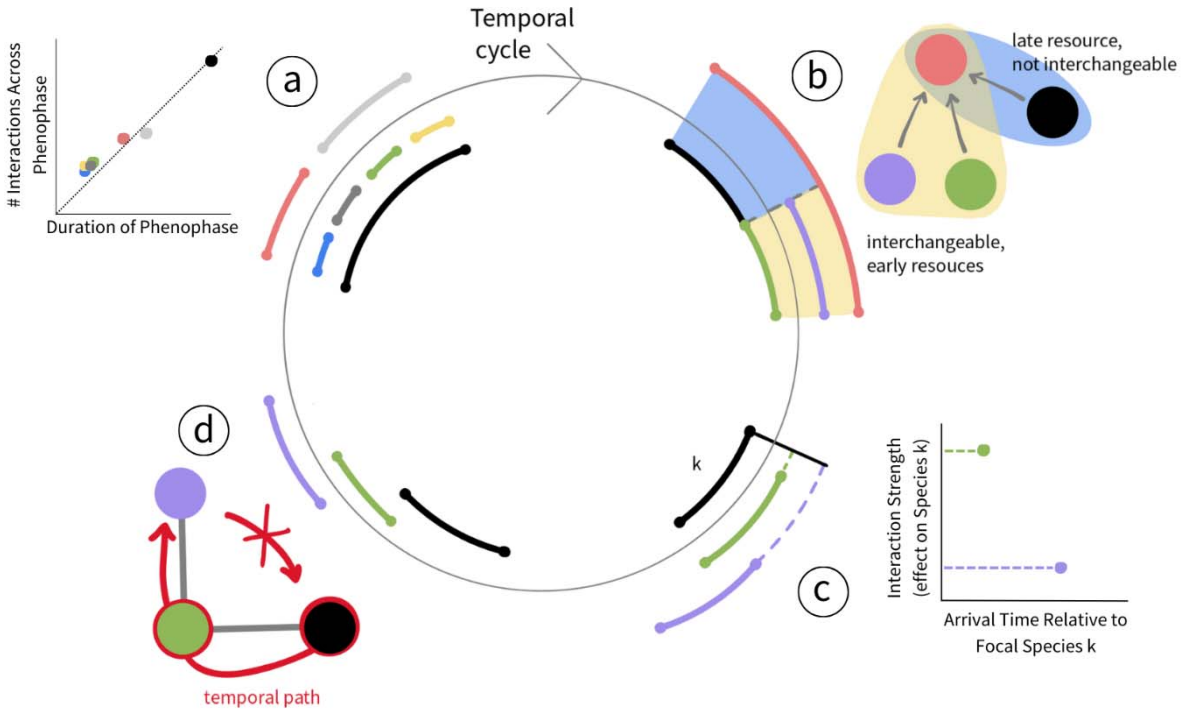

Temporal cycle
a
b
c
d
Interactions Across Phenophase
Duration of Phenophase
late resource, not interchangeable
interchangeable, early resouces
k
Interaction Strength (effect on Species k)
Arrival Time Relative to Focal Species k
temporal path

Figure 2

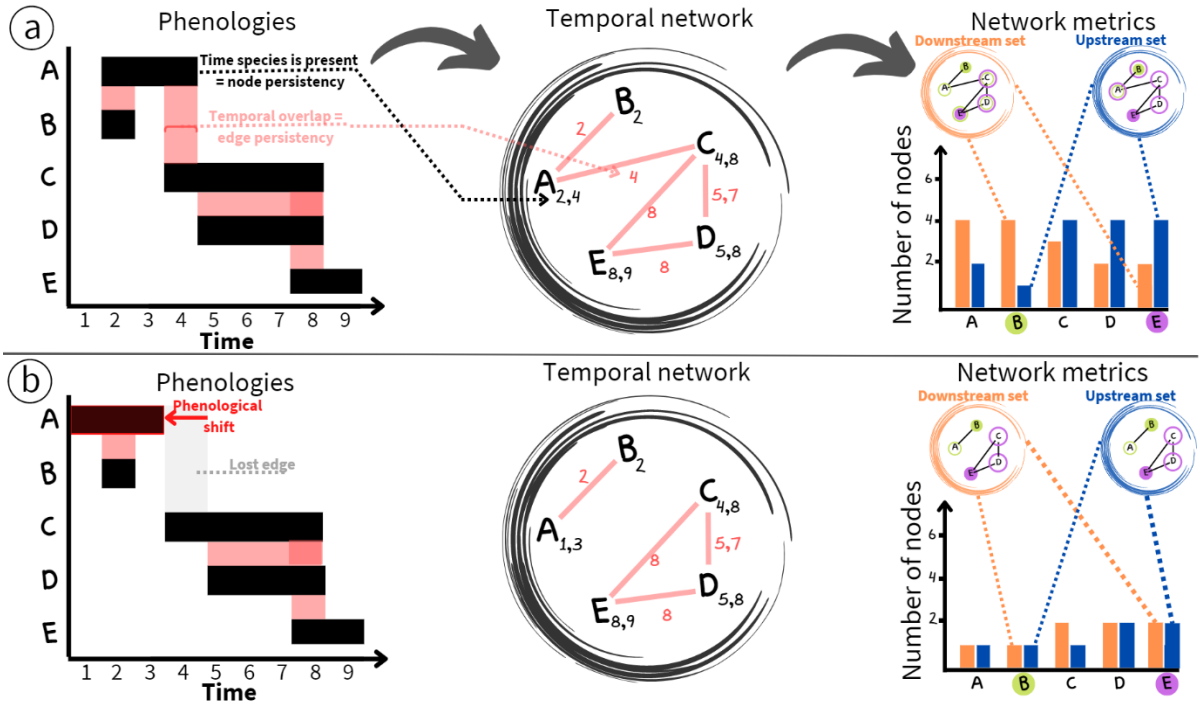
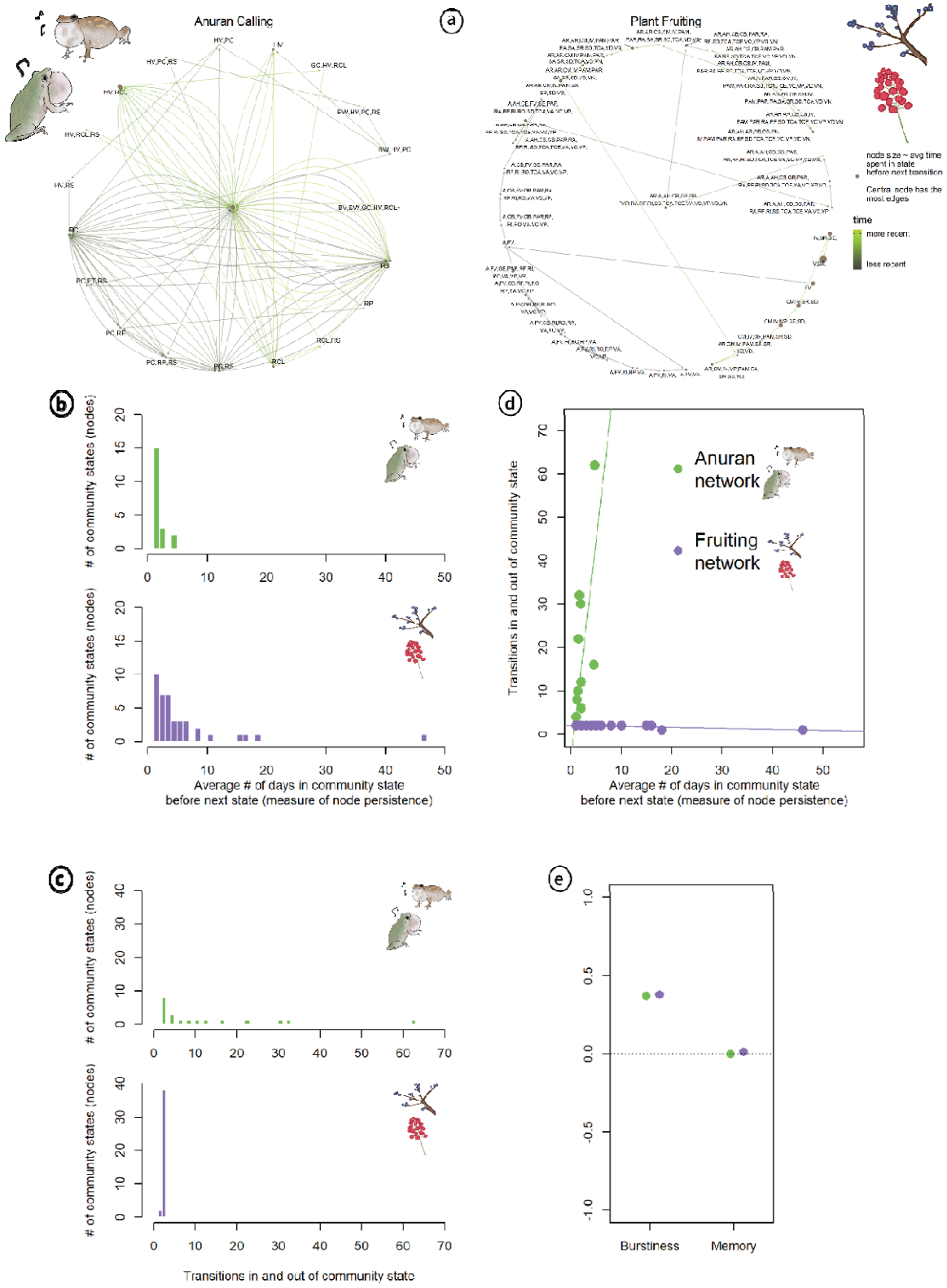

a
Phenologies
Time species is present
= node persistency
Temporal overlap =
edge persistency
A
B
C
D
E
1 2 3 4 5 6 7 8 9
Time
Temporal network
Network metrics
Downstream set
Upstream set
Number of nodes
b
Phenological
shift
Lost edge

Figure 3


a
Anuran Calling
Plant Fruiting
node size ~ avg time spent in state before next transition
Central node has the most edges
time
more recent
less recent
b
# of community states (nodes)
Average # of days in community state before next state (measure of node persistence)
c
Transitions in and out of community state
d
Anuran network
Fruiting network
Transitions in and out of community state
Average # of days in community state before next state (measure of node persistence)
e
Burstiness
Memory

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