Short communication

Sensitivity of plant–pollinator–herbivore communities to changes in phenology

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ABSTRACT

For many species in seasonal environments, warmer springs associated with anthropogenic climate change are causing phenological changes. Within ecological communities, the timing of interactions among species may be altered if the species experience asymmetrical phenological shifts. We present a model that examines the consequences of changes in the relative timing of herbivory and pollination in a community of herbivores and pollinators that share a host plant. Our model suggests that phenological shifts can alter the abundances of these species and, in some cases, their population dynamics. If historical patterns of interactions in a community change and herbivores become active before pollinators, the community could see a reduction in pollinators and an increase in herbivores, while if pollinators become active before herbivores, there could be a loss of stable coexistence. Previous studies have warned of the potential for climate change to cause large phenological mismatches whereby species that depend on one another become so separated in time that they can no longer interact. Our results suggest that climate change-induced phenological shifts can have a major impact on communities even in cases where complete phenological mismatches do not occur.

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1. Introduction

One characteristic of anthropogenic climate change is a longer temperate growing season, in part due to warm temperatures earlier in the spring (IPCC, 2007). For species with seasonal life histories, this means that ideal conditions for certain life-history events are occurring earlier than they have in the past. Some species appear to have the potential to adapt to the abiotic pressures imposed by changing climatic conditions (van Asch et al., 2007; Burgess et al., 2007), and many species are already exhibiting phenological shifts (Parmesan and Yohe, 2003; Root et al., 2003; Bertin, 2008). Responding to changing abiotic conditions, however, does not necessarily result in long-term persistence of a species. Persistence additionally requires that a species adapt to any changes that climate induces in other species with which it interacts. Understanding how a species will fare in the face of climate change therefore often requires an understanding of the community in which that species is embedded (Harmon et al., 2009).

When individual species change their phenologies, there is the potential for phenological mismatches: species that have historically undergone life history events on the same seasonal calendar may lose synchrony and therefore lose the ability to interact as they have in the past (Stenseth and Mysterud, 2002; Visser and Both, 2005; Durant et al., 2007; Both et al., 2009). Interactions among plants and their associated insects may be particularly sensitive to this type of mismatch (Harrington et al., 1999; Bale et al., 2002; Memmott et al., 2007; Hegland et al., 2009). For instance, a flowering plant must align its growing season with favorable weather, but it also must flower when pollinators are present, and herbivores and pollinators must emerge from overwintering at a time when both suitable climatic conditions and host plants are present. Synchrony among insect emergence and plant flowering is likely to be lost in a rapidly changing climate because different species may rely on weakly correlated or unrelated seasonal cues (van Asch and Visser, 2007) or respond differently to the same cues (Hodkinson and Bird, 2006). Indeed, many of the known examples of species showing phenological shifts are plants (Post et al., 2000; Fitter and Fitter, 2002; Root et al., 2003; Primack et al., 2004; Menzel et al., 2006) and insects (Visser and Holleman, 2001; Stefanescu et al., 2003; Gordo and Sanz, 2006), and there is already evidence that these shifts can result in asynchrony (Doi et al., 2008; Visser and Holleman, 2001).

In this study, we investigate the sensitivity of a plant–pollinator–herbivore community to changes in phenology. We focus on this type of community because it is both ubiquitous and, as explained above, likely to be impacted by climate change-induced phenological shifts. Very few studies have looked at relative phenological shifts in three or more species (but see Both et al., 2009), and, to our knowledge, none have looked at shifts in

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pollination and herbivory. A community-focused approach is particularly important because multiple interactions have been shown to combine in ways that alter ecological and evolutionary outcomes (Armbruster, 1997; Strauss, 1997; Herrera, 2000; Strauss and Irwin, 2004). The mix of beneficial pollinator services and detrimental herbivorous activity makes the impact of phenological shifts on the stability and dynamics of these communities difficult to intuit. For example, a plant would benefit from losing synchrony with its herbivore, but suffer from losing synchrony with its pollinator.

Past empirical (van Asch et al., 2007) and simulation (Memmott et al., 2007) studies have focused on how phenological asynchrony results in catastrophic outcomes; that is, the full or partial loss of species interactions caused by temporal separation. Instead, we ask whether the timing of springtime events is important, even when all three species are able to maintain interactions. Less dramatic disruptions are likely the norm so we believe there is great value in understanding their consequences. To that end, we present a simple model for exploring the importance of the timing of spring events in a plant–pollinator–herbivore community.

Our model tracks the abundances of a spring-flowering annual plant, a univoltine pollinator and specialist floral herbivore using a discrete-time framework. An annual plant was chosen because they have been shown to respond more quickly than perennials to climate change (Fitter and Fitter, 2002). The pollinator is modeled to represent any level of generalism or specificity for the focal plant. The herbivore can be modeled to have any level of generalism as well, although simulations suggest that many of our qualitative results are insensitive to the degree of herbivore generalism and so we present only the case of a specialist herbivore here. The plant–herbivore component of our model therefore describes systems such as sunflower beetles on annual sunflowers (Laird and Addicott, 2008), Edith's checkerspot butterflies on Torrey's blue-eyed Mary (Parmesan, 2000), and root-crown weevils on purple viper's bugloss (Sheppard et al., 2001), but the results are readily extended to many other systems. Because the plant is annual and both of the insects are univoltine, we assume an annual time-step. This assumption required us to construct new models since previously proposed models for plant–pollinator–herbivore communities operate in continuous time (Jang, 2002). Discrete-time models can be formulated to address dynamics at two time scales, by using functions that summarize within-year interactions in order to iterate between-year changes in population densities. We alter the within-year model to represent changes in one species' phenology relative to the others. This allows us to compare two alternative scenarios: (1) pollination occurs before herbivory each year, or (2) herbivory occurs before pollination. In these scenarios, both pollinators and floral herbivores have the opportunity to interact with the flowers and only the order of those interactions changes. Comparing scenarios (1) and (2) allows us to identify changes to the community brought on by shifts in species' phenologies.

2. Methods

Each growing season in our model begins with the flowering of plants. This is followed by pollination and then herbivory (scenario 1 above) or herbivory and then pollination (scenario 2). We assume that the herbivore has no preference between pollinated and unpollinated flowers. Next, the surviving pollinated flowers produce seeds, and the insects lay eggs according to the quantity of the floral resources that were available to them. These seeds and eggs determine the abundance of each species the following year.

We use the state variables F_t, P_t, and H_t respectively to denote the densities of flowers, pollinators, and herbivores at the start of year t. F_t' flowers survive herbivory in year t, and F_t'' survive herbivory and become pollinated. The fraction of flowers to survive herbivory, h, is a function of the number of herbivores per flower, and the fraction of flowers to become pollinated, p, is a function of pollinators per available flower. Using saturating type 2 functions to describe these species interactions,

$$h(H_t/F_t) = \frac{a}{a + H_t/F_t} = \frac{aF_t}{aF_t + H_t} \tag{1}$$

$$p(P_t/F_t^\bullet) = \frac{P_t/F_t^\bullet}{b + P_t/F_t^\bullet} = \frac{P_t}{bF_t^\bullet + P_t} \tag{2}$$

where a and b are constants determining the shapes of these functions. Our notation $F_t^\bullet$ represents F_t in the pollination-first scenario and $F_t' = h(H_t/F_t)F_t$ in the herbivory-first scenario. For either scenario, $F_t'' = p(P_t/F_t^\bullet)h(H_t/F_t)F_t$.

The maximum per capita growth rates of the flower, pollinator, and herbivore populations are r_F, r_P, and r_H. At a given density, the populations attain a fraction, given by the functions f_F, f_P, or f_H, of these maximum growth rates. Thus,

$$F_{t+1} = r_F f_F(F_t'')F_t'' \tag{3}$$

$$P_{t+1} = r_P f_P(F_t^\bullet, P_t)P_t \tag{4}$$

$$H_{t+1} = r_H f_H(F_t, H_t)H_t \tag{5}$$

Continuing with the assumption that species interactions can be described by type 2 functions, and assuming Beverton–Holt density dependence in the plant, we have

$$f_F(F_t'') = \frac{c}{c + F_t''} \tag{6}$$

$$f_P((F_t^\bullet + g_P)/P_t) = \frac{(F_t^\bullet + g_P)/P_t}{d + (F_t^\bullet + g_P)/P_t} = \frac{F_t^\bullet + g_P}{dP_t + F_t^\bullet + g_P} \tag{7}$$

$$f_H(F_t/H_t) = \frac{F_t/H_t}{k + F_t/H_t} = \frac{F_t}{kH_t + F_t} \tag{8}$$

The shapes of these functions are governed by the constants c, d, and k. In Eq. (7), g_P represents non-F resources used by the pollinator, determining its level of generalism or specialism. Although the model we present is specific for a specialist herbivore, adding a similar non-F parameter by changing F_t in Eq. (8) to $F_t + g_H$ does not appear to alter our qualitative conclusions in the three-species equilibrium. Note that when $F_t = 0$, the pollinator experiences Beverton–Holt density dependent population growth.

The full model is obtained by substituting Eqs. (1)–(2) and (6)–(8) into Eqs. (3)–(5). To facilitate analysis, we nondimensionalized this model using the following substitutions: $\tilde{F}_t = aF_t$, $\tilde{P}_t = adP_t$, $\alpha = 1/(ac)$, $\beta = bd$, $\gamma = ag_P$, and $\kappa = ak$. When pollination occurs before herbivory, the rescaled densities are then governed by:

$$\tilde{F}_{t+1} = \frac{r_F \tilde{P}_t \tilde{F}_t^2}{\alpha \tilde{P}_t \tilde{F}_t^2 + (\beta \tilde{F}_t + \tilde{P}_t)(\tilde{F}_t + H_t)} \tag{9}$$

$$\tilde{P}_{t+1} = \frac{r_P \tilde{P}_t(\tilde{F} + \gamma)}{\tilde{P}_t + \tilde{F}_t + \gamma} \tag{10}$$

$$H_{t+1} = \frac{r_H H_t \tilde{F}_t}{\kappa H_t + \tilde{F}_t} \tag{11}$$

When herbivory occurs before pollination, they are governed by:

$$\tilde{F}_{t+1} = \frac{r_F \tilde{P}_t \tilde{F}_t^2}{\alpha \tilde{P}_t \tilde{F}_t^2 + \beta \tilde{F}_t^2 + \tilde{P}_t(\tilde{F}_t + H_t)} \tag{12}$$