(A bit) Earlier or later is always better:

Phenological shifts in consumer-resource interactions

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Abstract Phenology is a crucial life-history trait for species interactions and it can have great repercussions on the persistence of communities and ecosystems. Changes in phenology caused by climate change can disrupt species interactions causing decreases in consumer growth rates, as suggested by the Match Mismatch Hypothesis (MMH). However, it is still not clear what the long-term consequences of such phenological changes are. In this paper we present models in which phenology and consumer-resource feedbacks determine long-term community dynamics. Our results show that consumer viability is constrained by limits in the amount of phenological mismatch with their resources, in accordance with the MMH. But the effects of phenological shifts are often non-monotonic. Consumers generally have higher abundances when they recruit some time before or after their resources because this reduces the long-term effects of overexploitation that would otherwise occur under closer synchrony. Changes in the duration of recruitment phenologies also have important impacts on community stability, with shorter phenologies promoting oscillations and cycles. For small community modules, the effects of phenological shifts on populations can be explained, to a great extent, as superpositions of their effects on consumer-resource pairs. We highlight that consumer-resource feedbacks and overexploitation, which are not typically considered in phenological models, are important factors shaping the long-term responses to phenological changes caused by climate change.

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1 Introduction

Phenology, the timing of plant and animal life cycles such as the first dates of flowering, the emergence of insects, and the migrations of birds, is an important aspect in the research of ecological interactions (Yang and Rudolf, 2010), evolutionary ecology (Gilman et al., 2012; Johansson and Jonzén, 2012), and community structure and dynamics (Kallimanis et al., 2009; Olesen et al., 2011; Encinas-Viso et al., 2012) among others. Since phenology plays such an important role at many scales of biological organization, there is much concern about the potential consequences of changes in species phenologies driven by global climate change (Parmesan and Yohe, 2003; Parmesan, 2007; Donnelly et al., 2011; Kerby et al., 2012).

A fundamental idea that helps to understand the effects of changes of phenology on population demographics is the Match Mismatch Hypothesis (MMH). The MMH posits that the growth rate of a consumer increases as its reproductive phenology becomes closer to the abundance phenology of its resources (Cushing, 1990). Conversely, growth rates decrease as the mismatch between resources and consumers increases. Although the MMH was originally applied to zooplanktivorous fish, it is now considered for a wide number of aquatic and terrestrial systems (Durant et al., 2005; Both et al., 2006; Durant et al., 2007; Miller-Rushing et al., 2010). Independently but very much related to the MMH, the amount of inter-specific temporal overlap has been frequently treated as a metric of interaction strength in non-consumptive relationships, such as interference competition (Ebenhöh, 1992; Encinas-Viso et al., 2012) and mutualisms involving services such as pollination or seed dispersal (Memmott et al., 2007; Encinas-Viso et al., 2012). In spite of this generalization, there is still little experimental and theoretical research on the consequences of phenological mismatches in systems comprising more than one consumer and its resource, and even less addressing the consequences of phenological shifts for the long-term dynamics of communities. The last issue is very important, because many predictions derived from simple application of the MMH fail to consider the effect of population sizes (Durant et al., 2005), and populations can display important changes from one year to another.

In order to investigate the effects of phenological shifts in multispecies systems, Nakazawa and Doi (2012) adopted a community module approach (Holt, 1997), with three species interacting as follows: tritrophic food chain, resource competition among two consumers, apparent competition between two resources sharing a common consumer, and intraguild predation. Phenology was incorporated as sinusoidal growth rates with periods equal to a year (Namba, 1984; Abrams, 2004), and the dynamics according to Lotka-Volterra equations. Phenological asynchrony between species was quantified by the phase difference between growth rate maxima. These authors found that phenological shifts strongly affects trophic cascades, indirect effects, competitive hierarchy and species coexistence.

The models of Nakazawa and Doi (2012) seem appropriate for species with several overlapping generations in the same year. However, more common species life-histories include maturation times to actively participate in the ecological interactions. For these species, events such as reproduction, recruitment or maturation take place periodically in a discrete or pulsed manner, while events such as deaths and consumption happen

continuously. We can expect important differences in the responses of the populations to phenological shifts between such contrasting life-histories. One important reason is that under continuous reproduction and maturation the consumer-resource feedbacks are instantaneous, whereas pulsed reproduction and delayed maturation introduce significant lags (e.g. a year) that can affect stability (May, 1974). Also, the periodic forcing in Nakazawa and Doi (2012) models make it difficult to know whether coexistence or competitive dominance are caused by shifts in phenology or by non-equilibrium dynamics. Finally, Nakazawa and Doi (2012) limited their study to shifts in the phenological peaks, not addressing the effects of changes in the duration of the phenophases, which is another important factor determining the overall amount of phenological matching (Miller-Rushing et al., 2010; Kerby et al., 2012).

This paper aims to improve our understanding of the impact of phenological mismatches in consumer-resource interactions. Our modeling approach is a hybrid of continuous time dynamics *within years* and discrete time dynamics *across years* (Pachepsky et al., 2008). We consider species with complex annual life cycles, where recruitment occurs in a pulsed manner. Thus, the top-down effects of consumers build-up across years as a consequence of time lags. In this way the effects of consumer-resource feedbacks, such as oscillations and trophic cascades, are not masked by external forcing, as it occurs when parameters become periodic functions (e.g. sine functions). Modeling phenologies as pulsed events allows us to study the effect of phenology duration, an important aspect of temporal overlap (Miller-Rushing et al., 2010), in addition to phenological shifts only. Our model also puts more emphasis on the mechanics of consumer-resource interactions between two species, their equilibrium, and long-term stability conditions. Our results show that overexploitation is an important factor shaping the long-term response due to phenological changes by climate change that is not considered by the MMH. This study is a step forward in understanding the combined effects of phenological changes and consumer-resource feedbacks in communities affected by climate change (e.g. warming).

2 Model and methods

Our model considers consumer-resource interactions between two species, and between three species arranged in four community modules (Holt, 1997; Nakazawa and Doi, 2012): (a) a consumer and two resources, in which resources face apparent competition, (b) resource competition, (c) a food chain, and (d) intraguild predation. The species have a demographic structure consisting of adults and offspring. The adults engage in consumer-resource interactions during a period of time that cannot last more than a year, after which all of them die. The adults produce offspring that do not interact in the present year, but that recruit as the new adults during the next year. Thus, we assume that the offspring is in a quiet stage such as seeds or eggs, and that recruitment means entering the adult stage by germination or eclosion. The recruitment phenology of species i is governed by a probability density function $\rho_i(t)$ with mean emergence date μ_i and standard deviation σ_i, where $t = [0, 365]$ in days (Figure 2, top row). This means that recruitment consists of an accumulation of cohorts, where the variation around the mean date of emergence reflects the heterogeneity of the individuals making the population. This approach in which recruitment is governed by a statistical distribution was used before to model the evolution of protandry in butterflies, where males and

females gradually emerge, interact and die during one season (Zonneveld and Metz, 1991; Zonneveld, 1992).

To introduce the model dynamics let us consider the simple case of one resource (species 1) and its consumer (species 2). Within a year, the time t runs from 0 to 365 days and the number of individuals of the resource $N_1(t)$ and the consumer $N_2(t)$ species in the adult phases change according to the set of ordinary differential equations (ODE):

$$\frac{dN_1}{dt} = \rho_1(t)n_1 - m_1 N_1 - a_{12} N_1 N_2 \tag{1}$$

$$\frac{dN_2}{dt} = \rho_2(t)n_2 - m_2 N_2 \tag{2}$$

where n_i are the number of offspring or propagules, e.g. seeds or eggs, available for recruitment during the year, m_i are first order mortality rates and a_{ij} is the consumption rate of i by j. All populations are absent just at the beginning of the year ($N_i(0) = 0$) and build up with phenologically determined recruitment rates $\rho_i(t)$. In the absence of any losses due to mortality or predation ($m_i = 0, a_{ij} = 0$), the integration of the ODE from $t = 0$ to 365 yields a number of adults that is equal to the number of propagules available at the beginning of the year, i.e. $\int_0^{365} n_i \rho_i(t)dt = n_i \int_0^{365} \rho_i(t)dt = n_i$. We will assume that $\rho_i(t)$ is a normal probability density function. Normal distributions span from $(-\infty, +\infty)$ instead of $[0, 365]$ as required, but the cutoff error can be kept below the typical rounding errors of numerical integration methods (more about this later). We also considered uniform distributions ($\rho_i(t) = {}^1/2\sigma_i$ for $\mu_i - \sigma_i \leq t \leq \mu_i + \sigma_i$, and 0 elsewhere), but we did not find important qualitative differences in the outcomes.

All living adults die at the end of the year and only their offspring will be available in the next year. A second set of ODEs accounts for the dynamics of offspring production for the resource $B_1(t)$, and the consumer $B_2(t)$, during the year:

$$\frac{dB_1}{dt} = \frac{b_1 N_1}{1 + cN_1} - d_1 B_1 \tag{3}$$

$$\frac{dB_2}{dt} = e_2 a_{12} N_1 N_2 - d_2 B_2 \tag{4}$$

where b_i is the maximum birth rate of the basal resource. Reproduction in basal resources is self-regulated by the factor $(1 + cN)^{-1}$ where c is an intra-specific competition coefficient. In the consumers e_i is a food to offspring conversion efficiency rate ($e_i < 1$). Although offspring are not playing the ecological roles of their parents in the present year, they can die due to causes not explicitly accounted by the model (e.g. seed/egg predation, or diseases). Appropriate death rates d_i were introduced to account for this fact. Notice that ODEs (3,4) run over a time span of 365 days, i.e. reproduction takes place during the whole year, in a mathematical sense. However, adult presence is negligible during most of the year due to recruitment happening around a few days, and adults dying after a few days or weeks (more about this later). Thus for all practical purposes, the breeding season lasts only a few months. We can also force breeding to happen in a fixed interval that is much smaller than 365 days, but this does not introduce significant changes in the outcomes.

There are two important reasons for modeling self-regulation by means of a fraction, instead of a linearly decreasing factor $(1 - cN)$ which is more familiar (e.g. in the logistic

model). The first reason is that the fractional factor can be derived from a mechanism in which reproduction depends on limiting resources (Schoener, 1974). To be more specific, let us say that the resource species uses a non-reproducing energy source (light, nutrients, detritus). The rate of offspring production of the resource species follows a mass action law like in the consumers (4), i.e. $\epsilon \alpha E N$, where E is the amount of energy available, α is the consumption rate by the resource species, and ϵ is an energy conversion efficiency. The dynamics of E can follow chemostat-like dynamics $dE/dt = I - \lambda E - \alpha E N$, where I is the energy inflow into the system and λ is its loss rate. If we assume that the energy dynamics is much faster than the dynamics of the resource species, then a steady-state ($dE/dt \approx 0$) can be attained with respect to the resource species, and we can substitute the steady-state energy availability $E \approx I/(\lambda + \alpha N)$, in the mass action law. We obtain the expression $\epsilon \alpha E N = \epsilon \alpha I N/(\lambda + \alpha N)$, which can be rewritten as $bN/(1 + cN)$, where $b = \epsilon \alpha I/\lambda$ is an energy-dependent birth rate, and $c = \alpha/\lambda$ a consumption-dependent competition coefficient. The second reason for our density-dependent factor has to do with the problem that a linear factor like $1 - cN$ can produce negative births. For example, if the past year produced a large enough number of eggs, it is possible that some day in the present year adult numbers are $N > 1/c$, causing negative births if we use a term such as $b(1 - cN)N$ in (3).

The final value of the B_i at $t = 365$ is obtained by solving the system of ODEs (1,2,3,4) numerically, and it becomes the value of n_i in the next year. Thus we can define the following offspring or propagule recurrences from year τ to year $\tau + 1$:

$$n_{1,\tau+1} = B_1(t = 365|n_{1,\tau}, n_{2,\tau}) \tag{5}$$

$$n_{2,\tau+1} = B_2(t = 365|n_{1,\tau}, n_{2,\tau}) \tag{6}$$

Summarizing, ODEs (1,2,3,4) govern the dynamics that occur within a year, whereas the recurrences (5,6) govern the long-term dynamics across several years, and ultimately the viability of the populations.

Phenological (a)synchrony is studied following the scheme of Nakazawa and Doi (2012): the recruitment peak of species 1 is fixed at $\mu_1 = 180$ (approximately mid-year) and the recruitment peaks of other species are shifted up to 100 days before and after species 1 in steps of 5 days. Table 1 lists the parameters of the model. Parameter values had to be chosen arbitrarily since we don't have the analytical means to determine which regions in parameter space allow the feasibility of the community modules. Nevertheless, we made the following important considerations. (i) μ_i and σ_i are such that the truncation of $\rho_i(t)$ at 0 and 365 causes very little error; for example if $\sigma_i = 20$, the earliest and the latest recruitment peaks, $\mu_i = 80$ and 280, are respectively ~4 standard deviations from the start and the end of the year, leaving ~0.01% of the distribution out. (ii) m_i is chosen such that the *average* life time of an adult is less than one month. This ensures that almost all adults become absent many months before the end of the year, i.e. phenophases are contained within a year for all practical purposes. Consequently, adult abundances (N_i) and mass action terms ($N_i N_j$) are negligible during most days of the year, and for practical purposes reproduction takes place during a short season even though the ODEs (1,2,3,4) consider 365 continuous days. (iii) The daily mortality must be significantly lower for the offspring compared with the consumers $d_i \ll m_i$. This is because the offspring must survive many more days than the adults in order restart the dynamics of the next year, whereas all adults are meant to die in the same year they were born. (iv) We use common values for most

of the parameters, in particular for the consumption and mortality rates, to make it easier to compare the species responses between the different modules. The electronic supplement provide additional results that check the robustness of our results, by halving or doubling the values of the parameters in Table 1.

The within-year dynamics (equations 1,2,3,4) are integrated using the Runge-Kutta(4,5) method. For the community modules the set of equations (1 to 6) is augmented and interactions are added as appropriate, always keeping species 1 as the reference with which phenological shifts are measured. Thus the following ODEs for the adults:

$$\frac{dN_1}{dt} = \rho_1(t)n_1 - m_1 N_1 - a_{12} N_1 N_2 - a_{13} N_1 N_3$$
$$\frac{dN_2}{dt} = \rho_2(t)n_2 - m_2 N_2 - a_{23} N_2 N_3 \tag{7}$$
$$\frac{dN_3}{dt} = \rho_3(t)n_3 - m_3 N_3$$

are used for the intra-guild predation (Fig. 4d, graph), for resource competition (Fig. 4b, graph) setting $a_{23} = 0$, and for food chains (Fig. 4c, graph) setting $a_{13} = 0$. For apparent competition we use the following ODEs:

$$\frac{dN_1}{dt} = \rho_1(t)n_1 - m_1 N_1$$
$$\frac{dN_2}{dt} = \rho_2(t)n_2 - m_2 N_2 - a_{21} N_2 N_1 \tag{8}$$
$$\frac{dN_3}{dt} = \rho_3(t)n_3 - m_3 N_3 - a_{31} N_3 N_1$$

in which the reference species 1 is the common consumer, making easier to compare species 2 and 3 under apparent (Fig. 4a, graph) and resource competition (Fig. 4b, graph). The corresponding equations for offspring production make use of the appropriate forms for resources (3), and for consumers (4). A recurrence equation of species 3 is added to the system (5,6).

3 Results

3.1 Phenological shifts between one resource and one consumer

The effects of phenological mismatches on the long-term dynamics between one resource (species 1) and one consumer (species 2) are illustrated in Figure 1. When the resource and consumer recruitment phenologies are similar ($\mu_1 \approx \mu_2$), the resource attains very low abundances due to high consumption. However, high consumption does not lead to high consumer abundances in the long-term. Instead, consumers attain higher abundances when they recruit some time before ($\mu_1 > \mu_2$) or after ($\mu_1 < \mu_2$) the resources. The reason for this pattern is that adult consumers kill only adult resources but not their offspring. Thus, as the recruitment of resources and consumers becomes closer in time, there will be less individuals of the resource population able to regenerate the resource stock for the next year. This effect accumulates over the years,

leading to net food scarcity for the consumers and lower populations. In contrast, when consumers start recruiting before or later than the resource, more resource individuals would be able to reproduce before dying or being consumed, and the next consumer generations would be facing food abundance and having larger populations. Support for this hypothesis can be seen in Figure 2 (middle row), where small consumer populations can keep down the resources under phenological coincidence, whereas much larger consumer populations still allow higher resource abundances under phenological mismatch. Summarizing, closer phenological match between the resource and its consumer leads to increased overexploitation, causing lower consumer abundances in the long-term.

Of course, if the consumers recruit too early or too late with respect to the resources (approximately by 100 or more days using our parameter values), the consumers attain very low abundances or go extinct, while the resources are able to attain their highest abundances, only limited by self-regulation. This is because a very large mismatch gives enough time for the earliest of the species (producer or consumer) to die off or to become too rare when the latest species recruits, causing consumption rates to drop towards zero, which is very good for the resource and very bad for the consumer. Overall, the profile of equilibrium abundances for the resource and the consumer is shown in Figure 1 where we see that the resource displays an exploitation valley, whereas the consumer is viable inside a constrained region where it displays a bimodal abundance pattern caused by overexploitation as discussed before. The fact that a year has a finite number of days, and that earlier recruiting consumers have more days to eat and reproduce than late recruiting consumers, is the reason for the asymmetry in the abundance profiles.

The long-term dynamics can display damped oscillations (Figure 2 bottom row), and persistent oscillations (Figure 3). Oscillations are a typical feature of consumer resource dynamics, caused by the inherent delay that exists between consumption and population growth. In simulations with the resource alone (not shown) we never found persistent oscillations. Thus, oscillations are not driven by the lag of the discrete-time long-term dynamics (equations 5,6). Oscillations tend to be permanent, and equilibrium return times longer, when (i) the consumer recruits a short time before the resource, and (ii) the width of the recruitment rate curves (σ_i) decrease, as seen in Figure 3. It turns out that under condition (i) the exploitation of the resource by the consumer is high according with Figure 1, and condition (ii) means that adult resources and consumers recruit in large numbers in a very short time. Oscillations are thus happening when interactions are stronger, i.e. they are more frequent. On the other hand, as recruitment spreads across more days (larger σ_i) and phenological mismatch further increases, interactions become less strong and the equilibrium becomes more stable.

The within-year dynamics can also reflect these dynamical behaviors. In cases that correspond to stable long-term dynamics, adult phenologies vary periodically in duration and maximum abundances, with long resource seasons matching short consumer seasons and vice-versa, until stable phenologies are achieved after many generations (Figure 2 middle row). In cases that correspond to permanent long-term oscillations, these variations continue forever (see supplement for illustration). Thus, whereas recruitment phenology $\rho(t)$ is independent of the dynamics, abundance phenologies $N_i(t)$ are partly determined by interplay of the within year (short-term) dynamics and across years (long-term) dynamics.

3.2 Phenological shifts in community modules

To study the long-term effects of recruitment asynchrony in three species community
modules, the model is run for 300 year/cycles, and the average of the recruit stock
abundances ($n_{i,\tau}$) of the last 20 years are plotted in the $x = \mu_2 - \mu_1, y = \mu_3 - \mu_1$ plane as contour lines. Figure 4 shows representative results (more available in
the supplement) using the default parameter values (from Table 1). We will call this
graphical representation introduced by Nakazawa and Doi (2012) the "phenological
space". The equilibrium abundances displayed in the phenological space are strongly
influenced by the patterns that occur in the case of one resource and one consumer (see
Figure 1), and to some extent they can be understood as superpositions of species-pair
patterns as described in more detail below.

Apparent competition (Figure 4a). In this module the consumer (species 1) displays
four abundance peaks in phenological space. Two of these peaks occur when both
resources (species 2 and 3) recruit together and the consumer recruits some time before
or after them ($\mu_2 \approx \mu_3 > \mu_1$ or $\mu_2 \approx \mu_3 < \mu_1$). This would be the same pattern as
in the case of a single resource (Fig. 2). The other two peaks correspond to situations
where the consumer recruits between the recruitment periods the two resources ($\mu_2 < \mu_1 < \mu_3$ or $\mu_3 < \mu_1 < \mu_2$). In all four cases the consumer peaks never occur when
all three species recruit simultaneously. The common consumer causes the resources to
indirectly affect each other negatively. When the recruitment phenology of one of the
resources (e.g. species 2) and the consumer are similar (e.g. $\mu_2 \approx \mu_1$), that resource
attains low abundances as expected. If we consider the second resource (e.g. species
3), we observe that the first resource attains even lower abundances (and may even
become extinct) when the second resource recruits some time before or after the first
resource-consumer pair (i.e. $\mu_1 \approx \mu_2 > \mu_3$ or $\mu_1 \approx \mu_2 < \mu_3$). We already observed
that consumers attain higher abundances when they recruit before or after a resource
(Fig. 2). Thus, when the second resource recruits before or after the common consumer
it may face a small decrease due to consumption, but at the same time it increases the
consumer's abundance, which poses additional pressures on the first resource which is
already experiencing intense consumption due to phenological matching.

Resource competition (Figure 4b). In this module the common resource attains
higher abundances when the two consumers recruit both too early, both too late,
or one too early and the other too late. Looking at the consumers separately, they
again display the pattern of having highest abundances when they recruit some time
before or after the resource, essentially repeating the pattern displayed in Figure 1.
Due to the exploitative nature of the competition, the abundance of one consumer
becomes smaller as the other consumer recruits closer in time to the resource, thus
creating distinctive regions of competitive dominance in phenological space. Although
most of the phenological space shows competitive exclusion and coexistence is close to
impossible when both consumers recruit together ($\mu_2 \approx \mu_3$), coexistence is possible
when one consumer recruits earlier than the resource and the other consumer later
than the resource ($\mu_2 < \mu_1 < \mu_3$ or $\mu_3 < \mu_1 < \mu_2$). When coexistence happens
under this circumstance, the consumer that recruits earlier is numerically favored. This
module illustrates how time has become the second dimension of the niche, allowing
the coexistence of two species on one resource at equilibrium. Coexistence occurs when
there is a right amount of segregation in time, allowing the earlier consumer to persist,
yet this consumer can not prevent resources from recruiting in quantities that are
sufficient to sustain the late recruiting consumer.

Both under *apparent* and *resource competition*, the competitors (species 2 and 3) interact indirectly, but the nature of the linking species (species 1 can be a consumer or a resource) determines contrasting orientations of their phenological niches (i.e. the alignment of the extinction zones of a consumer shifts 90 degrees between Figure 4a and b).

Food chain (Figure 4c). This module displays a top-down trophic cascade when the recruitment phenologies of the top predator and the intermediate consumer are closer, and both are earlier than the basal resource ($\mu_3 \approx \mu_2 < \mu_1$). The cascade does not occur when all species recruit closer ($\mu_3 \approx \mu_2 \approx \mu_1$), or when both consumers recruit together but after the resource ($\mu_3 \approx \mu_2 > \mu_1$). To understand why this occurs, let us consider for the moment that there is no top predator. Figures 1 and 4b indicate that the negative effects of consumers on resources are stronger in a time window not centered around perfect match scenarios, but some time ahead of the resource (e.g. $\mu_2 < \mu_1$). Under this scenario a top predator recruiting closer to the intermediate consumer ($\mu_3 \approx \mu_2$) can lessen the exploitation of the basal resource. In the opposite arrangement ($\mu_3 \approx \mu_2 > \mu_1$), the basal resource experiences less exploitation by the intermediate consumer, thus the indirect effect of a top predator would be less important for the resource. With respect to the relationship between the intermediate consumer and the top predator, we see again the pattern where the higher equilibrium densities occur when a consumer recruits just ahead of its resource ($\mu_3 < \mu_2$). Summarizing, the highest equilibrium abundances for the three species occur when the order of recruitment phenology is: top predator first, intermediate consumer second, basal resource last ($\mu_3 < \mu_2 < \mu_1$).

Intraguild predation (Figure 4d). This module presents features already seen in the food chain and resource competition modules. The basal resource displays roughly the same pattern of higher abundances when its consumers recruit too early or too late, with slightly augmented abundances when recruitment of intraguild prey and predator are similar ($\mu_2 \approx \mu_3$), which is the cascading effect seen in the food chain module. The abundance patterns of the intraguild prey resembles the pattern that occurs under resource competition, only this time its presence is greatly reduced when it coincides with the intraguild predator ($\mu_2 \approx \mu_3$). The intraguild predator on the other hand, is viable on a wider region of the phenological space, which is well approximated by the superposition of the corresponding regions in the food web and resource competition modules.

These abundance patterns in Figure 4 appear to be robust to changes in parameters that affect the time span of the interactions, such as the standard deviation of the recruitment distributions ($\sigma_i = 5$ or 20 instead of 10) and consumer mortality rates ($m_i = 0.05$ or 0.2 instead of 0.1), as well as changing the recruitment distributions from normal to uniform. Increasing the standard deviations of recruitment rates and decreasing consumer mortality rates result in wider niches for the consumers in all four modules. The effects are somewhat more complex for basal resources, but in most modules the increase of standard deviations and consumer mortalities tend to numerically favor the resources. We also ran additional simulations relaxing the assumption of parameter symmetry, for example by halving the consumption rate upon species 3 in apparent competition (a_{31}), or its consumption rate in the other modules (a_{i3}), from 0.3 (as in Table 1) to 0.15, and the superposition effect can still be seen. All these additional simulations can be seen in the supplement.

4 Discussion

4.1 Consumer resource dynamics

The two-species case is fundamental to understand the abundance and coexistence patterns later seen in the three-species modules. In our model phenological matching of resource and consumer recruitment phenologies increases resource mortality and hence smaller resource populations in the long-run. However, this does not translate into large consumer abundances. Instead, consumers display two abundance maxima, one when they recruit before and one when they recruit after the peak in resource recruitment (Figure 1). This bimodal response results from the interaction between overexploitation, stage-dependent consumption and phenology. Under phenological mismatch resources become partially released from exploitation, causing them to have wider phenologies and higher abundances (Figure 2, middle row), which more than compensates for the effect of the loss of phenological overlap on the consumer. A notable feature of this bimodal response is that the abundances for early recruiting consumers are significantly larger than for late recruiting ones. This is a consequence of the fact that the interactions are constrained to a period of a year, which causes late recruiting consumers to have less time to kill resources to make offspring. This same principle explains the optimality of protandry (males emerging earlier than females) in the models developed by Zonneveld and Metz (1991); Zonneveld (1992). Interestingly, Nakazawa and Doi (2012) (ND hereafter) also found that consumers achieve higher abundances when their reproductive phenologies occur earlier rather than later than their resources. However, they deemed such a result counter-intuitive and we are not sure that the same principle operates in their models because there is no distinction between within year and across years dynamics.

It is important to point out that the bimodal response in the consumer would not be expected by simple extrapolation from individuals to populations as in the original Match Mismatch Hypothesis (MMH). Individual responses (e.g. growth rates) to many abiotic and biotic factors are usually unimodal (e.g. there are single optima for temperatures, pH, food particle sizes, etc). Unless individual responses differ considerably (e.g. bimodal distributions of individual maxima), we would expect that populations also display unimodal responses to the factor considered (i.e. a single maximum of abundance when matching the most favorable condition). This reasoning only works if the consumers do not change the factors that determine the responses (e.g. consumers do not change temperatures), which is not the case here because the factor that affects the consumer is the resource being depleted. This highlights the role of feedbacks in the response of populations towards changes in phenology, as well as the shortcomings of considering bottom-up causalities only. A graphical support for this statement is in Figure 2: whereas recruitment phenologies are invariant ($\rho_i(t)$ functions, top row), the shape of abundance phenologies ($N_i(t)$, middle row) are molded by bottom-up and top-down effects acting over several generations.

Changes in phenology also affect the stability of interactions by leading to permanent oscillations or longer return times to the equilibrium (Figure 3). Although we are unable to demonstrate analytically whether oscillations during the discrete-time long-term dynamics are caused by overcompensation in single-species dynamics (like in the Ricker model) or by proper consumer-resource cycles, our simulations favor the second alternative. Firstly, the oscillations do not occur when the consumer is absent. Secondly, oscillations become permanent or last longer when interactions between con-

sumers and resources are stronger. And thirdly, the cycles have periods longer than six years, which falls within the range of periods expected for oscillating, discrete-time, predator-prey systems (Murdoch et al., 2003). Oscillations are well known to lead to extinction in laboratory predator-prey systems (Gause, 1934; Huffaker, 1958; Luckinbill, 1973) by increasing the effects of demographic stochasticity in population dynamics. Our simulations show that consumer-resource systems tend to be more stable as the amount of phenological mismatch increases and when recruitment occurs over longer times. Both factors provide a refuge effect in time, by decreasing the number of interactions per day, and refuges are known to enhance stability in exploitative systems (Gause, 1934; Huffaker, 1958; Luckinbill, 1973).

Although our main concern in this paper is to explore the consequences of phenological overlaps and mismatches for the long term dynamics, our approach also opens the possibility to explore how phenologies themselves are shaped by ecological interactions. As stated before, we assume invariant recruitment phenologies ($\rho_i(t)$), yet adult abundance phenologies ($N_i(t)$), and offspring production phenologies ($B_i(t)$) are dynamic. In the default scenario (Table 1, Figure 2) these phenologies settle down in the long term, whereas under cyclic dynamics (Figure 3) they keep varying periodically. Another interesting scenario concerns the case of ephemeral consumers, like many insects, that recruit in large numbers in a very short period (very low σ_i) and that disappear rapidly in a few days (large m_i). When these consumers recruit in synchrony with the much longer phenophases of the resources ($\Delta\mu \approx 0$), they can cause a bimodal shape in the resource abundance phenology and a biphasic resource production phenology. The dynamics of these scenarios can be seen in the supplementary material.

There are important differences between ND's work and ours. Both approaches consider top-down effects and consumer-resource feedbacks. However, in the ND model feedbacks are not only instantaneous by virtue of their continuous-time formulation, but their effects also act much faster as the gap in time between consumer and resource decreases. This is because when matching occurs, resource and consumer populations increase at their faster rates, simultaneously. In contrast, our model requires that newborn individuals wait until the next year in order to have any effect. In our model such lags potentially make top-down regulation stronger over several years, which can explain why we observe large overexploitation effects and bimodality in consumer abundances with respect to phenological mismatches, compared with ND (but read below). This comparison also highlights the potential role of voltinism. Our model only considers univoltine species, whereas the ND models could well approximate the case of multivoltine species, since multiple generations per year are possible. In order to explore the consequences of different patterns of voltinism, our model needs to be changed in appropriate ways (e.g. there would be two gaussians for bivoltine species in Figure 2, top row). Voltinism is thought to be a very important aspect of life history for consumer-resource interactions (Altermatt, 2009) and therefore altering voltinism can modify the frequency of interactions and the overall amount of phenological overlap, as well as change the relationship between the within-year and across-years temporal scales.

Another issue is that Lotka-Volterra oscillations in the ND model may also pass as phenological events if their periods when they are not forced are close to, or less than one year. This cannot happen in our model, since more than one year is required for any feedbacks to have an effect. Because of this, we are in a better position to tell apart the effects of phenology and complex dynamics while at the same time allowing them to influence each other. The sinusoidal forcings in the ND model could also

prevent competitive exclusion, by not allowing the system to achieve an equilibrium, thus making it more difficult to attribute competitive coexistence to phenological shifts or to non-equilibrium dynamics.

4.2 Community module dynamics

In scaling up from simple consumer-resource pairs to three-species modules, one of the most remarkable outcomes is that the abundance patterns in the phenological space are to a great extent superpositions of the abundance patterns of their constituent two-species modules. Our results are robust to some parameter changes as well as to changes of the recruitment distributions from normal to uniform (see supplement). The superposition of patterns influences the community in two ways. One way consists of additive and subtractive effects on niche breadth. This is best seen in the intraguild predation module, where the intraguild prey and the intraguild predator have their phenological niches respectively reduced and enlarged by comparison with the resource competition module. The other way concerns modifications in abundances. This is best seen again in the intraguild predation module, this time for the basal resource: in comparison with the resource competition module (Figure 4b), the resource displays increased abundances around the lower-left corner of its phenological space (Figure 4d), which is also the region where its densities are greatly enhanced in the food chain module (Figure 4c). The net effect of the superposition is lower than in the food chain because the top consumer is at the same time exploiting the resource and releasing it from consumption by the intermediate species.

There are limits, however, to the applicability of this superposition principle as a predictive rule. We presented the simulations using parameter symmetries in order to ease the comparisons, so it might be expected that under more general scenarios it will be more difficult to detect such superpositions (we also ran simulations without symmetries, and so far we found that the superposition effect often applies). Although we did not fully explore the conditions leading to oscillations (Figure 3), or the complex dynamics that could arise in multispecies systems (Hastings and Powell, 1991), exceptions can be seen even without invoking such details. This is the case of the food chain module. In the analysis with two species we concluded that a resource and its consumer attain high abundances when the consumer recruitment occurs some time before or after the resource, but not when in perfect synchrony because this causes overexploitation. Thus, by a simple extrapolation, one could say that the species in the food chain should attain higher abundances when they recruit in the following sequences: (i) top < intermediate < basal ($\mu_3 < \mu_2 < \mu_1$) and (ii) basal < intermediate < top ($\mu_1 < \mu_2 < \mu_3$). We see (i) occurring as Figure 4 shows, but we never see (ii). There is a simple reason for this: interactions are constrained to 365 days, which means that late emerging species have less days to make offspring. This is an important issue because the inflow of energy for each additional trophic level decreases (because of the loss rates m_i). Thus, the first alternative (i) can lead to increased abundances because each additional level shifts towards earlier dates, compensating for the energy transfer losses. In contrast, the second alternative (ii) places each additional level closer to the end of the year, with less days for consumption and thus offspring production. Interestingly, a recruitment sequence such as: basal < top < intermediate ($\mu_1 < \mu_3 < \mu_2$), which differs from (ii) by switching the order between intermediate and top species, leads to high abundances in many scenarios (results presented in the supplement). In

this sequence the top level consumer, which is the most affected by transfer losses, counts with more consumption days.

Models have considered time itself as a niche axis that can be partitioned, and temporal overlap has been taken as proxy for competitive effects (Fleming and Partridge, 1984; Ebenhöh, 1992; Schoener, 1974; Encinas-Viso et al., 2012). But time is different from other niche axes in a fundamental aspect. In "scalar" niche axes such as seed size, the consumption over a certain category of sizes (e.g. small seeds) does not, in principle, affect the availability of other categories (e.g. large seeds). By contrast, with a "directional" axis such as time, resource exploitation during earlier times has consequences over the availability of resources at later times (Loreau, 1989, 1992). As the saying goes "the early bird gets the worm". In scenarios where priority gives an advantage in competition, coexistence would be easier if early recruiting species leaves enough resources to the late recruiting species. This situation arises in our model when recruitment phenologies become wider (see additional simulations in the supplement). On the one hand, wider recruitment phenologies in the resource allows a more continuous supply over the year instead of a short episode falling under the exclusive control of one species; this makes the existence of competitors more independent of each other (Loreau, 1989, 1992). Experiments of competition between anurans in temporary ponds show that weaker species can benefit from delayed arrival, when resource levels have recovered following the metamorphosis and abandonment of stronger species (Lawler and Morin, 1993). On the other hand, wider recruitment phenologies can be seen as a bet-hedging strategy in the case of consumers, enabling some individuals to be closer to the resource peak in spite of the majority of the population experiencing a large mismatch (Kerby et al., 2012).

It remains an open question to what extend our predictions are robust with respect to changes in consumer numerical responses. We follow the custom that consumer reproduction increase with the resources and that mortality rates remain constant (Murdoch et al., 2003). An alternative formulation could be that consumption decreases mortality, thus increasing the number of days during which adults are alive and reproducing. Consumption can also increase maturation rates in pre-adult stages (Revilla, 2000). But one very important assumption of our model is that reproduction depends on consumption by adults, whereas in many cases reproduction depends on the amount of resources accrued during immature phases. In support of our assumption, Wheeler (1996) review many examples and mechanisms where adult consumption is required for oogenesis ("egg production in most Diptera completely depends on protein feeding by adult females" [sic]). In synovigenic parasitoids for example, adults can choose between infecting a host with eggs, or feeding from the host (and killing it) in order to produce more eggs (Rivero and Casas, 1999), thus adult resources can be a factor limiting reproduction. Our assumption concerning resource limitation only in the adults is not the most general scenario, but it makes much easier for us to track reproduction, since eaten food is converted into seeds/eggs. Otherwise, we would have to track eaten food by pre-adults, and discount the part of that food which is not going to produce seeds/eggs due to consumer deaths. We have reasons to think however, that as long as consumption is determined by phenology, overexploitation and feedbacks are going to have predictable consequences for the long-term fate of the populations. This is especially true for predation, which leads to the instantaneous killing of the preys. This causes an instantaneous decrease in the reproductive potential of the prey population, irrespective of whether the predator population increases instantaneously or not, and irrespective of whether consumption affects weight gain, size at maturity,

or survival, all of them factors that enhance the consumer's numerical response. This decrease in the preys must be stronger when the temporal overlap between preys and predators increase, leading to overexploitation and smaller abundances for everybody in the long-term.

4.3 Real communities and the effects of climate change

So far we only know about one field study that related the phenologies, interaction strengths and demographics of a consumer-resource system over more than one year, under a climate change context: the flower head weevil (*Rhinocyllus conicus*) and platte thistle (*Cirsium canescens*) interaction (Russell and Louda, 2004). In one of two localities studied, the displacement of weevil phenology towards earlier dates with respect to the plant occurred in parallel with an increase in weevil numbers, besides the fact that interaction strength (i.e. herbivory, measured as egg load per flower) actually decreased. Although such an outcome can be predicted by our model (i.e. a little earlier is better), this study took place in an open system, where phenologies and interactions can be altered by many factors that are difficult to control (e.g. dispersal). In order to test predictions about the role of consumer-resource feedbacks under phenological shifts, experiments under controlled conditions are necessary. In this respect, it would be enlightening to manipulate consumer and resource recruitment timings over several generations, in order to determine the long-term consequences of phenological (mis)matches among interacting species. An interesting system might be amphibians in temporary ponds (Wilbur, 1997), where experiments show the critical importance of priority effects and prey-predator asynchrony on survival and development (Morin, 1987; Lawler and Morin, 1993; Morin, 1999). So far these experiments have been performed over one cycle or generation only; proper modifications would be needed in order to run them for several cycles, such as keeping the metamorphosed adults for the next rounds (instead of propagules such as eggs of seeds in our model). Another interesting setting in which to test the effect of interaction timings are bacteria-phage systems, where bacteria and phages can be inoculated at entirely controlled times, and their production (cells and virions) mechanically separated and used in recurrent generations, hundreds in a single year (Joshua Weitz, personal communication).

Our predictions concerning the long-term effects of phenological shifts depend on the relative importance of consumer-resource feedbacks in real ecosystems. Several studies support the idea that the MMH must be modified to take into account the effects of population sizes (Durant et al., 2005, 2007). In addition, the recent work of Durant et al. (2013) shows that statistical models of top-down regulation by consumers can sometimes explain better the effects of phenological mismatches than corresponding models where regulation is bottom-up. The effects of species abundances, bottom-up and top-down regulations, support an enhanced role of consumer-resource feedbacks, but their importance still awaits more direct empirical demonstration. In this context space becomes an important factor, since the effect of feedbacks on the consumers may be restricted to systems of small spatial scales (Durant, personal communication). According to our model, moderate mismatches in recruitment phenology between consumers and resources (Figure 2 top row, for $\Delta\mu = \pm 50$) leads to wider resource phenologies in the long-term (Figure 2 middle row, for $\Delta\mu = \pm 50$), which up to certain limits more than compensates for the decrease of overlap that would result if the phenologies were invariant.

The start of many phenologies is advancing as a consequence of warming (Parmesan, 2006; Parmesan and Yohe, 2003), but the speed of change varies across different taxa. This creates mismatches and new matches between resources and consumers, which are expected to be bad and good, respectively, for consumers according to the tenet of the MMH. But sometimes the empirical evidence suggest an opposite pattern if climate change is considered in a broader perspective. For example, Rockwell et al. (2011) found that the average phenological overlap between polar bears and snow geese in western Hudson Bay has been increasing as a result of warming, causing the decline of geese. But the climate is also predicted to become more variable (Salinger, 2005), which according to Rockwell et al. (2011) will cause enough environmental stochasticity in geese phenology, preventing permanent overlap and overexploitation, and thus ensuring a more stable energy supply for the bears. Such prediction is in line with our findings of decreased overexploitation and increased consumer viability in terms of abundance, under moderate scenarios of mismatch. Mesocosm experiments also support the hypothesis that overexploitation has negative effects on the consumers when warming causes phenological coincidence instead of mismatch (Aberle et al., 2012).

Another prediction generated by our model is that earlier consumer recruitment caused by warming results in higher abundances, because early recruiting consumers have more days per year to eat and reproduce. The results of Ozgul et al. (2010) support such a "time is resource" argument. They showed that earlier recruitment of marmots in sub-alpine environments caused by warming, give these herbivores more time to eat and gain weight before the next hibernation, leading to higher population growth rates and abundances. A field study in the Netherlands by Both et al. (2006), indicates that climate change has caused mismatches between egg laying by flycatchers and the peak in caterpillar abundances, leading to flycatcher population decline. They found that the decline is more severe (~90%) in areas were caterpillar peaks shifted before egg laying compared with the decline (~10%) in areas were the peak shifted after egg laying. These authors argue that since flycatchers are bivoltine, later peaks in food abundance gives them some chance to have a second brood in the year, but earlier peaks gives them little time to match their food and having at least one brood. This is why arriving (in place of recruiting) earlier (food peak later) is less bad than arriving later (food peak earlier).

We treated recruitment phenologies in the form of pulses (Figure 2, top row). Phenologies are usually quantified at the population level (Miller-Rushing et al., 2010) and thus the width of the pulses reflects the inherent variability of individuals in the populations. This variability is caused by genetics or phenotypic plasticity, for example. In addition, the phenology of interacting individuals (Figure 2, middle row) is shaped by mortality rates (or migration, transition to other life stages, etc.), as well as by the dynamics in the previous years. Therefore it is very difficult to make generalizations about how changes at the individual level will be reflected in the shape of the phenologies. We can argue, for example, that warmer years could result in a rapid accumulation of degree-days in all individuals and a more synchronous recruitment, i.e. narrow recruitment curves. On the other hand, development could be constrained by factors that are not expected to change as a consequence warming, such as photoperiod in the case of plants (Dunne et al., 2003), or it can speed growth in size such that mortality decreases (Kristiansen et al., 2011), leading to longer phenologies. Finally, warming can increase insect voltinism, with important consequences for the management of seasonal pests and conservation (Altermatt, 2009) (see also section 4.1).

4.4 Conclusions

Our model predicts that consumer populations require minimum amounts of phenological overlap with their resources in order to be viable, which is in line with the Match Mismatch Hypothesis (MMH). However, the degree of match or mismatch of their life cycles alone is insufficient to account for the long-term effects of phenological shifts that arise because of changes in the environment. This is because the MMH does not account for consumer-resource feedbacks, which can turn resource overexploitation into a significant issue. Furthermore, as a consequence of top-down regulation, we predict that moderate amounts of phenological mismatch can result in a more sustainable resource supply, making a positive contribution to the consumer population in the long term. We also highlight that aspects of life-history such as lags in development and voltinism can have important effects on the relationship between phenology and population dynamics, but more research is still necessary in this respect. In the context of simple communities it is possible to predict to some extent the consequences of phenological shifts, by the superposition of their effects of on consumer-resource pairs. Our models also help to understand and predict how the changes in the timing and duration of phenologies triggered by climate change, are translated into changes in the abundances of resources and consumers in real-life settings.

References

Aberle, N., B. Bauer, A. Lewandowska, U. Gaedke, and U. Sommer (2012). Warming induces shifts in microzooplankton phenology and reduces time-lags between phytoplankton and protozoan production. *Marine Biology 159*(11), 2441–2453.

Abrams, P. A. (2004). When does periodic variation in resource growth allow robust coexistence of competing consumer species? *Ecology 85*, 372–382.

Altermatt, F. (2009). Climatic warming increases voltinism in European butterflies and moths. *Proceedings of the Royal Society B: Biological Sciences 277*(1685), 1281–1287.

Both, C., S. Bouwhuis, C. M. Lessells, and M. E. Visser (2006). Climate change and population declines in a long-distance migratory bird. *Nature 441*(7089), 81–83.

Cushing, D. H. (1990). Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Advances in Marine Biology 26*, 249–293.

Donnelly, A., A. Caffarra, and B. F. O'Neill (2011). A review of climate-driven mismatches between interdependent phenophases in terrestrial and aquatic ecosystems. *International Journal of Biometeorology 55*, 805–817.

Dunne, J. A., J. Harte, and K. J. Taylor (2003). Subalpine meadow flowering phenology responses to climate change: integrating experimental and gradient methods. *Ecological Monographs 73*(1), 69–86.

Durant, J. M., D. Hjermann, T. Anker-Nilssen, G. Beaugrand, A. Mysterud, N. Pettorelli, and N. C. Stenseth (2005). Timing and abundance as key mechanisms affecting trophic interactions in variable environments. *Ecology Letters 8*(9), 952–958.

Durant, J. M., D. O. Hjermann, T. Falkenhaug, D. J. Gifford, L.-J. Naustvoll, G. Sullivan, B. K.and Beaugrand, and N. C. Stenseth (2013). Extension of the match-mismatch hypothesis to predator-controlled systems. *Marine Ecology Progress Series 474*, 43–52.

Durant, J. M., D. O. Hjermann, G. Ottersen, and N. C. Stenseth (2007). Climate and the match or mismatch between predator requirements and resource availability. *Climate Research 33*(3), 271–283.

Ebenhöh, W. (1992). Temporal organization in a multi-species model. *Theoretical Population Biology 42*, 152–171.

Encinas-Viso, F., T. A. Revilla, and R. S. Etienne (2012). Phenology drives mutualistic network structure and diversity. *Ecology Letters 15*(3), 198–208.

Fleming, T. H. and B. L. Partridge (1984). On the analysis of phenological overlap. *Oecologia 62*(3), 344–350.

Gause, G. F. (1934). *The Struggle for Existence.* Baltimore, MD: Williams & Wilkins.

Gilman, R. T., N. S. Fabina, K. C. Abbott, and N. E. Rafferty (2012). Evolution of plant-pollinator mutualisms in response to climate change. *Evolutionary Applications 5*(1), 2–16.

Hastings, A. and T. Powell (1991, June). Chaos in a three-species food chain. *Ecology 72*(3), 896–903.

Holt, R. D. (1997). Community modules. In A. C. Gange and V. K. Brown (Eds.), *Multitrophic Interactions in Terrestrial Ecosystems*, pp. 333–349. 36th Symposium of the British Ecological Society: Blackwell Science.

Huffaker, C. B. (1958). Experimental studies on predation: dispersion factors and predator-prey oscillations. *Hilgardia 27*, 795–835.

Johansson, J. and N. Jonzén (2012). Game theory sheds new light on ecological responses to current climate change when phenology is historically mismatched. *Ecology Letters 15*(8), 881–888.

Kallimanis, A. S., T. Petanidou, J. Tzanopoulos, J. D. Pantis, and S. P. Sgardelis (2009). Do plant-pollinator interaction networks result from stochastic processes? *Ecological Modelling 220*, 684–693.

Kerby, J. T., C. C. Wilmers, and E. Post (2012). Climate change, phenology and the nature of consumer–resource interactions: advancing the match/mismatch hypothesis. In T. Ohgushi, O. J. Schmitz, and R. D. Holt (Eds.), *Trait-Mediated Indirect Interactions: Ecological and Evolutionary Perspectives*, pp. 508–525. Cambridge University Press.

Kristiansen, T., K. F. Drinkwater, R. G. Lough, and S. Sundby (2011). Recruitment variability in North Atlantic cod and match-mismatch dynamics. *PLoS ONE 6*(3), e17456.

Lawler, S. P. and P. J. Morin (1993). Temporal overlap, competition, and priority effects in larval anurans. *Ecology 74*(1), 174–182.

Loreau, M. (1989). Coexistence of temporally segregated competitors in a cyclic environment. *Theoretical Population Biology 36*(2), 181–201.

Loreau, M. (1992). Time scale of resource dynamics and coexistence through time partitioning. *Theoretical Population Biology 41*(3), 401–412.

Luckinbill, L. S. (1973). Coexistence in laboratory populations of *Paramecium aurelia* and its predator *Didinium nasutum. Ecology 54*(6), 1320–1327.

May, R. M. (1974). *Stability and Complexity in Model Ecosystems*. Princeton Landmarks in Biology. Princeton: Princeton University Press.

Memmott, J., P. G. Craze, N. M. Waser, and M. V. Price (2007). Global warming and the disruption of plant–pollinator interactions. *Ecology Letters 10*(8), 710–717.

Miller-Rushing, A. J., T. T. Høye, D. W. Inouye, and E. Post (2010). The effects of phenological mismatches on demography. *Philosophical Transactions of the Royal Society B: Biological Sciences 365*(1555), 3177–3186.

Morin, P. J. (1987). Predation, breeding asynchrony, and the outcome of competition among treefrog tadpoles. *Ecology 68*(3), 675–683.

Morin, P. J. (1999). Productivity, intraguild predation, and population dynamics in experimental food webs. *Ecology 80*, 752–760.

Murdoch, W. W., C. J. Briggs, and R. M. Nisbet (2003). *Consumer-Resource Dynamics*. Number 36 in Monographs in Population Biology. Princeton: Princeton University Press.

Nakazawa, T. and H. Doi (2012). A perspective on match/mismatch of phenology in community contexts. *Oikos 121*(4), 489–495.

Namba, T. (1984). Competitive co-existence in a seasonally fluctuating environment. *Journal of Theoretical Biology 111*(2), 369–386.

Olesen, J. M., J. Bascompte, Y. L. Dupont, H. Elberling, C. Rasmussen, and P. Jordano (2011). Missing and forbidden links in mutualistic networks. *Proceedings of the Royal Society B: Biological Sciences 278*(1706), 725–732.

Ozgul, A., D. Z. Childs, M. K. Oli, K. B. Armitage, D. T. Blumstein, L. E. Olson, S. Tuljapurkar, and T. Coulson (2010). Coupled dynamics of body mass and population growth in response to environmental change. *Nature 466*(7305), 482–485.

Pachepsky, E., R. M. Nisbet, and W. W. Murdoch (2008). Between discrete and continuous: Consumer-resource dynamics with synchronized reproduction. *Ecology 89*, 280–288.

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution and Systematics 37*, 637–69.

Parmesan, C. (2007). Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biology 13*(9), 1860–1872.

Parmesan, C. and G. Yohe (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature 421*(6918), 37–42.

Revilla, T. A. (2000). Resource Competition in Stage-structured Populations. *Journal of Theoretical Biology 204*, 289–298.

Rivero, A. and J. Casas (1999). Rate of nutrient allocation to egg production in a parasitic wasp. *Proceedings of the Royal Society of London B 266*(1424), 1169–1174.

Rockwell, R. F., L. J. Gormezano, and D. N. Koons (2011). Trophic matches and mismatches: can polar bears reduce the abundance of nesting snow geese in western Hudson Bay? *Oikos 120*(5), 696–709.

Russell, F. L. and S. M. Louda (2004). Phenological synchrony affects interaction strength of an exotic weevil with platte thistle, a native host plant. *Oecologia 139*(4), 525–534.

Salinger, M. J. (2005). Climate variability and change: past, present and future–an overview. *Climatic Change 70*(1), 9–29.

Schoener, T. W. (1974). Resource partitioning in ecological communities. *Science 185*, 27–39.

794   Wheeler, D. (1996). The role of nourishment in oogenesis. *Annual Review of Entomology 41*(1), 407–431.

796   Wilbur, H. M. (1997). Experimental ecology of food webs: complex systems in temporary ponds. *Ecology 78*, 2279–2302.

798   Yang, L. H. and V. H. W. Rudolf (2010). Phenology, ontogeny and the effects of climate change on the timing of species interactions. *Ecology Letters 13*(1), 1–10.

800   Zonneveld, C. (1992). Polyandry and protandry in butterflies. *Bulletin of Mathematical Biology 54*(6), 957–976.

802   Zonneveld, C. and J. A. J. Metz (1991). Models on butterfly protandry: virgin females are at risk to die. *Theoretical Population Biology 40*(3), 308–321.

804 **Tables**

Parameter	Value	Description
μ_i	80 to 280 d	mean of the recruitment rate distribution ($\mu_i = 180$ for species 1)
σ_i	10 d	standard deviation of the recruitment rate distribution
a_{ij}	$0.3\,\mathrm{ind}^{-1}\,\mathrm{d}^{-1}$	consumption rate of j on i (when it applies)
b_i	$2\,\mathrm{d}^{-1}$	maximum per-capita reproduction rate of a resource
c	$0.01\,\mathrm{ind}^{-1}$	strength of density dependence for resources
e_i	0.2	food to offspring conversion efficiency of a consumer
m_i	$0.1\,\mathrm{d}^{-1}$	adult mortality rate
d_i	$0.001\,\mathrm{d}^{-1}$	offspring mortality rate

Table 1 Parameters of the model with their default values (d=day, ind=individuals).

Figure Captions

Fig. 1. Long-term equilibrium abundances for resources and consumers versus number of days of phenological mismatch ($\Delta\mu = \mu_2 - \mu_1$).

Fig. 2. Effects of shifts in recruitment phenologies for one resource and one consumer. The three columns correspond to different shifts of the consumer (blue, species 2) recruitment peak with respect to the resource (green, species 1) recruitment peak. The top row shows the recruitment rates along the year. The middle row shows stable abundance phenologies (after 100 years) of the resource and consumer adult populations, i.e. their phenologies in terms of abundances, as well as their offspring production (dash lines, same colors as for adults). The bottom row displays the long-term dynamics, the (net) offspring produced each year.

Fig. 3. Long-term dynamics (offspring) of resources (green, species 1) and consumers (blue, species 2) for different amounts of phenological mismatch ($\Delta\mu = \mu_2 - \mu_1$) and standard deviation of the recruitment rate distribution ($\sigma = \sigma_1 = \sigma_2$).

Fig. 4. Equilibrium abundances in the four community modules: (a) apparent competition, (b) resource competition, (c) food chain, (d) intraguild predation. The horizontal (vertical) axis gives position of the recruitment peak of species 2 (species 3) with respect to species 1. Above (below) the diagonal axis the recruitment peak of species 3 lies before (after) that of species 2. Abundances are scaled with respect to the maximum attained for each species, increasing from blue to red. The lowest contour line corresponds to an abundance of 1, and lower abundances (white background) are considered extinctions.
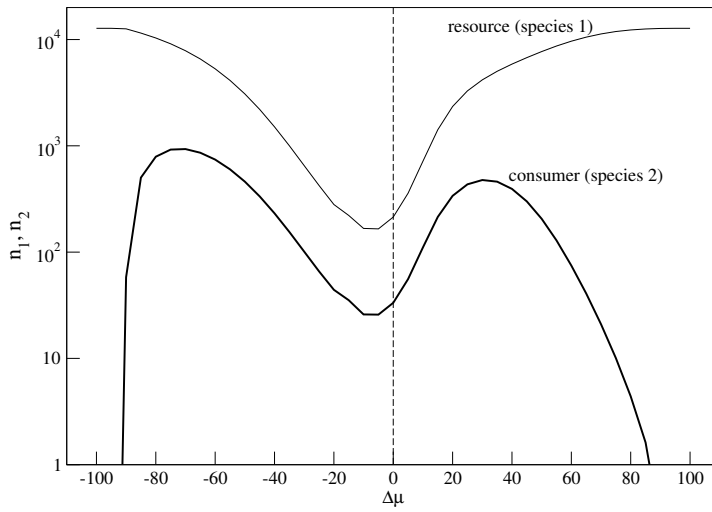
806 **Figures**

Fig. 1 Long-term equilibrium abundances for resources and consumers versus number of days of phenological mismatch ($\Delta\mu = \mu_2 - \mu_1$).
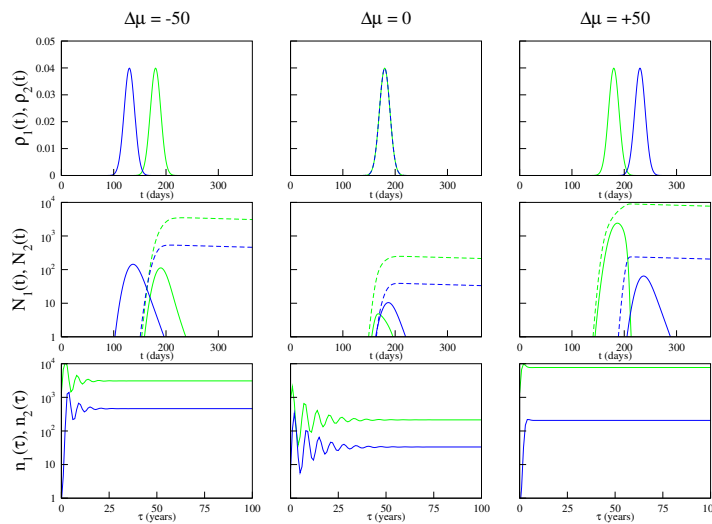

Fig. 2 Effects of shifts in recruitment phenologies for one resource and one consumer. The three columns correspond to different shifts of the consumer (blue, species 2) recruitment peak with respect to the resource (green, species 1) recruitment peak. The top row shows the recruitment rates along the year. The middle row shows stable abundance phenologies (after 100 years) of the resource and consumer adult populations, i.e. their phenologies in terms of abundances, as well as their offspring production (dash lines, same colors as for adults). The bottom row displays the long-term dynamics, the (net) offspring produced each year.
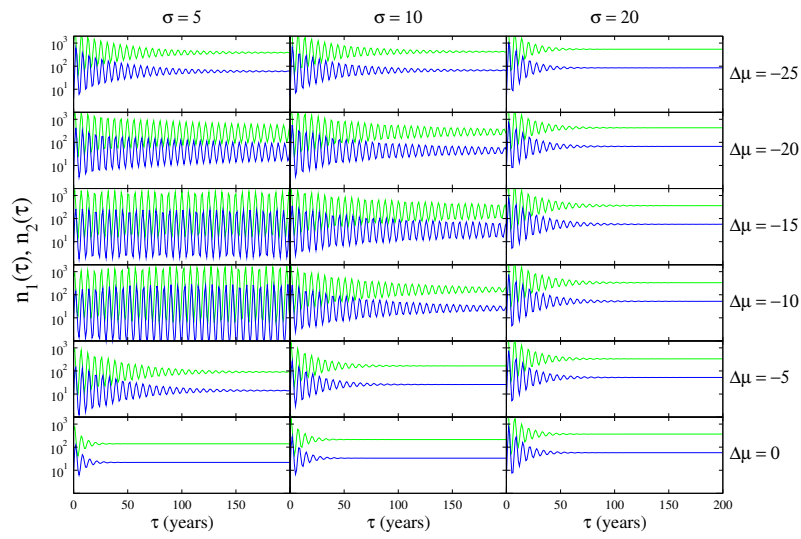
Fig. 3 Long-term dynamics (offspring) of resources (green, species 1) and consumers (blue, species 2) for different amounts of phenological mismatch ($\Delta\mu = \mu_2 - \mu_1$) and standard deviation of the recruitment rate distribution ($\sigma = \sigma_1 = \sigma_2$).
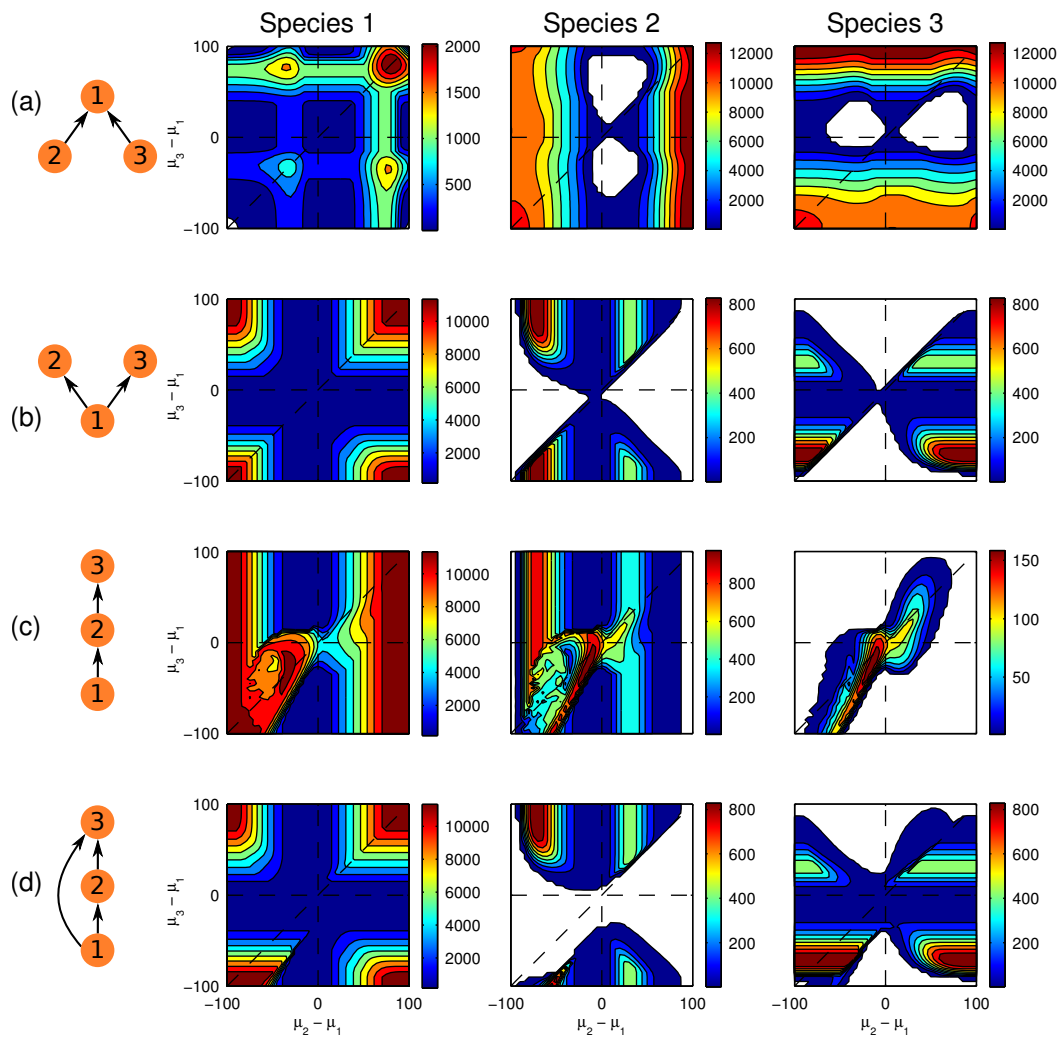
Fig. 4 Equilibrium abundances in the four community modules: (a) apparent competition, (b) resource competition, (c) food chain, (d) intraguild predation. The horizontal (vertical) axis gives position of the recruitment peak of species 2 (species 3) with respect to species 1. Above (below) the diagonal axis the recruitment peak of species 3 lies before (after) that of species 2. Abundances are scaled with respect to the maximum attained for each species, increasing from blue to red. The lowest contour line corresponds to an abundance of 1, and lower abundances (white background) are considered extinctions.