Time is of the essence: A novel 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 species interactions, energy flow, nutrients, information, diseases, and how perturbations cascade through the system. Yet, our understanding of community structure has relied heavily on static approaches that do not capture key features of this dynamic temporal dimension of communities. Here we propose a conceptual and methodological framework to quantify and analyze this temporal dimension. Conceptually, we split the temporal structure into two definitive features, sequence, and duration, and discuss how they are linked to key concepts in ecology. We then outline how to capture these definitive features using perspectives from temporal graph theory. While we focus on how ongoing research in phenology and species interactions easily integrates into our proposed framework, we also describe how this framework applies to other outstanding questions in community ecology. As climate change reshuffles ecological communities worldwide, integrating the temporal dimensions of communities is not only imperative to resolve the fundamental processes that shape natural ecosystems, but also essential to predict how these systems may change in the future.

The temporal dimension of communities

Communities are structured across two fundamental dimensions: time and space. Research on spatial structure has increased rapidly in the past decades and transformed the way we think about natural communities, by emphasizing the importance of spatial structure in species distributions (e.g. metapopulations & metacommunities, macro-ecology) [1-4]. In comparison, we still know surprisingly little about the temporal structure of communities, which has only

recently gained renewed attention as a line of research [5-7]. 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 [8], create an urgency to develop frameworks explicitly focusing on the temporal dimension of community structure to fill this conceptual gap [6, 9-12].

Temporal patterns and shifts in community composition and species interactions are a hallmark of any natural community. Their importance manifests in several key ecological concepts, like the temporal niche [13-16], the window of opportunity [17, 18], and the seasonal timing of life history events (phenology) [19-22]. 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 most ecological networks is fixed and time-invariant such that only the abundance of species may change over time [9, 23, 24]. When analyzing empirical patterns, studies of community structure typically use a single data snapshot in time or aggregate time points to calculate key biodiversity metrics, thereby potentially overlooking transient states and important ecological processes present at the community level, such as seasonality [25]. As a consequence, our current understanding of the temporal structure of natural communities is severely limited, with little knowledge about 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.

Given that ecologists have long appreciated the temporal 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 methodological framework for analyzing the temporal structure and the

logistical challenges in obtaining the fine-scaled temporal data required, which can require a lot of resources or new technologies. To help fill these gaps, we propose a new conceptual and methodological framework to quantify and analyze the temporal structure of natural communities. First, we define the temporal structure of communities and discuss their relevant ecological concepts. We then give a brief introduction to temporal networks and suggest how and why they can theoretically capture the definitive features of temporal structure in natural communities, by applying perspectives from temporal graph theory. We end by applying this temporal network 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?

Unlike space, time is unidirectional: it always moves forward, it never stops, and we can't go back. This means that events and processes from the past can affect events and processes that happen in the future, but not the other way around. Given this directionality, the temporal structure is fundamentally about the *sequence* (order) and *duration* of and between events. Take a piece of music for example. Knowing all notes played in a melody does not tell you how it sounds. What makes any melody unique from others is the sequence of notes (relative timing), how long each note is played, and the pauses in 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 dynamics of natural communities and how they 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).

For a more concrete ecological example of this concept, consider the cycle of an annual plant community: at the start of every year, the new offspring of species start to "arrive" and interact with other members. During their ontogeny, their interactions change (ontogenetic niche shifts) before they "leave" the community (e.g. enter dormancy or die). The respective phenology of a species determines the timing of these events (i.e. when and at what stage they interact with other species) and the combination of all phenologies summarizes the temporal structure of a community. Relative differences in when phenophases start (e.g. the first day of hatching) determine the sequence of appearances of species and the time intervals between new appearances. Overlapping phenophases created by relative starting times and durations of phenophases restrict what direct interactions are even possible, the maximum interaction durations, and time intervals between interactions. Subsequent annual cycles may follow a similar but not identical temporal distribution of events compared to past years. There is clear evidence of a temporal structure to ecological interactions in any natural system.

Why is temporal community structure so important?

Describing the temporal structure of natural communities clearly requires more effort and data than the traditional static approach (e.g. taking a single snapshot or aggregating all observations), but is it really worth the effort? Why should we care about temporal community structure, and what new insights can we gain from analyzing it? The answer to this question becomes quickly apparent if we think about how many longstanding ecological concepts and contemporary studies rely on key elements of temporal structure (sequence and duration of/between events) to ultimately make sense of the causality and predictability of community structures and dynamics.

Knowing when and for how long species are present and active in a community is key to building a foundational understanding of which species interact and how they interact (**Figure**

1). The potential for species to directly interact is, at minimum, restricted by their temporal co-occurrence; a predator cannot consume a prey, and a bee cannot pollinate a flower, if they are not both present at the right stage at the right time(s). As a consequence, species interactions are closely linked to their temporal presence (**Figure 1**). For instance, analyses of mutualistic networks found that species with longer phenophases had on average more interactions and thus were more likely to take a central position closer to the core of the interaction network [26] (**Figure 1b**). However, because species went through a sequence of interactions, they only had one or a few interactions at any given point in time. For consumers, this meant most of their resources were not interchangeable, so species that may appear as a generalist in a cumulative network (static, aggregated across time) may be a "sequential specialist" (**Figure 1d**). In the case of competition, species often intentionally reduce their temporal overlap with competitors, a phenomenon called temporal niche partitioning [13, 15]. Of course, a single snapshot of a community would simply miss these and many other potential patterns. Thus, knowing the sequence of species' arrival and the duration of their stay is not only essential to identifying what interactions are possible but can also reveal the forces that structured life histories and community composition.

The outcomes of interactions may also depend on the duration and sequence of events. Interspecific interactions that last longer are likely stronger [27]. For example, a pollinator that only overlaps with a plant for a few days will likely have a much smaller impact on that plant than a pollinator that is present for the entire duration of the plant's flowering period (**Figure 1a**) [28]. Furthermore, the sequence of species' arrivals in a community and the time interval between arrivals often determine the per-capita interaction strength and thus the outcome of interactions (e.g., competition or predation), especially when interactions occur among growing

individuals [12]. An early arriver may have a competitive advantage over species that arrive later, and this advantage often depends on the difference in relative arrival times [29-32]. As a consequence, long-term coexistence and competitive dominance strongly depend on the relative timing and sequence of interactions [12]. Similarly, predation rates (and thus the strength of trophic cascades) can decline with a delay in predator arrival relative to its prey [33]. Such timing effects (also called priority effects or historical contingencies) are well documented in animal, plant, and microbial systems and determine the long-term dynamics and structure of aquatic, marine, and freshwater communities [34]. These studies emphasize how the key elements of temporal structure (sequence and duration) determine all possible aspects of species interactions and play a central role in shaping biodiversity patterns.

At the community and ecosystem level, the duration and chronological order of temporal co-occurrences limits the possible pathways through which diseases, energy, water, key organic and inorganic elements, and perturbations cascade through the ecosystem. Early-arriving species could indirectly affect many species that arrive later, even if they never co-occur with them (legacy effects), e.g. by passing on an infection, altering the environment [35], consuming a competitor of a later arriving species [36, 37], or by changing the community composition that later arriving species experience [38]. This potential to affect other members in the community 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) [39], and the species that arrive last can only affect a limited number of species with which they co-occur (**Figure 1c**). Similarly, 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. As for the

importance of duration at the community and ecosystem levels, the continuous deposition of electrolytes through bison urine, including potassium that might otherwise easily leach out of plants upon a one-time application, appears to facilitate more efficient use of nutrients in grassland plants [40]. Explicitly accounting for plausible chains of events and their durations as constrained by temporal community structure helps us better discern the relative importance and functional role of individual species, community dynamics, and ecosystem processes.

The need for a general framework to quantify temporal community structure

Because various studies and related ecological concepts make use of the sequence and duration of (or between) events to understand community dynamics, we believe in the merits of establishing a general quantitative framework designed to capture the key features of temporal community structure. Current approaches to analyzing the temporal structure of communities have largely operated independently of each other but fall into two broad research areas: phenology and interaction networks. Each approach has strengths and limitations in capturing both the complexity of communities and key features of temporal structure.

To date, phenology studies have predominantly focused on the onset or duration of phenological events of single species [20, 41, 42], pairwise correlations of these events [43, 44], and the temporal overlap of interacting pairs of species (e.g. trophic mismatch) [27, 45-47]. While these and other studies have been fundamental in documenting the temporal coordination and variability of interactions, many other 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. Such bursts of activity can only be identified 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. Similarly, the ecological consequences of phenological shifts may only become fully apparent in a community context (e.g. when shifts create temporal partitioning). 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 used in current phenological studies.

Studies on interaction networks of communities, on the other hand, prioritize a multi-species perspective to capture how communities change [9, 48]. In interaction networks, species are represented as nodes and links indicated observed interactions (e.g. predator consuming prey, or pollinator visiting a flower) between species pairs. By focusing on changes in observed interactions between community members, these studies have provided important new insights into the temporal dynamics of communities. For example, while the composition and interactions of communities can rapidly turn over across years, seasons, and even days, some structural patterns at the network level (e.g. nestedness, connectivity, etc.) may change comparatively little [49-51]. These results suggest that there may be general "rules" that determine community structure, but those rules can only be observed when we consider the whole network of interactions.

However, existing approaches using interaction networks come with their own limitations. They largely use a static network or biodiversity metrics that do not account for the timing,

sequence, and duration of events. Thus, they miss information on the key components that define the temporal structure of communities and that can drive many ecological processes. Furthermore, the effort associated with quantifying many interactions at a time often comes at the cost of a small number of repeated observations separated by long time intervals (months or even years) [9]. Indeed, with the notable exception of certain plant-pollinator systems, it is often simply not logistically possible to even observe interactions at short temporal scales. The coarse temporal resolution necessitated by such logistical constraints inevitably misses much of the temporal structure of communities, e.g. precisely how long species and interactions occur, in what sequence they appear, or by how much time they are separated. Furthermore, many studies combine time points to generate temporally aggregated (cumulative) networks. Unfortunately, the structure of these aggregated networks changes with the temporal scale over which observations are aggregated [49], which may further limit what we can learn about interaction structure in communities. Nevertheless, having the ability to analyze a more complete history of communities is imperative to understanding the roles that interacting species play in maintaining or altering community and ecosystem trajectories.

In summary, despite important 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. As the field collects more information on the phenology and interactions of species co-occurring in communities, greater complexities in their data analysis inevitably emerge. At a minimum, we hope this review helps researchers design their projects in ways that tie these data complexities back to the properties of the temporal structure described above. Especially in this age of unprecedented environmental change, doing so should help the field move toward the much-needed, temporally explicit frameworks of change in ecological communities.

A new approach to studying the temporal structure of natural communities

Here we propose to combine the strengths of both phenology and interaction network concepts to build temporally explicit networks from phenology data to study the temporal structure of natural communities in full. Temporal networks (also called time-varying, or dynamic networks) differ from traditional static networks because each node (vertex) and link (edge) in the network is only active during certain time points or periods [52]. Crucially, all nodes and links have time stamps or time intervals showing when interactions or transitions occur (shown explicitly in **Figure 2**). Therefore, temporal networks explicitly track when events occur. They break down cumulative networks to capture temporal structure—the sequence and duration of or between events. Metrics or algorithms for temporal networks respect the unidirectional flow of time in the network topology so that implausible chains of events suggested by the topology alone won't get considered. The study of temporal networks is still ongoing, but it is a rapidly growing interdisciplinary field. Temporal networks have been used to describe a range of systems, from public transportation to neurons in the brain [52]. These networks could prove useful in practice as long as the activities or dynamics captured in the network change at a similar timescale as changes in the network topology. We believe this holds for many cases in community ecology where changes in species interactions captured in the network topology result from these species undergoing phenological shifts. Thus, temporal networks are ideally suited to describe the temporal structure of natural communities, despite these networks having received little attention in community ecology so far.

Building temporal networks from phenology data

A key challenge in analyzing the temporal structure of communities lies in creating a temporal network with enough consecutive data points at a sufficiently fine-grained temporal

resolution. Observing interactions at fine time scales is very difficult and time-consuming at best, and often simply not feasible for many natural systems. Furthermore, to study long-term trends and the effects of climate change, we prefer and, in many cases, require long-term observations (on the scale of decades), which only exacerbates the already daunting logistical challenges.

Thankfully, phenology data are comparatively easy to collect for most organisms at a relatively fine and long temporal scale. Indeed, we already have a rich body of phenology data for a wide range of 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 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 [53] can greatly help to reduce the manpower 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) [53-55]. Importantly, phenology data provide key information about the temporal structure of communities by documenting the presence and activity of species and their life history stages. Therefore, we can use phenology data to create temporal networks and then adapt existing tools and metrics or develop novel ones to gain detailed insights into the temporal structure of communities. This approach also puts changes in the temporal distribution of a species (e.g. phenological shift) in a community context

rather than treating each temporal shift as an isolated instance, thereby increasing our ability to detect ecologically meaningful changes in a community.

The process of building temporal phenology networks is, conceptually, fairly intuitive (**Figure 2**). Following traditional approaches, we can build a network where a species represents a node, and its phenology determines the time stamps (interval) for that node. Depending on the system, a node may thus just 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 (also known as edges) show relationships between nodes to represent when two species are active at the same time 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 temporal networks, links are sometimes called "contacts" to emphasize a time-limited information exchange [56].

This representation of a community helps capture the temporal structure of species in a given system. We focus here on species co-occurrence since most phenology data is recorded at this level (see the *Future directions* section below for an example of how this approach can be applied to another type of temporal ecological data). Formulated in this way, temporal networks help identify which direct and indirect interactions are even possible. While they cannot show that the interactions are also necessarily realized, the networks set boundary conditions such that any additional information on species interactions would further restrict the topology of these co-occurrence networks. For instance, one could restrict the co-occurrence network to only show trophic interactions (e.g. bipartite plant-pollinator webs may only represent links between plants and their pollinators). Similarly, species or individuals could be grouped in various ways, e.g. by

traits, functional roles, life stages, or time (see **Box 1 and Figure 3** for an example where time-stamped links signal transitions between community states). Ultimately, the type of network structure decided depends on the specific questions of interest and available information. This choice will affect the interpretation of temporal patterns and determine the metrics used to quantify them.

Quantifying temporal community structure using temporal graph theory

Converting species' phenologies into temporal networks opens the door to calculate a range of metrics that could provide new and deeper insights into the temporal relationships of species and the organization of natural communities. Some of these metrics for temporal networks are unique to temporal analyses, while others build on static network metrics by accounting for the unidirectionality of time. Here we highlight a subset of temporal network metrics (**Table 1**) that we believe are among the most conceptually straightforward and biologically meaningful for analyzing temporal community networks built from phenology data.

The most basic quantity of any network explains how a node (e.g. species) is connected to other nodes. In a temporally explicit network, the unidirectionality of time (i.e. time always moves forward) means that this relationship between nodes has to follow a time-respecting "walk" (sequence) of adjacent nodes and links. Importantly, these "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* can indirectly affect node *C* (via *A*), but nothing from *C* can propagate to *B*, since signals cannot travel back in time.

Connectance metrics that we call "*upstream set"* and "*downstream set"* (**Table 1**) show how species are connected to other community members that appeared before them and those that

come afterward, respectively. For instance, we can compare the *downstream set* 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). Connectivity also depends on transmissibility—how easily and fast a signal or substance can travel across a community. In static networks, this is typically measured as the "*shortest path*", i.e. the smallest number of nodes that need to be traversed to connect one node to another. In temporal networks, this is sometimes called "*flow*" [57]. Distances between nodes can be measured in two ways in temporal networks: the number of nodes that need to be traversed (*distance*), or the actual time required to travel from one node to another (*latency*). Perturbations or infectious diseases can spread faster in communities with shorter average *latency*. Together, all these connectance metrics (**Table 1**) give important insights into the functional role of species and their relationships.

Other metrics, such as *burstiness*, *memory*, *node*, and *link* persistency (**Table 1**), focus on the duration of, or between events to quantify the permanence/transience of temporal network structures, including temporal turnover of interactions. A high level of burstiness could help identify windows of opportunity (e.g. favorable environmental conditions, resource pulses) or temporal guilds. Link persistency may correlate with interaction strength and therefore could help identify which interactions are particularly important for a given species, 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). Combining multiple metrics could elucidate how life histories lend themselves to species' functional roles, how species utilize resources (e.g. looking for correlations between a node and link persistence or source set), or how species' phenologies form the structure and complexity of communities (e.g.

test if networks with higher node and link persistency also have shorter average latency or higher source set, etc.). Altogether, these metrics for phenological data not only capture important network properties such as connectivity, transmissibility, and persistence but also sequence and duration, the key features of temporal structure (**Table 1**).

Temporal networks have not been widely applied to phenological data, which means 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 analyzing temporal communities. For instance, how can temporal networks incorporate count data from phenological datasets to summarize the relative durations of co-occurrences? How can comparisons of temporal networks further our understanding of observed, predicted, or simulated ecological time series outside static approaches?

Dealing with practical considerations in the analysis

The size of any temporal network scales with the length of the analyzed period. Results of several temporally explicit metrics can differ based on the length of time over which network structures get quantified. This is particularly important for metrics that rely on time-respecting path lengths since they typically have positive correlations with the length of the period considered. Therefore, as best practice, any analyses of temporal community structure should have a clearly defined time window *t.* Fortunately, when analyzing phenology data, the temporal window is often set by the calendar year, or the system itself, especially in temperate regions, e.g. the melting of snow in spring and the start of the first snow in fall. That being said, these boundaries can be blurred for some systems, e.g. when individuals or life stages stay active all year round. In this case, researchers have to either identify other biologically meaningful time windows (ex: 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, we recommend that researchers clearly communicate the time windows used in their analyses and standardize network metrics by the length of time windows when comparing temporal networks with variable time windows.

Second, visual representation of temporal networks becomes difficult when exceeding a certain size, and the technical support for calculating temporal network metrics is currently limited to those with ample experience in computer programming. However, several packages specializing in temporally explicit networks already exist, and many of these packages have regular updates implementing new functions for network metrics (R packages: networkDynamic, tsna, ndtv; Python packages: straph, snap-stanford, teneto, tnetwork). Furthermore, several metrics like burstiness and memory have applications beyond network analysis and therefore do not necessarily rely on network-specific software. For other 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 temporal networks and the development of new comprehensive guides [58], we anticipate that more user-friendly options will emerge over the next decade.

Dealing with phenology data limitations

The analysis of temporal (phenology) networks can provide new insights into the temporal structure of communities, but it is important to keep potential data limitations and caveats in mind to decide when this approach will be most useful. Like all network approaches, it becomes more powerful the more nodes (species) are included. Similarly, very short or sparse time series may not contain enough information to reveal certain temporal patterns. Some metrics like memory require a minimum number of time points (**Table 1**). However, these

caveats simply reflect the fact that the analysis is focused on the temporal dynamics of communities which inherently requires more data than single species or snapshot approaches.

Phenology data is becoming more and more available, but some data can be incomplete. For instance, phenology datasets may only have start dates that happen once per species per year (ex: first flowering, first emergence). Without a biological notion of both start and end times or time points shared by more than one species, a temporal network reduces to a temporal path or chronological sequence of events. Nevertheless, temporal patterns with this limited data may still exist and can be analyzed using several different approaches. First, we can still apply network metrics that depend less on the network topology, such as burstiness, memory, sub-path length, and latency (**Table 1**). Second, this type of data still provides important information on the temporal structure and how species may carry out functional roles and phenological shifts over time (see **Supplement 1** for an example of an empirical application using data set on the leafout of woody plants). It may also help to find the center and spread for the chronological rank of phenological events across calendar years (**Supplement 1 Figures S1, S2**). Third, when working with multiple sequences of phenological events, we can learn to adapt sequence analysis methods used in other fields. Developments in this kind of analysis continue to add tremendously to the understanding of evolutionary histories [59], and temporally explicit sequence analyses help social scientists compare human life course trajectories [60, 61]. What if phenology research started applying these sequence analysis approaches to study temporal patterns? Could they open up new lines of inquiry or help better answer existing research questions in community ecology?

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 [5]. To predict how systems will change, we first need to understand what the temporal structure of communities looks like and what mechanisms drive this structure. To date, progress in answering these questions has been hampered by a lack of available methods and limited time series data. Our temporal framework is specifically aimed to help overcome this limitation.

Through visual and quantitative assessment of temporal networks of phenology data, researchers can quantify and compare temporal structures of communities across time, space, and different ecosystems (see **Box 1** and **Figure 3** for a worked example). We have already highlighted how many of the different metrics can be used to answer questions about the functional roles and the relationships between species within a community, or how energy, nutrients, information, diseases, and perturbations "flow" through an ecosystem (see *Quantifying community structure using temporal graph theory* section above and **Table 1**). Additionally, our framework can provide new ways to quantify the "temporal niche" of species, by putting them in a temporally explicit community context and revealing previously hidden functional differences between species across ecosystems and space. For example, species that interact 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 are likely to show different responses to species extinctions and other environmental perturbations. Temporal differences uncovered using this framework could help explain differences in the extinction risk of species or population declines when guiding conservation efforts, especially in areas with comparable spatial characteristics.

After identifying similarities and differences in temporal networks of phenology data, we can determine and analyze their drivers. For instance, perhaps weak burstiness and memory of

fruiting plant communities for a year (**Figure 3e**) could arise from plant species starting but not ending their fruiting phenophases in the same month. This source of variation ties into environmental conditions and/or species life histories. However, weak burstiness and memory could also arise from a different observed temporal distribution of plant fruiting caused by separate or additional factors (ex: herbivory). Ultimately, identifying the key drivers of temporal structure will require that we compare structural patterns across a wide range of different systems or/and how systems change over time. Once identified, an important next step will be to determine how the structural differences affect the dynamics of these systems when responding to biotic and abiotic change. Answering these and many related questions is fundamental to our ability to understand and predict how natural communities will respond to future perturbations and climate change, especially in areas with comparable spatial characteristics.

Temporal networks also provide new tools to study the ecological consequences of phenological shifts. We would like to reiterate that while past studies have largely 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 big consequences at the community level depending on the temporal position of species relative to other community members (e.g. advancing phenology of species A in **Figure 2** fundamentally alters networks structure and affects metrics of all species, while 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 the functioning of the existing ecosystem) and the groups likely to be the most affected by phenological shifts. Consequences predicted from these networks generate *apriori* hypotheses that researchers could test experimentally.

Finally, the analysis of temporal networks can also be applied to other types of data. For instance, recent advances in genetic methods have improved Quaternary paleo-records [62], which have emerged as an important way to explore the long-term dynamics of communities and how they are linked to climate change [63, 64]. 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 temporal networks that study how communities have changed in the distant past. Since both types of data document co-occurrences, temporal 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 [62].

Like spatial ecology, integrating temporal structure into community ecology has the potential to fundamentally alter our understanding of the key forces and processes that shape natural communities. As a loose analogy, natural communities have temporal similarities and differences, just like how certain pieces of music are similar or different in various aspects of their composition. Our framework provides an important first step toward building a temporally explicit framework for community ecology. Building this framework is particularly important to understand and predict how natural ecosystems with change, as climate change continues to reshuffle the temporal structure of natural communities worldwide. The next challenges include the collection, access, and analysis of this temporal data to shed new light on this understudied dimension of natural systems.

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.

Box 1: ***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 it can be used to compare the temporal structure of communities using publicly available data sets on two very different systems; one on anuran calling in Texas [27] and the other on fruiting phenology in Thoreau's Concord [65] (**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 temporal networks is still the same (see **Figure 1**), 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 (**Figure 3a**). The anuran-calling temporal network is characterized by 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 **Figure 3b** and c, respectively). This arises because most species have more than a single time interval during which they are active and because species 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 **Figure 3b**) are more central and act as “hubs” connecting different community states. In contrast, the fruiting network is characterized by a sequential turnover of community states, because species are typically only fruiting during a single period. As a consequence, there is a much clearer temporal hierarchy with a simpler causal structure (who comes first and could

influence later arrivers) and 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 temporal 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 **Figure 3e**) and no clear autocorrelation in times between community shifts (memory in **Figure 3e**). These examples illustrate just some of the various analyses that can be performed with our approach to better comprehend the common and unique temporal structures and functions of natural communities.

503 **Table 1: Example of useful metrics that quantify different aspects of the temporal structure of natural communities.**

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 temporal network under the constraint that the next link to be traversed is activated at some point in time after the current one.	This is a foundation for many temporal network metrics and establishes a potential **causal relationship**. It assures that the connection between nodes (e.g. species) and temporal 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 *which* and *how many species could be "influenced" by a focal species*. This includes species (can be represented in nodes) that do not have direct temporal overlap with the focal species. The distribution of downstream sets across all species can be used to identify species that play a central role in connecting the network or could exert a disproportionate influence on others. (see **Figure 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 that have 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 **Figure 2** for a worked-out example)

			In combination with the downstream set, the upstream set helps determine how well-connected a species is. This 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). Can provide new insights into *what the functional roles of species (or other groups) are in a community*, by resolving relationships between species in a temporal context. At the community and ecosystem level, the pace of phenological shifts identified by this metric suggests *how perturbations, energy, or infections "flow" through a community and at what time scale*.
	Time-dependent – betweenness centrality	Measures the fraction of shortest paths that go through a node	Measures how well connected a node is to others. Can be used to *identify the relative level of importance of a node in terms of its ability to act as an intermediary to other nodes in a network*.
Duration of events	**Node persistency**	Period a node is present	Essentially indicates *how long species are present/active*. Likely to be correlated with connectivity metrics. (see **Figure 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 **Figure 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 temporal 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 **Figure 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 **Figure 3** for a worked-out example) §

*Definitions and use of temporal network metrics vary among studies. Here we largely follow those in [66]

§ Relatively simple formula [67, 68] to implement in code

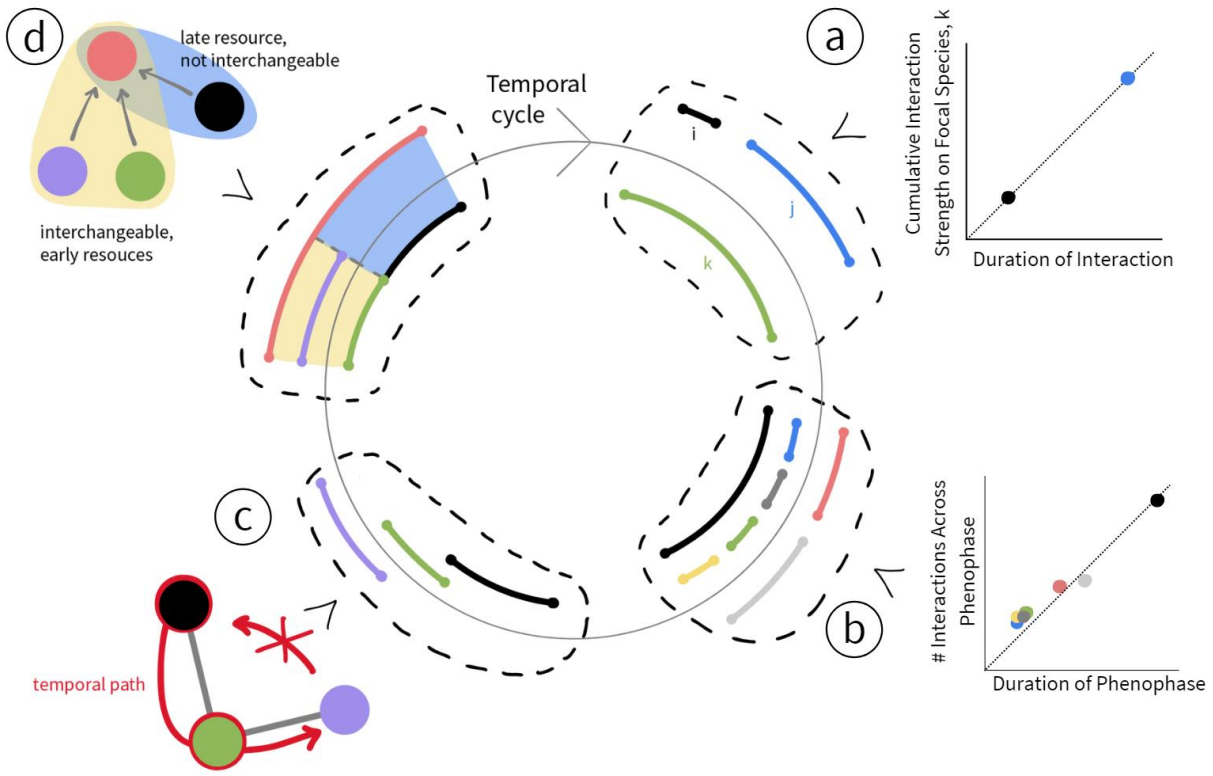


Figure 1. Temporal structure, as defined by the sequence and duration of and between events, influences many aspects of species interactions. Our four examples (a-d) may happen simultaneously or in different orders and were arranged arbitrarily along a cyclical rather than linear timeline to emphasize 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)** The temporal overlap/co-occurrence of species determines how long species interact which is positively correlated (e.g. linear) with the strength of interactions (effect of species *j* vs *i* on green species, $\alpha_j > \alpha_i$). **(b)** How long species are present (length of phenophases) typically correlates positively with the number of interactions per species (e.g. black species has more interaction than green or grey). **(c)** 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. **(d)** Consumers that appear as generalists in static networks (coral) often feed on resources that occur during different periods (purple, green, black) and thus are not interchangeable.

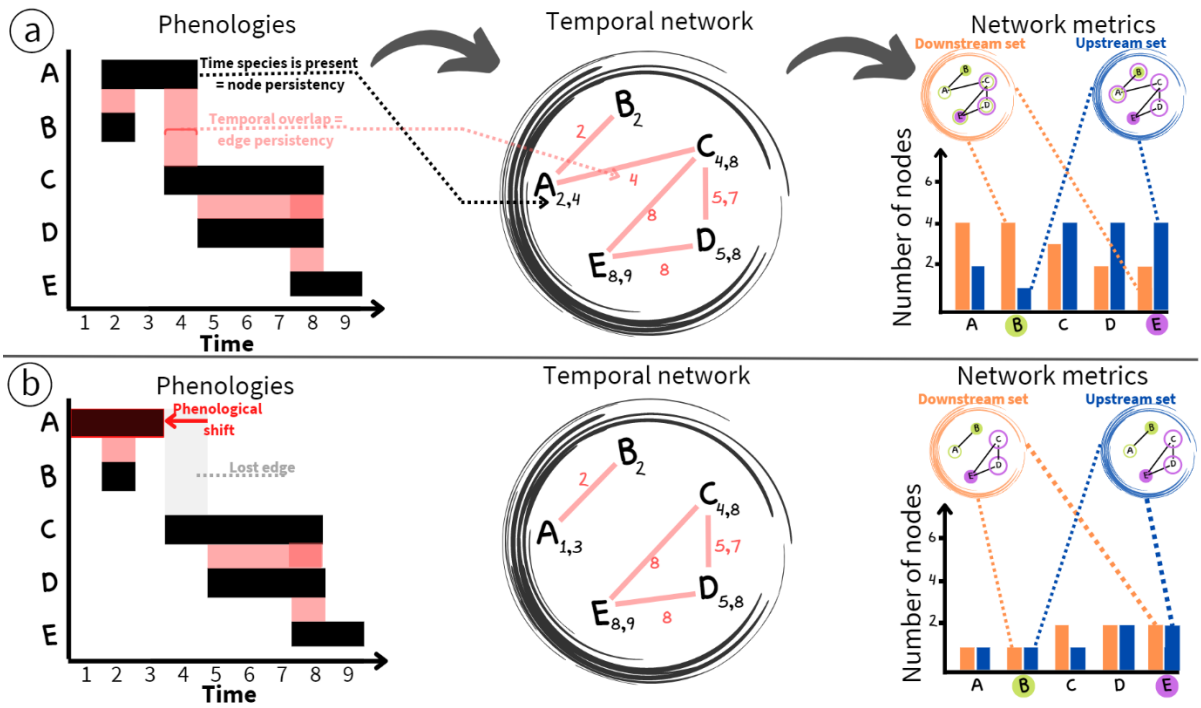
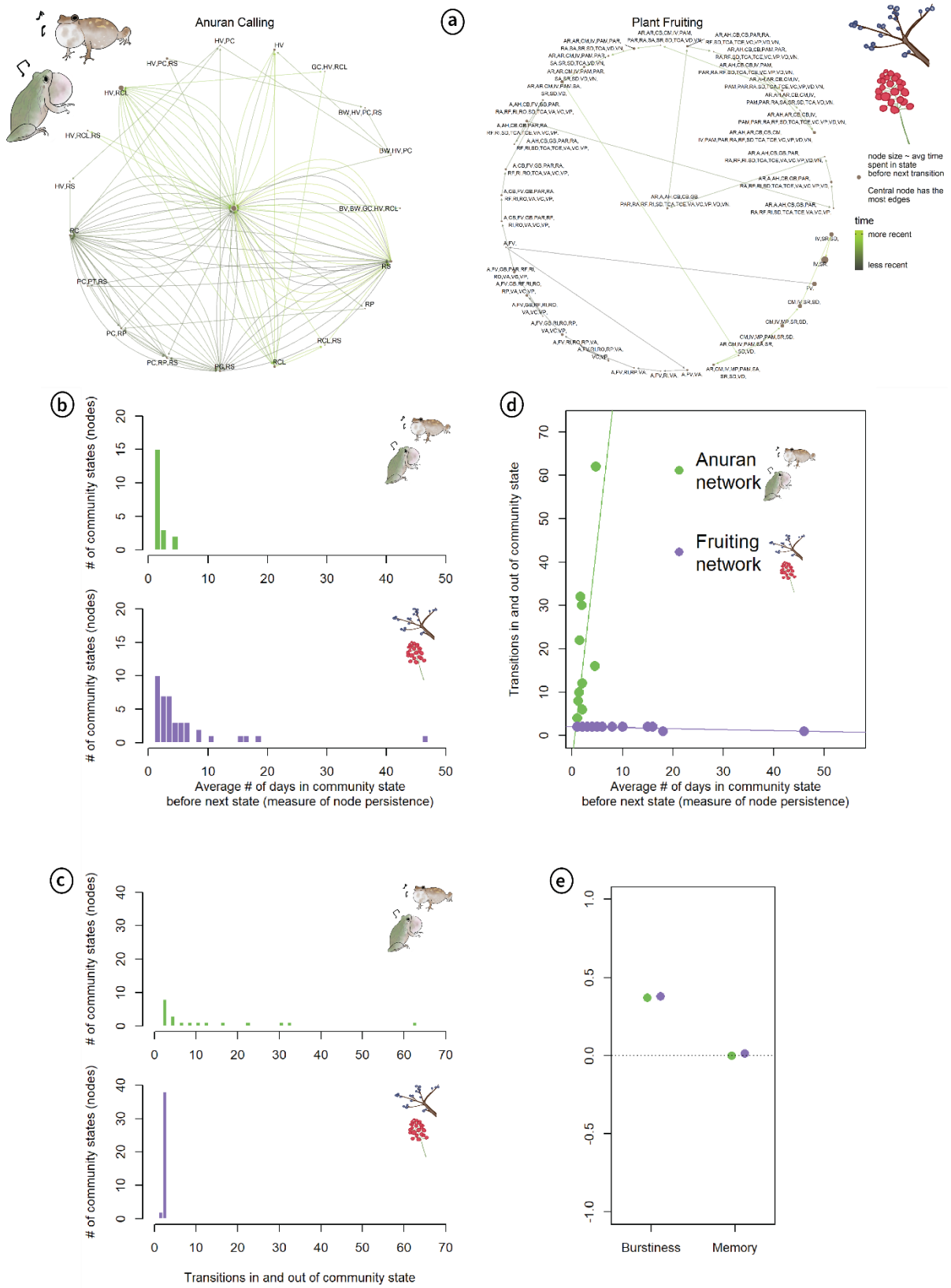


Figure 2. Steps to build, analyze, and compare temporal networks using phenology data. The start and end date of a phenophase are used to quantify when species are present and active in a community (black bars in left column). This is recorded for all species in a community. We than can calculate the temporal overlap/co-occurrence of species (red bars). From a network perspective, length of the phenophase (black bar) and overlap (red bar) indicate the persistency of nodes and links respectively. This phenology data is then used to build temporal networks of communities (middle column), where nodes are species with corresponding time stamps that indicate when a species is present. This can either be a single time point, a time interval with start and end date, or multiple points or intervals if species re-enter a community. Links that connect nodes (species) are given by temporal co-occurrence of species with their corresponding time stamps (red bars). Once these temporal networks are constructed, we can calculate a range of temporal network metrics that explicitly account for the temporal sequence of events (see **Table 1**). For instance, we can find the "downstream set" and "upstream set" for each species (bar graphs on right) to determine how species influence each other given the temporal sequence

of species occurrences/phenologies (see **Table 1** for full definitions). Circular inserts show graphical example of how those two metrics are calculated for focal species B and E, with solid circle indicating a focal species and open circle indicating corresponding (by color) source or set of influence species. These metrics are sensitive to the relative temporal position of a species and sequence of temporal overlap. They not only provide new insights into basic temporal structure of communities but can also be used to gain deeper understanding of functional role of species. For instance, species that appear earlier often have a larger downstream set of nodes but a smaller upstream set than species that appear late (e.g. B vs E in 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 shifts in a single species can therefore lead to dramatic changes in network structure and metrics, especially when this results in the loss of an link that connects temporally separated groups of species (e.g. 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.


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
# of community states (nodes)
Transitions in and out of community state
d
Transitions in and out of community state
Anuran network
Fruiting network
Average # of days in community state before next state (measure of node persistence)
e
Burstiness
Memory

552

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 size of the node 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 **Figure 1**). 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. Colors of links indicate the relative order of transitions (light green = near end of calendar year, dark brown = near start of calendar year). The anuran network (left) is based on daily calling data over the course of a ~1-year breeding season at one pond in Texas, USA in the early 2000s [27], while the plant fruiting network (right) comes from Massachusetts, USA based on estimates during 1850-1860 [65]. Frequency plots show 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 1** for metric details).

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Supplement 1

We examine the temporal structure of leafout in seven woody tree or shrub species in Concord, MA [65]. A visual inspection shows that in this system the timing of leafout varies between years and species (**Figure S1**). A more quantitative follow-up might involve computing burstiness and memory of leafout events per year, but given the low number of these events per year, we find value in turning to alternative metrics to assess variation between years. For instance, we can quantify the level of this variation by finding the sequence (relative order) of these events through chronological rank and their relative timing (**Figure S2**). Chronological rank focuses exclusively on the order events and ignores the amount of time between events assigned to different ranks. In **Figure S2a**, we resolve ties in the chronological rankings by averaging the successive ranks the tied species would have been assigned had they not been tied (ex: all 3 species tied for 2nd get the average of ranks 2, 3, and 4; this is known as the "midrank" method). In contrast, relative timing, as calculating here, better accounts for time between leafouts. We calculated the relative timing by dividing when the leafout happened relative to the first leafout of the year (units in days) by the number of days between the first and last leafout of the year. Discrepancies in variation between chronological rank and relative timing would suggest differences in the length of time intervals between different chronological ranks. In turn, an event ranked 2 and not 3 may matter more than an event ranked 6 and not 7, for example. Whether this matters depends on the context under which the metrics get calculated and interpreted. Generally speaking, for the leafout events, **Figure S2** suggests that the sequence of leafout events and the spacing between these events remain conserved across years.

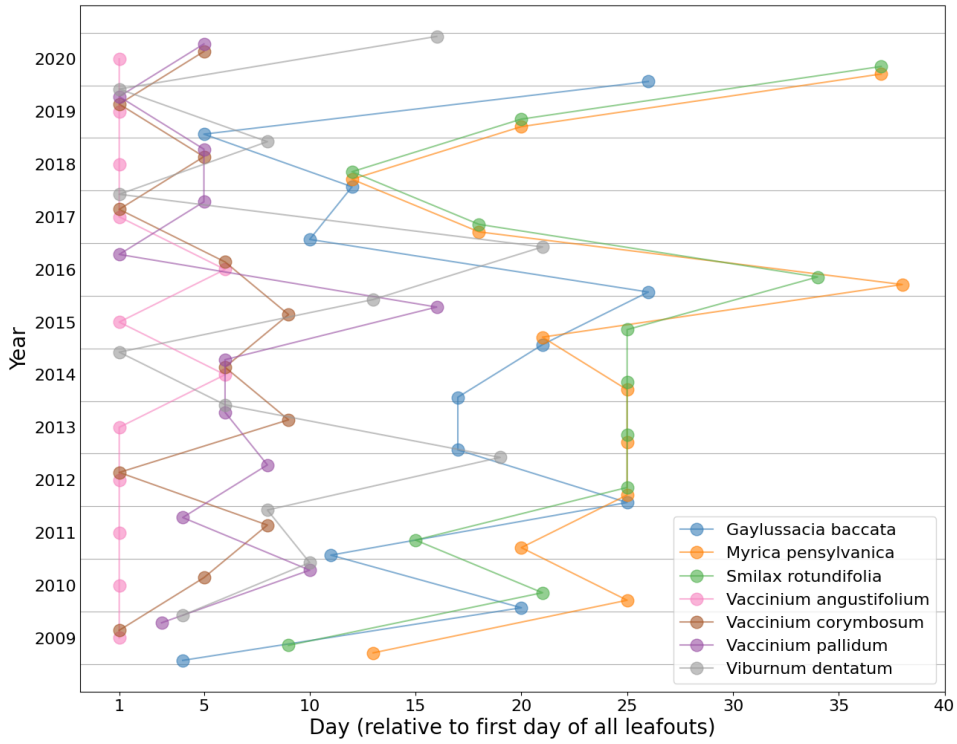

Figure S1. Relative order of leafout events by species in Concord, Massachusetts, USA from 2009 through 2020. Along the x-axis, the species with the first leafout event of a given year gets assigned Day 1. All subsequent leafout events for the other species that year have time points computed relative to Day 1. Along the y-axis, gray horizontal lines separate leafout events by year. The vertical positioning of points within years holds no information beyond helping to visually distinguish points between species.

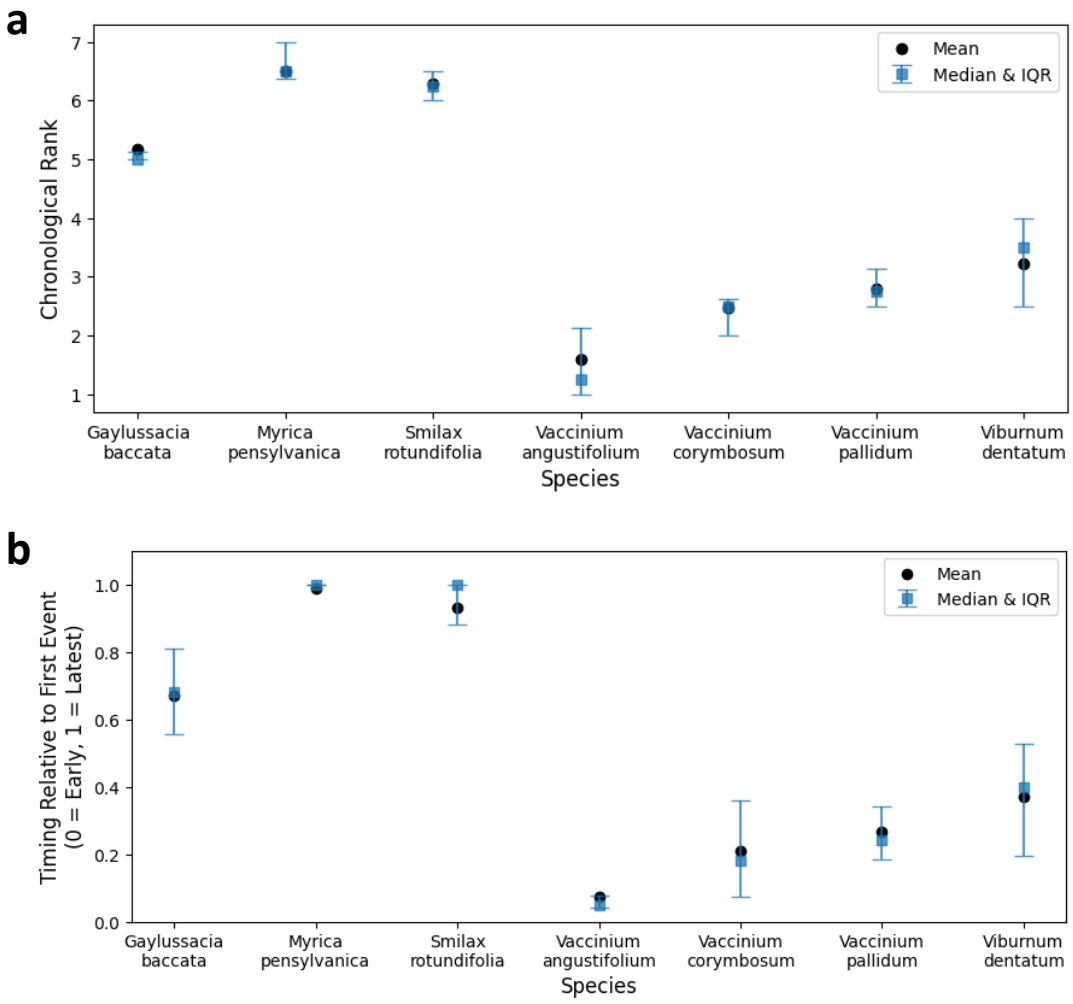

Figure S2. Summarizing the order of leafout events by species in Concord, Massachusetts, USA across years. Black points and blue squares come from computing the mean and median, respectively, of metrics shown on the y-axis in plots **(a)** and **(b)** across 12 years (2009-2020, 1 value per metric per year). Blue error bars capture the interquartile range (IQR), or 25th through 75th percentile of the annual metrics for each species.