A perspective on match/mismatch of phenology in community contexts

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Climate change has significant impacts on phenology of various organisms in a species-specific manner. Facing this problem, the match/mismatch hypothesis that phenological (a)synchrony with resource availability strongly influences recruitment success of a consumer population has recently received much attention. In this article, we discuss extending the conventional pairwise concept and demonstrate a community module-based approach as an initial step for exploring community consequences of species-specific phenological shifts caused by climate change. Our multispecies match/mismatch perspective leads to the prediction that phenological (a)synchrony among interacting species critically affects not only population recruitment of species but also key dynamical features of ecological communities such as trophic cascades, competitive hierarchies, and species coexistence. Explicit identification and consideration of species relationships is therefore desirable for a better understanding of seasonal community dynamics and thus community consequences of climate change-induced phenological shifts.

Phenology, the timing of life-history events such as breeding, migration, leaf unfolding and flowering, is a crucial factor for population dynamics (Inouye et al. 2000, Post and Forchhammer 2002, Kudo et al. 2008). The importance of phenology in population dynamics has been emphasized by the match/mismatch hypothesis, which states that if the most energy-expensive period of the consumer's reproductive phenology occurs close to the peak availability of the resource, then recruitment of the former will be high (Cushing 1990). This is a classical concept that stems from fishery biology focusing on recruitment success of fish populations supported by plankton production (Cushing 1990). During the last decade, this concept has received considerable attention for its applications to various organisms and various interspecific interactions (Buse et al. 1999, Bale et al. 2002, Winder and Schindler 2004, Both et al. 2006, Doi et al. 2008). Behind this trend, there is a growing concern that climate change has significant impacts on species phenology, seasonal population dynamics, and thus interaction (a)synchrony between species (Durant et al. 2005, 2007, Visser and Both 2005, Miller-Rushing et al. 2010, Thackeray et al. 2010).

Numerous studies have shown that in various organisms, phenological events are now occurring earlier or later than in past decades (Root et al. 2003, Parmesan 2006, Doi 2008, Doi et al. 2008, Post et al. 2008a, Both et al. 2009). Such phenological shifts are largely attributable to climate change (IPCC 2007). Climate change affects physical and biological processes differently and thus can have different phenological effects on different trophic levels or species (Inouye et al. 2000, Winder and Schindler 2004, Gordo and Sanz 2005, Both et al. 2006, Durant et al. 2007, Doi et al. 2008). As a consequence, climate change can synchronize or desynchronize the phenology of interacting species. Examples can be found in diverse interspecific interactions, such as those between primary producers and herbivores (Buse et al. 1999, Inouye et al. 2000, Bale et al. 2002, Winder and Schindler 2004, Both et al. 2006), between predators and their prey (Strasser and Günther 2001, Both et al. 2006, Otterson et al. 2006), and between plants and pollinators (Gordo and Sanz 2005, Doi et al. 2008).

In view of the match/mismatch hypothesis, the different extents or directions of the phenological shifts among interacting species may have significant implications for community structure and dynamics (Alheit 2009, Walther 2010). For example, Winder and Schindler (2004) reported that abundance of *Daphnia* declined and that of rotifers increased following the advancement of diatom and rotifer bloom phenology. At present, however, much remains unknown about how species-specific phenological shifts influence ecological communities (Miller-Rushing et al. 2010, Van der Putten et al. 2010). This is partly because the match/mismatch hypothesis has usually been tested for pairwise species interactions or because most studies have focused on short-term impacts on population recruitment (or foraging success) rather than long-term (i.e. over many seasonal cycles)

consequences on population and community dynamics within interaction networks (Cushing 1990, Durant et al. 2005, 2007, Kristiansen et al. 2011). Thus, there is a need for a framework for the match/mismatch concept in community contexts and its implications for long-term community dynamics.

In a recent review, Gilman et al. (2010) discussed the utility of a community module-based approach to better understand how local community structure would be altered by species-specific spatial distribution shifts under climate change. This approach simplifies complex food webs into tractable subunits of strongly interacting species and can help elucidate how interspecific interactions will influence and be influenced by the population dynamics within a community (Holt 1997). In this article, we also adopt the community module approach and expand the pairwise match/mismatch concept. Our aim is to propose a multispecies match/mismatch perspective of phenology and apply it to community module models as an initial step for exploring community consequences of species-specific phenological shifts. To develop our argument, we first present conceptual models for short-term predictions on population recruitment in community contexts, and then explore simple numerical models including species-specific reproductive phenology for long-term predictions on community structure. These theoretical frameworks allow the conventional match/mismatch concept to account for multispecies interactions and explicit population dynamics, respectively.

A conceptual extension of the pairwise match/mismatch hypothesis: short-term effects on population recruitment

The conventional match/mismatch hypothesis explains that recruitment of a consumer population decreases with an increasing phenological mismatch with a resource in a consumer–resource interaction; that is, the length of the period during which the resource is available is crucial for the consumer population (Fig. 1a). Here we extend the pairwise concept by adding another species. As such, we develop community modules consisting of three species (i.e. tritrophic food chain, exploitative competition, apparent competition, and intraguild predation) and briefly describe how the consumer's recruitment in a pairwise trophic interaction could be altered in the presence of additional species.

First, we add a top predator feeding on the consumer, developing a tri-trophic food-chain module (Fig. 1b). In this scenario, matching with predator phenology will affect negatively the consumer's recruitment by imposing predation pressure. If this effect is large, the consumer may decrease regardless of synchrony with resource phenology; in other words, escaping the period during which predation risk is high, rather than matching with resource phenology, may be crucial for the consumer. For example, Parry et al. (1998) reported that survivorship of later hatching cohorts of Lepidoptera was reduced more drastically by predation. Their study suggests that phenological (a)synchrony with predator has also significant impacts on recruitment success (also see Both et al. 2009). Adding a competitor (i.e. an exploitative competition module) will give qualitatively similar results (Fig. 1c), where it can be seen that matching with competitor phenology decreases the consumer by

reducing the resource availability. Meanwhile, adding alternative resource (i.e. an apparent competition module) will cause a positive effect on the consumer, because it prolongs the total period during which a resource(s) is available (Fig. 1d). Predictions are more complex in an intraguild predation module. Suppose that the competitive species (added in Fig. 1c) preys not only on the resource but also on the consumer (i.e. intraguild predation) (Fig. 1e). In this scenario, the consumer suffers from poor recruitment with increasing phenological synchrony with the competitive predator because of combined effects of resource competition and predation pressure, and the negative effects are more severe than those predicted in the tri-trophic food-chain (Fig. 1b) or exploitative competition module (Fig. 1c). However, if the competitor (added in Fig. 1c) serves as a prey for the consumer, then we can expect that matching with phenology of the competitive prey causes a positive or negative effect on the consumer's recruitment (Fig. 1f), the sign of which will be determined by the relative reliance of the top consumer on the basal resource and competitive prey and the rate at which the competitive prey consumes the basal resource. These predictions are straightforward, yet relatively few studies have explicitly tested the effects of multispecies interactions on seasonal population recruitment (Cushing 1990, Durant et al. 2005, 2007, Kristiansen et al. 2011).

Our conceptual models based on the multispecies match/mismatch perspective suggest that recruitment success of a consumer population can be quantitatively or even qualitatively different in community contexts from that expected based on the pairwise match/mismatch hypothesis. This suggestion implies that the identification of species relationships and the nature of interspecific interactions enable us to come closer to mechanisms underlying population recruitment in seasonal environments. In the next section, we will explore the mathematical models describing long-term dynamics of the four community modules developed above.

Numerical simulations including species-specific reproductive phenology: long-term effects on community structure

As mentioned above, the conventional match/mismatch concept has focused on relatively short-term impacts of interaction (a)synchrony on population recruitment or foraging success. In order to explore the long-term demographic consequences, we need to develop mathematical models in which species densities are computed dynamically rather than input a priori. Here we purposely formulate minimum three-species community-module models including species-specific reproductive phenology without attempting to incorporate other known factors affecting population dynamics (e.g. stage structure). For instance, a tri-trophic food chain is modeled as follows:

$$dN_1/dt = p_1(t)r(1 - N_1/K)N_1 - a_{21}N_1N_2$$
$$dN_2/dt = p_2(t)a_{21}b_{21}N_1N_2 - d_2N_2 - a_{32}N_2N_3$$
$$dN_3/dt = p_3(t)a_{32}b_{32}N_2N_3 - d_3N_3$$

This model describes the changes in population densities of the basal resource N_1, intermediate consumer N_2, and

(a) pairwise interaction

(b) adding top predator

(c) adding competitor

(d) adding alternative resource

(e) adding competitive predator
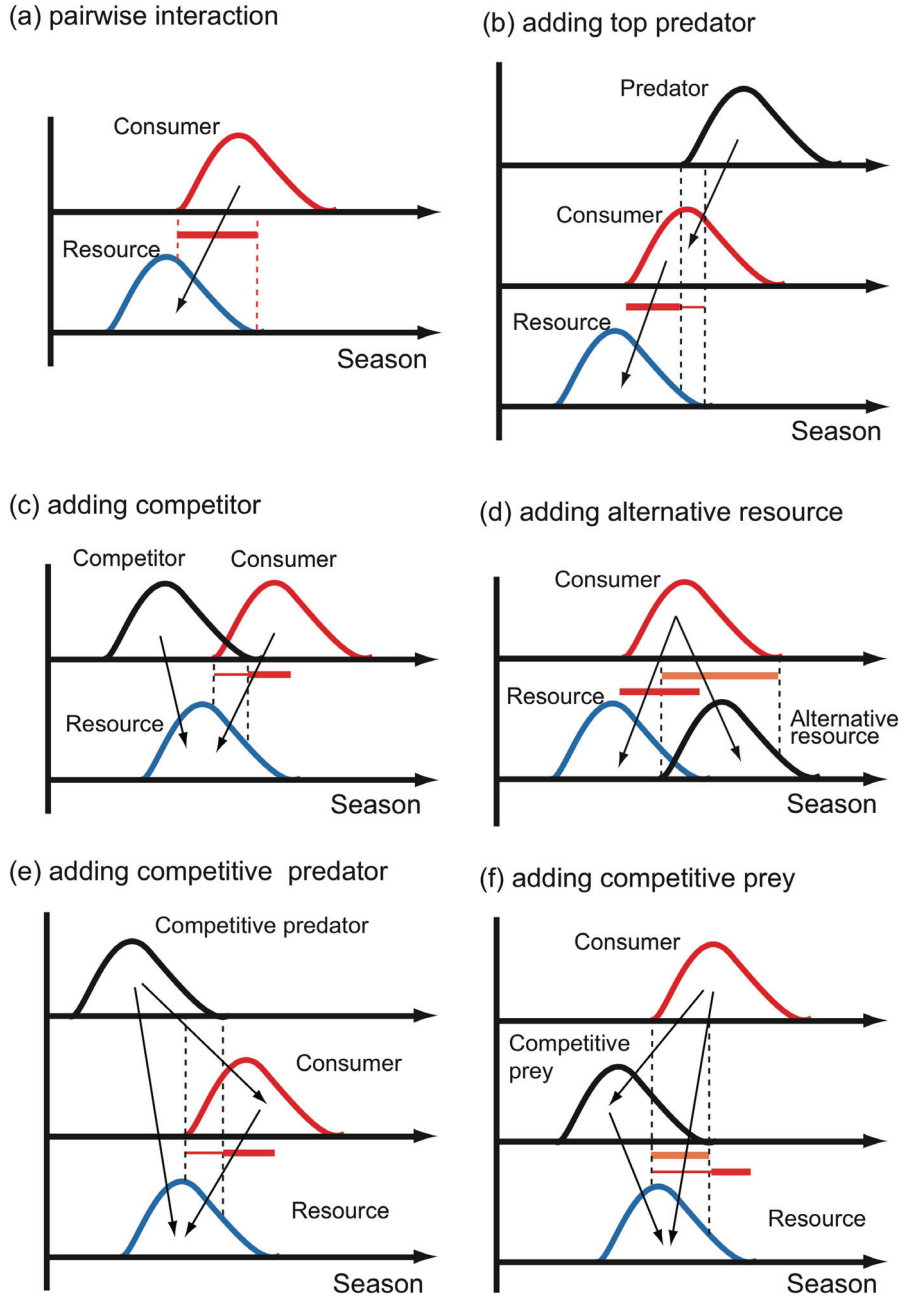
(f) adding competitive prey

Figure 1. Phenological match/mismatch in community modules. Here we consider several scenarios in which one species is added to (a) a consumer-resource interaction as (b) a top predator (i.e. a tri-trophic food-chain), (c) a competitor (i.e. exploitative competition), (d) an alternative resource (i.e. apparent competition), (e) a competitive predator, or (f) a competitive prey. Note that the scenarios in (e) and (f) both result in an intraguild predation module. Red, blue and black curves indicate seasonal population dynamics of the consumer, resource, and newly added species, respectively. Arrows indicate trophic interactions between species. Red horizontal bars represent the period during which the consumer interacts with the resident resource, and the thin ones reflect that phenological match with the added species causes negative effects on the consumer due to (b) predation pressure, (c) resource competition, or (e) both. Orange bars in (d) and (f) indicate that phenological match with the added species has a positive effect on the consumer.

top predator N_3. We make the simplest assumptions: the resource exhibits logistic growth, all trophic interactions are linear, and heterotrophs have density-independent natural mortality rates. The time-varying function $p_i(t)$ represents reproductive phenology of species i. Note that reproductive phenology in our models indicates seasonal variations in reproductive efficiency or activity governed by environmental cues (e.g. temperature and precipitation) rather than by

resource acquisition. The functional form may be determined by empirical data or specific assumptions. For simplicity and as is common in the literature (Namba 1984, Abrams 2004), we opt here for sinusoidal functions:

$$p_i(t) = 1 + u_i \sin\{2\pi(t - v_i)/T\}$$

where T, u_i, and v_i represent seasonal period, amplitude, and timing of the reproductive peak, respectively. We apply

this modeling scheme to the other community modules (see Supplementary material Appendix 1 for formulations).

We performed numerical simulations using the four community module models (Supplementary material Appendix 1). For the model simulations, we first calculated community dynamics over 30 seasonal cycles and then evaluated the average population densities of the species for the last half period (i.e. 15 seasonal cycles). Here we present representative results (Fig. 2), in which we manipulated the reproductive peak timing (i.e. v_i) of each species independently,
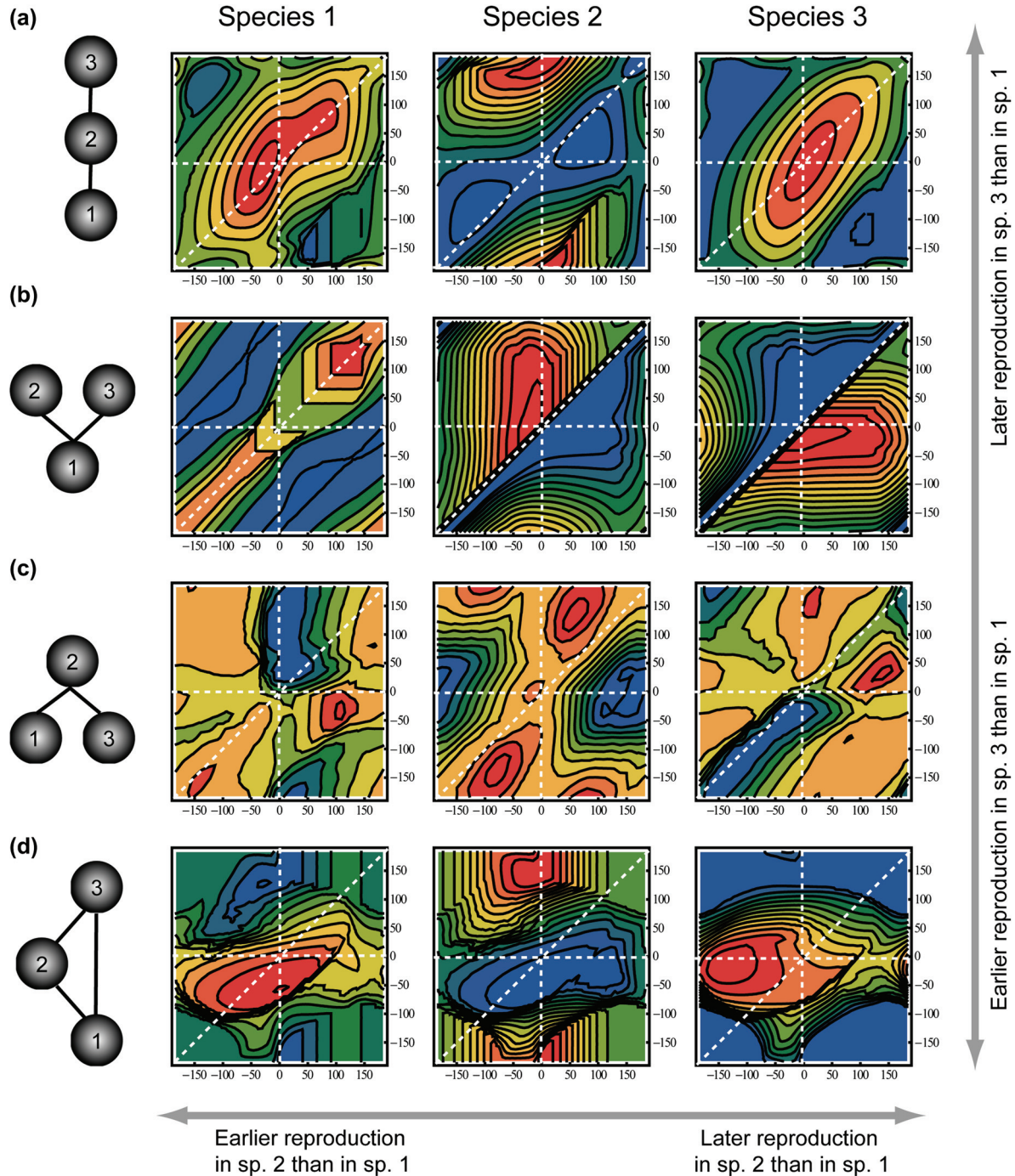

Figure 2. Long-term average densities of species in community modules for different levels of reproductive (a)synchrony. We consider four three-species community modules: (a) tri-trophic food chain, (b) exploitative competition, (c) apparent competition, and (d) intraguild predation. In each module, species 1 is a primary producer and species 2 utilizes it, whereas species 3 occupies different niches in different modules. We drew the panels using the phenology of species 1 as a yardstick. The x- and y-axis represent time lags of the reproductive peaks between species 1 and 2 and between species 1 and 3, respectively (i.e. $v_2 - v_1$ and $v_3 - v_1$): positive (or negative) values indicate that the reproduction of species 2 or 3 peaks after (or before) that of species 1. The white lines indicate pairwise synchrony, where two of the three species have the same peak timing. Where the three lines cross there is perfect synchrony between all three species. Red and blue colors indicate high and low densities, respectively. Color coding is scaled in each panel and density values are omitted for clarity. See Supplementary material Appendix 1 for model formulations and parameter values used.

fixing the other parameters. In a tri-trophic food chain, phenological (a)synchrony significantly affects the magnitude of cascading top–down effects (Fig. 2a). The basal resource has a high density when the top predator has synchronized phenology with the intermediate consumer (i.e. $v_2 \approx v_3$), whereas the predator has a low density in asynchrony with the consumer, allowing it to reduce the resource. In exploitative competition, an earlier-reproducing consumer (i.e. species 2 when $v_2 > v_3$) generally has a greater competitive advantage, probably because a later-reproducing consumer cannot sufficiently utilize the resource (Fig. 2b). As a result, a drastic shift in dominance occurs between the two consumers. Such an order effect is not clear in apparent competition between the two resources sharing a consumer. The resources are likely to be depleted when in synchrony with the consumer (i.e. $v_1 \approx v_2$ or $v_2 \approx v_3$; Fig. 2c). The generalist consumer achieves a high density by having the reproductive peak timing between the two resources (i.e. $v_1 < v_2 < v_3$ or $v_3 < v_2 < v_1$). This is probably due to a long period of resource supply. The intraguild predation module is a combination of the above ones. Therefore, while it exhibits similar patterns to those described above, some patterns are significantly modified by the combined structure (Fig. 2d). For example, cascading top–down effects exist as in a tri-trophic food chain, although the intraguild predator may have a low density even when in synchrony with intraguild prey (i.e. $v_2 \approx v_3$). Overall, our numerical simulations indicate that phenological (a)synchrony among interacting species can critically affect key dynamical features of ecological communities such as trophic cascades, competitive hierarchies, and species coexistence. Such predictions cannot be made from the conventional match/mismatch concept.

In fact, modeling phenology using periodic functions (in particular, sinusoidal functions) has been widely conducted to describe seasonal population dynamics (Namba 1984, Abrams 2004). However, the structural diversity of community modules and phenological (a)synchrony among species have not been fully considered, and thus the classical approach for seasonal population and community dynamics can be applied more intensively to climate change issues. Importantly, we observed some counterintuitive predictions. For example, the exploitative competition module predicted that a consumer can do well even when it reproduces earlier that its resource and also that the two consumers can coexist based on a single resource in some parameter spaces (Fig. 2b). We therefore consider that a more detailed analysis of each community module will be useful, although this is beyond our scope here.

Although we did not explicitly consider temporal processes by which climate change alters species phenology, we can derive important implications for community consequences of species-specific phenological shifts. For example, it was predicted that in exploitation competition, earlier reproduction has a greater advantage (Fig. 2b), which is consistent with the observation that the abundance of rotifer increased and that of *Daphnia* declined following the advancement of diatom and rotifer bloom phenology (Winder and Schindler 2004). We also note that the present modeling scheme provides the prediction that in a pairwise trophic interaction, the population density of a higher trophic level generally decreases with an increasing phenological mismatch with a lower trophic level (unpubl.), as documented in many empirical studies (Post and Stenseth 1999, Root et al. 2003, Edwards and Richardson 2004, Gordo and Sanz 2005, Kudo et al. 2008, Doi et al. 2010). Therefore, although still preliminary, we think that our numerical predictions based on the multispecies match/mismatch perspective captures some representative community consequences of species-specific phenological shifts induced by climate change.

Toward a better understanding community consequences of species-specific phenological shifts

Our multispecies match/mismatch perspective of phenology clearly demonstrates the importance of species relationships for seasonal community dynamics and thus community responses to species-specific phenological shifts, and opens several new and important avenues for further research. Most importantly, there is a need for empirical tests of our predictions and data-driven modifications of the models. Most previous studies to date have elucidated outcomes of phenological match/mismatch in pairwise species interactions. Much remains unknown about the species-specificity of climate-induced phenological shifts and its expected community-level effects in natural settings (Thackeray et al. 2010). This line of investigation requires information about species relationships and phenology of key demographic traits and obviously is a significant research challenge. However, such attempts are considered very promising for future research and supported by recent studies showing the importance of species relationships for community responses to climate change (Post and Pedersen 2008, Harmon et al. 2009, Gilman et al. 2010, Lavergne et al. 2010, Van der Putten et al. 2010).

Many more specific questions also need to be addressed based on the multispecies match/mismatch perspective in both empirical and theoretical research. For example, we can ask how climate change affects community structure when phenological shifts occur simultaneously in different traits, such as foraging and mortality, in addition to reproduction. This is very likely because life-history parameters are bioenergetically related to one another, and thus climate change may regulate multiple traits in complex ways. Ozgul et al. (2010) showed that in a hibernating mammal, earlier arousal from hibernation has led to a longer growing period and larger body mass, which in turn has resulted in a decline in adult mortality and triggered an abrupt increase in population size. It is also expected that climate-induced changes in individual growth modify stage-structured species relationships (Post et al. 2008b, Seebens et al. 2009, Yang and Rudolf 2010). Further studies need to expand simple species-based community modules to study how life history and stage structure of species can influence community responses to phenological shifts. Another possible strategy of model extension is to assume behavioral flexibility allowing for changes in resource use or anti-predator defense. Many species can adjust their behaviors depending on resource availability or predation risk, which often has significant consequences for population and community dynamics (Tansky 1978, Nakazawa et al. 2009, 2010). For example,

a herbivore may switch to use another host plant, by which the herbivore can maintain phenological synchrony with its resource. Models and empirical data are needed to address the community consequences of such behavioral flexibility to adjust the mismatching of phenology. Finally we note that there are many more possible situations in reality than we can describe here; for example, when climate change causes spatial distribution shifts in a species-specific manner (Sparks et al. 2005, Gavin and Hu 2006, Hassall et al. 2007, Parmesan 2007, Gilman et al. 2010), when species form mutualisms with one another (Gordo and Sanz 2005, Doi et al. 2008) or when evolution occurs in response to climate change or phenological shifts in other interacting species (Van Asch et al. 2007, Hoffmann and Sgrò 2011).

Conclusion

In the present study, we extended the conventional match/mismatch concept of phenology for population recruitment in a pairwise consumer–resource system to account for multispecies interactions and long-term community dynamics. Our theoretical frameworks provided valuable insights into how seasonal population recruitment in a pairwise trophic interaction could be altered in the presence of additional species (Fig. 1) and how community dynamics are mediated by phenological (a)synchrony among interacting species (Fig. 2). At the same time, we realized that we are still at the early stage of our understanding of how ecological communities are organized in seasonal environments and could be altered by climate-induced phenological shifts and interactions with other factors. Both theoretical and empirical advances are needed to establish and refine the multispecies match/mismatch perspective and more accurately predict community responses to climate change. Models and experiments that explicitly consider species phenology and interaction topology are inevitably more complex than those that ignore them. However, given the ubiquity and importance of species-specific climate responses in community structure, the potential gains in understanding warrant the additional effort. The community module approach we sketch here can be an initial step in the process.

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