The Interplay Between Phenology and Community Dynamics

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Among the evidence of the impact of global warming in ecosystems, the advancement of activity seasons (flowering, pollination, breeding) towards earlier dates of the year is one of the best documented. Because species metabolisms respond differently to temperature changes, and because other constraints are at play (photoperiod, precipitation, resources), one of the most important predictions is the rapid loss of many interactions and the creation of new ones, with uncertain consequences for biodiversity and ecosystem functioning. Thus phenology, the study of the timing of periodic biological phenomena, is to play an increasingly important role in ecological theory, forecasting, and policies. Predicting the consequences of phenological changes in ecosystems is a difficult challenge, because there are multiple simultaneous time scales involved: the short-term scale of interactions between individuals, whose strength depends on phenological overlap; the mid-term scale, where the outcomes of the interactions determine population dynamics and phenologies too; and the long-term scale, where phenologies evolve in response to natural selection. I propose a research program designed achieve a comprehensive understanding of the role of phenologies in ecosystems. This proposal is organized around four modeling projects concerning the roles of (a) interactions, (b) spatial organization, (c) evolution and plasticity, and (d) metabolism.

The first and most extensive project will study the role of interaction phenology on small (modules) and large communities (networks). This project also lays the ground for rest of the proposal. The cornerstone idea is that consumers do better when their activity periods match with those of their resources (Match Mismatch Hypothesis), and resources do better by avoiding such state of affairs. However, consumer–resource feedbacks, indirect interactions and interaction types (mutualisms vs antagonisms) strongly modulate the response of populations and communities to phenological change.

The second project will study the interplay between species phenologies and spatial dynamics. One of the most important factors behind population viability is the distribution over regions large enough to prevent total extinction, as well as the ability to disperse between localities. Local survival relates with the local pattern of interspecific interactions, which depends on phenology. This allows for synergies between phenology and spatial organization acting on metacommunities. In addition, dispersal itself can be phenologically determined (migration seasons). The third project will study phenological changes due to natural selection and phenotypic plasticity, under the conditions studied by the first two projects (multiple interactions, spatial settings). The fourth project will link phenological events with climate via metabolic theories, in order to predict the response of communities to projected global warming.

The projects in this proposal will make use of intensive simulations (differential equations, individual based models), informed by real data on interaction networks and species activity calendars. However, there is also room for analytical approaches that will enlighten our understanding of the feedbacks involved between phenology and species interactions. Parts of this proposal will rely heavily on an extensive network of collaborators.

1 Project proposal

Why phenology?

Phenology (from the greek *phainō*: to show, to bring to light, make to appear + *logos*: study, discourse, reasoning) is the scientific study of periodic biological phenomena, such as flowering, breeding, and migration, in relation to climatic conditions. The study of phenological events is perhaps as old as the rest of the ecological sciences [1]. Phenology allows to connect the realm of physical factors such as light, temperature and precipitation, with the seasonality displayed by individuals, populations and communities [2].

A renewed interest in phenology has grown over the past decade, as several works documented a tendency towards early spring events of many taxa in many ecosystems (Figure 1), and the relationship of these timing shifts with global warming [3, 4, 5]. Due to differences in physiology and ecological constraints, different taxa and different trophic levels tend to change their phenologies at different rates [6, 7, 8], resulting in changes of life history, population viability, biodiversity and community dynamics [9, 10, 11, 12]. More recent research using data from mutualistic communities, in particular plant–pollinator networks, has shown that phenology plays an important role in shaping the patterns of interaction networks [13, 14, 15], and that warming could have caused the alteration, complete elimination or the creation of new interactions [16, 17]. This has important consequences for the long term stability of communities under the threats of habitat and biodiversity loss, according to some modeling studies [18, 19, 20].
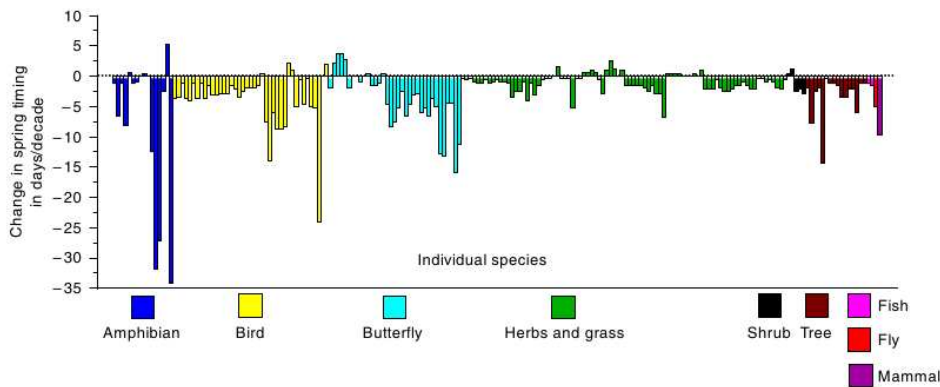

Figure 1. Changes in timing of spring events in days decade^{-1}. Each bar represents a species. Negative values indicate advancement (earlier phenology through time) while positive values indicate delay (later phenology through time). (Source: 7).

But the role of phenology in shaping the structure and dynamics of communities is more than a simple matter of temporal coincidences. In competition for example, early arriving species can gain competitive advantage by growing larger and stronger than latecomers [21, 22], and many species undergo drastic ontogenetic changes determined by phenology, resulting in changes of interaction type [23]. For plants, phenological constraints can determine their spatial distributions over extended areas [24]. As we can see, phenology has consequences for many ecological processes, spanning several spatial scales and levels of organization.

Changes in phenology affect important human affairs such as agriculture [25]. Knowledge of migration phenology can inform us better about the spread of infectious diseases [26]. Thus, it is very important for practical and theoretical reasons, to get a better understanding of the role of phenology on the organization and dynamics of ecological communities.

Theoretical background

Ecological communities are complex adaptive systems made of many components at different levels of organization (individuals, populations, species), arranged as dynamical structures (food webs, interaction networks, metacommunities). The interactions between their components are often non-linear and operate on different spatial and temporal scales. Not surprisingly, our capacity to predict the dynamics of communities, and perhaps more important, their response to perturbations, is quite limited. The models employed to understand and predict the dynamics of communities were originally developed under quite simplistic assumptions, in analogy with ideal physical systems (ideal gases, mass action laws) [27, 28]: all members of a population are alike, they interact with each other no matter the distances separating them. Over time, important details such as demographic structure [27, 29], limits on coexistence [30, 31], interaction complexity [32, 33, 34], spatial effects [35, 36], and evolution [37, 38], have been addressed. Ecological modeling has improved in the last decades thanks to the computer revolution, and with the development of individual based simulations [39, 40].

Although phenology plays important roles in communities, its inclusion into mainstream ecological theories has been rather limited. There are quite elaborated models relating phenology and viability for single populations in time and space [24], but they tend to ignore inter-specific interactions. Most ecological models try to predict the fate of communities over time scales that are much longer than the species phenophases. The consequences of phenology are simply ignored or at best averaged, in order to avoid the complexities involved in analyzing multiple time scales simultaneously. As a result, some relevant information concerning conditions for species coexistence is inevitably lost [41]. When phenology is explicitly considered in communities, I have knowledge about three ways to do it.

One is by considering the Match Mismatch Hypothesis (MMH). The original MMH [42] relates the reproductive success of marine fishes with the temporal synchrony between fish larvae recruitment and the peak in their food abundance (zooplankton). Owing to its simplicity, the MMH has been applied to freshwater and terrestrial systems [43, 44]. Under a MMH framework, peaks in seasonal food abundances can be used as appropriate yardsticks to measure phenological (a)synchrony [6] among species. However, the success of this approach is mixed, because fitness depends on many sequential steps (e.g. adult feeding, oogenesis, egg laying, chick rearing), all of them requiring some degree of resource synchrony [45]. Another issue is that the original MMH is a bottom-up hypothesis which does not consider the long term effect of consumer–resource feedbacks [12, 46].

Another form to consider phenology is in the context of niche partition theories, in order to explain conditions for coexistence in competitive communities [31]. Under this approach time is treated as one dimension of the hutchinsonian niche, and the strength of competition between two species is considered to be proportional to the overlap of their "temporal niches" [47], e.g. if "early is to small food item" as "later is to large large food item", then "early species" and "later species" compete weakly, but a "mid-time species" competes strongly with the former two. This kind of argument has been called upon to explain the segregation of flowering phenophases [48]. This view however, ignores the fact that time is unidirectional, with the past determining the future. Consider priority effects: an early arriving species could deplete all resources during April, leaving nothing for a species arriving in June; but a third species arriving in August may have better luck because resources had enough time to replenish. This highlights that non-coincident species can still affect each other via third parties. Another example: sequentially flowering species competing for pollination services can in theory help each other by ensuring a constantly abundant population of their pollinators [49].

A third way to consider phenology is by its role in shaping interactions. In recent times the availability of large phenological databases has made possible to follow the seasonal assembly of large interaction networks [15, 13], as well as long term changes in their topology [16, 17]. For mutualistic networks this causes changes in connectance and nestedness [50], properties that strongly affect their stability and robustness against interaction loss [51, 20].

Proposal goals

I am aiming for a comprehensive synthesis of the role of phenology in ecological communities. Thus, I will consider themes such interaction dynamics, spatial distribution and dynamics, adaptation and metabolism. The projects of this proposal will address the following general questions:

1. What are the long term consequences of patterns of temporal organization, i.e. phenophase distributions, on the dynamics of communities?

2. How does interaction network architecture modulate the effects of phenology? Do mutualistic networks respond differently than food webs?

3. How does the population dynamics in one year shapes the phenological events in future years? How important is the feedback between phenology and ecological interactions?

4. How does natural selection and phenological plasticity affect the phenophases of interacting species? To what extent environment and interactions constrain adaptation?

5. How to link physical factors with the chronology of ecological interactions? Can we use such knowledge to predict the consequences of climate change?

A framework to achieve these goals

The core idea behind the this proposal is that phenological events affect several processes that ultimately determine biodiversity and function in ecological communities. These effects are modulated by the mesh of species interactions, the dispersal of populations in space, individual adaptations and changes in the environment. In order to achieve the goals stated before, this proposal will comprise four projects addressing these factors. The scope of the projects are displayed in Figure 2, and there is a great amount of overlap among them. I expect this to be a comprehensive approach towards unraveling general patterns concerning the interplay between phenology and communities.

Project A will explore the consequences of phenology on the dynamics of interacting populations, starting with small sets of species and scaling up to large communities. A central idea of this project is the Match-Mismatch Hypothesis (MMH) discussed before, as well as the dynamical feedbacks that can alter species phenologies over longer ecological time scales (e.g. years). This is largest of all four projects in terms of scope, development, data availability and use of computational resources. This project will support the development of projects B, C and D, which explains why it takes more space in this document. For this project I already obtained some partial results [51, 52, 20], as well as the technical expertise needed to approach the other projects.

Project B will study how phenology and spatial organization drive community dynamics. In a recent paper [20], I showed that in spatial contexts habitat destruction and phenological alterations can act synergistically, making mutualistic networks very fragile against interaction loss. I will further explore this subject for consumer–resource networks. This project will also explore the seasonality of migration and alterations of phenological organization by invasive species.

Project C addresses the fact that phenophases, which depend on individual traits, can evolve and adapt due to natural selection and phenotypic plasticity. This adaptability of phenology is constrained by trade-offs, interactions (e.g. matching resources while mismatching predators), and density- and frequency-dependent effects. This will determine which species will be able to change fast enough in the face of climate change.

Project D will seek to use general rules of physiology (e.g. metabolic theories) in order to link the periodical nature of climate and the timing of ecological interactions. Climate seasonality is affected by natural drivers (e.g. Earth's rotation) and human actions (e.g. global warming).
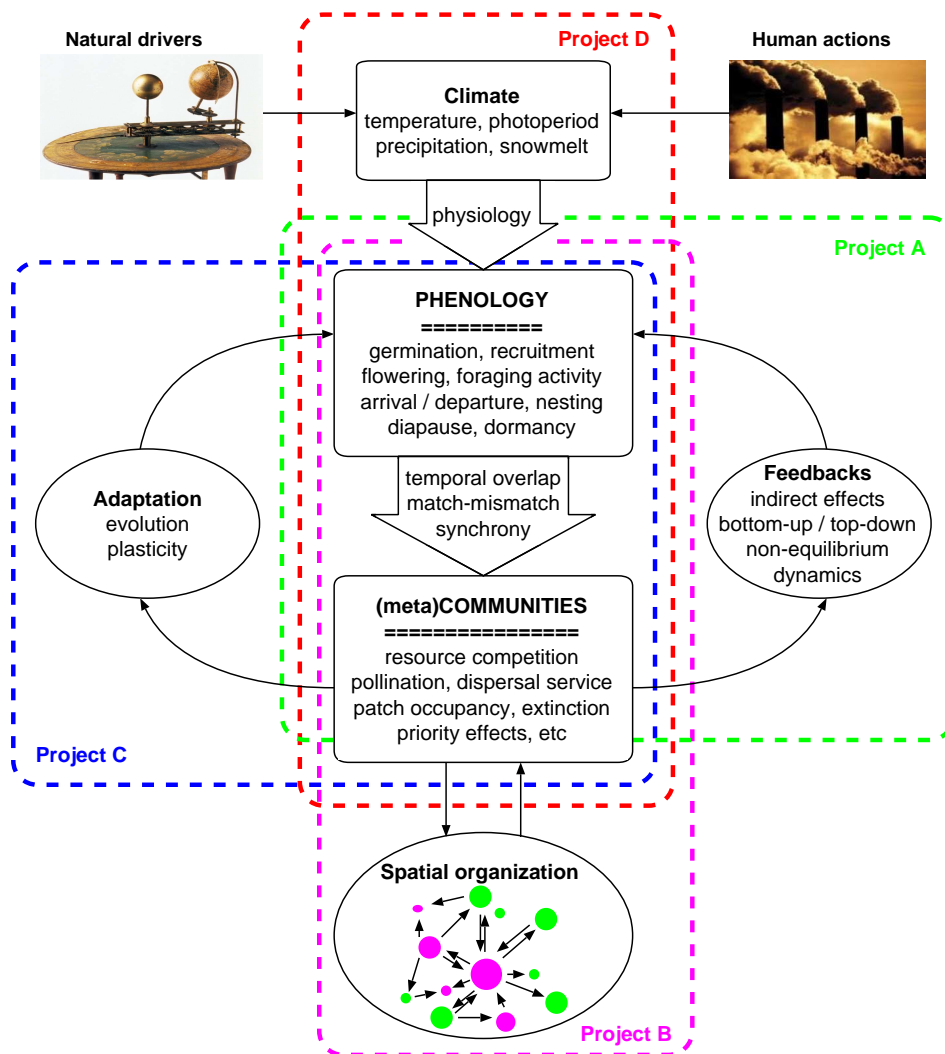
Figure 2. Framework to study the interplay between phenology and community ecology. Four projects will address the ways in which interactions (A), spatial dynamics (B), adaptation (C) and climate changes (D) condition the consequences of phenology for communities.

2 Research projects

Project A. The temporal organization of ecological networks

In order to study the role of phenology on ecological interactions, population dynamics and communities, it is necessary to start from simple but solid foundations. A convenient starting point is a system of two species like in Figure 3, interacting as a prey and predator, competitors, or mutualists for example. A certain model in continuous or discrete time governs the population dynamics of the species (e.g. Lotka–Volterra equations), parameterized by growth and mortality rates, and by interaction parameters (e.g. consumption rates, handling times). Simple pairwise interactions can be aggregated as community modules [53] in order to study processes such as resource competition, apparent competition or intraguild predation to name a few. Several community modules can be condensed to form interaction networks (e.g. food webs, mutualistic networks).

Figure 3 illustrates three ways in which I will incorporate phenology in community modules and large networks. I will use some example scenarios to describe how to relate these three schemes with the parameters governing interaction dynamics.

Time-dependent parametrization. Assume that species N is a plant and P herbivore. Photosynthesis depends on solar radiation, which increases and declines within a year. In contrast, foraging activity can depend on temperature, which also varies within a year. As a result, growth (b) and herbivory (a) rates become periodic functions of time (e.g. sine functions) with periods of 365 days each, and the difference in time between the peaks of $b(t)$ and $a(t)$ quantifies the phenological asynchrony between the species. This kind of approach has been applied to small community modules [54].

Temporal overlap. Assume that N_i represent $i = 1, \ldots, n$ plants and P_j represent $j = 1, \ldots, m$ pollinators. The interactions among them depend explicitly on the amount of time of their common presences, i.e. their days of temporal overlap. For example, if the pollination rate for plant–pollinator pair is a when they coincide during four days, it will be o $2a$ if their coincidence increases by two days, or $a/2$ if halved to two days. These approach has been used to study the consequences of temporal segregation in very large competitive and mutualistic communities [55, 56, 51, 20].

Semi-discrete dynamics. The populations undergo continuous or discrete dynamics embedded into larger, discrete intervals of time, e.g. years. Phenology is modeled by pulsed events of recruitment from propagules (e.g. seeds, eggs) produced in the preceding year, and interactions between preys and predators in the present year determine their respective number of propagules for the next year. The timing (mean date) and duration (standard deviation) of the recruitment phenology determines the abundance phenology of a species, which can vary across years as a consequence of the interactions. This approach as been used on few occasions, for very simple systems [57, 52].

These approaches have different strengths and weaknesses. Under *Time-dependent parametrization* it is easy to link growth parameters and seasonal drivers such as temperature [58] or solar radiation [59]. This approach slightly modifies the most common models used to describe species interactions [54, 60]. However, an important issue of this approach is that some interactions can lead to periodical dynamics by themselves. Such endogenous oscillations (e.g. prey–predator) and the forced oscillations (seasonal) can mask each other or interact in ways that makes it difficult to assess the importance of phenology in driving community dynamics. On the other hand, this issue is a potential research subject.

The *temporal overlap* scheme does not require important modifications of conventional modeling frameworks (e.g. Lotka-Volterra competition models). It's major appeal is to enable the use of a large number of readily available phenological calendars of large communities, mostly from plant–pollinator networks [16, 13, 17]. These calendars have very simple information, just the records of the first and last days of an important event such as flowering in plants or flight activity in pollinators. In a few cases, these recordings were made at different years, allowing us to study
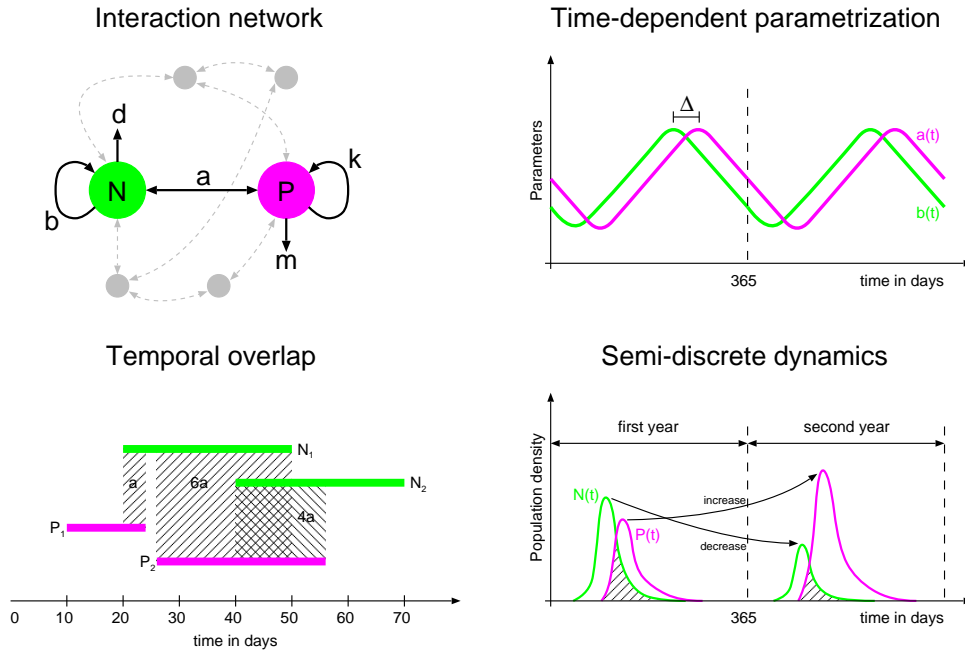
Interaction network

Time-dependent parametrization

Temporal overlap

Semi-discrete dynamics

Figure 3. Embedding phenology within communities. A species pair (green and magenta) within an *interaction network* (circles connected by double headed arrows) displays the growth (b,k) mortality (d,m) and interactions (a) parameters governing population dynamics. Under *time-dependent parametrization* some parameters vary in time, with a certain amount of phenological (a)synchrony (phase difference Δ). Under *temporal overlap,* interaction parameters are functions of the number of days of coincidence between species (width of stripped areas). Under *semi-discrete dynamics* the populations recruit and vanish in pulses describing their phenologies. Population pulse overlap (stripped area) determines species interaction strength (scaled by parameter a), and also the shape of the pulses (width and height) in future years (e.g. plants decrease, herbivores increase).

the consequences of phenological changes of large numbers of species in a given community. Overall, this methodology adds a missing feature in many studies of interaction network robustness, which is information concerning relative interaction strengths among species.

The first two schemes assume that the dynamics develops without interruption, every day of every year. In contrast, *semi-discrete dynamics* acknowledges the fact that there are times in the year during which the interaction of interest is in fact nonexistent [41]. This happens for many reasons: some species can be in diapause, insects can be pupating instead of foraging, migratory birds have not yet arrived, grasses cannot start flowering because the soil is covered with ice, etc. The semi-discrete approach however, is so far analytically untractable, and its implementation demands numerical simulation [57, 52, 61].

Using these approaches, the interplay between phenology and communities will be studied under two scales organizational complexity: small community modules and large interaction networks.

Phenology and community modules

An important direction in this subproject is to characterize the responses of small sets of interacting populations, i.e. community modules [53], towards phenological shifts. The Match Mismatch Hypothesis (MMH) tells us that consumers would perform better when matching with their resources, whereas resource species would perform better under mismatch with their consumers. In the case of a mutualistic interaction, the MMH would predict that temporal (mis)match would always be (un)favorable for two species.

The next step in complexity will consider a third species, whose phenology matches the two other species with variable degrees. From this point, predictions from the MMH will be conditioned by the arrangement of the interactions, top- versus bottom-up effects, resource competition, apparent competition and indirect effects. A first exploration using *time-dependent parametrization* [54], revealed that phenological (a)synchrony affects not just population recruitment, but also

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key dynamical features such as trophic cascades, competitive hierarchies, and species coexistence. Under *semi-discrete dynamics*, we made [52] two important predictions. The first is that higher synchrony between preys and predators can lead to low predator population abundances in the long term. This is a consequence of overexploitation, which is not accounted in by the original MMH, and this has been observed in a context of arctic climate change [12]. The second prediction for tree-species modules is that temporal niches (temporal windows of species viability) display superposition effects as a consequence of interactions (e.g. being enlarged or reduced, respectively by alternative resources or competitors). Empirical confirmation for this prediction would require multi-generational experiments. In order to see if superposition effects are robust, simulations will be performed in community modules with four, five and six species arranged according to different network motifs [62], e.g. food chain, intraguild predation, pyramidal webs (*with C. Melián*). This subproject will employ consumer–resource approaches. This will also work for pollination and seed dispersal mutualisms, by modeling floral resources and fruit production in an explicit manner [63, 64].

My work with community modules revealed important predictions regarding the limits of competitive coexistence under temporal segregation. The Competitive Exclusion Principle (CEP) states that everything else equal, two consumers cannot stably coexist in competition for a single resources [30]. However, long term stable coexistence can be achieved under conditions of semi-discrete dynamics [52] by temporal segregation (i.e. one consumer before and the other after the resource peak; see also [41, 65, 56]). A research question here (*with V. Krivan*) is to see to which extend can semi-discrete dynamics be collapsed into the much simpler temporal overlap parametrization, for two competitors (i.e. not telling which species comes before and which after the resource peak): are they still able to coexist, thus violating the CEP?

Phenology and interaction networks

This subproject will look at the consequences of phenological organization and phenological shifts in large communities (e.g. 20 species or more). The goal of many studies of interaction networks is to relate network statistics such as link connectance, nestedness and degree distributions with the network's tolerance against species removals or population stability [66, 67, 18, 50, 68]. In doing this, interaction strengths (e.g. parameters like a in Fig. 3) are typically set as 0 (interaction absent) or 1 (interaction present), or randomly sampled without any relation with real network properties. As it turns out, empirical studies and simulations [13, 14, 15] reveal that interaction frequency, a reliable proxy of interaction strength [69], can be highly variable within and across years. By considering this, simulations predict that phenology can drive the dynamics of mutualistic networks [51], or it can interact synergistically with threats such as habitat loss [20].

At the moment phenology and interaction networks have been linked under the *temporal overlap* scheme (Fig. 3). This is because the phenological data associated with interaction networks take the form of presence/absence calendars, and information about abundance phenology, growth rates, etc, is generally incomplete. This methodology will be revised by simulation and the correlations between interaction strength and temporal overlap properly tested using empirical data (*with A. Richards*). Why is this important? because one may ask: is the loss of 5 interaction-days equally harmful when a phenophase lasts 2 weeks instead of 4?, how important are species-specific tolerances against the loss of interaction-days?

So far, my research only addressed mutualistic networks (pollination and seed dispersal), since the data on phenology and interaction patterns for these are readily available. I am looking forward to use data on antagonistic networks (e.g. food webs, host-parasite, competitive guilds, see Methods) in order to develop a more general understanding on the role of phenology on large communities. For example we discovered [51] that in mutualistic–competitive networks, phenological overlaps reinforce plant–pollinator mutualisms, but at the same time it unbalances plant–plant and pollinator–pollinator competition, threatening coexistence. This is a consequence of parameterizing interaction models with *temporal overlap* schemes. I am curious to see if *semi-discrete dynamics* schemes (*with F. Encinas-Viso and R. Ramos-Jiliberto*) would relax the coexistence requirements [52].

Project B. Phenology in spatial contexts

Communities are embedded in complex landscapes which condition the interactions that occur at the local scales, e.g. habitats, patches, micro-sites. In turn, interactions at local scales determine which species survive and disperse between different localities, and by extension regional biodiversity. Thus, metacommunity theories [70] are necessary to understand how the interplay between spatial organization and phenology determines biodiversity [20]. My work in this direction will generally consider large interaction networks, but community module approaches will remain useful for certain problems.
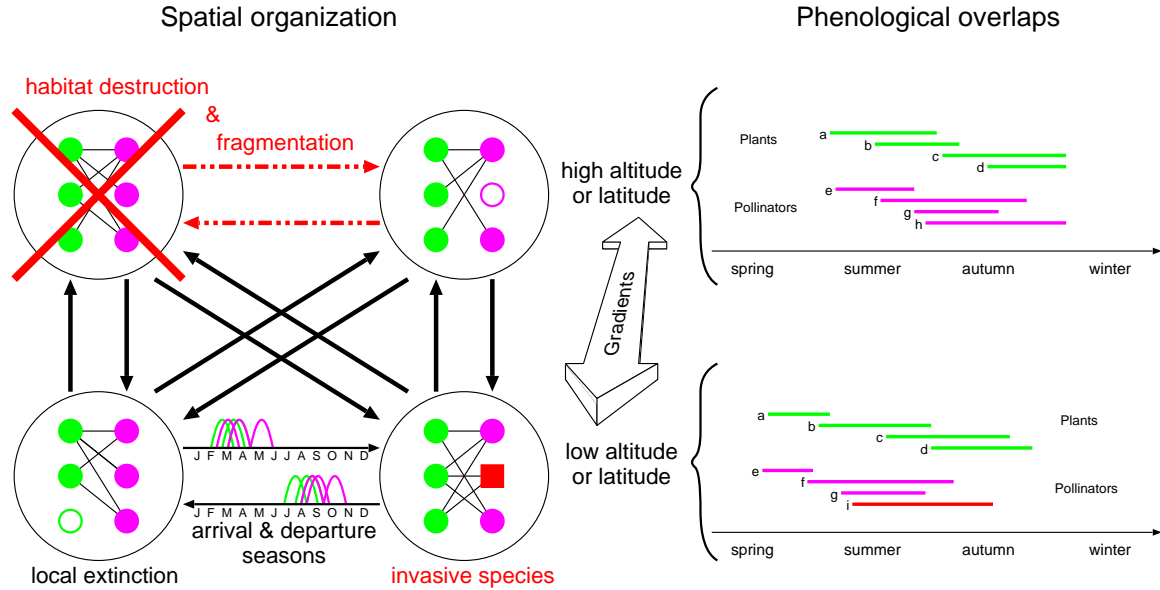

Figure 4. Spatial and temporal organization of interaction networks. Interacting species (green and magenta disks) spread over a metacommunity by dispersal events (arrows). Phenological overlaps determine local survival and extinctions, thus presences or absences (filled or open disks). Dispersal itself be can seasonally determined. Metacommunities will face alterations such as habitat destruction (X), fragmentation (broken arrows) and substitution of species with altered phenologies (square, species 'i' substituting species 'h'). Phenologies themselves can vary across environmental gradients.

Figure 4 summarizes the main topics to be explored under this project. Spatial dynamics will be considered implicitly [35] or explicitly [36]. Implicit space considers an infinite amount of patches in which a species can be present or absent. Thus each species occupy a certain proportion (%) of patches in the metacommunity [68, 18], and the distance between patches plays no role in the dynamics. Explicit space considers a finite amount of patches. The state of a population in a given patch is given by its local population size or by its occupancy (present/absent). With explicit space the distance between patches plays an important role in the dynamics. In both approaches, the regional abundance of a species depends on the balance between inter-patch dispersal and local extinction. A species dispersal and extinction rates depends on local events of reproduction and mortality, which will depend on the phenological overlap with their resources (increase growth, decrease mortality) and predators (increase mortality).

Dispersal can also be directly dependent on phenology. This will permit to explore the effect of arrival and departure seasons of migratory species, which determine territory acquisition [71], match/mismatch with local resources and priority effects [21], and the seasonal spread of infections [26] (*with J. Mellard*). We will study the effect of spatial gradients (e.g. temperature decrease with altitude), which are known to affect phenologies and the extend to which temporal uncoupling affects species performances [72] (*with F. Encinas-Viso*).

Empirically recorded interaction networks do not usually provide information about their spatial distribution. For this reason, spatial dynamics will be implicitly modeled for them. We

will employ statistical approaches to fit phenologically informed models (based on interaction calendars) with presence/absence or relative occupancy data when available (*with B. Haegeman and A. Richards*).

The extent to which phenology and its changes affect metacommunities depends strongly on other environmental stressors and perturbations. Our recent simulation study [20] predicts that habitat destruction and interaction loss due to phenological mismatch act synergistically, raising the vulnerability of mutualistic networks to catastrophic collapse. We argue that this is because mutualisms are characterized by positive feedbacks that reduce system stability. Future work will address these synergies in food webs, which are characterized by multiple negative feedbacks instead. Finally, another perturbation that will be studied is species substitution. Invasive species can have very different phenologies than the native ones they displace [73]. I will consider different amounts (%) of species substitutions to see how they affect the performance of interaction networks (*with F. Encinas-Viso*).

Project C. Adaptation and evolution of phenologies

Phenologies result from environmental conditions and individual traits that are plastic and evolvable. Under natural selection, phenologies will change under the limits imposed by climatic constraints that define fundamental niches (e.g. solar radiation, temperature, precipitation). The Match Mismatch Hypothesis (MMH) predicts that species would evolve to match their resources and to mismatch their natural enemies (e.g. predators, competitors), see Figure 5. However, the reality is more complex [74], because of trade-offs between conflicting goals. For example, migratory birds face increased pressure to arrive early to acquire breeding sites, but this can offset their chicks from the local resource peak [71].
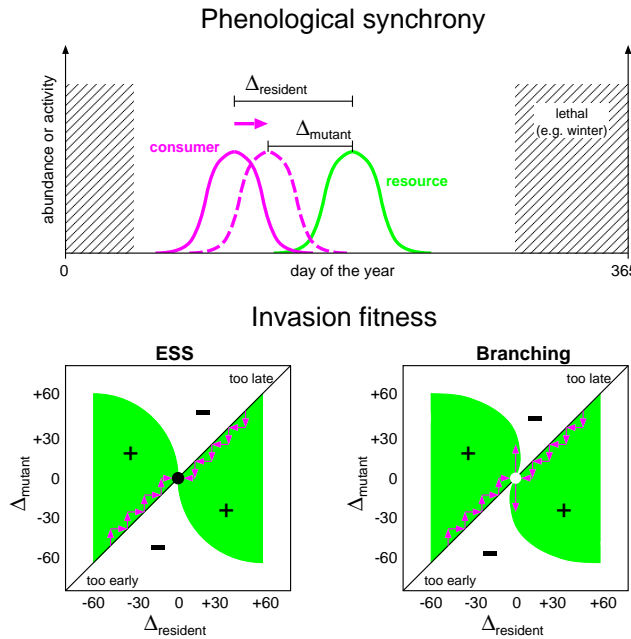

Figure 5. Evolution of phenological traits. A consumer has a certain amount of asynchrony (Δ) between its phenology (magenta curve) and its resource phenology (green curve), but this can change as a result of mutations (arrows) in a resident population. Only mutations along the invasion fitness gradient (from $-$ to $+$, with 0 at the diagonal) can invade and replace resident populations, increasing synchrony as a result. Phenological match can be an evolutionary stable strategy (ESS, black spot), or it can lead to a fitness minimum (white spot), promoting disruptive selection by evolutionary branching.

This project will explore the evolution of phenologies in small communities and in large interaction networks. I will use Adaptive Dynamics (AD) theory [75] to model evolutionary changes.

AD has a number of advantages over traditional approaches (e.g. mendelian and quantitative genetics). AD deals with phenotypic evolution (i.e. genetic architecture is not considered), it assumes a separation of scales between ecological dynamics (fast) and evolutionary change (slow), and it allows the treatment of density-dependent fitnesses by linking them with population dynamical models. However, some assumptions of AD such as time scale separation, small mutational steps and asexual reproduction, are not usually met together. These shortcomings will corrected using individual based simulations [40] (*with F. Encinas-Viso*).

One of the first questions that will be addressed is under which conditions temporal matching with resources becomes an evolutionarily stable strategy (*with C. de Mazancourt*). Phenological synchrony can lead to overexploitation and small consumer populations in the long term [52]. Small populations may evolve very slowly (low genetic diversity), are affected by genetic drift, or can go extinct. In addition, close phenological matching will cause strong resource competition. Thus there are reasons to think that adaptation can lead populations to fitness minima instead of maxima, promoting disruptive selection and evolutionary branching [75] (Figure 5), and increasing the diversity of phenologies. Subsequent work will deal with the coevolution between resource and consumer phenologies, but in a context of large organizational complexity, e.g. mutualistic networks and food webs (*with M. Loreau*). The AD approach is also useful for this kind of task [38].

Recent research points out that evolution may not be fast enough to ensure phenological adaptation in the face of climate change, but phenotypic plasticity could [76]. This is another question that will be explored by this project (*with V. Krivan*). Phenotypic plasticity will include diet changes in consumer–resource modules, and interaction rewiring for large networks.

Project D. Linking warming with phenology and communities

The current paradigm relating temperature and physiological rates is the Arrhenius equation used by the Metabolic Theory of Ecology (MTE) [58]. It is a common practice to link population model parameters such as growth and mortality rates directly with temperature (e.g. b(Temp) in Figure 3) under the MTE [60], and then let the temperature vary according to a seasonal schedule (i.e. Temp(day of the year)) to explore the consequences of a variable environment on community dynamics [59].

However, the relationship between phenological events and temperature has been commonly and very successfully explained by means of the degree-day concept, a proportional measure of heat accumulation linked to development [77]. Degree-days, for which there is abundance of data [78], will be used to bracket starting end ending days of phenological calendars (for models using *temporal overlaps*) or to construct recruitment curves (for models using *semi-discrete dynamics*). In this way, the consequences of potential warming trends [79] on interaction networks will be simulated and compared (*with J. Mellard*).

3 Overview of tools and methods

The projects in this proposal depend strongly on simulation of large systems of differential equations. Approaches such as s*emi-discrete dynamics* and spatially explicit modeling, adaptive dynamics and individual based models require replications in order to achieve robustness in the outcomes. These tasks can be done relatively quick using parallel computing, with free software such as the GNU Scientific Library and the Python programming language. Data analysys and parameter fitting will employ the R language. Simulations will be done locally (desktop computers, small clusters), or with external computer clusters (e.g. Genopole Toulouse http://www.genotoul.fr) if needed.

Source codes, methods and working papers (preprints) will be hosted in online revision systems such as https://bitbucket.org/ or https://github.com/. Model generated data will be available at online repositories such as Dryad http://datadryad.org/.

When possible, real networks and phenological calendars will used to parametrize simulation models. Data will be obtained from the most recent literature on the subject and from public databases such as:

- Interaction Web Database (NCEAS): https://www.nceas.ucsb.edu/interactionweb/

- Web of Life (Bascompte Lab): http://www.web-of-life.es

- USA National Phenology Network: https://www.usanpn.org/

- Pan European Phenology Project: http://www.pep725.eu/

Some models for project D will require information about degree-days, which are usually reported in agricultural journals. A Database of Thermal Requirements from project PRATIQUE is available:

- https://secure.fera.defra.gov.uk/pratique/publications.cfm

4 Integration into the Research Team

The Centre for Biodiversity Theory and Modelling (CBTM) at the Station d'Ecologie Expèrimentale du CNRS a Moulis (SEEM) provides the ideal working conditions for the development of these projects, in terms of collaboration, discussion and facilities. The stated mission of the CBTM is to lay the theoretical foundations of an integrative biodiversity science able to meet the great challenges of the current biodiversity crisis. The local research team provides expertise in metacommunity theory and spatial complexity (Michel Loreau, Bart Haegeman), adaptation under climate change (Michel Loreau, Claire de Mazancourt, Jarad Mellard), and linking theory with data (Bart Haegeman, Adam Richards). My recent work at the CBTM has lead to publications on the topics proposed here [52, 20], and the head of the group is familiar with the modeling challenges at hand [55, 41, 65].

The SEEM is also a convenient venue for the realization of scientific meetings and workshops, and it will allow the access to important computing facilities (via the Genopole Toulouse). Its strong association with the University Paul Sabatier makes the SEEM ideal for involving students in some of the projects.

Collaborators

The wide scope of this project will require a network of collaborators locally (Moulis) and from abroad. A first list of collaborators include:

- Michel LOREAU (DR, CNRS, Moulis, France). *Biodiversity theory and modeling, metapopulation dynamics, phenology*

- Claire de MAZANCOURT (DR, CNRS, Moulis, France). *Consumer–resource dynamics, mutualistic models, eco-evolutionary dynamics*

- Bart HAEGEMAN (DR, CNRS, Moulis, France). *Dispersal and consumer–resource dynamics*

- Jarad MELLARD (Postdoctoral fellow, CNRS, Moulis, France). *Eco-evolutionary dynamics, consumer–resource coevolution*

- Adam RICHARDS (Postdoctoral fellow, CNRS, Moulis, France). *Statistical methods, bayesian statistics, high performance computing*

- Francisco ENCINAS-VISO (Postdoc, CSIRO, Canberra, Australia). *Network theory, mutualistic models, individual based modeling, phenology*

- Carlos MELIÁN (Associate professor, EAWAG, Kasnatienbaum, Switzerland). *Network theory, individual based modeling*

- Rodrigo RAMOS-JILIBERTO (Associate Professor, University of Chile, Santiago de Chile, Chile). *Network theory, food web modeling, phenology*

- Vlastimil KRIVAN (Professor, University of South Bohemia & Academy of Sciences, Ceske Budejovice, Czech Republic). *Dynamical systems, mechanistic models, foraging theory, mathematical analysis*

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