Phenology, ontogeny and the effects of climate change on the timing of species interactions

Louie H. Yang[1†] and V. H. W. Rudolf[2]*[†]

[1]*Department of Entomology, UC Davis, CA 95616, USA*

[2]*Department of Ecology & Evolutionary Biology, Rice University, Houston, TX 77098, USA*

*Correspondence: E-mail: volker.rudolf@rice.edu

[†]*These authors contributed equally to this work.*

Abstract

Climate change is altering the phenology of many species and the timing of their interactions with other species, but the impacts of these phenological shifts on species interactions remain unclear. Classical approaches to the study of phenology have typically documented changes in the timing of single life-history events, while phenological shifts affect many interactions over entire life histories. In this study, we suggest an approach that integrates the phenology and ontogeny of species interactions with a fitness landscape to provide a common mechanistic framework for investigating phenological shifts. We suggest that this ontogeny–phenology landscape provides a flexible method to document changes in the relative phenologies of interacting species, examine the causes of these phenological shifts, and estimate their consequences for interacting species.

CLIMATE CHANGE AND THE TIMING OF SPECIES INTERACTIONS

In recent years, the effects of global climate change on species and ecosystems have become increasingly apparent (Parmesan & Yohe 2003; Parmesan 2006; Intergovernmental Panel on Climate Change 2007). Numerous ecological studies have now pointed to an important general pattern of species' responses to climate change around the world: on average, seasonal life-history events such as leaf unfolding, flowering, insect emergence, or the arrival of migratory birds are occurring earlier than they have in the historical past (Dunn & Winkler 1999; Walther *et al.* 2002; Parmesan & Yohe 2003; Gordo & Sanz 2005). Despite this prevailing trend, however, it has also become evident that species within the same community often show variable phenological responses to climate change (Visser & Both 2005; Miller-Rushing & Primack 2008; Both *et al.* 2009). For example, an unusually warm spring in northern Japan lead to substantial phenological advances in the flowering of several spring-ephemeral plants relative to their pollinating bees, resulting in dramatically decreased seed production of bee-pollinated species (Kudo *et al.* 2004). In general, while many species have shown advances in the seasonal timing of their

life-history events to varying degrees, some species have shown no discernible phenological changes, and others have demonstrated delayed seasonal phenologies (Beebee 1995; Parmesan & Yohe 2003; Gordo & Sanz 2005; Both *et al.* 2009).

These differential responses across species indicate that climate change is altering the relative timing of species interactions and influencing which ontogenetic stages interact with each other (Visser & Both 2005; Memmott *et al.* 2007; Both *et al.* 2009). For example, a recent long-term study in the Netherlands showed different phenological responses to climate change for the relative timing of oak leaf unfolding, the peak biomass of caterpillars, the breeding of insectivorous birds and the breeding of an avian predator, resulting in the disruption of stage-structured interactions across four trophic levels (Both *et al.* 2009). Given that species interactions can strongly determine the structure and dynamics of many natural communities, some of the most profound effects of climate change are likely to be driven by changes in the timing of biotic interactions between species. The effects of these altered interactions can be as strong or stronger than the direct abiotic effects of climate change (Parmesan 2006). While it has become increasingly evident that differential changes in phenologies

can disrupt the temporal coordination of longstanding and potentially coevolved species interactions (Stenseth & Mysterud 2002; Winder & Schindler 2004; Post *et al.* 2008), the broad implications of these disruptions are still not well-understood. However, it is clear that we cannot expect to understand the consequences of phenological changes by investigating single species in isolation. Instead, understanding the full implications of climate change will require an integrated and mechanistic understanding of how climate change is affecting phenology, ontogeny and the timing of species interactions.

PHENOLOGY, ONTOGENY AND THE TIMING OF SPECIES INTERACTIONS

The phenologies of ontogenies

Phenological studies have traditionally examined the timing of key life-history events relative to calendar dates (Lieth 1974; Fitter & Fitter 2002; Schwartz 2003). More recently, however, a growing number of studies have begun to consider changes in the timing of life-history events for one species relative to those of an interacting species (Durant *et al.* 2005; Visser & Both 2005). These studies have refocused attention on the ecological consequences of disrupting species interactions. However, most studies of phenological mismatch have continued to emphasize the timing of single life-history events, such as flowering time or peak resource demand, for one focal species instead of examining the entire ontogenies of both interacting species. While an emphasis on specific life-history events may be sufficient to understand some short-term ecological interactions, many interactions extend and change over the lifetime of the organism and are strongly affected by the ontogenetic stages of the interacting species. For example, most competitive and predator–prey interactions are size-structured (Ebenmann & Persson 1988; Wilbur 1988; Schwinning & Weiner 1998; Rudolf 2008a, b), and most plant-herbivore interactions change over ontogeny (reviewed in Boege & Marquis 2005). How are these extended interactions being affected by climate change?

At a mechanistic level, climatic change may drive phenological shifts by accelerating or decelerating the developmental rates of species (Gillooly *et al.* 2002; Van Nouhuys & Lei 2004), or by altering the timing of environmental cues that affect a species' appearance in the community (Kemp & Bosch 2005; Levine *et al.* 2008; Tottrup *et al.* 2008). For example, the developmental rate of the dark-coloured caterpillar *Melitaea cinxia* is strongly affected by basking in direct sunlight, while the developmental rate of its light-coloured specialist parasitoid *Cotesia melitaearum* is primarily influenced by air temperature (Van Nouhuys & Lei 2004). As a result, climatic changes in the

patterns of spring warming and sunshine can differentially influence the relative phenologies of these two species through changes in their developmental rates. By comparison, climatic changes can also affect environmental cues that determine a species' appearance in the community through processes such as migration (Tottrup *et al.* 2008), germination (Levine *et al.* 2008), hatching (Dunn & Winkler 1999; Visser & Holleman 2001) or emergence from dormancy (Kemp & Bosch 2005). Importantly, both types of changes are likely to affect the entire phenology of a species' life-history, not just the timing of specific life-history events. As a result, understanding the consequences of many phenological shifts will require an understanding of stage-structured species interactions.

Species interactions over ontogeny

Studies of stage-structured species interactions have long emphasized and illustrated the importance of ontogenetic variation over the entire life-history of individuals. Fundamental individual traits such as size, behaviour, resource use and defenses against consumers often vary considerably between ontogenetic stages (Werner 1994; Boege & Marquis 2005; Benton *et al.* 2006). For example, many plants show ontogenetic patterns in their tolerance of and resistance to herbivory (Boege & Marquis 2005), and many animal species switch between herbivorous and carnivorous feeding habits over ontogeny (i.e. life-history omnivory; Werner & Gilliam 1984; Polis & Strong 1996). As a consequence, individuals across a diversity of taxa often experience significant ontogenetic shifts in both the *type* and *strength* of their species interactions over ontogeny (for example, Fig. 1).

Shifts in species interaction type

Qualitative changes in species interactions over ontogeny are ubiquitous in natural communities and well-established in most taxa, including a diversity of plants, invertebrates and vertebrates (Wilbur 1980, 1988; Werner & Gilliam 1984; Polis 1991; Boege & Marquis 2005; Rudolf 2008b). In predator–prey interactions, juvenile predators often compete with their future prey, resulting in a shift from competition to predation during ontogeny (Maly 1976; Werner & Gilliam 1984; Persson & Greenberg 1990; e.g. Fig. 1a). When the prey outgrows the predator and reaches a size refuge, predation can also shift to competition (Boone *et al.* 2002; Rudolf & Armstrong 2008), or the role of the predator and the prey can even be reversed (Wissinger 1992; Magalhaes *et al.* 2005; e.g. Fig. 1a). For example, the late filling of temporary ponds can delay the hatching of *Ambystoma opacum* salamander larvae relative to hatching times of the salamanders *Ambystoma talpoideum* or *Ambystoma maculatum*. When this phenological shift occurs, *A. opacum* is
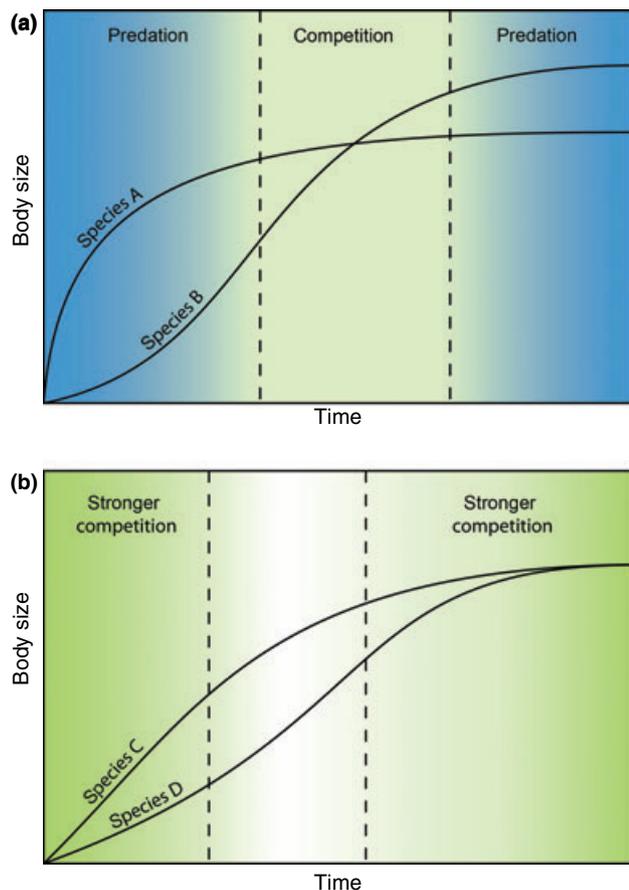
Figure 1 Both the *type* and *strength* of species interactions can change over time, due to differences in relative ontogenies and phenologies of interacting species. For example, (a) relative changes in phenology and ontogeny can lead to shifts from predation to competition or *vice versa*, or to a complete role reversal. This specific example represents a hypothetical system where predation rates increase with differences in size and competition is strongest for individuals with similar size. Over the course of the interaction, there are successive periods when species A preys upon species B, when both species compete, and when species B preys upon species A. In this panel, the blue regions represent interaction phases that are dominated by predatory interactions, while the green region represents the interaction phase that is dominated by competitive interactions. Conversely, (b) even without a change in interaction type, the strength of interactions often varies over time due to changes in stage-structured interactions. In this specific example, species C and D experience stronger competitive interactions early in ontogeny and late in ontogeny, when both interacting individuals show similar body sizes. In this panel, the intensity of the green gradient represents the intensity of competitive interactions between species C and D. This example could be relevant to a range of competitive interactions; for example, where similarly sized predators compete for common prey items or where similarly sized plants compete for below-ground resources at similar root depths.

often not large enough to prey on the other two species, shifting the dominant interaction type from predation to competition (Boone *et al.* 2002; Urban 2008). Similar changes in interaction type have been documented in copepod interactions where changes in temperature cues between years alter the relative hatching and developmental times of two interacting species, thereby changing their relative phenologies and shifting the dominant interaction type from competition to predation and *vice versa* (Maly 1976).

In plant–herbivore interactions, herbivores often become pollinators over ontogeny, resulting in transitions between herbivory and mutualism. For example, interactions between hawkmoths (*Manduca sexta*, Sphingidae) and their host plants (typically Solanaceae, including *Datura wrightii*) often include an ontogenetic window of intense herbivory during the larval stages, followed by the highly effective pollination of these same host plants in the adult stages (Adler & Bronstein 2004; Alarcon *et al.* 2008; Bronstein *et al.* 2009).

By comparison, many interactions among plants may also transition through ontogenetic periods of facilitation as well as competition. While the observation of 'nurse plants' facilitating the establishment of heterospecifics is relatively widespread in abiotically stressful environments (Stachowicz 2001), these facilitative interactions can readily shift to competitive interactions over the ontogenies of the two interacting plants (Callaway & Walker 1997), with substantial changes occurring even within a single growing season (Holzapfel & Mahall 1999). Whether and when such transitions occur depends on the specific combination of interacting ontogenetic stages, suggesting that phenological shifts could fundamentally alter the nature of many species interactions.

In general, such shifts demonstrate that the fitness consequences of phenological shifts that appear early in the ontogeny of a species can be fundamentally different from the effects observed at later ontogenetic stages. For example, the relatively early seasonal appearance (or accelerated developmental rate) of a prey species may decrease its predation risk early in life, but increase the negative effects of competition with its former predator later in life. For interactions between plants and their pollinating herbivores, phenological shifts may allow the plant to avoid costly herbivory early in the growing season, but ultimately reduce the likelihood of successful pollination during the flowering period. Similarly, relative shifts towards increasingly early germination of an annual plant in a shrub-facilitated nurse plant interaction could potentially reduce net facilitation during establishment while increasing later competitive interactions, due to seasonal changes in the abiotic context and the relative ontogenies of the species. Thus, assessing the consequences of phenological mismatch

at any one particular life-stage can often provide a misleading estimate of the cumulative lifetime effects. This emphasizes the importance of integrating over the entire ontogeny of the interaction and accounting for changes in interaction type to reliably estimate the net effects of phenological shifts on species interactions.

Phenological shifts in interaction strength within interaction types

Even in systems where the fundamental interaction type remains unchanged, there is often continuous ontogenetic variation in the effects (i.e. fitness consequences) of interactions over the course of a season (e.g. Fig. 1b). Ontogenetic stages are often represented by individual body size, and body size is arguably one of the main factors that determines the strength of species interactions in the broadest possible sense (for a recent review, see De Roos *et al.* 2003). For example, competitive dominance can increase over ontogeny, as has been observed for interference competition between predatory larval salamanders (Ziemba *et al.* 2000; Rudolf 2006) and for light competition between plants (Schwinning & Weiner 1998). In other systems, however, younger stages are more efficient in exploiting limiting resources and outcompete older stages, thus resulting in decreasing competitive ability over ontogeny, as observed for food competition in fish (Persson *et al.* 2004; Bystrom & Andersson 2005) or tadpoles (Werner 1994). In predator–prey systems, predation risk may decrease over ontogeny if predators are gape-limited and the prey grows faster than the predator (Taylor *et al.* 2001; Urban 2007), or increase over ontogeny if predators actively prefer larger prey (Rudolf 2008a,c). In plant–herbivore interactions, young plants often experience greater insect herbivory than older plants (Coley 1980), while the opposite pattern is commonly observed for mammalian herbivory (Boege & Marquis 2005). Moreover, the costs of herbivory also appear to be strongly stage and context dependant, with some plants showing greater tolerance to herbivory at early stages (Weltzin *et al.* 1998), and other plants showing greater tolerance at later stages (Maschinski & Whitham 1989; Boege *et al.* 2007), with a general trend towards reduced tolerance at intermediate seedling stages (Boege & Marquis 2005). Similarly, pathogen virulence is often more severe for older hosts (Thompson 1988; Woodland & Blackman 2006), but is sometimes more severe for younger hosts (Wilson-Rich *et al.* 2008). Consequently, even within a general interaction *type* (e.g. competition, predation, parasitism or mutualism), phenological shifts in species interactions can either have positive or negative effects on individual species depending on how the per-capita interaction *strength* changes over ontogeny. However, while several previous studies have investigated ontogenetic-dependence in a range of

species interactions, these studies have usually considered ontogenetic variation in only one interactor (but see Maly 1976; Abramoff *et al.* 2004; Cameron *et al.* 2007). Accounting for changes in both interaction type and interaction strength over the ontogeny of both interacting species will be necessary to develop a mechanistic framework to predict the individual fitness effects of phenological shifts and may at least partly explain variation in the impact of phenological shifts observed within different types of species interactions.

The effects of phenological shifts will not be negative for all interacting species, as varied effects are likely to result from the disruption of different competitive, predator–prey, host–parasite and mutualistic interactions. For example, phenological shifts between the timing of bud burst in oaks and the emergence of their herbivores has strong negative consequences for the herbivore but may actually benefit the oaks by reducing herbivory (Visser & Holleman 2001). By comparison, phenological shifts in the seasonal coordination of mutualistic plant–pollinator interactions may commonly be expected to have negative consequences for both interactors, and specialist interactors may be expected to experience more severe consequences than generalists (Bascompte *et al.* 2003; Memmott *et al.* 2007; Hegland *et al.* 2009). However, hypotheses distinguishing how phenological shifts are likely to affect different kinds of species interactions have remained untested (Tylianakis *et al.* 2008).

In general, the effects of phenological shifts on interacting species seem to be largely determined by (1) how the interaction *type* and/or *strength* changes over their ontogenies and (2) the relative phenologies of the interacting species (i.e. what ontogenetic stages interact with each other). Ontogenetic variation and stage-structured species interactions are important general features in the majority of natural systems, including many systems that are likely to experience shifting phenologies due to climate change. We suggest that integrating the ontogeny and phenology of species interactions could provide a useful framework that allows novel predictions of the consequences of phenological changes for interacting species.

THE NEED FOR A MECHANISTIC FRAMEWORK

Recognizing the wide range of potential consequences that could result from phenological shifts in species interactions, we believe that the addition of more focused, local and mechanistic studies will be necessary to investigate how phenological responses to climate change are likely to affect species interactions and the fitness of species. As Visser & Both (2005) have suggested, studies investigating the relative phenologies of interacting species will require a different 'yardstick' than traditional approaches based on calendar dates. They proposed a framework in which changes in the timing of key life-history events for multiple species are

presented together to provide an intuitive graphical representation that compares changes in the relative phenologies of interacting species. Such efforts are useful to address ecological questions about species interactions, but even this framework is limited by its focus on specific life-history events (e.g. flowering, bud burst, clutch initiation or emergence from dormancy) instead of determining the stage-specific per-capita effects of interactions between species over the entire course of their interaction, and in ways that are more readily incorporated into stage-structured models of species interactions.

Here, we propose a conceptual framework (the *phenology–ontogeny landscape*, Fig. 2) to document shifts in the phenologies of two interacting species and examine the ecological consequences of these shifts. Instead of documenting phenological shifts relative to calendar dates, this approach represents the ontogenies of two interacting species as separate axes of a phase plane relative to each other to examine the range of possible pairwise interactions between different ontogenetic stages. A *phenological interaction path* through this landscape space describes the series of stage-structured interactions that occur between two interacting species over the course of a season (Fig. 2a). The phenology–ontogeny landscape provides a flexible graphical representation describing the relative timing of two ontogenies over the entire duration of the species interaction. For example, Fig. 2a provides one heuristic example comparing how changes in the appearance phenology or developmental rate of interacting species may be documented as different interaction paths in a phenology–ontogeny landscape. This approach can provide a useful framework for structuring future observations, monitoring changes in the relative timing of species life histories, comparing the relative timing of interactions in different communities, suggesting mechanisms behind observed phenological shifts and predicting how changes in the relative timing of life histories are likely to affect many different kinds of species interactions.

Experimental studies can extend this framework to examine the fitness implications of these phenologically shifted interaction paths, contributing a valuable third dimension to the phenology–ontogeny landscape (Fig. 2b–d). Although specific methods for parameterizing the fitness dimension of a phenology–ontogeny landscape will vary among systems and species, we suggest a general experimental approach to estimate fitness effects over the phenology–ontogeny landscape by limiting the pairwise interactions between different ontogenetic stages of two interactors. A series of experiments would be conducted in which two species are allowed to interact only during a relatively brief time interval of their life-history (i.e. an 'interaction window', see Fig. 2b). Replicated trials representing different combinations of two ontogenetic stages would provide standardized measures that can be used to

parameterize the fitness surface of the phenology–ontogeny landscape (Fig. 2c). This fitness dimension describes the per-capita interspecific effects of one interactor on the other, where each cell represents the fitness effect of a specific stage-structured interaction window. The phenological interaction path indicates the series of fitness effects experienced over the duration of the interaction. Comparing the fitness effects of different phenological interaction paths allows one to estimate how phenological shifts are likely to affect the fitness of the focal species at various points in its ontogeny and suggest the strength of selection imposed by different scenarios of observed or simulated phenological shift.

In summary, this framework extends previous approaches in four key ways: (1) first, it emphasizes the importance of considering phenological shifts relative to the ontogenies of interacting species in the community, rather than calendar dates. This emphasizes the consequences of phenological shifts for community dynamics, and provides a graphical method to distinguish between the mechanisms underlying phenological shifts (i.e. relative changes in the timing of appearance cues vs. relative changes in developmental rates; e.g. see Fig. 2a); (2) second, it integrates the phenology and ontogeny of both interacting species over the entire duration of their interaction, instead of focusing on single species and specific life-history events. This makes the phenology–ontogeny landscape approach applicable to a wide range of extended interactions, and inherently incorporates changes in the strength and type of species interactions over ontogeny; (3) third, it estimates the stage-specific empirical data that are essential to parameterize standard stage-structured models, allowing existing model frameworks to consider the population dynamics and evolutionary responses of species under different scenarios of phenological shift; (4) finally, it aims to provide a robust method of documenting phenological shifts applicable across several interaction types, to allow future comparative studies to look for general patterns among the causes and consequences of phenologically shifting species interactions.

Because it focuses both observational and experimental approaches on detailed investigations of specific pairwise species interactions, the phenology–ontogeny landscape complements existing efforts to assess climate change effects over much broader scales (e.g. Betancourt *et al.* 2005; Morisette *et al.* 2009). Importantly, the phenology–ontogeny landscape approach requires coordinated and repeated observations of two interacting species within a community, and such datasets are not common in the literature (but see Maly 1976). We believe that this detailed approach has become especially necessary and relevant now, because of the temporal complexity and multiple consequences inherent with phenological shifts. Given this complexity, we note that this framework will not be readily applicable to all systems of
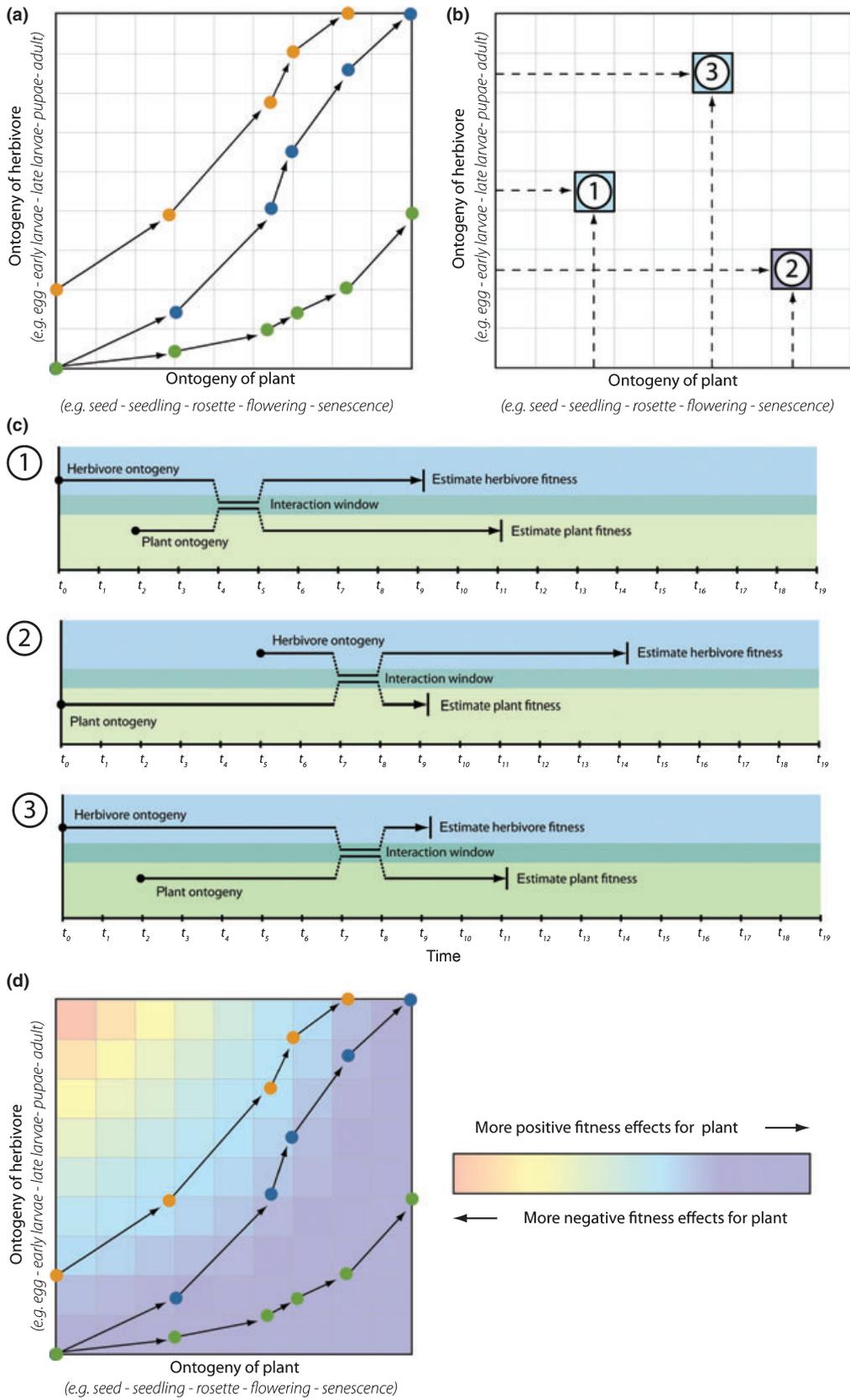
Figure 2 The phenology–ontogeny landscape graphically describes the relative timing of two interacting species' ontogenies over the entire duration of the species interaction. The series of stage-structured interactions that occur between two interacting species over the course of a season is represented by a phenological interactions path, where each point along this path represents coincident observations of both interactors in the same community. (a) An observational phenology–ontogeny landscape, showing three possible phenological interaction paths documented for a hypothetical plant–herbivore interaction. The blue path shows the baseline interaction phenology, the orange path shows an alternative interaction phenology in which the appearance of the herbivore is advanced relative to the plant, and the green path shows an interaction phenology where the developmental rate of the plant is accelerated relative to the herbivore. Although these data points are shown without error bars for clarity, horizontal and vertical error bars could be used to represent the degree of phenological variability or synchrony within a population at each observation period. (b) Experimental manipulations that limit the interaction interval may be used to probe the fitness consequences of stage-specific interaction combinations of each interactor. A general framework for parameterizing the fitness landscape of a phenology–ontogeny landscape would require experimental manipulations that limit the temporal window for species interactions in a systematic manner. (c) For example, to estimate the fitness effects for each of the numbered interaction windows, herbivores and plants that were otherwise maintained separately would be allowed to interact at different combinations of life stages. In this figure, arrows represent the ontogenies of the herbivores and the plants; the circle at the beginning of the arrow represents age zero, and the vertical line at the end of the arrow represents the point at which fitness is estimated. Interactions between the plant and herbivore would only be allowed to occur during the interaction window. For example, to parameterize the cell numbered ①, a cohort of herbivores must be initiated at time t_0 and a cohort of plants must be initiated at time t_3; these plants and herbivores are only able to interact during the interval from t_4 to t_5. The fitness of these individuals would be assessed at reproduction or at senescence. Similar methods could be used to parameterize cells ② and ③. The mean reproductive success of these individuals could be normalized relative to control individuals that were maintained in the absence of the interaction of interest; time–slice interactions that tend to increase fitness would yield positive fitness effects relative to the controls, while time–slice interactions that tend to decrease fitness would yield negative fitness effects relative to the controls. To optimize experimental effort, the extent of the estimated landscape surface could be limited to only those pairwise interactions that are considered plausible or relevant, or standard methods for extrapolating response surfaces could be used to estimate the entire fitness surface (e.g. Inouye 2001); the most appropriate resolution of the landscape will depend on the degree to which the species interactions change over ontogeny. (d) Fitness estimates for either species can then be used to parameterize the fitness dimension. In this example, the plant is the focal species, and the stage-specific fitness effects are represented as a colour grid. Each surface represents the fitness effects for one focal interactor, but the reciprocal fitness effects on the other interacting species can be represented in a second phenology–ontogeny landscape. The phenological path can be used to examine the fitness consequences of observed and simulated phenological shifts for stage-structured interactions at various points in the ontogeny of the interacting species, and provide valuable information that can be used in stage-structured models to investigate species' ecological and evolutionary responses to phenological shifts.

interest. However, we believe that the fundamental approach of the phenology–ontogeny landscape provides a useful method for many systems that allows us to take important first steps towards examining the potential consequences of phenological shifts. This approach broadens the realm of phenological shifts to include many systems where interactions are changing quantitatively, or where the mis-match of specific life-history events may be less evident, or less important.

Many new questions will undoubtedly follow. Even as we seek to integrate considerations of phenology and ontogeny into our basic understanding of pairwise species interactions, important future challenges urge us to consider how more complex multispecies community interactions (English-Loeb & Karban 1992; Both *et al.* 2009), the role of evolutionary responses (Van Asch *et al.* 2007), and other important drivers of environmental change such as habitat fragmentation (Tylianakis *et al.* 2008) are likely to affect the consequences of phenological shifts. We suggest these as important directions for continued and future investigation, synergistic with the detailed analysis of specific pairwise interactions.

In particular, the phenology–ontogeny framework suggests several questions for the evolutionary ecology of species responses to phenological shifts. The phenology–ontogeny landscape would provide a valuable roadmap to begin anticipating evolutionary responses to phenological shifts, as the actual responses of species in nature are likely to integrate both complex ecological processes and evolutionary responses in unexpected ways. For example, in a study of winter moth (*Operophtera brumata*) and pedunculate oak (*Quercus robur*) interactions, Van Asch *et al.* (2007) documented strong fitness consequences of phenological shifts for winter moths in lab experiments, and substantial heritable genetic variation in the effects of different temperature regimes on the timing of egg hatch. A simulation model that combined these data with climatic projections predicted a strong adaptive response among winter moths to minimize phenological shifts, a result that is inconsistent with ongoing observations of substantial phenological shifts in the winter moth–penduculate oak interaction (Van Asch *et al.* 2007). One strong explanation for this result is that winter moths may be responding to phenological shifts by shifting to alternative host trees with more favourable leaf unfolding phenologies (Van Asch *et al.* 2007). This example illustrates a key challenge in forecasting species responses to phenological shifts, as many species are likely to have multiple avenues for integrating ecological and evolutionary responses in complex natural systems.

CONCLUSIONS

While the direct abiotic effects of climate change on individual species have become increasingly evident (Walther *et al.* 2002; Thomas *et al.* 2004; Intergovernmental Panel on Climate Change 2007), the effects of climate change on species interactions are more complex and less clear (Visser & Both 2005). Given the widespread importance of stage-structured species interactions and the mounting evidence of variable phenological responses to climate change, it seems clear that we now need to develop a more detailed understanding of how phenological shifts are likely to affect interactions throughout the life-history of species. We believe that studies focused on integrating the phenology and ontogeny of stage-structured species interactions will be necessary to understand the complex consequences of climate change.

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