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To cite this article: Clàudia Payrató-Borràs *et al* 2024 *J. Phys. Complex.* **5** 025013

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OPEN ACCESS

RECEIVED
6 November 2023REVISED
2 April 2024ACCEPTED FOR PUBLICATION
30 April 2024PUBLISHED
14 May 2024

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Beyond the aggregated paradigm: phenology and structure in mutualistic networks

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E-mail: carlos.gracia.lazaro@gmail.com**Keywords:** phenology, mutualism, competition, ecological networks, entropy, ecological modelingSupplementary material for this article is available [online](#)

Abstract

Mutualistic relationships, where species interact to obtain mutual benefits, constitute an essential component of natural ecosystems. The use of ecological networks to represent the species and their ecological interactions allows the study of structural and dynamic patterns common to different ecosystems. However, by neglecting the temporal dimension of mutualistic communities, relevant insights into the organization and functioning of natural ecosystems can be lost. Therefore, it is crucial to incorporate empirical phenology -the cycles of species' activity within a season- to fully understand the impact of temporal variability on network architecture. In this paper, by using empirical datasets together with a set of synthetic models, we propose a framework to characterize the phenology of plant-pollinator communities and assess how it reshapes their portrayal as a network. Analyses of three empirical cases reveal that non-trivial information is missed when representing the network of interactions as static, which leads to overestimating the value of fundamental structural features. We discuss the implications of our findings for mutualistic relationships and intra-guild competition for common resources. We show that recorded interactions and species' activity duration are pivotal factors in accurately replicating observed patterns within mutualistic communities. Furthermore, our exploration of synthetic models underscores the system-specific character of the mechanisms driving phenology, increasing our understanding of the complexities of natural ecosystems.

1. Introduction

Mutualistic relationships, which for centuries had been mainly overlooked as fascinating but marginally relevant, are today known to play a crucial role in shaping natural ecosystems [1]. In mutualistic communities, individuals from different species interact through activities that provide them mutual benefits such as food, shelter or an increase in reproductive success—being pollination of plants by animals the most characteristic example. The explosion of network science in the 90s fostered the development of a holistic understanding of these communities using the language of ecological networks [2], which allowed investigating the existence of widespread structural or dynamical patterns despite ecosystem's differences in species composition, climate or location [3–5].

In the context of community ecology, the network's nodes typically represent different species, while the links (which might be weighted or binary) depict the ecological interactions among them. In the particular case of mutualistic networks, the nodes may be moreover separated into two different sets or guilds—e.g. plants and pollinators—such that the links representing the mutualistic interaction only exist between nodes of different guilds, resulting in a so-called bipartite network. This representation can then be enhanced, for

instance, by adding other kinds of ecological interactions like competition for common resources, which then leads to a bilayered depiction of the community [6].

Here, we will attempt to understand how by neglecting the temporal dimension of real mutualistic communities, that is, by working with the aggregated version of the interaction networks, we can lose relevant insight into the organization and functioning of natural ecosystems. In this sense, we will incorporate into the network formalism the information about empirical phenology, namely the biological activity cycles of species that, to a certain extent, constrain and articulate how ecological relationships occur among individuals. This endeavor, although largely overlooked, is not entirely new [7–11] and, in fact, during recent years the need of moving towards a more realistic depiction of ecological communities has been stressed more than once [2, 12–14].

Indeed, some studies have begun to shed light on these aspects [15–17]. For instance, it has been shown through empirical data analysis that temporal variation in networks leads to different structural outputs compared to aggregated networks [15], highlighting the importance of considering temporal dynamics for understanding mutualistic systems. Similarly, it has been emphasized the necessity of integrating flowering time distribution patterns with other factors to uncover the dynamic nature of community assembly processes in co-flowering communities [16]. Furthermore, Duchenne *et al* developed a dynamic model comparing the influence of phenology versus morphology on the structuring of mutualistic networks, suggesting that facilitation may occur independently of competition, which underscores the need for a more nuanced understanding of temporal dynamics in mutualistic systems [18]. Regarding the influence of abiotic factors on phenology, Theobald *et al* [19] conducted research demonstrating that climate-induced changes can drive phenological reassembly in mountain wildflower meadow communities. They observed that these communities adapt their phenological periods in response to changing abiotic factors, such as temperature and precipitation. Although their focus is not specifically on facilitation, their findings contribute to our understanding of how environmental changes can impact the temporal dynamics of mutualistic communities. Moreover, recent research underscores the importance of considering the seasonal organization of interactions, or seasonal structure, in understanding not only community structure but also its stability [20]. Their findings suggest that empirical seasonal structures contribute to enhancing community stability by promoting diverse and resilient communities while maintaining robustness to species extinctions, highlighting the significant role of seasonal dynamics in shaping the stability of ecological networks.

Although phenology certainly plays a part in different types of ecological mutualism, in this work we will focus on its implications for plant-pollinator communities, both because it is a paradigmatic example in which seasonality is strongly marked and also because, despite the aforementioned data limitations, the phenology of plants and pollinators is, in general, better documented than that of other mutualistic species [21]. In fact, recent studies shed light on the importance of considering seasonal variation, temporal scale-dependence and shifts in phenologies for understanding the dynamics of plant-pollinator communities [22, 23]. Rabeling *et al* reveal how extreme cycles of drought and precipitation in seasonally dry Neotropical habitats impact the dynamics and stability of plant-pollinator communities, pointing out the vulnerability of these communities to seasonal changes in resource availability [22]. Similarly, Schwarz *et al* remarked on the strong temporal scale-dependence of plant-pollinator network structure and advocate for considering multiple temporal scales to fully appreciate the causes and consequences of interaction network structure [23]. Furthermore, regarding the effect of phenology on other relationships, such as competition, Rudolf proposes a conceptual framework incorporating seasonal timing of species interactions to examine how changes in phenologies influence the long-term dynamics of natural communities, emphasizing the crucial yet currently understudied role of phenology in driving coexistence and biodiversity patterns [13]. Additionally, it has been shown the significance of facilitative interactions among concurrent species, further contributing to our understanding of the complex dynamics within mutualistic communities [24]. Collectively, these studies emphasize the need for a more comprehensive assessment of temporal dynamics in mutualistic communities and provide valuable insights into the mechanisms driving their structure and stability.

Along this paper we will address this problem by examining the effects on the perceived network architecture of taking into account -at least partly- the temporal dimension of mutualism, using information extracted from two empirical datasets on plant-pollinator communities provided by [25, 26]. These studies include simultaneously the information mentioned before, that is: the observed networks of interactions, the starting dates of activity and the phenophases of each species. The first dataset [25] depicts a set of woodland sites in Illinois (USA) observed during the springs of 2009 and 2010, from which we obtained one network. The second dataset [26] gathers a two-year study conducted in Lesvos Island (Greece), from which we extracted two networks (one per year). Moreover, we will not only consider their consequences for mutualistic relationships but also for intra-guild competition for common resources.

Accordingly, the present paper is organized as follows: first, we complete this introduction by reviewing some basic notions and recent advances in the study of phenology; next, we propose a framework to characterize empirical phenology and we propose a set of synthetic models in order to study the structural consequences of phenology beyond the scarce number of open datasets; third, we present a structural characterization of two real datasets taking into account the variation of three interaction networks during the season and compare these observations with the explorations produced by synthetic models that include stylized characteristics of the phenology; and finally, we conclude with a discussion of these results and some unresolved, future challenges.

1.1. From cherry blossom to phenocams

The bloom of flowers in spring, the arrival of the first migratory birds and the shedding of leaves in fall are all simple yet beautiful examples of phenological events that undeniably shape, since ancient ages, our perception and narration of time. Our language and culture are full of references to this sort of phenomenon and their timing, from words like ‘late bloomer’ to Aristotle’s famous phrase ‘*one swallow does not make a summer*’. Naturally, hence, we can find as well ancient instances of documented phenological patterns, some of them spanning over several centuries like that of the cherry blossom [27, 28]. In fact, this kind of sequential data has been used to reconstruct springtime temperatures of undocumented old periods [28, 29].

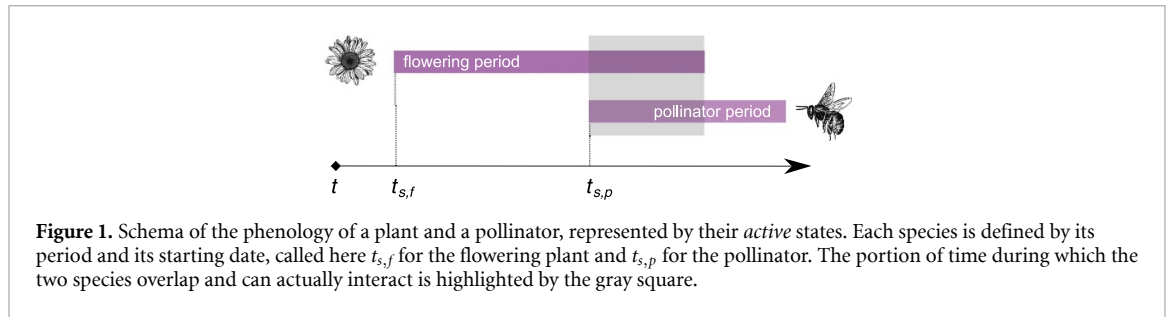
While these datasets were constructed by relying, basically, on visual and small-scale observations, during the last decades technological advances have permitted a multiplication and diversification of the means to measure the phenology of both plants and animals [30]. Such methodologies range from citizen science projects where participants collect and share individual observations of phenology in their local area [31], to the use of sophisticated remote sensing tools based on satellite data [32] or public cameras connected to the Internet [33], the so-called phenocams [34]. Nurtured by these methodological advances as well as spurred by the investigations on how climate change influences phenology [35, 36], nowadays we face an undeniable increase in the quantity and the quality of documented phenology [37]. Moreover, recent research underscores the significance of examining complete phenological distributions, rather than relying solely on partial assessments like the first date of flowering, to understand the effects of climate change on phenology [38].

Paradoxically, though, this copious amount of phenological data comes at relative help when trying to better understand mutualism over time. This is due to the fact that public empirical information on both the network of interactions *and* the timing of their mutualistic activity is rather scarce. Consequently, previous studies examining the effect of phenology on mutualistic communities either focus on a very reduced number of highly-resolved networks [7, 10, 39], either they succeed in keeping the big numbers of phenological data at the expense of roughly approximating the patterns of mutualistic relationships—that is, by neglecting the real complex networks of interactions [18]. A third approach, yet, is to explore instead synthetic models either for phenology or for the network of interactions [8, 17, 40]. In this work we chose to use the latter in order to handle the problem of data scarcity.

1.2. Ecological and evolutionary determinants of phenology

The study of the phenology involves all temporal aspects of species’ life cycle, regarding on the one hand the timing of their various stages of development and on the other hand the onset and duration of different biological processes such as flowering, germination, etc. Such timing is determined by a myriad of factors, similarly to what occurs with mutualistic interactions in general [41]. Indeed, both biotic and abiotic forces shape the phenology of species, which, in addition, is thought to be subject to evolutionary change [42, 43]. To complicate things further, several sources of intra-species phenological variability occur simultaneously: inter-annual [7, 44], geographical [45] and last but not least, among different individuals of the same population, even those coexisting on the same site and at the same season [43].

All in all, from a statistical viewpoint a few general patterns have been identified. In particular, we will focus on two fundamental phenological quantities of plant-pollinator systems that are well characterized: the *starting dates*, that is, the time at which the flowering—in the case of plants—or the pollination—for animals—begins, and secondly the so-called *periods*, that is, the length or duration of this active state, during which mutualistic interactions are possible. Certainly, this selection of phenological indicators is far from being exhaustive, and other works have modeled the different stages of plants and pollinators in more realistic detail [10]. In our approach we will approximate this complex landscape of temporal variability by focusing only on the adult phase of the species, and moreover, reducing the whole possible set of biological processes and stages to a couple of states: *active*, namely when the species could potentially hold a mutualistic relationship—i.e. pollinate or be pollinated—, or *inactive*. This sort of simplification is not novel and other works have adopted analogous approaches [8, 25, 35]. In figure 1 we depict this schematic representation of a hypothetical plant and its pollinator.



Regarding the periods of activity, in general, both plants' and pollinators' periods tend to follow right-skewed distributions, with a small number of species exhibiting a long phenophase while a large number of species are active only during a short time [40, 46]. Particularly, Kallimanis *et al* [40] examined the statistical distribution of period lengths in a Mediterranean scrub community observed over four years by Petanidou *et al* [47] and concluded that the distribution of pollinator's periods could be fitted by a decreasing exponential, while plants' followed a lognormal distribution. On the other hand, a lognormal shape for both plants and pollinators' periods and a normal distribution for plants in one of the years of their observation has been identified in a plant-pollinator system in the Arctic [7].

In what concerns the onset of flowering and pollinating activity, a complementary measure that is often used is the *middle date*. In this sense, evidence suggests that middle dates tend to be relatively synchronized [42, 48]. For example, both in [7, 46] it was observed that most active periods temporally coexist at a peak, probably due to a similar reaction to a common set of physicochemical stimuli such as temperature, photo-period, humidity, etc [42]. In statistical terms, this would correspond to a scenario where the middle dates are relatively clustered, as modeled for instance in [40] using a normal distribution. At the same time, genetic factors seem to play an important role in determining the timing of flowering or pollinating activity, which contributes to explaining the heterogeneity of starting dates. For instance, it has been hypothesized that species may spread along the season in order to minimize competition. While the evidence supporting this hypothesis may have been a topic of debate in the past [42], it is now widely acknowledged that competition plays a significant role in structuring phenological organization within communities. This recognition has been supported by numerous studies highlighting the importance of competition in shaping phenological dynamics [8, 16]. Additionally, recent research has further elucidated the complex interactions between competition, facilitation, and environmental factors in driving phenological patterns [17].

This short introduction illustrates the complexity of the temporal dimension of plant-pollinator communities. Moreover, the relevance of phenology goes beyond the individual characterization of species' traits, since it regulates as well the ecological interactions within the community, affecting both their occurrence and intensity. Understanding how this may modify the structure of ecological interactions beyond the limits of the aggregated paradigm is crucial if we aim to produce a refined depiction of natural systems. In order to do so, in the next sections we first define a general framework to model the effects of phenology on mutualistic networks, then describe the three empirical plant-pollinators communities under study and finally expose our findings in the results section.

2. Definitions and models

Along this section we introduce the tools and models to explore the effects of phenology on a plant-pollinator community: first, we define the mutualistic and competitive networks of interactions; second, we describe how we may account for empirical phenology using overlaps and a coarse-grained temporal representation of networks; finally, we present a set of basic toy-models to produce synthetic configurations of phenology using both mechanistic and statistical principles.

2.1. Mutualistic and competitive network

In order to assess the effects of phenology on the plant-pollinator community, we will not only consider the mutualistic relationship among different species but also indirect interactions like competition for shared mutualistic resources [49], which naturally emerge among species of the same kind. The negative effects of these antagonistic interactions are known to coexist with mutualism, leading to a trade-off between costs and benefits [6, 50].

Therefore, we start by defining the undirected biadjacency matrix of mutualistic interactions $B_{i,k}$ of size $N_P \times N_A$, where N_P is the number of plants and N_A is the number of animals, such that:

$$\begin{aligned} &\text{if } B_{i,k} = 1 \text{ then plant } i \text{ and animal } k \text{ engage in a mutualistic interaction,} \\ &\text{if } B_{i,k} = 0 \text{ then species } i \text{ and } k \text{ do not share any mutualistic interaction.} \end{aligned} \quad (1)$$

To be able to calculate the consequences of phenology also among competitors, we need to infer the network of competitive interactions based on shared mutualistic resources. We do so following [6], namely, projecting the empirical biadjacency matrix of mutualistic interactions $B_{i,k}$ into the subspace of intra-guild interactions such that:

$$\begin{aligned} &\text{if } B_{i,k}B_{j,k} = 1 \\ &\quad \text{then plants } i \text{ and } j \text{ compete for the pollinating services of animal } k, \\ &\text{if } B_{i,k}B_{j,k} = 0 \\ &\quad \text{then } i \text{ and } j \text{ do not compete for the resources of pollinator } k, \end{aligned} \quad (2)$$

which leads to a competitive network between all pairs of plant species i and j . Analogously, we can define the competitive interactions among two pollinator species k and l as follows:

$$\begin{aligned} &\text{if } B_{i,k}B_{i,l} = 1 \\ &\quad \text{then pollinators } k \text{ and } l \text{ compete for the flower resources of plant } i, \\ &\text{if } B_{i,k}B_{i,l} = 0 \\ &\quad \text{then } k \text{ and } l \text{ do not compete for the resources of plant } i. \end{aligned} \quad (3)$$

Altogether, this provides a bilayered depiction of the ecological community, such that the observed network of pollinating contacts not only mediates the explicit mutualistic interactions, but also the implicit, competitive relationships among species of the same guild [6].

2.2. Empirical overlaps

The most straightforward consequence of introducing phenology into an aggregated network is the modification of the amount of temporal coexistence—the so-called *overlap*—among species. Indeed, we find a continuum of possible scenarios ranging from full concurrence to absence of overlap, as shown in figure 2. These overlaps concern either two species in the mutualistic case or three species—two species of the same kind and the shared resource—when considering the competition.

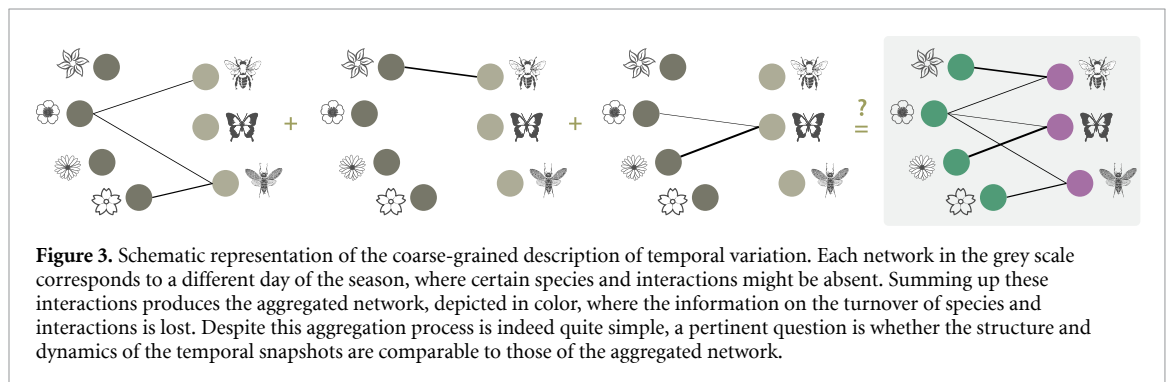
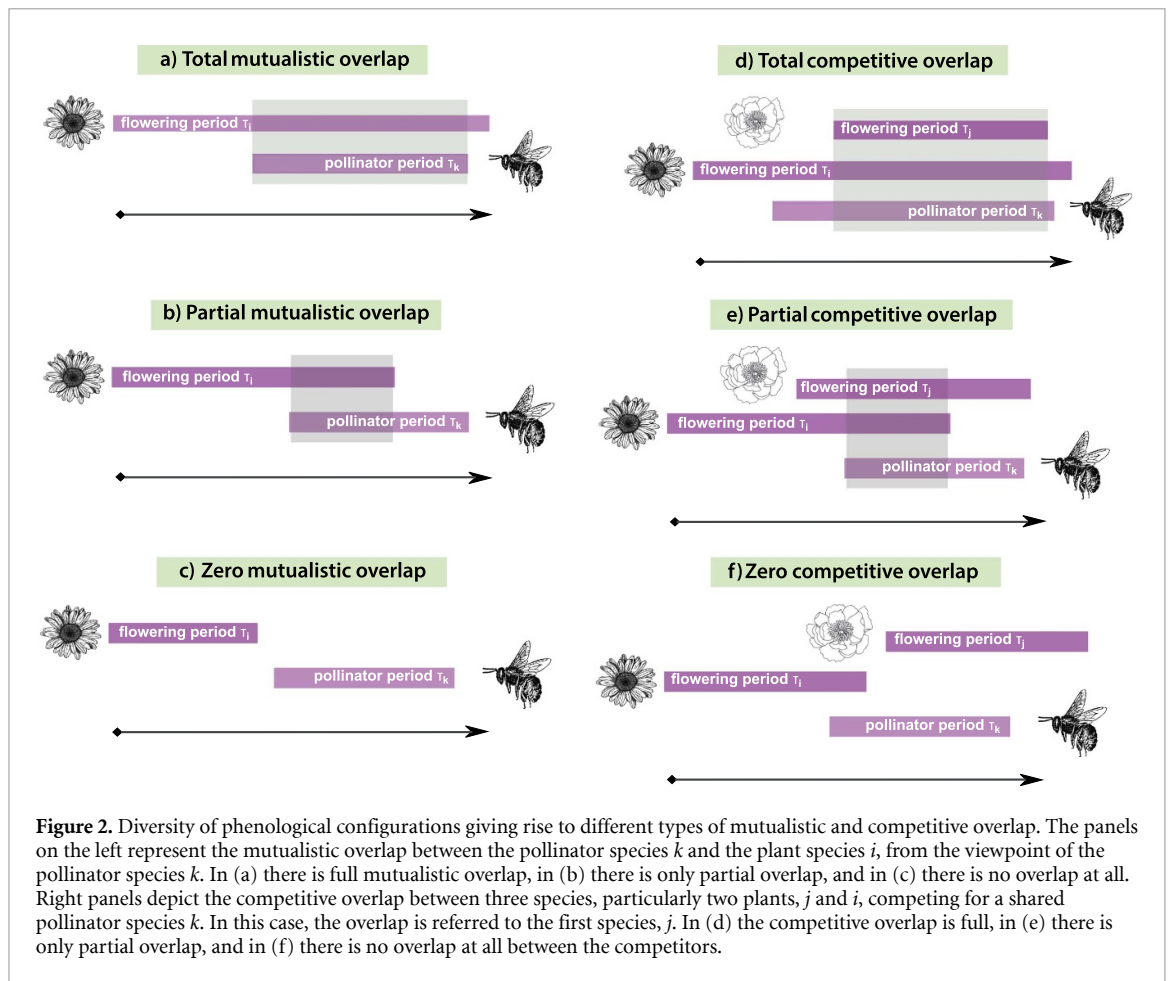
Within this framework, we can introduce a set of phenological coefficients $\{\Phi\}$ and $\{\Omega\}$ to quantify the effect of the phenological overlap on, respectively, the mutualistic and the competitive interactions. In the particular case of a plant species i interacting mutualistically with a pollinator k and competitively with another plant j , we define these coefficients as follows:

$$\Phi_{ik}^p = \frac{\tau_{ik}}{\tau_i}, \quad (4)$$

$$\Omega_{ijk}^p = \frac{\tau_{ijk}}{\tau_i}, \quad (5)$$

where τ_i stands for the period of flowering of the plant species i , τ_{ik} represents the temporal overlap between the period of the plant species i and that of its pollinator k (see figures 2(a)–(c) for a graphical representation), and finally τ_{ijk} stands for the overlap between plants species i and j and their pollinator k (see figures 2(d)–(g) for an example). An analogous set of coefficients can be drawn for the pollinators.

Note that, as can be seen in equations (4) and (5), the overlaps are pondered by the period of activity of the species—in the example above, the plant i —, which means that each coefficient is always referred to a certain plant or animal species. This particular normalization implies, moreover, that the effect of the temporal overlap is non-symmetric among the interacting partners and hence, in general, $\Phi_{ik}^p \neq \Phi_{ki}^A$.



2.3. Coarse-grained temporal sequence of networks

In order to better understand how the perceived structure of the network changes if we take the empirical phenology into account, we construct as well a discrete temporal sequence of networks. Here, each element corresponds to a different *snapshot* of the system, taken at a different moment of the season. In particular, given that the degree of detail of the empirical phenologies under study is narrowed to *days*, we construct a set of daily networks. That is, each network represents the mutualistic interactions observed among plants and pollinators on a given day.

To construct this sequence of networks, we use the empirical information on the starting and ending dates of activity of plants and pollinators, then remove from the daily network certain mutualistic links among species whenever they do not coincide in time—i.e. when their phenological overlap, as defined in equation (4), is zero. Additionally, we remove inactive species as well as active species with no interactions—i.e. zero degree.

On the whole, this provides a coarse-grained description of the community as shown in figure 3, that, even if it is not a pure temporal network, it does account to a great extent for the intra-annual temporal variation, moving beyond the static network formalism. In order to characterize this variation, we measure a

set of fundamental structural features for the different coarse-grained networks of the daily sequence: the number of active nodes -that is, species-, the number of active links -either mutualistic or competitive interactions- and the maximum degree -i.e. the largest number of interactions held daily by one species. We do so both for the mutualistic and the competitive network defined above. The choice of these properties is motivated by the fact that they have been often linked to dynamical properties of the network [51], as happens for instance with connectivity and stability [5] or degree and species persistence [52, 53].

2.4. Characterization of the empirical distributions of periods

Given that the organization of the duration of the activity of plants and pollinators might be a strong determinant of the structure of the daily networks, we are interested in characterizing the empirical distributions of periods provided by the datasets. In particular, we fit a variety of functional forms on the cumulative distributions using a maximum likelihood estimation. Then, we test the quality of the fit by performing a Kolmogorov-Smirnov test by bootstrapping, as explained in detail in the supplementary material.

In detail, we test three different functional forms: lognormal, exponential, and beta function. As aforementioned, the first two distribution types have been claimed to correctly describe some empirical observations, while we introduce the latter as a generic fitting.

2.5. Synthetic toy-models

In order to evaluate how our results depend on the details of the empirical dataset, we develop a group of toy models that, under different assumptions, produce synthetic configurations of phenology compatible with a given mutualistic network. As aforementioned, in our framework, the phenology of each species is defined by two elements: the starting date and the period of activity. Here, we will focus on determining the starting dates while preserving the empirical periods. This particular choice aims at reducing the number of free parameters of the model and hence the size of the phase space of possible configurations of phenology. This keeps, moreover, some the main characteristics of real data discussed earlier, such as a right-skewed distribution of the phenophases. While other works have explored the effects of varying as well the duration of the periods [10], our scope here is to eventually provide a set of toy-models that rely on simple mechanisms and thus setting the periods reduces the complexity of the problem.

Therefore, the starting dates will be treated as parameters to be set by the synthetic model, under the condition that mutualistic partners share a non-zero mutualistic overlap. This requirement ensures that the binary mutualistic network is kept equal to the observed one, constituting a formalism that focuses explicitly on modeling the phenology.

Before entering into further details about the different synthetic models, let us briefly discuss the particularities and consequences of preserving the network of interactions. As aforementioned, we will construct a model under the requirement that the phenological overlap among mutualistic partners is comprised in the range $(0, 1]$, excluding the zero in order to ensure that the two species still interact. This means that, strictly speaking, we will only keep the *binary* mutualistic network. In other words, the general idea consists in constructing a synthetic phenology that is *compatible* with the given network treated in binary terms.

In this line of thought, the constraint that mutualistic partners share non-zero phenological overlap may be written as an inequality for each species' starting date. For instance, let us take a plant species i with period p_i^P and unknown starting date $t_{0,i}^P$, which interacts with an animal species j with period p_j^A and an unknown starting date $t_{0,j}^A$. In order to ensure that their periods overlap, it must be fulfilled that:

$$t_{0,j}^A - p_i^P + 1 \leq t_{0,i}^P \leq t_{0,j}^A + p_j^A - 1, \quad (6)$$

where we have assumed a daily coarse-graining, such that the minimal overlapping unit is one day. In order to ensure that all interacting species share phenological overlap, we may write an inequality analog to equation (6) per each link in the bipartite network. Then, if we take the starting dates as unknown variables, we can view the problem of constraining the starting dates as a multivariate system of linear inequalities composed by N unknown variables and L inequalities (where N and L are respectively the number of nodes and the number of links of the network). Note that both $\{t_0^P\}$ and $\{t_0^A\}$ are unknown, which means that the system of inequalities is coupled.

Furthermore, in order to ensure that the resulting distribution is realistic, we may introduce an additional set of constraints. In particular, we impose a lower and upper bound for the starting dates of activity, which ensures that the community exhibits some seasonality, a characteristic that has been empirically observed [40, 42]. If we represent by l the lower bound and by u the upper bound delimiting the season, then the condition on the starting date of an arbitrary species i can be written as:

$$l \leq t_{0,i} \leq u - p_i + 1. \quad (7)$$

Overall, equations (6) and (7) represent a coupled system of linear inequalities, where the parameters to be determined are the starting dates. Although a problem of this kind might not generally have a feasible solution, in our particular case the existence of some trivial solutions—e.g. the same starting dates for all species—warrants that the system is consistent.

Within this framework, we present a group of approaches that, under different assumptions, permit determining the set of synthetic starting dates while fulfilling the conditions in equations (6)–(7). In particular, we explore four possible scenarios, corresponding to different fundamental hypotheses about the main factor governing the species' phenology, namely: (i) species' periods tend to be synchronized, (ii) species seek to organize their activity as to minimize their intra-guild competition for mutualistic resources, (iii) the variance associated to middle dates of activity is maximized, (iv) in the absence of further information, the starting dates can be determined using a minimal model of maximum entropy.

As can be observed, each of these assumptions relies on a single dominant factor. Indeed, hypothesis (i) and (ii) are mechanistic, in the sense that they place the emphasis on environmental and ecological drivers of the phenology. Instead, the scenarios (iii) and (iv) function as non-mechanistic models based on statistical properties of the distribution of starting times, regarding either their dispersion or their entropy. Of course, since biotic and abiotic forces do not act separately, one could construct a more complex model where various of these factors operate simultaneously. In this sense, these synthetic models constitute a first-order approach, which helps to understand the consequences of each of these hypotheses concerning the phenology. In what follows, we define each of these models one by one and describe how we numerically implemented them.

2.5.1. Synchronized phenology

This model is based on the assumption that the level of synchronization in the community is high, hence most species' activity temporally coincide with the peak of the season. As we reviewed in the introduction, empirical evidence suggests that seasonal systems usually exhibit non-negligible synchronization, in the sense that the flowering and pollination of species tend to occur simultaneously. Several hypotheses have been proposed to account for this pattern, from the presence of abiotic pressures such as the temperature, the precipitation, or the photoperiod—disregarding genetic differences or biotic constraints—[43], to the existence of facilitative interaction among concurrent species [24], which obtain an ecological benefit of overlapping their periods of activity. All in all, it is still not clear how the mentioned factors interplay among themselves and with other possible forces to give rise to the observed heterogeneity in starting dates [43].

In order to attempt to reproduce this pattern, we construct a model where species' periods are approximately centered. To do so, we set the middle dates around the peak of the season and then slightly perturb them, following the numerical procedure detailed in the supplementary material. This leads to phenological configurations where species are considerably—but not perfectly—synchronized. Indeed, introducing this imperfection is crucial for two reasons: first, to account for the aforementioned heterogeneity in starting and middle dates of activity; second, because a perfectly synchronized system is trivial, in the sense that all species fully overlap, recovering hence the aggregated case.

2.5.2. Minimization of the intra-guild competition

This second model is built upon the hypothesis that the periods of the species are located along the season so as to avoid, as far as possible, overlapping with other species that exploit a common mutualistic resource—i.e. pollinating services in the case of plants or flower availability for pollinators. As discussed above, there seems to be an increasing amount of evidence that suggests that this mechanism can be a governing factor in organizing phenology [54–56].

In order to construct a phenological configuration that minimizes the competition among species, we implement a global search algorithm that optimizes an objective function under the constraints in equations (6) and (7) (see the supplementary material for the numerical details). In this particular model, the objective function corresponds to the total competitive phenological overlap among species.

2.5.3. Maximization of the variance

We now turn our attention to models that focus directly on the statistical properties of the system's phenology. As a first approach, we propose a model based on maximizing the dispersal of the periods along the season. In particular, we maximize the variance of the middle dates of activity. Indeed, if we define the middle time t_M of a species i as:

$$t_{M,i} = t_{0,i} + \frac{p_i - 1}{2}, \quad (8)$$

then its variance $\text{Var}(t_M)$ is an approximate measure of the dispersion of the activity of both plants and pollinators along the season. Once again, the maximization of this quantity is done under the condition that mutualistic interactions present in the aggregated network still occur. The numerical procedure to do so is explained in the supplementary material.

2.5.4. Maximization of the entropy

Following a similar line of thought, we propose a second model to produce phenological configurations that is based on their statistical properties. In particular, we refine the former approach by characterizing the distribution with a more sophisticated and robust indicator, namely, entropy [57]. This is a plausible alternative to maximizing the variance which may especially outperform the latter when the distribution is multimodal.

Our choice of the maximum entropy hypothesis for generating synthetic networks is rooted in its widespread application across various scientific disciplines as a neutral and unbiased approach to modeling ecological systems [58–61]. This hypothesis has been successfully employed in modeling species distributions and the structure of ecological networks [57], offering valuable insights into the dynamics of complex systems.

Let us define the entropy within the constructed framework for describing phenology. We start by defining a random variable x_i as the number of species whose middle date of activity t_m takes place at a given date t_i . Then, its corresponding probability $p(x_i)$ will be:

$$p(x_i) = \frac{\text{number of species with } t_m = t_i}{\text{total number of species}}. \quad (9)$$

Given this random variable, it is possible to define its Shannon–Gibbs entropy as follows:

$$S = - \sum_i p(x_i) \ln p(x_i). \quad (10)$$

It is straightforward to see that in a scenario of perfect synchronization, the middle dates of activity are the same for all species. That is, if we name such a date by the index k , then $p(x_k) = 1$, and the information entropy is zero.

Maximizing the entropy defined in equation (10) under the constraints imposed by the network of interactions results in a maximum entropy model that randomizes the distribution of periods of the species, yet using only the minimal amount of necessary information. The particular details of how this model was implemented can be found in the supplementary material.

3. Datasets

In order to assess the consequences of phenology on the perceived network structure, we analyzed two public datasets [25, 26] which contain observations of mutualistic interactions in plant–pollinator systems together with their phenology. In particular, they provide the data to construct three empirical networks. We detail the peculiarities of each dataset below.

3.1. The Illinois dataset

This dataset [25] corresponds to a set of woodland sites in Carlinville, Illinois (USA), observed during the springs of 2009 and 2010 from March to May. The observed network of mutualistic interactions contained originally 26 spring-blooming herbaceous plants and 54 bee species. However, 2 plant species did not exhibit any interaction in the empirical network, so we obtained eventually a 24×54 network.

The dataset also included the observed phenology, specifically the starting and ending dates of the active stages of both plants and pollinators. Using those, we extracted as well their periods of activity and the middle dates.

3.2. The Lesvos Island dataset

This dataset is based on a two-year study conducted in Aglios Stefanos, Lesvos Island (Greece) during the springs of 2011 and 2012 from April to July [26]. It includes information on both the network of mutualistic interactions and the phenology. Aggregated over the two years, the resulting network is composed of 41 plant species and 168 pollinators.

Table 1. Results of fitting different functional forms, disentangled into plants and pollinators. We show the p -value of the fit, marked with asterisk good quality fits, that is, those which do not significantly differ from the estimated distribution (p -value > 0.05). The p -values are obtained by performing a Kolmogorov–Smirnov test between the fitted distribution and the empirical sample, then comparing it to the corresponding K-S distribution sampled by bootstrap as explained in the supplementary material.

Dataset	Lognormal fit		Exponential fit		Beta function fit	
	Plants	Pollinators	Plants	Pollinators	Plants	Pollinators
Illinois	0.021	0.018	0.001	0.001	0.63*	0.18*
Lesvos Island 1st year	0.67*	0.014	0.029	0.001	0.41*	0.001
Lesvos Island 2nd year	0.50*	0.001	0.018	0.001	0.02	0.001

Remarkably, a large portion of the pollinator species is present in only one of the seasons. In particular, out of the total 168 pollinator species observed over the two years, only 67 species (39.9%) were persistently found in both seasons, while 53 species (31.5%) were observed just during the first year, and 48 species (28.6%) just during the second year of observation. This implies that not only there is an important turnover of interactions among the two consecutive years, but also there is a considerable species turnover, as suggested as well by previous studies [7, 11].

In order to obtain the network of interactions specific to each year, we removed those interactions present in the aggregated network whose periods of activity do not overlap according to the information concerning phenology. In such cases, it is clear that the interaction was not possible due to the lack of phenological overlap and hence we can remove it from the yearly network. After doing so for each season, we removed as well those species that no longer hold mutualistic interactions—i.e. they have degree zero. As a result, both year-specific network sizes are reduced to 34 plant species and 113 pollinators in the first year and 38 plant species and 104 pollinators in the second year of observations.

4. Results

4.1. Distribution of periods

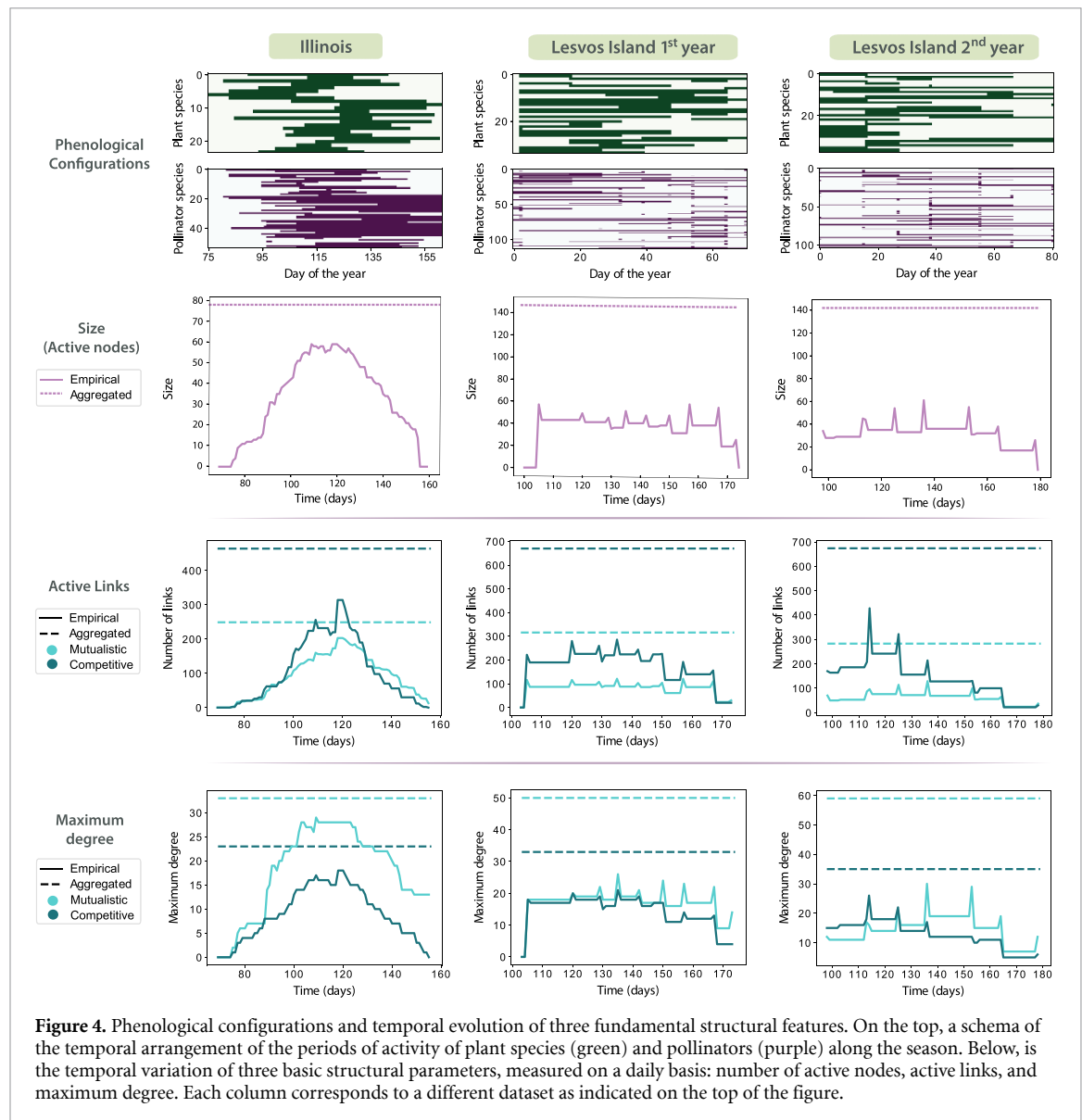
We start by examining the distribution of the duration of the activity of plants and pollinators as explained in the Methods section. The results of the p -value for the KS-test of the three trial fits—lognormal, exponential, and beta function—are reported in table 1, where we highlight in bold the good-quality fits. As can be seen, the Illinois dataset is better fitted by the beta function, while in the Lesvos Island dataset, we can fit a lognormal to the distribution of plants' periods but we found no unique fit for the pollinators.

In general terms, the distribution of periods of the Illinois dataset is less heterogeneous, while the Lesvos Island distributions are clearly righter-skewed. This is especially notorious for the periods of the pollinators, among which we find a large proportion of species with very short phenophases. A plot of the empirical distributions together with the best-fitting function can be found in the supplementary material. We will show later how these differences among empirical distributions entail, in turn, the observed differences among the structure of the daily networks and their aggregated counterparts.

4.2. Temporal variation of the structure

Now that we have characterized the differences among the empirical phenology of the two datasets, we turn our attention to the coarsened-grained networks in order to address the question of how the perceived structure of the ecological network changes if we take phenological information into account. Figure 4 provides a summary of the daily variation of fundamental structural properties over time, for each of the empirical networks in our dataset. To begin with, our results show that in both cases the temporal measures are significantly smaller than their aggregated counterparts. However, we observe a non-negligible quantitative difference among datasets: in the Illinois dataset, the maximum of the peak represents around the 75%–80% of the aggregated counterpart, whereas in both instances of the Lesvos Island dataset, this quantity descends to less than 30%–40%. Additionally, the comparison of the results for the two systems shows that the variation of their network structural properties exhibits a strikingly different pattern over the season. Indeed, while in the Illinois dataset, the three quantities show a marked peak approximately at the middle of the season, in the Lesvos Island dataset they stay relatively stable, with some spikes that could respond to a myriad of factors—from variations in observational efforts to resource pulses.

Apart from the differences among datasets, we also observe quantitative distinctions between mutualistic and competitive interactions. To start with, in the subplots depicting the active links in figure 4 we can observe that in the aggregated network the total number of competitive links is much higher than the number of mutualistic links. This is due to the fact that there are two guilds and hence two sets of intra-guild competitive interactions. Strikingly, the relative decrease in connectivity observed when introducing



phenology is significantly larger for competition than for mutualism. Indeed, when regarding mutualistic interactions the peak of daily activity in the Illinois dataset represents, as aforementioned, 75%–80% of its aggregated counterpart, but only around 60% for competitive links. This gap is still larger for the Lesvos Island dataset, pointing out the fact that phenology seems to impact differently at the two types of interactions.

4.3. Comparison with synthetic models

We now proceed to test the performance of the different generative models of synthetic phenologies proposed above. To do so, we will adopt as input the observed network of interactions—which is to be preserved—, and the empirical distribution of periods. The latter will allow us to focus on the quality of the methodology to produce the starting dates alone, without introducing additional sources of noise.

In order to examine the adequacy of each model to reproduce the empirical phenological patterns, we start by extracting the synthetic starting dates corresponding to each of our three datasets (see the supplementary material for the explanation of the numerical methods). Then, we characterize the synthetic phenologies with the methods and definitions described in section 2. That is, we calculate, on the one hand, the distribution of phenological coefficients defined in equations (4) and (5), and, on the other hand, we couple the phenology to the network structure and compute the change of some basic structural features along time. Along the rest of this section, we will explain and discuss the results of comparing these synthetic measures with the empirical observations.

Table 2. Results of the K-S two sample test among the synthetic distribution and the empirical distribution. We show the KS distance between the two samples; the cases in which the null hypothesis is rejected, that is, those where the two samples do significantly differ (p -value < 0.05), are indicated with an asterisk. The smaller the KS distance, the smaller the discrepancy between the two samples. The numerical implementation to calculate these distances is described on the supplementary material.

Model /Dataset	Mutualistic overlap		Competitive overlap	
Synchronized	Plants	Pollinators	Plants	Pollinators
Illinois	0.052	0.051	0.008	0.021*
Lesvos Island 1st year	0.015	0.010	0.002	0.002
Lesvos Island 2nd year	0.009	0.009	0.001	0.0017
Minimum competition	Plants	Pollinators	Plants	Pollinators
Illinois	0.100*	0.103*	0.036*	0.031*
Lesvos Island 1st year	0.012	0.013	0.002	0.0015
Lesvos Island 2nd year	0.007	0.008	0.001	0.001
Maximum variance	Plants	Pollinators	Plants	Pollinators
Illinois	0.066*	0.069*	0.027*	0.028*
Lesvos Island 1st year	0.015	0.014	0.004	0.003
Lesvos Island 2nd year	0.011	0.011	0.003	0.002
Maximum entropy	Plants	Pollinators	Plants	Pollinators
Illinois	0.040	0.042	0.010	0.015*
Lesvos Island 1st year	0.009	0.007	0.001	0.001
Lesvos Island 2nd year	0.006	0.007	0.001	0.0016

4.3.1. Distribution of overlaps

We first study the distribution of the phenological coefficients defined in equations (4) and (5). In order to compare the empirical and the synthetic distributions, we perform two different statistical measures: (a) a two-sample Kolmogorov-Smirnov test and (b) the calculation of the Kullback–Leibler divergence (see the supplementary material for the numerical details).

Using (a), we analyzed separately the competitive and mutualistic overlaps on the one hand, and the distributions for plants and for pollinators on the other hand, as summarized in table 2. In particular, for the Illinois dataset, the null hypothesis that both samples come from the same distribution is rejected for the models that minimize the competition and maximize the variance, which is hence incompatible with the empirical data. The model with centered times and maximum entropy is generally compatible with the observed phenology, except for the distribution of coefficients associated with the competition among pollinators. Instead, for the Lesvos Island dataset, the four models are compatible with the data.

In order to differentiate which model better reproduces the empirical phenology in the cases in which, according to the KS test, various models are statistically compatible, we carry out (b), that is, the calculation of the KL-divergence. Indeed, the KL distance measures the amount of information lost when we approximate the empirical distribution by the synthetic one, and therefore it can be used as a statistical criterion for model selection. In table 3 we can observe that the model based on maximum entropy generally provides the best approximation, except for the second year of the Lesvos Island dataset, in which it is slightly outperformed by the model based on minimizing the competition. It is also interesting to observe that the second-best model is not the same among datasets: while the second-best model for the Illinois dataset is the one with synchronized phenology, in the Lesvos Island dataset it is the model which minimizes the competition.

4.3.2. Structural features

Secondly, in order to complement the information provided by depicting the phenological coefficients, we calculate the daily networks resulting from considering the phenology. This again produces a sequence of synthetic networks, each corresponding to a given date, as represented in figure 3. Repeating the procedure detailed in section 3.2. now for each synthetic model, we calculated a few basic structural quantities as a function of time: the size -number of active species-, the number of active links -that is, of active mutualistic interactions- and the maximum degree -largest number of mutualistic interactions hold by a single species-.

With this information at hand, we can perform a comparison between the product of each synthetic model and the empirical observations, specifically addressing the change in fundamental structural properties over time. To quantify these correlations, we calculated the corresponding Pearson coefficient for

Table 3. Results of the K-L divergence among the synthetic distributions and the empirical distributions of overlap, either among mutualistic or competitive partners. The smaller the KL-divergence, the smaller the difference between the two samples. Further details on the definition and numerical implementation of this measure can be found in the supplementary material.

Dataset / Model	D_{KL} mutualism		D_{KL} competition		
Illinois	Plants	Pollinators	Plants	Pollinators	Average
Synchronized	0.035	0.038	0.002	0.014	0.022
Minimum competition	0.095	0.101	0.026	0.033	0.064
Maximum variance	0.042	0.056	0.010	0.019	0.032
Maximum entropy	0.022	0.032	0.003	0.008	0.016
Lesvos Island 1st year	Plants	Pollinators	Plants	Pollinators	Average
Synchronized	0.0116	0.0053	0.0014	0.0010	0.0048
Minimum competition	0.0050	0.0073	0.0009	0.0004	0.0034
Maximum variance	0.0111	0.0047	0.0032	0.0008	0.0049
Maximum entropy	0.0055	0.0051	0.0005	0.0005	0.0029
Lesvos Island 2nd year	Plants	Pollinators	Plants	Pollinators	Average
Synchronized	0.0048	0.0036	0.0008	0.0008	0.0025
Minimum competition	0.0018	0.0035	0.0005	0.0005	0.0015
Maximum variance	0.0080	0.0036	0.0019	0.0005	0.0035
Maximum entropy	0.0019	0.0035	0.0005	0.0007	0.0016

Table 4. Maximum Pearson correlation among the empirical and the null expectation of the structural properties along time.

Dataset/Property	Maximum Pearson coefficient for each null model			
Illinois	Synchronized	Max variance	Min competition	Max entropy
Maximum degree	0.98	0.88	0.93	0.98
Number of links	0.98	0.87	0.78	0.98
Size	0.99	0.79	0.92	0.98
Average	0.99	0.85	0.88	0.98
Lesvos Island 1st year	Synchronized	Max variance	Min competition	Max entropy
Maximum degree	0.78	0.76	0.91	0.91
Number of links	0.74	0.71	0.89	0.83
Size	0.81	0.58	0.89	0.85
Average	0.78	0.69	0.90	0.86
Lesvos Island 2nd year	Synchronized	Max variance	Min competition	Max entropy
Maximum degree	0.90	0.67	0.87	0.93
Number of links	0.85	0.78	0.89	0.85
Size	0.89	0.63	0.90	0.88
Average	0.88	0.69	0.88	0.88

different values of time lag between the distributions. By doing so, we are taking into account the possibility that the null model reproduces well the empirical scenario but in a delayed or advanced time. That is, we are relaxing the assumption of perfect matching between the empirical and the synthetic starting dates, focusing instead on the relative position among the starting dates of different species. In table 4 we show the maximum value of the Pearson correlation calculated following this procedure (technical details can be found in the supplementary material).

The study of table 4 reveals that the analysis of the network structure leads to similar results to the aforementioned analysis of the phenological overlap. Indeed, the better fitting models for the Illinois dataset are the ones based on synchronized phenology and maximum entropy, while for the Lesvos Island dataset, the maximal correlation is found for the model which minimizes intra-guild competition and, again, the one maximizing the entropy.

Overall, these multiple statistical tests reveal at least two general conclusions. On the one hand, we find that each dataset is better described by a distinct mechanistic assumption, i.e. the synchronization of the species' phenologies in the Illinois dataset and the minimization of the competition in the Lesvos Island dataset. This disparity seems to reflect the substantial divergences between the two communities'

phenologies, which we described in detail in section 3.1. On the other hand, the temporal networks' features are accurately reproduced by the statistical model that maximizes the entropy associated with the distribution of the middle dates of activity, despite the considerable differences between the two datasets. What this latter finding suggests is that the observed network of interactions together with the periods of each species provide sufficient information to reproduce, fairly closely, the observed temporal patterns of activity. This is particularly interesting given the mentioned differences among datasets, which provide, to a certain extent, a warranty of generality despite the limited data at our disposal. This finding does not imply that, forcedly, the starting dates of activity are set at random, but that the information enclosed in the corresponding network of interactions and the species' periods may be sufficient to reproduce well the main characteristics of the community's phenology.

5. Conclusions

Along this paper, we have addressed the challenge of moving beyond the aggregated paradigm by incorporating some of the temporal variability that plant-pollinator communities exhibit throughout the year. In particular, we have focused on seasonal ecosystems, assessing the daily change in both inter-guild, mutualistic relationships and intra-guild, competitive interactions.

The analyses carried out by using both synthetic models and empirical data have revealed, in the first place, that non-trivial information is lost when portraying the real network of interactions by a static representation, that is, neglecting its temporal dimension. First, we have observed that the consequences of introducing the empirical phenology into the network formalism are system-dependent, and hence no general pattern can be expected *a priori* nor the daily networks could be reproduced by knowing only its aggregated counterpart. Moreover, the process of aggregation not only disregards the richness of temporal variability, but it also tends to overestimate the value of the main fundamental structural features, agreeing with previous results [9, 15, 22, 23]. This is especially relevant given that structural features like the degree or the connectivity are consistently used to characterize, respectively, the relative vulnerability of species [52, 53] or the community stability [5]. Last but not least, neglecting phenology seems to impact differently competition and mutualism, being the gap between the aggregated and the daily connectivity much larger for the competitive links. This can be of interest for those models that aim at evaluating the effects of combining different ecological relationships, either competition or facilitation [6, 17]. In particular, our results agree with recent findings [20] pointing out that phenology may favour mutualism over competition, hence fostering community stability.

In light of the limitations of the aggregated paradigm, and driven by the scarcity of available datasets, we proposed a group of models to produce, given a fixed mutualistic network, a compatible hypothetical phenology. Additionally, we utilized empirical period data, which significantly contributed to enhancing the accuracy and realism of our models. The comparison of these results with the empirical datasets revealed that the soundness of certain mechanisms is, at least in the first-order approach we have adopted here, specific to the particular system under consideration. We have found that the purely statistical assumption of maximizing the entropy associated with the distribution of middle dates performs generally well, as we have tested in two dissimilar empirical examples. Importantly, the remarkable performance of the maximum entropy hypothesis is partly explained by the fact that, actually, the network of interactions is closely dependent upon the starting dates, in the sense that the mutualistic contacts observed corresponded, forcedly, to concurrent species—a condition that, indeed, we impose to our models. Therefore, preserving the network of interactions is a strong constraint, which could justify the general adequacy of this model.

In perspective, these synthetic models offer a methodological set that might prove useful in different aspects. On the one hand, they can be exploited as a group of models to construct synthetic ensembles under simple rules, as long as a network of interactions and a distribution of periods—either real or modeled as well—are provided. On the other hand, they can also be applied as null models that permit testing a variety of null hypotheses, from the mechanistic forces shaping the phenology to the existence of temporal, structural, or dynamical patterns. By offering a set of possible null models for phenological organization, our study fills an important gap in the literature and provides a valuable tool for investigating the mechanistic forces shaping phenology. At this point, it is worth reminding as well that ours is just a first approach to modeling the temporal variability of networks. In particular, we considered the description level at which species are active or inactive during a certain fraction of the season. However, it could be possible to refine the scale of description to include the weekly or even daily turnover of interactions, a sort of hyper-realistic depiction of the temporal variability of the network that is gaining attention during the recent years [39]. This is due, partly, to the technological advances that permit monitoring phenology in great detail, and therefore it is probable that in the coming years, we will find a rising number of this type of studies [30, 37].

In the bigger picture, the interest in moving towards a more realistic portrayal of interacting systems is not exclusive to ecology, and indeed the study of temporal complex networks has received great attention in recent years [62]. How this change of paradigm will eventually challenge our understanding of natural systems is something we are just now beginning to explore.

Data availability statement

The datasets analyzed in this paper were released by [25, 26] and are publicly available, respectively, at: <https://doi.org/10.5061/dryad.rp321> and https://figshare.com/articles/dataset/Data_from_Disentangling_the_role_of_floral_sensory_stimuli_to_pollination_networks_/5663455

The code for the synthetic models of this article is available at: <https://github.com/cclausal/synphen>

Acknowledgments

The authors would like to acknowledge and thank A Kantsa for sharing some valuable clarifications on the construction of the Lesvos Island dataset, as well as additional information on the starting and final dates of the pollinator's activity. We acknowledge partial support from the Government of Aragon, Spain, and 'ERDF A way of making Europe' through Grant E36-23R (FENOL) and from Ministerio de Ciencia e Innovación, Agencia Española de Investigación (MCIN/ AEI/10.13039/501100011033) Grant No. PID2020-115800GB-I00 to C G L and Y M. CP and LH acknowledge the support of Labex MME-DII, Grant No. ANR reference 11-LABEX-0023.

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