

REVIEW AND SYNTHESIS

Seeing through the static: the temporal dimension of plant–animal mutualistic interactions

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Abstract

Most studies of plant–animal mutualistic networks have come from a temporally static perspective. This approach has revealed general patterns in network structure, but limits our ability to understand the ecological and evolutionary processes that shape these networks and to predict the consequences of natural and human-driven disturbance on species interactions. We review the growing literature on temporal dynamics of plant–animal mutualistic networks including pollination, seed dispersal and ant defence mutualisms. We then discuss potential mechanisms underlying such variation in interactions, ranging from behavioural and physiological processes at the finest temporal scales to ecological and evolutionary processes at the broadest. We find that at the finest temporal scales (days, weeks, months) mutualistic interactions are highly dynamic, with considerable variation in network structure. At intermediate scales (years, decades), networks still exhibit high levels of temporal variation, but such variation appears to influence network properties only weakly. At the broadest temporal scales (many decades, centuries and beyond), continued shifts in interactions appear to reshape network structure, leading to dramatic community changes, including loss of species and function. Our review highlights the importance of considering the temporal dimension for understanding the ecology and evolution of complex webs of mutualistic interactions.

Keywords

Ant–plant mutualism, mutualistic networks, plant–pollinator interactions, plant–seed disperser interactions, temporal dynamics, temporal scale.

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“We may perhaps regard the organisms, both plants and animals, occupying any given habitat, as woven into a complex but unstable web of life. The character of the web may change as new organisms appear on the scene and old ones disappear during the phases of succession, but the web itself remains.” Yapp (1922, pp. 11)

“When the factor of time is introduced it is immediately seen that each place has several fairly distinct communities (distinct in characteristic composition of species, not in the sense of possessing entirely different species) which come out and transact their business of feeding and breeding at different times.” Elton (1927 pp. 97–98)

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“Vos siempre cambiando, ya no cambiáis más.” (You are always changing, you’ll never change) El Cuarteto de Nos (2006).

INTRODUCTION

Interspecific interactions link species in space and time to form ecological communities. These interactions determine species coexistence, and the persistence and stability of communities (Cowles, 1899; Elton, 1927; Hutchinson, 1957; Thébault and Fontaine, 2010; Levine *et al.*, 2017; Alroy, 2018). Although there is a widespread appreciation that species interactions can vary substantially through time at multiple scales—from hours, to days, seasons, years, decades and beyond (McMeans *et al.*, 2015; Trøjelsgaard and Olesen, 2016)—our current empirical understanding of species interaction networks still comes predominantly from a temporally static perspective (Polis, 1991; Memmott, 1999; Dunne, 2009; Bascompte and Jordano, 2014). Whereas this temporally static approach to ecological networks has identified a series of general patterns regarding the structure, function and stability of ecological networks (Pascual and Dunne, 2005; Thébault and Fontaine, 2010; Bascompte and Jordano, 2014; Valdovinos, 2019), the processes that determine the structure of ecological networks take place at particular time scales (Fig. 1) (Ricklefs, 1987, 2004). Thus, by aggregating the temporal dimension of species interaction networks, we may be obscuring the underlying biology that we aim to understand, limiting our ability to predict community responses to environmental change.

In this paper, we provide a conceptual road map for exploring, understanding and interpreting temporal dynamics of ecological networks, focusing on plant–animal mutualistic networks: (1) we begin with a synthesis of the literature to date that has considered the temporal dynamics of plant–animal mutualistic networks; (2) we then discuss the general mechanisms underlying temporal variation in interactions at multiple temporal scales; and (3) we end by considering

research frontiers in the study of temporal networks. Throughout, we argue that a more thorough understanding of the temporal dimension of these networks will provide insight into the basic ecology and evolution of species interactions and improve our ability to forecast species interactions, their stability and the functions they provide in light of rapid global change.

A LITERATURE REVIEW OF TEMPORAL DYNAMICS IN PLANT–ANIMAL INTERACTION NETWORKS

Summary of the studies and the temporal scales they investigate

The increasing availability of studies explicitly considering the temporal dynamics of plant–animal mutualistic networks provides the opportunity for the synthesis of this body of research. To this end, we surveyed the literature for studies of plant–pollinator, plant–seed disperser and plant–ant mutualistic networks (through August 2019) that focused explicitly on the temporal dimension: studies addressing a question referring explicitly to some aspect of time and considering temporally explicit network data. We included studies concerning the effect of temporal data aggregation on various network properties (e.g. Basilio *et al.*, 2006; Petanidou *et al.*, 2008; Vizentin-Bugoni *et al.*, 2016; Sajjad *et al.*, 2017), and excluded those that considered phenology but focused only on aggregate static networks (e.g. Vázquez *et al.*, 2009b; Vizentin-Bugoni *et al.*, 2014). A complete list of the studies included in our survey is available in Table S1. We begin with a brief summary of the temporal scales investigated in these studies, and then discuss the types of questions researchers have explored and the general patterns emerging from these studies.

Our survey revealed 75 studies that investigated the temporal dynamics of plant–animal mutualistic networks. Most studies focused on plant–pollinator mutualisms ($n = 52$), whereas a smaller subset of studies focused on seed dispersal ($n = 11$) and plant–ant mutualisms ($n = 12$; Fig. 2a). The majority of these studies addressed within-year temporal

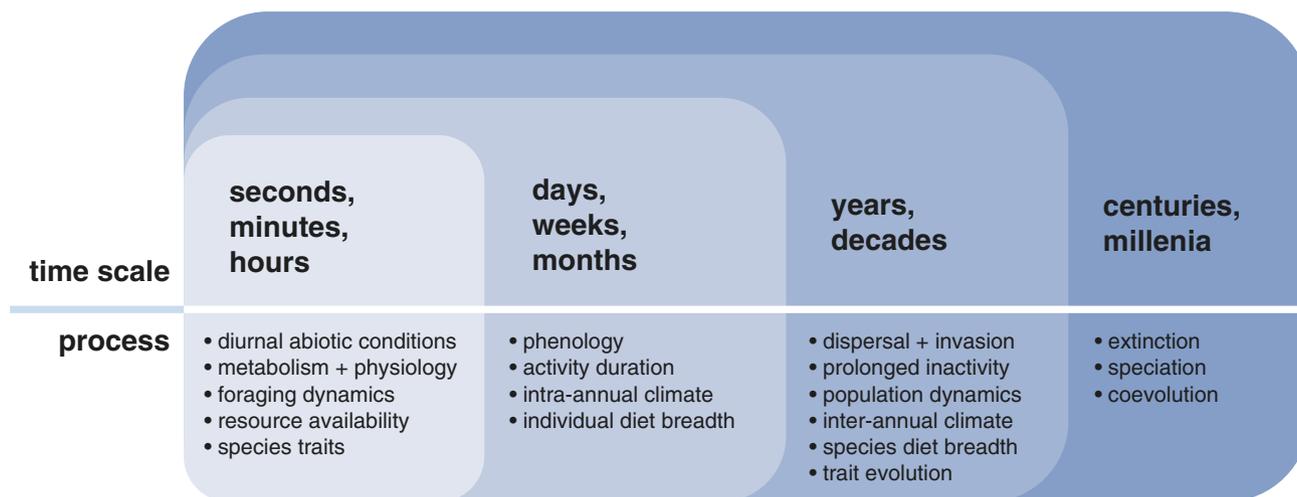


Figure 1 Conceptual road map of the ecological and evolutionary processes that occur at different time scales. Although processes are put into discrete categories here, many are likely to operate over a range of time scales (e.g. for an individual, diet breadth may be best represented over days, weeks, or months, but for a species, diet breadth may be better represented by years or decades).

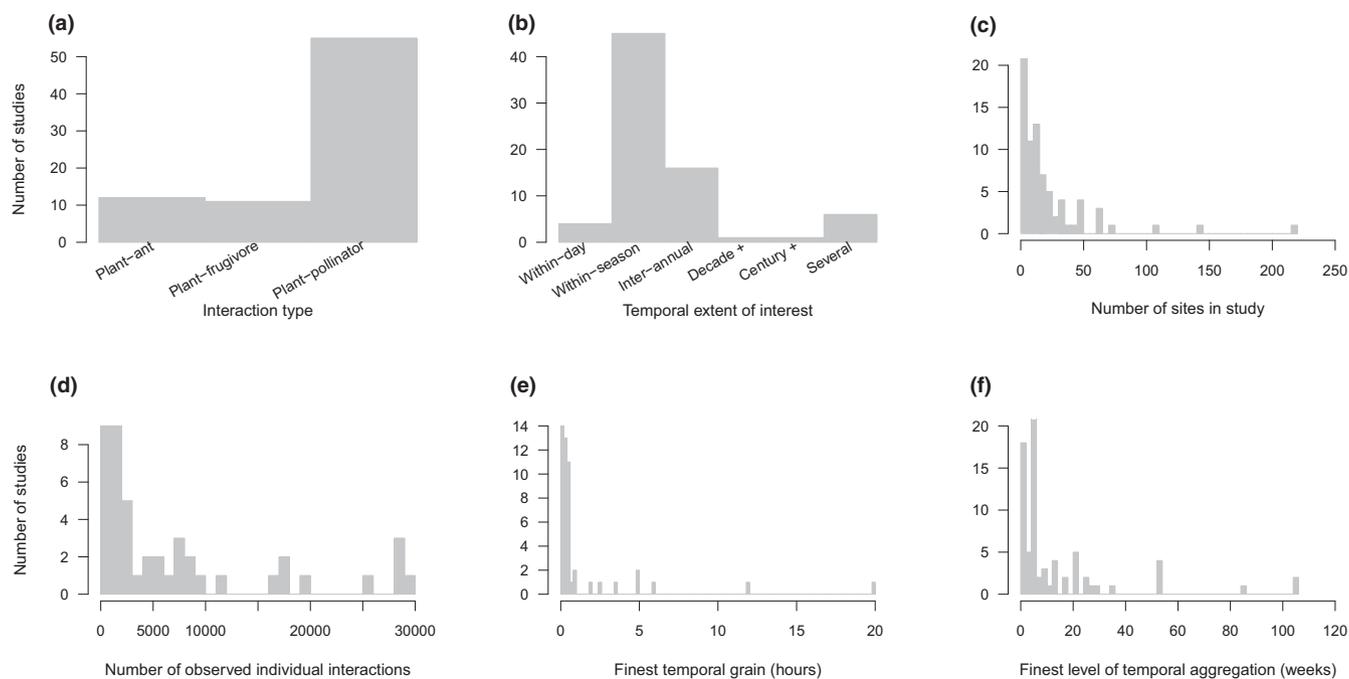


Figure 2 A quantitative summary of studies investigating the temporal dynamics of plant–animal mutualistic networks. (a) Number of studies in each of the types of plant–animal mutualistic interactions considered in our review. (b) Temporal extent of interest. (c) Number of sites included in each study. (d) Number of interactions (e.g. animal visits to a plant) recorded per study. (e) Finest sampling grain of each study in hours. (f) Finest level of temporal aggregation of each study in weeks.

dynamics ($n = 44$), followed next by those that explored inter-annual temporal dynamics ($n = 16$), and few conducted at finer or broader temporal scales (Fig. 2b). Thus, although the broadest temporal extent (the time span of a study; see Box 1 for definitions) included in our literature survey was 120 years (Burkle *et al.*, 2013), 37% of studies had a temporal extent of 1 year or less, 65% 2 years or less, very few more than 3 years, and even fewer a decade or more (Fig. 2b; Table S1).

Most studies were spatially replicated, although the number of sites included ranged widely (Fig. 2c). There was substantial variation in the number of observed interactions, with the majority of studies including fewer than 10 000 individual interactions (e.g. the total number of flowers visited or fruits consumed) and some including nearly 30 000 (Fig. 2d). For most studies, the finest reported temporal grain (the minimum temporal resolution of data collection; see Box 1) ranged from 1 to 30 min (Fig. 2e). Because interaction sampling at the finest temporal grain is likely to be an incomplete representation of the interaction network, it was common for studies to aggregate interaction data across multiple sampling periods prior to analysis (Box 1). The most common temporal analysis grain was 4 weeks or fewer (Fig. 2f). Virtually all studies aimed at documenting some pattern of temporal variation in species interactions and network structure (or both), but most studies also went beyond pattern description, additionally exploring potential mechanisms underlying temporal network dynamics (Table S1).

Because of the central importance of sampling effects in the interpretation of ecological patterns (e.g. Blüthgen *et al.*, 2006, 2008; Vázquez *et al.*, 2009b; Vizentin-Bugoni *et al.*, 2014; Fründ *et al.*, 2016; Schwarz *et al.*, 2020), it is important

to address whether the attributes of scale discussed in the preceding paragraphs are related to the detection of interactions and could therefore lead to sampling artefacts. For example if the detection of interactions in networks is related to attributes of temporal scale (such as temporal sampling grain, temporal analysis grain and temporal extent; Box 1), we may expect that at broader temporal scales, and with more sampling, there would be an increase in the detection of interactions, which may therefore bias patterns of network structure. In a recent meta-analysis, Schwarz *et al.* (2020) investigated the temporal scale-dependence of the structure of 30 temporally resolved plant–pollinator networks, finding that the completeness of interaction sampling did not change with the temporal extent of studies nor the temporal scale of data aggregation. Additionally, Schwarz *et al.* (2020) found that temporal variation in network structure was related to variation in species richness, which increased with sampling effort, and species turnover, which increased with temporal extent. Yet, although species richness and sampling effort were important predictors of temporal variation, these two factors were insufficient to explain why network structure changes across temporal scales. As a simple test of sampling effects in the studies included in our literature review, the total number of interactions recorded within studies (i.e. the total number of animal visits to plants, such as the number of flowers visited by pollinators, the number of fruits removed by seed dispersers or the number of individual ants recorded at plants) exhibited a weak positive correlation with the temporal sampling grain at which the data were collected (Spearman's $r = 0.14$), a weak positive correlation with the temporal analysis grain (Spearman's $r = 0.26$) and a moderate positive

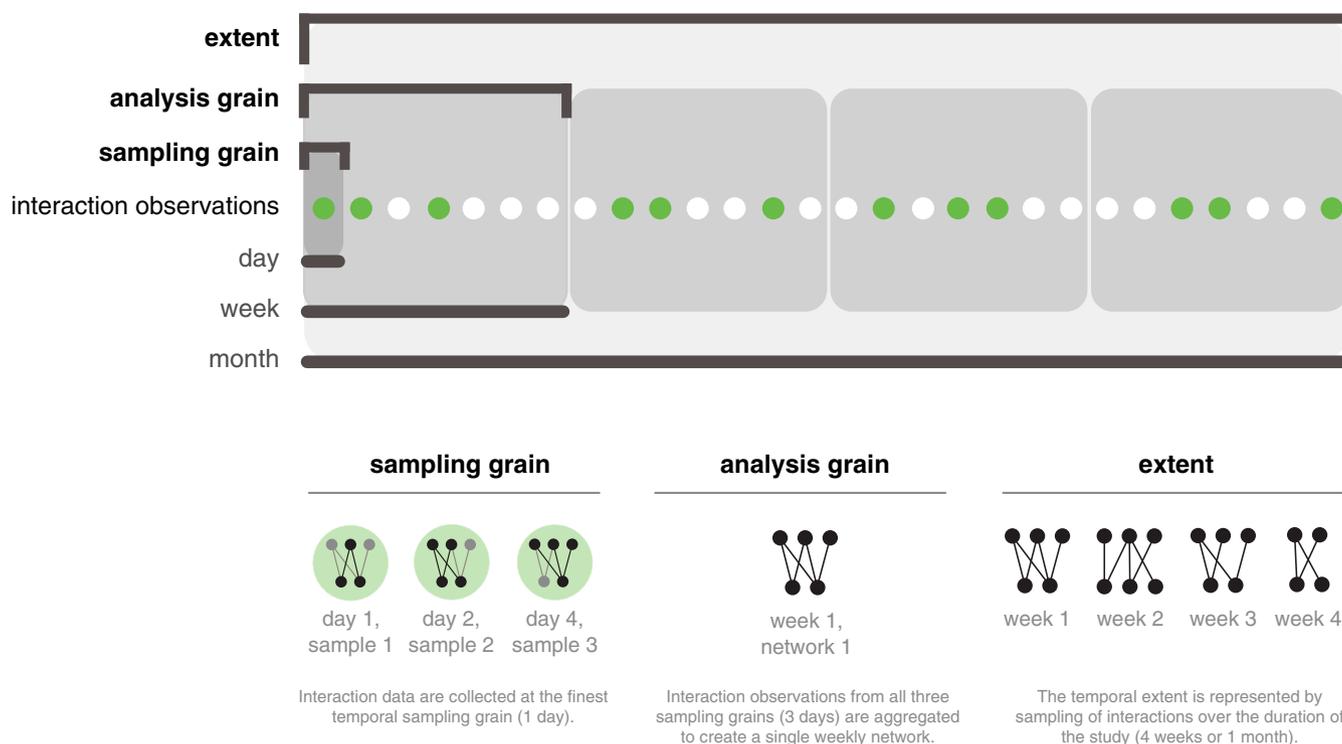


Figure 3 (Box 1). Concepts of temporal scale relevant to the study, analysis and interpretation of ecological networks.

Box 1. Defining temporal scales.

Scale is of fundamental importance in ecology and evolution. The term 'scale' is used frequently, yet its various meanings and definitions are similarly numerous. As in spatial ecology (Forman and Godron, 1986; Turner, 1989; Wiens, 1989), there are several attributes of temporal scales that are relevant for ecological and evolutionary processes. Three concepts of temporal scale are relevant to the study, analysis and interpretation of temporal variation in interaction networks (i.e. sets of time-slice networks): (1) *temporal sampling grain*, (2) *temporal analysis grain* and (3) *temporal extent* (Fig. 3). *Temporal sampling grain* and *extent* are both properties of the data and sampling methods, whereas the *analysis grain* is a property of the analysis.

The *temporal sampling grain* refers to the minimum temporal resolution at which data were gathered and temporal information is preserved. In this illustrated example, the sampling grain is represented by a single day of interaction sampling, whereby all interaction observations are pooled within a single day at the time of data collection. The *temporal analysis grain* (i.e. the level of data aggregation) is the temporal resolution over which the investigator decided to aggregate the data for the purposes of analyses; the level of aggregation could be the same as sampling grain (i.e. a single day), but is often of a coarser temporal resolution because of the need to include replicated samples to construct meaningful networks. In our illustrated example (Fig. 3), the analysis grain is represented by a week, whereby all daily interaction observations are pooled to construct a single weekly network.

The *temporal extent* refers to the total time span encompassed by the study. Here, the temporal extent is represented by 4 weeks (or 28 days) over which interaction sampling occurred. In practice, temporal extent can be thought of in more than one way. For example the maximum temporal extent deals with the total duration of the study from the first day of sampling until the last, whereas the representative temporal extent deals with the biological timeframe encompassed by the study (here, 1 month, 1 season, or 1 year, depending on the research question). An additional component of temporal scale that is relevant for the study of temporal variation in interaction networks is *temporal sampling frequency*. In our illustrated example, the temporal sampling frequency can be defined as three sampling events per week.

Depending on the goals of the study, the level of aggregation may change. As an alternative example, if the research question was to investigate day to day temporal variation, the analysis grain would be represented by networks constructed from interaction observations from a single day (and therefore, the sampling grain and temporal extent would still remain the same).

[Correction added on 2 November 2020, after first online publication: the position of Box 1 has been corrected.]

correlation with temporal extent of the study (Spearman's $r = 0.51$). In other words, interaction detection does increase somewhat as the temporal sampling grain and the temporal extent of the study increases, suggesting that the detection of interactions may be at least partly influenced by these attributes of temporal scale. However, these relationships are relatively weak overall, and a substantial fraction of the variation in interaction frequency appears to be independent of the temporal scale at which the data were collected and analysed. Consistent with the meta-analysis conducted by Schwarz *et al.* (2020), these findings suggest that sampling effects have relatively minor effects on the detection of interactions in plant–animal mutualistic networks, and most important, that sampling effects are unlikely to explain all the observed variation in network structure across different temporal scales.

Synthesis of primary findings

Within-day temporal dynamics. The general pattern emerging from *within-day* studies is that the composition and structure of mutualistic interaction networks can vary substantially over the course of a single day. However, to date, relatively few studies have focused on these very short time scales ($n = 5$); nevertheless, it appears that within-day variation is related to the relatively rapid (behavioural) response of both plants and animals to changing biotic and abiotic contexts (e.g. temperature, light). For example Fründ *et al.* (2011) found that the composition of plant–pollinator interactions in meadow sites in southern Germany can change from morning to afternoon as a result of pollinator-mediated flower closure and a concomitant shift in pollinator behaviour in response to reduced floral resources later in the day. Similarly, Baldock *et al.* (2011) found that the network properties of plant–pollinator interactions in a Kenyan savanna habitat can progressively change over the course of a day. Here, variation in network structure may derive from changes in pollinator activity and resource use throughout the day, as well as changes in the availability of floral resources (Willmer and Stone, 2004; Fründ *et al.*, 2011; Ogilvie and Forrest, 2017). As a final example, in a comparison between diurnal and nocturnal moth–pollen transport networks in a boreal pine forest, Devoto *et al.* (2011) observed that although the structural properties of these networks varied little between day and night, there was substantial variation in interaction composition among moths and the plants they visited.

Within-year (and within-season) temporal dynamics. The general pattern emerging from *within-year* studies is that there is considerable turnover of mutualistic interactions from day to day, week to week and month to month, and such variation can contribute strongly to variation in the structural properties of these networks. For example CaraDonna *et al.* (2017) observed high week to week turnover of plants, pollinators and their interactions across the summer growing season within a subalpine ecosystem; such temporal turnover of species and their interactions gives rise to substantial temporal variation in both the structural properties of the interaction networks and the structural positions of species within these networks (CaraDonna and Waser, 2020). Within-season variation appears to be related to

temporal variation in species phenology (i.e. activity periods), abundance and traits that occur within a season, although the importance of each likely depends on the particular system. Within-season studies have also quantified the contribution of interaction rewiring (i.e. interaction flexibility) to the turnover of interactions, revealing that it can account for a lot of interaction turnover in some ecosystems (CaraDonna *et al.*, 2017), but less so in others (Simanonok and Burkle, 2014). To date, many studies have explored *within-year* variation in network structure (Fig. 2b). These studies typically aggregate interaction networks over various time spans, including a single day (Olesen *et al.*, 2008; Rasmussen *et al.*, 2013), 1 week (Simanonok and Burkle, 2014; CaraDonna *et al.*, 2017; CaraDonna and Waser, 2020), 2 weeks (Carnicer *et al.*, 2009; Kaiser-Bunbury *et al.*, 2010), 1 month (Cuartas-Hernández and Medel, 2015; Ramos-Robles *et al.*, 2016) or several months (Plein *et al.*, 2013). The discrepancies in temporal data aggregation procedures across these studies appear to be based on the seasonal dynamics of the different study systems, the specific research question being addressed, as well as logistical and sampling constraints (Olesen *et al.*, 2008; Carnicer *et al.*, 2009; Cuartas-Hernández and Medel, 2015; Ramos-Robles *et al.*, 2016).

Several additional studies took an alternative approach to investigate the temporal dimension of *within-year* mutualistic networks (Vázquez *et al.*, 2009b; Olesen *et al.*, 2011a; Vizenin-Bugoni *et al.*, 2014; Olito and Fox, 2015; Biella *et al.*, 2017; Peralta *et al.*, 2020). These studies did not focus explicitly on *within-year* temporal variation as stated above, but instead implicitly considered the temporal dimension of aggregated interaction networks by incorporating phenological overlap between plants and animals. This approach allows researchers to assess the importance of among-species phenological variation for interaction probabilities and ultimately network structure. Collectively, these studies provide indirect evidence that *within-year* temporal variation consistently plays an important role in determining the overall structure of cumulative interaction networks.

Inter-annual temporal dynamics. The general pattern emerging from *inter-annual* studies of mutualistic networks ($n = 16$; Table S1) is that there is high turnover of species and interactions from year to year, but low variation in network structure. In other words, the structural properties of interaction networks can remain relatively stable from 1 year to the next even with substantial changes in the composition of species and their interactions (Petanidou *et al.*, 2008)—a pattern that contrasts to what is observed within-years (e.g. CaraDonna and Waser, 2020). This inter-annual variation may in part result from the relatively low inter-annual turnover among species forming the network core, and relatively high rates of turnover among peripheral species (Petanidou *et al.*, 2008; Díaz-Castelazo *et al.*, 2010; Olesen *et al.*, 2011b; Fang and Huang, 2012; Chacoff *et al.*, 2018). Interestingly, however, in an analysis of the interannual dynamics of a plant–pollinator network over 6 years, Miele *et al.* (2020) found that the structural positions occupied by species within the network change widely among years, so that species forming the network core during some seasons and years are peripheral in other seasons and years. Similarly, Ponisio *et al.* (2017) found that even the

most persistent pollinator species were also highly variable in terms of their network position. These findings indicate that structural positions of species within the network can change widely among years.

Temporal dynamics at the broadest temporal scales. The limited evidence available (two studies, Table S1) suggests that mutualistic networks can change dramatically in terms of species and interaction composition over broad temporal scales, while exhibiting only modest change in aggregate structural properties. For instance Díaz-Castelazo *et al.* (2013) studied mutualistic ant-plant interactions across two decades (1989–1991, 1998–2000 and 2010–2011), finding that although there was considerable change in species and interaction composition, network structure remained constant. Here, network nestedness, connectance and modularity all remained virtually unchanged across the three time slices over 20 years even as highly connected species (i.e. network hubs) shifted. Interestingly, these temporal patterns observed across two decades are similar to those occurring across fewer years (<10), suggesting that network structure may persist with relatively high turnover of species and interactions for many years. However, at the even broader temporal scale of a century, and in conjunction with dramatic environmental change, network structure appears to be more dynamic. Using a series of historic datasets, Burkle *et al.* (2013) investigated how environmental change influenced a plant–pollinator network over a 120-year time period. Environmental change (climate change and habitat loss) led to pollinator extinctions, loss of interactions and the formation of new interactions among remaining species. All these changes together contributed to changes in network structure (lower nestedness) and loss of function (reduced pollination quality).

Given that longer-term interaction data are generally unavailable, alternative approaches can be employed to help illuminate what may happen over substantially broader temporal scales that far exceed any research program and the life of a single researcher. For example Albrecht *et al.* (2010) used a space-for-time-substitution approach to study the assembly of plant–pollinator networks across a deglaciation chronosequence in Switzerland, representing a temporal extent of approximately 8–130 years. This study revealed that community and interaction diversity increased with time since deglaciation (a major environmental change), and that the pollination networks became more generalised and more nested. This approach provides valuable insight, but we do note that a space-for-time-substitution is an imperfect proxy for the temporal dimension, as pollinator individuals can easily move among different stages of the chronosequence.

Another alternative approach to reconstruct historic mutualistic networks is to use palaeontological data. For example Pires *et al.* (2014) combined contemporary ecological and palaeontological data to reconstruct megafaunal seed-dispersal interactions in Brazil over a 12 000-year period and compared these palaeo networks to modern day networks. Interestingly, similar research conducted on antagonistic predator–prey networks (food webs) indicates that although structural properties of Pleistocene and modern-day networks may be similar, changes in the composition of species and their traits in response to species extinctions and human activities rendered the networks

more susceptible to collapse (Pires *et al.*, 2015). While such research has suggested that network structure may have played a role in megafaunal extinctions at the end of the Pleistocene, ‘the past is foreign’, and hence network reconstructions always remain uncertain to some degree (Telford *et al.*, 2016).

Theoretical modelling approaches are yet another way in which to study temporal dynamics of ecological networks over the broadest temporal scales. For example there are several modelling approaches that make predictions of network responses to perturbations over long time frames (reviewed in Valdovinos, 2019). Such theoretical models rely on realistic representations of the basic ecology of species interactions and the consequences of these interactions for population dynamics. Although these models build on empirical interaction data collected over relatively short time spans (e.g. several years), they still represent powerful tools to explore network dynamics and responses to perturbations over time spans that would be unfeasible to study empirically.

Given the rarity of long-term interaction datasets, alternative approaches are necessary to improve our understanding of the temporal dynamics of mutualistic networks at the broadest temporal scales (Fig. 1). Due to the dearth of data to fully parameterise mathematical and computational models, we still contend that there is no replacement for empirical long-term studies, which are essential for understanding and forecasting the long-term dynamics of ecological interactions under the rapid global change currently underway.

MECHANISMS DRIVING TEMPORAL VARIATION IN INTERACTIONS

The great temporal variation in plant–animal mutualistic interactions described earlier leads to the question of how and why such variation occurs. Mechanistically, a link can be gained or lost due to changes in the presence–absence of species within the community or because species that are present switch their interaction partners. For example at finer time scales, interactions are gained and lost as new species become active and inactive from seconds to months; at broader time scales, interactions are lost because not all species are active in every year, and because of prolonged inactivity or local extinctions; and at the broadest time scales, interactions are gained because new species successfully immigrate to the community, or emerge via *in situ* speciation. Although the proximate mechanisms of link dynamics are essentially the same across temporal scales, the specific drivers (ultimate mechanisms) underlying the gain and loss of links, as well as their implications for network structure, can vary widely. For simplicity, we focus our discussion of the drivers of temporal variation in interactions to how links are gained or lost, but in all cases, the same ideas can be extended to changes in the link intensity.

Evolutionary processes that generally occur over very long time periods set the stage for interactions to play out by placing constraints on which species co-occur in time (and space), and which traits allow or prevent the formation of interactions (although the evolution of novel traits can also occur over much finer time scales; see below). Across all temporal scales, the gain and loss of interactions among species depend

on a series of trait-mediated filters. First, species must temporally co-occur, which means they must have matching physiological requirements that determine their activity over the course of a single day, a season and multiple years. Once the condition of temporal co-occurrence is met, the formation of interactions will be constrained by other interaction relevant traits (e.g. morphology) that allow for the formation of certain interactions, and prevent the formation of others. Finally, even if these conditions have been met, species must be present at a sufficiently high abundance for interactions to occur (i.e. a species may be functionally absent if its abundance is too low to be encountered by potential interaction partners). Thus, it is important to understand how the different traits of species, which are shaped by evolutionary processes, set the stage for the realisation of interactions within local communities at various temporal scales, thereby shaping the emergent structure of the network.

At the finest temporal scales (seconds, minutes, hours), links form and dissolve rapidly due to changes in the activity or inactivity of species within a community. Over the course of a single 24-h day, a physiological window of activity for animals and plants will be set first by abiotic conditions, such as temperature, light and precipitation (e.g. Ewusie and Quaye, 1977; Stone *et al.*, 1999). Within this window of opportunity, over the course of seconds, minutes and hours, an active animal makes specific foraging decisions involving the temporal availability of resources across the landscape (e.g. Dukas and Real, 1993; Waser *et al.*, 2018). When and how different animals navigate a given resource landscape will be influenced by species-specific physiology and energetic demands (e.g. metabolism, body size), as well as competition among other foraging animals (Calder, 1984; Stephens and Krebs, 1986). For example for a desert solitary bee, daytime temperature variation creates a window of foraging opportunity, but foraging patterns within this window are based upon the daytime variation in floral food resources (Stone *et al.*, 1999). Similarly, in a controlled greenhouse experiment, bumblebees showed daytime variation in their floral resource use, whereby links are formed first among the highest quality resources, and when no longer available, are replaced with lower quality resources (Vaudo *et al.*, 2014). Once plants are functionally active, they can alter the formation of interactions with animal mutualists over seconds, minutes and hours by varying the presence and availability of rewards, often in response to forager activity. For example many species of flowering plants are able to modify their rewards over the course of the day by making them available only at certain times (Stone *et al.*, 1999; Fründ *et al.*, 2011), by replenishing rewards intermittently throughout the day (Luo *et al.*, 2014), or by replenishing rewards only after they have been removed (Castellanos *et al.*, 2002). For both plants and animals, these time-variant strategies influence which links are gained or lost, and ultimately the overall structure of the interaction network at the scale of a single day (Fig. 4).

Over somewhat broader temporal scales, from several days, to several weeks, to several months, the gain or loss of interactions will depend on which species temporally co-occur over the course of a season (as well as their traits and relative abundances; Vázquez *et al.*, 2009a, b). In other words, the abiotic and biotic factors that give rise to species' activity

times within a season will determine phenological overlap among species, which will ultimately constrain the potential for interaction formation. For example in highly seasonal ecosystems, the short flowering period of plant species and the brief flight periods of many pollinator species strongly contribute to the rapid gains and losses of plant–pollinator interactions across the growing season (Olesen *et al.*, 2008; Simanonok and Burkle, 2014; CaraDonna *et al.*, 2017). Even in ecosystems with less pronounced seasonality (e.g. tropical ecosystems) where species are active for much longer periods of time (e.g. several months), there can still be considerable variation in which interactions form at any given time (e.g. Kaiser-Bunbury *et al.*, 2014). In any ecosystem, once the condition of phenological overlap is met, morphological traits, variation in species abundances, and species interaction flexibility can all come in as important determinants of which interactions form (Kaiser-Bunbury *et al.*, 2014; Simanonok and Burkle, 2014; CaraDonna *et al.*, 2017). The relative importance of these factors will likely depend on their relative magnitude of variation, as factors with greater variation are arguably more likely to be important determinants of the occurrence of interactions and their functioning (Vázquez *et al.*, 2005; CaraDonna *et al.*, 2017; Chávez-González *et al.*, 2020).

At the temporal scale of years and decades, links are gained and lost via interannual variation in the presence and absence of species. Processes driving interannual variation in the presence or absence of species (as well as their abundance) includes population dynamics and inter-annual climate variation, which may represent directional trends, periodicity or perturbations. For example interannual variation in drought conditions may drive the presence or absence of numerous species within a local community (e.g. Tilman and El Haddi, 1992; Minckley *et al.*, 2000). Obviously, if species are absent year to year, then none of their interactions will form; yet in their absence, new interactions may form among the remaining species. More dramatically, prolonged abiotic change, or large-scale perturbations, can lead to the local extirpation of a species, which will necessarily lead to the loss of its interactions; on the other hand, these same conditions may result in the arrival of a new species via invasion or dispersal, which will result in the establishment of new interactions with the resident species (Olesen *et al.*, 2002; Lopezaraiza-Mikel *et al.*, 2007; Aizen *et al.*, 2008; Bartomeus *et al.*, 2008; Vilà *et al.*, 2009; Kaiser-Bunbury *et al.*, 2011; Burkle *et al.*, 2013). Which interactions do form among temporally co-occurring species in any given year will again depend on the abundance of species that are present and the expression of their phenological and morphological traits. Interestingly, however, all of this variation in interannual gain or loss of interactions contributes to only minimal interannual variation in network structure (Petanidou *et al.*, 2008; Chacoff *et al.*, 2018). Finally, the evolution of novel traits from one year to the next may also give rise to the formation of new interactions or the loss of others. For example Schemske and Bradshaw (1999) found that a mutation in a gene with a large effect on *Mimulus* flower color resulted in an 80% decline in bee visitation to these flowers. Similarly, Ramsey (2011) found that genome duplication resulted in a substantial increase in the

Mechanisms of temporal change

Species pool changes

- active species
- inactive speices
- dispersal or invasion
- speciation
- extinction

Interaction changes

- active link
- inactive link
- link gain or loss due to rewiring
- link gain due to dispersal or speciation
- link gain or loss due to species turnover

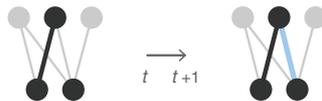
Interaction changes occurring at different temporal scales

cumulative (static) interaction network



The cumulative interaction network is a static representation of all of the observed interactions among all species across a given time period. For simplicity, the cumulative network is defined here as all of the interactions among resident species over many years. In practice, defining the cumulative network depends on the question of interest, as observing all interactions among every possible species across all time periods is logistically challenging.

seconds, minutes, hours



An interaction is gained between two active species over seconds, minutes, or hours. ●

days, weeks, months



Interactions are gained as new species become active within a year. ●

Interactions are lost as species become temporarily inactive within a year. ●

An interaction is lost due to rewiring. ●

years, decades



Interactions are gained as new species become active over years or decades. ●

Interactions are gained due to dispersal (or invasion) of a new species. ●

Interactions are lost as not all species are active in every year. ●

centuries, millenia



Interactions are gained among new species due to speciation. ●

Interactions are lost due to the permanent extinction of species. ●

Figure 4 Conceptual diagram illustrating the various mechanisms underlying changes in interactions occurring at different temporal scales. The illustrations of interaction changes within each network are meant to provide examples of change that are characteristic of different temporal scales (i.e. these changes are not exhaustive).

flowering duration of *Achillea millefolium*, which can promote the formation of many new interactions. Although the evidence presented in these two studies is indirect, both cases provide clear evidence that trait evolution (from one year to the next) is likely to bring about interaction changes.

At the broadest temporal scales—over several decades, centuries and millennia—links can be lost due to regional or global extinction of species, and links can be gained due to speciation. For example Burkle *et al.* (2013) observed the loss of many plant–pollinator interactions in response to the regional extinction of approximately 50% of the local bee species. Here, the loss of species and their interactions contribute to changes in network structure that ultimately degrade its stability (Burkle *et al.*, 2013). Over these broader temporal scales, evolutionary and coevolutionary processes can modify life history and phenotypic traits that, in turn, mediate species interactions (Jordano *et al.*, 2003; Thompson, 2005). For instance the evolution of various species traits, such as pollinator tongue length and floral corolla size and shape, or animal mouth size and fruit size, will depend on the community context and will allow (i.e. phenotypic match) or prevent (i.e. phenotypic mismatch) interactions between those species when they encounter each other (Darwin, 1862; Guimarães *et al.*, 2011; Lomáscolo *et al.*, 2019).

It is also critical to consider that virtually all the mechanisms of interaction formation operating at different temporal scales can be substantially altered by global change. Climate change, land-use change and species invasions all have the immense potential to influence which species are present, when they are present, and in what abundances—all of which can reshape the formation of interactions and the structure and stability of networks at different temporal scales. Take climate change as one example, which has clear consequences for the physiology, phenology, population abundance and range dynamics of many organisms worldwide (e.g. Walther *et al.*, 2002; Parmesan and Yohe, 2003; Williams and Jackson, 2007; Pörtner and Farrell, 2008). Changes in abiotic conditions (such as temperature increases and reductions in precipitation) can alter the physiology of individual organisms, which can affect interaction formation at the finest scales (e.g. diurnal activity patterns). At somewhat broader temporal scales, species-specific phenological shifts can reshuffle the timing and overlap among potentially interacting organisms within a year, influencing the probability of interaction formation, turnover of interactions and network structure. In addition to shifts in timing, climate-driven changes in inter-annual population abundance can alter the likelihood of interaction formation from one year to the next. Over time, climate-driven range shifts can bring about the introduction of new species within local communities, with the potential to alter who interacts with whom. When all these changes are persistent over the long term, they may lead to evolutionary change in interaction relevant traits (e.g. Miller-Struttman *et al.*, 2015), local extirpation of species, degradation of network structure and loss of ecosystem functions (e.g. Burkle *et al.*, 2013). On the one hand, it is clear that global change has obvious consequences for the mechanisms of interaction formation, and therefore the temporal dynamics of plant–animal mutualistic networks at various temporal scales, but on the other hand, it

is clear that we are only beginning to understand the full range of consequences resulting from global change.

Finally, we must bear in mind that in addition to the above mechanisms, the network structure we record in our field studies may be also partly result from sampling effects (Vázquez *et al.*, 2009a; Fründ *et al.*, 2016; Dormann *et al.*, 2017). These sampling issues include observer error (distortions of a real ecological pattern resulting from errors made by the observers or from methods they use), sampling incompleteness of interactions, and heterogeneous detection probability of interactions (Vázquez *et al.*, 2009a). As we discuss in the next section, teasing apart real biological mechanisms from sampling artefacts is one of the key future challenges in the study of the temporal dynamics of ecological networks.

RESEARCH FRONTIERS IN THE STUDY OF TEMPORAL NETWORKS

The study of mutualistic networks without consideration of temporal variation overlooks a major dimension of how assemblages of species interact, evolve and respond to change. As we have shown, many studies to date have empirically quantified temporal variation in mutualistic network structure over various temporal scales, from hours, to days, weeks, months, years, decades and beyond (Fig. 2). Our survey of the literature suggests that there are some general patterns that emerge from the study of temporal variation in mutualistic interactions at specific time scales, and such patterns appear to be linked to mechanisms that operate at these specific time scales. Nevertheless, knowledge gaps still remain, and such patterns should be viewed as hypotheses to be tested. As we look ahead, we see three major areas of research frontiers in the study of the temporal dynamics of mutualistic networks: (1) gain a more mechanistic understanding of the factors underlying temporal variation in mutualistic networks, (2) develop and refine analytical tools for the effective study, quantification and prediction of temporal dynamics in mutualistic networks, and (3) make continuous and concerted effort to disentangle true biological patterns from those arising from sampling effort.

The explicit study of the drivers of temporal variation in mutualistic interactions is not only important for understanding their basic ecology and evolution, but it is also necessary for mitigating consequences of global change on these important interactions and ensuring that conservation efforts are most effective. As we have outlined above, there are various proximate mechanisms underlying how interactions are gained and lost from one time point to the next, but accurate prediction of how and why interactions change in any given ecosystem will depend on the understanding of their ultimate mechanisms. For example, what are the relative contributions of abiotic and biotic factors in giving rise to individual species interactions, their temporal flexibility, and the emergent structural properties of a network at different temporal scales? Does the relative importance of these factors vary predictably by ecosystem and mutualism type? In other words, might the temporal dynamics of pollination networks respond to abiotic and biotic variation much differently than seed dispersal networks, and might this play out differently if the mutualistic

network is within the context of an arctic ecosystem compared to a tropical ecosystem? And, critically, how will abiotic and biotic drivers interactively influence mutualistic responses to various global change drivers, including land-use change, species invasion and climate change, all of which occur with characteristic timing, duration and frequency? In particular, how might the interaction patterns that emerge across temporal scales change in response to continued global change? For example we tend to observe inter-annual stability in the structure of plant–animal mutualistic networks, despite relatively high turnover of species and interactions—but might such inter-annual temporal stability breakdown when the mechanisms underlying such patterns continue to shift dramatically (e.g. Burkle *et al.*, 2013)? And although we tend to observe variable network structure and relatively high species turnover within a year, might more extreme changes in abiotic and biotic conditions render networks more susceptible to disturbance at certain times of the year (e.g. CaraDonna and Waser, 2020)?

The rigorous study of the temporal dimension of ecological networks is still in its infancy (Holme, 2015), and as such, there is a need to develop and refine analytical tools for addressing new and outstanding questions. In ecology, most commonly static networks are constructed at a particular temporal analysis grain (Box 1), summary metrics are calculated from these networks, and these metrics are then compared across networks as a means to explore temporal variation in network structure. Another relatively common approach is the quantification of interaction turnover from one time slice to the next, which can help to understand temporal variation in interaction composition. Additional approaches have been developed in other fields (reviewed by Blonder *et al.*, 2012; Holme, 2015) and are now gaining more attention in ecology. For example estimating the flow and spread of perturbations through interaction networks (e.g. presence of an invader or a novel resource; Valdovinos *et al.*, 2009; Kaiser-Bunbury *et al.*, 2010; Arroyo-Correa *et al.*, 2020); assessing how the network roles of individual species change through time (e.g. Cirtwill *et al.*, 2018; Bramon Mora *et al.*, 2020); quantifying the temporal persistence of species, their interactions and structural components of networks (e.g. Bramon Mora *et al.*, 2018; Chacoff *et al.*, 2018), and linking temporal flexibility and interaction reorganisation to network structural stability (e.g. Saavedra *et al.*, 2016, 2017). Thus, there is much opportunity for advancing our understanding of the temporal dynamics of mutualistic networks by incorporating novel analytical methods to the ecological toolbox.

Finally, in order to achieve a better understanding of the causes and consequences of temporal variation in mutualistic networks, it is critical to disentangle variation due to sampling effects from variation driven by biological factors. As with the common problem of detection of species, a non-observed interaction may be present in the wild, but was not observed by the researcher, which may bias our understanding of the temporal dynamics of species interactions. Further analytical and experimental work is needed toward this end. As one example of research addressing this issue, Schwarz *et al.* (2020) used a structural equation modeling approach with 30 temporally resolved plant–pollinator networks to disentangle

the direct and indirect effects of temporal scale, species richness, species turnover, link rewiring and sampling effort on network structure. This approach illustrated that species richness and sampling effort were indeed important predictors of network structure, but were not enough to explain variation across temporal scales; furthermore, their analyses revealed that after accounting for variation in species richness, network structure was increasingly shaped by its underlying temporal dynamics (species turnover and link rewiring). With the increasing availability of time-series network data, occupancy models like those used for estimating species occurrences (MacKenzie *et al.*, 2005; Royle *et al.*, 2005) can be used to estimate the probability that an interaction is present but not observed (M'Gonigle *et al.*, 2015; Weinstein and Graham, 2017b, a). DNA metabarcoding is another promising approach (Bell *et al.*, 2017) to increase interaction sampling completeness and may be particularly powerful when combined with more traditional sampling methods. For the study of the temporal dimension of mutualistic networks to move forward, we must not underestimate the importance of sufficient sampling effort—the key is to generate robust methods that allow teasing apart real ecological and evolutionary drivers of network structure and dynamics from sampling artefacts.

CONCLUSIONS AND PROSPECTS

We have argued that the study of mutualistic networks as temporally dynamic entities is a better match to the reality of ecological systems and provides insights into relevant aspects of their underlying biology. Our review of the literature reveals consistent and characteristic temporal variation in the composition and structure of mutualistic networks at different temporal scales. Of course, the studies we have examined vary widely in their aims and methodologies, so the conclusions we draw from them are tentative and should be regarded as hypotheses to be tested rather than hard-wired facts. At the finest temporal scales (i.e. days, weeks, months) mutualistic interactions are highly dynamic, which leads to considerable variation in the structural properties of networks. Rapid temporal variation at these finer time scales appears to be driven by the physiology, behaviour and interaction relevant traits of temporally active organisms. At intermediate temporal scales (i.e. years, decades), interactions still exhibit high levels of temporal variation from one time slice to the next, but there tends to be more consistency in the emergent structural properties of the networks compared to finer temporal scales. Interaction variation at these intermediate time scales appears to be driven by processes involving population abundance, dispersal and invasion, and trait evolution. Finally, at the broadest temporal scales (i.e. many decades, centuries and beyond), gradual shifts in interactions can eventually reshape interaction network structure, leading to dramatic changes in the community, including interaction loss and species extinctions, while also giving rise to novel interactions. As we look into the future, more rigorous and thoughtful study of the temporal dimension of mutualistic networks promises to provide insight not only into the ecology and evolution of interacting species, but also into how

species and entire communities may respond to various disturbances.

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AUTHORSHIP

All authors conceived the study during a workshop organised by DPV and TMK. PJC, LAB, BS, JR and DPV wrote a first draft of the manuscript, and all authors contributed to the final version of the manuscript. PJC designed all conceptual figures. BS conducted the initial literature survey.

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SUPPORTING INFORMATION

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

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