



Modeling herbivore competition mediated by inducible changes in plant quality

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Competition between herbivorous insects often occurs as a trait mediated indirect effect mediated by inducible changes in plant quality rather than a direct effect mediated by plant biomass. While plant-mediated competition likely influences many herbivores, progress linking studies of plant-mediated competition in terrestrial phytophagous insects to longer-term consequences for herbivore communities has been elusive, and there is little relevant theory to guide this effort. We present simple models describing plant-mediated interactions between two herbivorous insects or other functionally equivalent organisms. These models consider general features of plant-mediated competition including specificity of elicitation by and effects on herbivores, positive and negative interactions among herbivores, competition independent of changes in plant biomass, and the existence of multiple relevant plant traits. Our analyses generate four important conclusions. First, herbivores competing strongly via only one plant quality phenotype exhibit a limited range of outcomes. These include coexistence and competitive exclusion of either herbivore, but do not include initial condition dependence. Second, when the outcome of competition is competitive exclusion, the herbivore that persists is the one that can do so under the highest inducible reductions in plant quality. Third, competition via more than one inducible phenotype can exhibit a wider range of outcomes including multiple equilibria and initial condition dependence. Finally, transient dynamics may not predict the eventual outcome of competition when changes in plant quality are slow relative to herbivore population growth, especially when herbivores compete through multiple phenotypes. We interpret our results in terms of competition outcomes reported in the literature, and suggest directions for the future empirical study of herbivore competition mediated by inducible changes in plant quality.

Trait mediated indirect interactions (or interaction modifications) are interactions where an indirect effect is mediated by changes in organismal traits (physical or behavioral) rather than by changes in density. There is growing evidence of the prevalence of trait-mediated indirect interactions from a variety of taxa (reviewed by Werner and Peacor 2003). While trait-mediated indirect interactions are still rarely included in models of multi-species interactions, theoretical and empirical studies suggest their potential importance in both short-term studies of communities and longer-term community dynamics and structure (Bolker et al. 2003, Werner and Peacor 2003).

Competition between phytophagous insects is emerging as an example where trait-mediated indirect interactions may have potentially widespread community effects. Such competition was once thought to be rare, but studies documenting negative interactions among phytophagous insects are increasingly common (reviewed by Denno et al. 1995, Kaplan and Denno 2007). Renewed interest in competition between herbivorous insects has been fueled in part by growth in our understanding of changes in host-plant quality induced by herbivore feeding (Karban and

Baldwin 1997, Walling 2000). The seeming prevalence of induced changes in plant quality suggests that competition between phytophagous insects is often occurring as a trait-mediated indirect effect (Ohgushi 2005, Kessler and Halitschke 2007). Competition studies include numerous cases of herbivore species influencing each other's performance through effects on the host plant, even when herbivores occupy the plant at different times (Harrison and Karban 1986, Viswanathan et al. 2007), or in different locations such as roots versus leaves (Kaplan et al. 2008). A wide variety of plant defenses and other traits can be influenced by herbivore damage, and plant responses may vary with the type of damage received (Denno et al. 1995, Karban and Baldwin 1997, Walling 2000, Ohgushi 2005, Kessler and Halitschke 2007). Effects of one herbivore on another can be due to the induction (Stout et al. 1998, Viswanathan et al. 2005, 2007, Kaplan et al. 2008) or suppression (Walling 2000, Zarate et al. 2007) of plant defensive traits, or due to changes in other traits such as nutritional content (Denno et al. 2000, Sandstrom et al. 2000). This complexity can result in specificity in the elicitation of plant responses (different herbivores cause different changes in the plant) and specificity in the effect of

induced plant changes on the herbivores (different herbivores may respond differently to the same plant traits).

A recent meta-analysis of studies addressing competition in phytophagous insects (Kaplan and Denno 2007) reinforces the argument that it differs markedly from competition described by traditional conceptual frameworks. In particular, Kaplan and Denno (2007) found that competition between phytophagous insects is 1) often highly asymmetrical (and may include facilitation when mediated by plant quality), 2) likely to occur between species that belong to different feeding guilds and that are spatially and/or temporally separated, and 3) often of the same magnitude regardless of the amount of plant biomass consumed. While these results deviate from expectations from traditional competition theory, they are consistent with the idea that competition among phytophagous insects is commonly a trait-mediated indirect effect of plant quality rather than quantity. Thus, availability or access to plant biomass may be largely unimportant in determining the outcome of competition, making the factors leading to the structure and dynamics of phytophagous insect communities somewhat cryptic.

Mathematical models of competition are abundant, and some of these have included trait-mediated indirect effects (reviewed by Bolker et al. 2003, Abrams and Nakajima 2007). However, most modern competition theory – including that investigating indirect effects – describes competition as being mediated by changes in the density or availability of a dynamic resource or prey (Armstrong and McGehee 1980, Tilman 1982, Abrams 2003, Amarasakare 2003, Abrams and Nakajima 2007). In contrast, a focus on biomass dynamics in terrestrial plant–insect systems is potentially counterproductive given that the strength of competition between phytophagous insects may frequently be independent from changes in biomass (Kaplan and Denno 2007). Rather, inducible changes in terrestrial plant phenotypes should be viewed as changes in host plant quality rather than changes in biomass quantity (Karban and Baldwin 1997, Agrawal 2005, Kaplan and Denno 2007), as has been done in limited modeling studies of effects of induced plant changes on the dynamics of single species of phytophagous insect herbivores (Edelstein-Keshet and Rausher 1989, Lundberg et al. 1994, Morris and Dwyer 1997, Underwood 1999, Underwood et al. 2005). To our knowledge, no modeling study of competition between phytophagous insects has explicitly considered effects of inducible terrestrial plant defenses. Changes in biomass available for consumption that are mediated by inducible defenses have been shown to have substantial effects on stability in models of aquatic food chains (Vos et al. 2004), yet we argue that a qualitatively different model structure is required to address inducible defenses in terrestrial plants, where multiple individual insects compete on the same plant over time versus systems where individual predators eat entire algal or zooplankton individuals. Without a well developed body of theory to draw upon, it is difficult to formulate specific predictions for particular systems (e.g. ‘species A and B will suppress species B over time’), or to design experiments appropriate for assessing the long-term consequences of plant-quality mediated competition.

In this paper we present simple models describing competition between two phytophagous insects or other

functionally equivalent organisms as a trait-mediated indirect interaction generated by inducible changes in plant quality. These models consider general features of plant quality mediated competition that have arisen in the empirical literature (e.g. specificity of elicitation and effects, positive and negative interactions, competition independent from resource biomass, and the existence of multiple relevant plant pathways or traits). These models should not be taken as descriptions of any particular phytophagous insect system. Instead, we have chosen to begin with minimally detailed models because this allows us to focus on general features and point to potential future directions for the field as opposed to making system-specific predictions; we expect it will be interesting to add additional details about mechanisms of induction and/or herbivore behavior to these basic models. With this study, we also hope to provide a framework for future theoretical and empirical work so that researchers can move towards predictions about the importance of plant quality-mediated competition for coexistence or the relative abundance of phytophagous insect competitors.

Model motivations and formulations

We model the population dynamics of two species of competing herbivores, H_1 and H_2 , feeding on a collection of plants or plant parts possessing inducible changes in quality. We define plant quality by modeling the levels of inducible phenotypes (or other changes in quality) I that affect herbivore reproduction and survival. We assume that populations are ‘well mixed’, i.e. we ignore within-population variation in induction (Edelstein-Keshet and Rausher 1989, Lundberg et al. 1994) and herbivore densities (i.e. aggregation, Underwood et al. 2005). Following the results of Kaplan and Denno (2007) discussed in the introduction, we do not model plant demography or biomass, focusing only on the average level that induced defenses or phenotype changes have achieved in the population. We revisit the potential implications of these assumptions in the discussion.

When two populations compete, both intra- and interspecific competition contribute to their dynamics. Many previous empirical studies have clearly established that phytophagous insects can have either positive or negative effects on the densities of other species (Kaplan and Denno 2007). Far fewer empirical studies have addressed both intra- and interspecific effects for competing herbivores in a single system, but again these studies indicate that interactions can range from simple (all intra- and interspecific effects negative, Denno et al. 2000) to complex (both positive and negative intra- and interspecific effects, Van Zandt and Agrawal 2004). Our models represent three scenarios inspired by interactions that have been observed empirically, although a complete description of these scenarios is not yet available for any particular system. Because Kaplan and Denno (2007) report that 32/243 of studies surveyed include facilitation mediated by inducible changes in plant quality, we include this feature in two of our models. The qualitative forms of these models are illustrated in Fig. 1 and their mathematical details are given below.

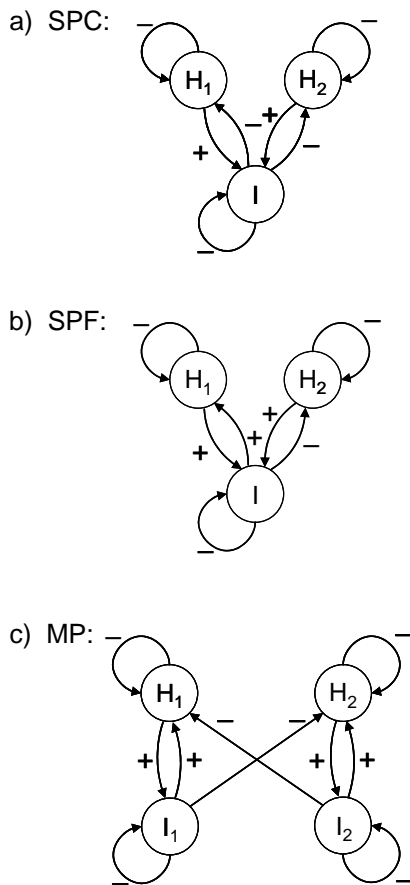


Figure 1. Diagrams illustrating interactions assumed in the three models. Arrows indicate direct causal effects; signs indicate whether these are positive or negative effects. (a) In the single phenotype competition (SPC) model, two herbivore species H_1 and H_2 compete indirectly by inducing changes in a quality phenotype I and each species has negative intraspecific competition. Denno et al. (2000) finds this pattern for two planthopper species feeding on *Spartina alterniflora* (intraspecific effects on both herbivores negative $(-, -)$ and interspecific effects on both herbivores negative $(-, -)$). (b) In the single phenotype facilitation (SPF) model, a competitor herbivore H_1 benefits from induced changes in plant quality, while a facilitator herbivore H_2 suffers. Viswanathan et al. (2005) finds a similar pattern for flea beetles *Psylliodes affinis* and tortoise beetles *Plagiometriona clavata* feeding on *Solanum dulcamara* (intraspecific effects $-, 0$ and interspecific effects $-, +$). (c) In the multiple phenotype (MP) model, each herbivore species elicits changes in independent induced plant quality phenotypes I_1 and I_2 . Herbivores benefit from increases in the phenotype they elicit, and suffer from increases in the phenotype elicited by their competitor. Van Zandt and Agrawal (2004) finds a similar pattern for weevils *Rhyssomatus lineaticollis* and monarch larvae *Danaus plexippus* feeding on *Asclepias syriaca* (intraspecific effects $+, +$ and interspecific effects $-, 0$). For the three empirical studies cited here, a ‘+’ indicates a significant positive effect at $p < 0.05$ (facilitation), a ‘-’ indicates a significant negative effect (competition) and ‘0’ indicates no significant effect.

Single phenotype competition (SPC) model

We begin with a simple model of a reciprocally negative plant-mediated competitive interaction (Fig. 1). Our model extends Lotka–Volterra competition such that competition

between two herbivore species is mediated indirectly by a single inducible defense or plant quality phenotype (Fig. 1a),

$$\begin{aligned} \frac{dH_1}{dt} &= r_1 H_1 \left(\frac{K_1 - H_1 - f_1(I)}{K_1} \right) \\ \frac{dH_2}{dt} &= r_2 H_2 \left(\frac{K_2 - H_2 - f_2(I)}{K_2} \right) \\ \frac{dI}{dt} &= \underbrace{\rho_1(I, H_1) + \rho_2(I, H_2)}_{\text{elicitation by herbivory and self-inhibition}} - \underbrace{\delta I}_{\text{induction decay}} \end{aligned} \quad (1)$$

The induced defense level could represent a single trait or the combined effects of several traits that, because of cross-talk (Karban and Baldwin 1997) or shared resource pools, act in concert and function as a single quality phenotype. In the absence of induced changes in plant quality, each herbivore population j grows logistically up to a carrying capacity K_j that is set by external factors for which there is no interspecific competition (e.g. intraspecific competition for oviposition or foraging sites; predation or parasitism). Induced defenses lower the population growth rate of species j with effect $f_j(I)$, and species j elicits increases in the induced defense (i.e. decreases in quality) at rate $\rho_j(I, H_j)$. Specificity of induction effect occurs when $f_1(I) \neq f_2(I)$ and specificity of elicitation occurs when $\rho_1(I, H_1)H_1^{-1} \neq \rho_2(I, H_2)H_2^{-1}$. Changes in induced defenses exhibit self-limitation, $\frac{\partial \rho_j}{\partial I} < 0$, such as would occur due to nutrient

limitation or autotoxicity (Baldwin and Callahan 1993), and decays at a constant per unit rate δ (e.g. as observed by Underwood 1998).

Single phenotype facilitation (SPF) model

Several studies report positive plant-mediated interspecific and intraspecific effects for some herbivores, often without describing the responsible mechanism (Karban and Baldwin 1997, Stout et al. 1998, Van Zandt and Agrawal 2004, Kaplan and Denno 2007), although facilitation by induced susceptibility to herbivory may be mediated by either chemical (Lu et al. 2004) or morphological changes (Utsumi and Ohgushi 2008) in the plant and by orienting behavior of the herbivore (Hitchner et al. 2008). Thus, we model an asymmetric interaction (Fig. 1b) where one herbivore species is facilitated with effect $g(I)$ from induced changes in the plant phenotype,

$$\frac{dH_1}{dt} = r_1 H_1 \left(\frac{K_1 - H_1 + g(I)}{K_1} \right) \quad (2)$$

The dynamics of herbivore H_2 and the induced quality level I are as described in Eq. 1. Changes in plant quality caused by H_1 have a negative effect on H_2 , so we refer to H_1 as the competitor herbivore. Since changes in plant quality caused by H_2 have a positive effect on H_1 , we refer to H_2 as the facilitator herbivore.

Multiple phenotype (MP) model

Plants may possess multiple induction pathways and quality phenotypes (e.g. secondary compounds, Walling 2000), and these phenotypes may have different effects on different

herbivore species (Karban and Baldwin 1997). For example, different herbivore species may induce alternative secondary compounds, and then respond differently to varying concentrations of these compounds. We therefore present a multiple phenotype model where we consider two species of herbivores that are each capable of eliciting the production of a separate phenotype (Fig. 1c). Our model reflects an empirical scenario described by Van Zandt and Agrawal (2004; Fig. 1c) where each induced phenotype change has a positive effect on the eliciting herbivore's density (i.e. facilitation) while having a negative effect on the density of the non-eliciting (competing) herbivore,

$$\begin{aligned} \frac{dH_1}{dt} &= r_1 H_1 \left(\frac{K_1 - H_1 - f_1(I_2) + g_1(I_1)}{K_1} \right) \\ \frac{dH_2}{dt} &= r_2 H_2 \left(\frac{K_2 - H_2 - f_2(I_1) + g_2(I_2)}{K_2} \right) \\ \frac{dI_1}{dt} &= \rho_1(I_1, H_1) - \delta_1 I_1 \\ \frac{dI_2}{dt} &= \rho_2(I_2, H_2) - \delta_2 I_2 \end{aligned} \quad (3)$$

We are assuming for simplicity that each herbivore can only directly elicit changes in its own beneficial induced phenotype and the induced phenotypes have no direct effects on one another at the level of the plant population (although 'cross-talk' could still occur at the level of individual plants). We also assume the same restrictions on functional forms as for Eq. 1 and 2, making this model a general model of which the SPC and SPF models are special cases. The links between the MP model and SPC and SPF models will allow us to explore which combinations of competitive and facilitative interactions tend to lead to behavior described by the simpler SPC and SPF models.

Analyses and results

We analyze the three models above with a focus on equilibrium outcomes in order to provide insights into how competition occurring as a trait-mediated indirect interaction resulting from induced changes in plant quality might influence long-term herbivore population dynamics and community structure. However, because of seasonal or stochastic environmental variation, ecological systems may often not attain equilibrium, and, even when they do, following herbivore dynamics over the generations required to approach equilibrium can be logistically difficult. Therefore we also present transient dynamics, which are most relevant to the results of the short-term experiments or highly variable systems common in the literature.

Equilibrium outcomes in the single phenotype competition (SPC) model

The SPC model exhibits three potential outcomes: extinction of H_1 , extinction of H_2 , and coexistence (Supplementary material Appendix 1). We explore these outcomes using a simple form of Eq. 1 where induction has different

strengths of effect on herbivore growth rates but herbivores do not differ in the strengths with which they induce changes in plant quality,

$$f_j(I) = \gamma_j I \quad \text{and} \quad \rho_j(I, H_j) = \begin{cases} (\alpha - \beta I) H_j & \text{for } I < \frac{\alpha}{\beta} \\ 0 & \text{for } I \geq \frac{\alpha}{\beta} \end{cases} \quad (4)$$

Here, γ_j is the per unit reduction in the growth rate of herbivore j caused by induction of defense or quality changes, α is the maximum per capita induced defense or quality change elicitation rate, and β is the per unit reduction in the elicitation rate due to plant self-limitation. This simplification increases the ease of analysis, yet our qualitative results are general for models in the form of Eq. 1 (Supplementary material Appendix 1).

We examine these three outcomes using the zero isoclines of the system. Fig. 2 presents examples of isoclines for each observed outcome of competition; isoclines for each herbivore are presented unconventionally assuming that it has equilibrated with induced changes in quality for simplicity. Results inferred from isoclines are identical to those yielded from traditional invasion analysis (Supplementary material Appendix 1).

Indirect density-dependence resulting from feedbacks between induced changes in quality and the herbivore populations causes the isoclines to be concave towards the origin. For comparison, two-species Lotka-Volterra competition with linear competition coefficients possesses linear isoclines, while similar equations with density-dependent competition coefficients typically possess either concave or convex isoclines (Ayala et al. 1973). The isocline of each herbivore j intersects its own axis at its equilibrium in the absence of the other herbivore species i ,

$$H_j^* |_{H_i=0} = K_j - \gamma_j I^* = \frac{1}{2\beta} \left\{ \beta K_j - \alpha \gamma_j - \delta + \sqrt{(-\beta K_j + \alpha \gamma_j + \delta)^2 + 4\delta \beta K_j} \right\} \quad (5)$$

and intersects the axis of the other herbivore i when

$$H_j^* = 0 \quad \text{and} \quad H_i^* = \frac{\delta K_j}{\alpha \gamma_j - \beta K_j} \quad (6)$$

Equation 6 is true when $\alpha \gamma_j > \beta K_j$, i.e. induced changes in quality must possess the ability to drive H_j extinct (Fig. 2a). If $\alpha \gamma_j < \beta K_j$ induced changes in quality can not reach a high enough level to drive H_j extinct – even when the competing herbivore is held at infinitely large densities – and the H_j isocline never crosses the competing herbivore species' axis (Fig. 2b).

We use these results to delineate conditions that lead to each possible outcome of the SPC model. When $\alpha \gamma_j > \beta K_j$ for $j = 1, 2$, the conditions leading to the different outcomes are as follows:

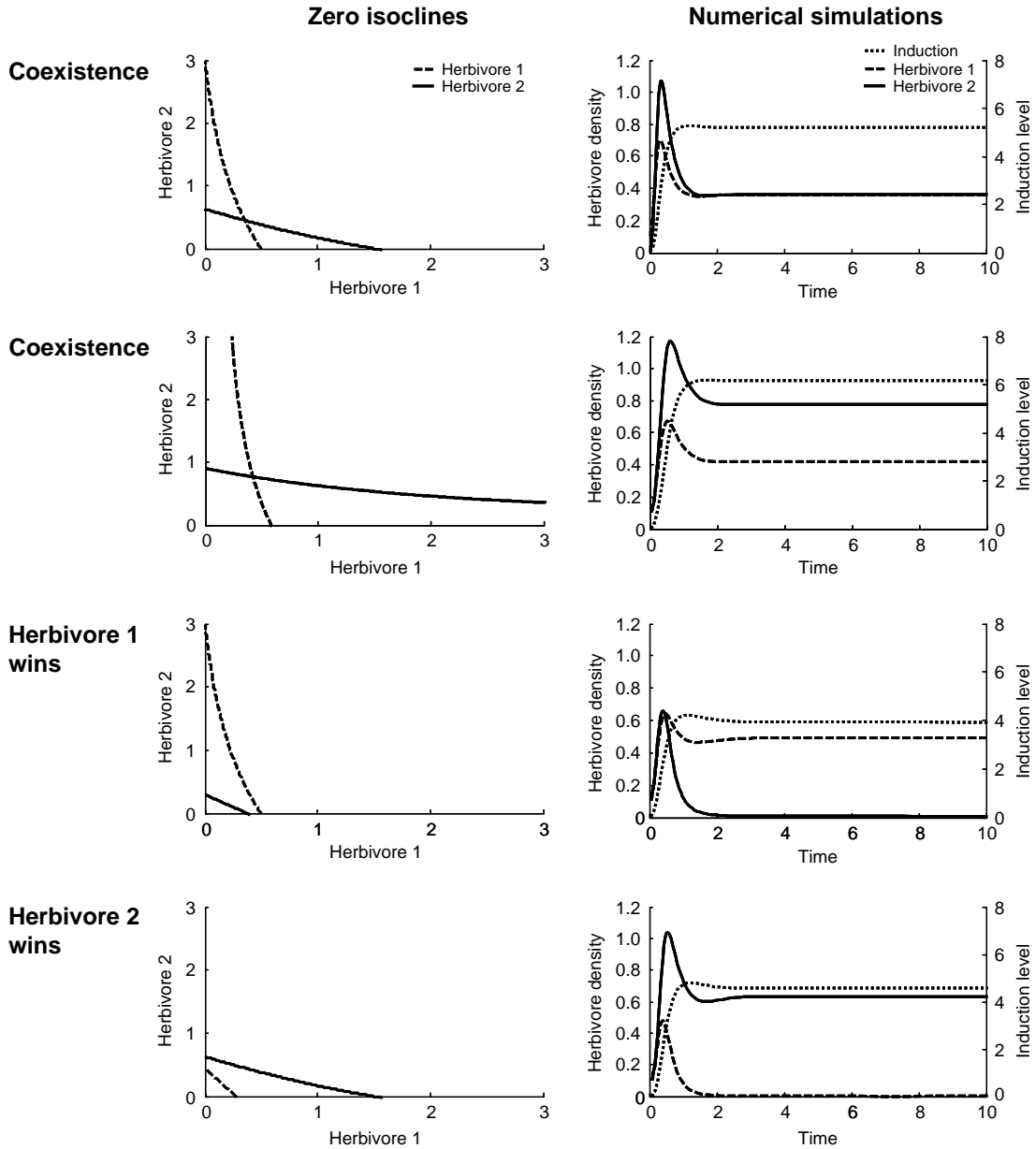


Figure 2. Examples of coexistence and extinction outcomes for the SPC model. Plots on the left are isoclines that represent the combination of herbivore and levels of induced plant quality changes where the density of herbivore do not change ($\frac{dI}{dt} = 0$ and $\frac{dH_j}{dt} = 0$, $j = 1, 2$). Plots on the right present numerical simulations of the outcome illustrated to its left. Parameters used for the first coexistence scenario where $\alpha\gamma_j > \beta K_j$, $j = 1, 2$: $\alpha = 10$; $\beta = 1$; $d = 0.75$; $r_1 = 10$; $r_2 = 10$; $K_1 = 1$; $K_2 = 2$; $\gamma_1 = 0.125$; $\gamma_2 = 0.3$. Parameters used for the second coexistence scenario where $\alpha\gamma_j < \beta K_j$, $j = 1, 2$: same as above; $\gamma_1 = 0.095$; $\gamma_2 = 0.199$. Parameters used for H_2 extinction scenario: same as first coexistence scenario; $\gamma_2 = 0.6$. Parameters used for H_1 extinction scenario: same as first coexistence scenario; $\gamma_1 = 0.27$.

- 1) Both herbivores coexist when $\frac{\delta K_1}{\alpha\gamma_1 - \beta K_1} > H_2^*|_{H_1=0}$ and $\frac{\delta K_2}{\alpha\gamma_2 - \beta K_2} > H_1^*|_{H_2=0}$
- 2) H_1 excludes H_2 when $\frac{\delta K_1}{\alpha\gamma_1 - \beta K_1} > H_2^*|_{H_1=0}$ and $\frac{\delta K_2}{\alpha\gamma_2 - \beta K_2} < H_1^*|_{H_2=0}$
- 3) H_2 excludes H_1 when $\frac{\delta K_1}{\alpha\gamma_1 - \beta K_1} < H_2^*|_{H_1=0}$ and $\frac{\delta K_2}{\alpha\gamma_2 - \beta K_2} > H_1^*|_{H_2=0}$
- (7)
- Coexistence is always guaranteed when $\alpha\gamma_1 < \beta K_1$ and $\alpha\gamma_2 < \beta K_2$. If $\alpha\gamma_j < \beta K_j$ but $\alpha\gamma_i > \beta K_i$, species i will be able to coexist with species j when

$$\frac{\delta K_i}{\alpha \gamma_i - \beta K_i} > H_j^*|_{H_i=0} \quad (8)$$

While the results in Eq. 7 and 8 appear cumbersome, their ecological interpretation is straightforward. An herbivore can be driven extinct by induced defenses or other changes in plant quality when the quality change required to do so is less than that generated by the competing herbivore at its equilibrium in isolation. The herbivore that wins in competition is able to persist at higher densities in the presence of induced defenses or other changes in plant quality. Unsurprisingly, these results are similar to the coexistence criteria from Lotka–Volterra competition; namely, that species must compete more strongly intra-specifically than inter-specifically in order to coexist.

In contrast to Lotka–Volterra competition, the possible equilibrium outcomes in the SPC model are never dependent on initial conditions. Initial condition dependence arises in Lotka–Volterra competition when both species compete inter-specifically more strongly than intra-specifically. These dynamics can not occur in the SPC model because competition is mediated by dynamic feedbacks between the two herbivore competitors and induction of changes in plant quality. At least one species therefore competes more strongly with itself over a range of densities: as its own density goes up, the herbivore causes concomitant increases in induced defenses or other changes in plant quality. These results do not depend on the precise functions defining the induction effect, f_j , and induction elicitation, ρ_j , in Eq. 1, as long as the signs of these functions lead to the relationships pictured in Fig. 1. Changing the functional forms can however alter the relative frequency of the different outcomes, which we

illustrate using an example in Supplementary material Appendix 2.

Equilibrium outcomes in the single phenotype facilitation (SPF) model

Since the competitor species benefits from species specific induced increases in plant quality, there are only two outcomes for the SPF model Eq. 2: coexistence, and extinction of the facilitator species.

Consider Eq. 2 and 4 where the competitor receives a linear benefit from species specific increases in plant quality, $g(I) = \phi I$ (9)

The isocline of the competitor intersects its own axis at the equilibrium density

$$H_1^*|_{H_2=0} = K_1 + \phi I^* = \frac{1}{2\beta} \left\{ \beta K_1 + \alpha \phi - \delta + \sqrt{(-\beta K_1 - \alpha \phi + \delta)^2 + 4\delta\beta K_1} \right\} \quad (10)$$

and trends away from the facilitator axis as the density of the facilitator increases (Fig. 3); the competitor has a higher equilibrium density in the presence of the facilitator species than in its absence. The intersection points of the facilitator's isocline are the same as in the SPC model. Thus, the facilitator will coexist with the competitor when

$$\alpha \gamma_2 < \beta K_2 \quad \text{or} \quad \frac{\delta K_2}{\alpha \gamma_2 - \beta K_2} > H_1^*|_{H_2=0} \quad \text{and} \quad \alpha \gamma_2 > \beta K_2, \quad (11)$$

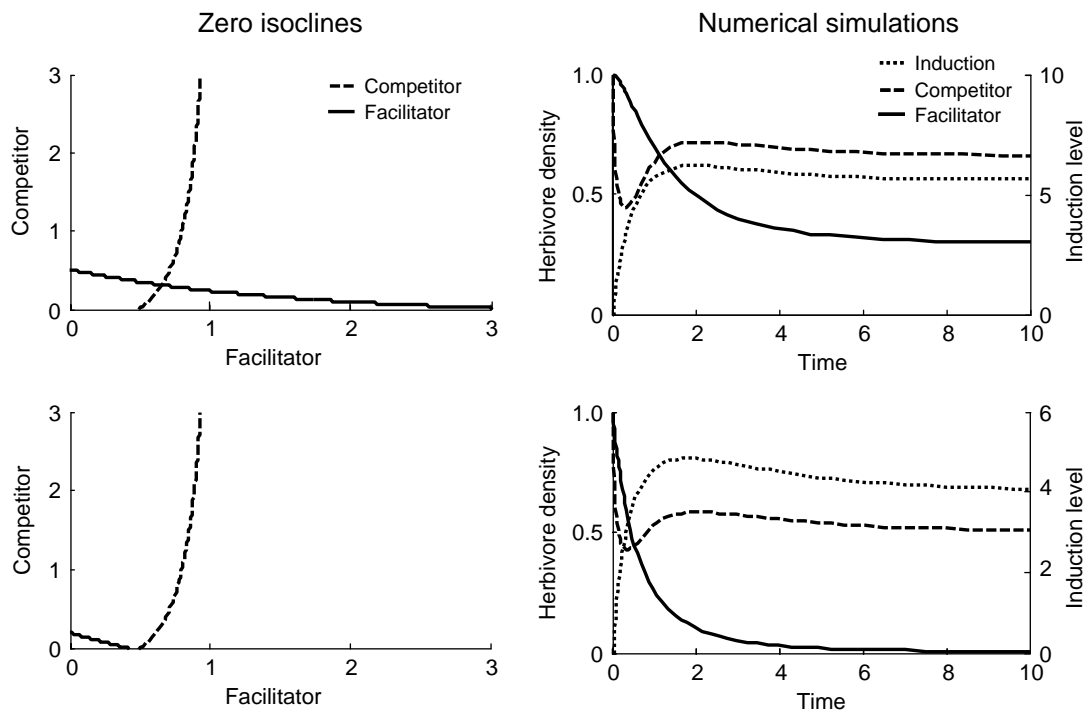


Figure 3. Examples of coexistence and extinction outcomes for the facilitation model. Parameters used for the coexistence scenario: $\alpha = 10$, $\beta = 1$, $\delta = 0.75$, $r_1 = 1$, $r_2 = 1$, $K_1 = 0.1$, $K_2 = 1$, $\gamma_1 = 0.1$, $\gamma_2 = 0.125$. Parameters used for competitor extinction scenario: same as above, $K_2 = 0.4$.

and otherwise goes extinct. The interpretation of this criterion is similar to that of the competition model; the facilitator is able to coexist when the induced change in plant quality required to drive it extinct is larger than the change in plant quality elicited by the competitor when the facilitator is not present. These qualitative results again hold for other versions of the SPF model as long as the signs of the induced change in plant quality and competition functions are similar among models.

Equilibrium outcomes in the multiple phenotype (MP) model

The MP model exhibits a much broader array of dynamical behaviors than the SPC and SPF models. Numerical simulations demonstrate that the MP model possesses four possible behaviors: extinction of H_1 , extinction of H_2 , coexistence, and extinction or coexistence determined by initial conditions. This last condition is not possible in the SPC or SPF models. For ease of comparison, we adopt the same functional forms as Eq. 4 and 9.

Isoclines of the MP model are no longer monotonic because of the complex feedbacks between the two herbivores and induced plant quality phenotypes. The isoclines are composed of two branches that join at a singularity and are no longer monotonic when this point is positive (Fig. 4). The shapes of these isoclines can allow for multiple crossing points that correspond to equilibria under many parameter values. Although these equilibria are not necessarily all stable, more than one typically is, leading to initial dependence in the outcome. This scenario shares many similarities with the initial condition dependent outcome in simple Lotka–Volterra competition, where strong interspecific competition relative to intraspecific competition de-stabilizes the coexistence equilibrium. However, unlike Lotka–Volterra competition, all observable outcomes of competition – extinction of H_1 or H_2 and coexistence – can be possible under the exact same parameter values in the MP model as a result of the effects of herbivore facilitation by induced changes in plant quality (Fig. 4).

Despite their complex shape, the herbivore isoclines still intersect their own and their competitor's axes at only one point each,

$$H_j^*|_{H_i=0} = K_j + \phi_j I_j^* = \frac{1}{2\beta_j} \left\{ \beta_j K_j + \alpha_j \phi_j - \delta_j + \sqrt{(-\beta_j K_j - \alpha_j \phi_j + \delta_j)^2 + 4\delta_j \beta_j K_j} \right\} \quad (12)$$

and

$$H_j^* = 0 \quad \text{when} \quad H_i^* = \frac{\delta_i K_j}{\alpha_i \gamma_j - \beta_i K_j} \quad \text{and} \quad \alpha_i \gamma_j > \beta_i K_j \quad (13)$$

The intersection of H_j 's isocline with H_i 's axis is now determined by the effects on H_j of the phenotype induced by H_i . The beneficial effects of I_j on H_j do not appear in Eq. 13 because H_j does not elicit induced changes in plant quality I_j when at zero density. However, H_j will elicit I_j even at small densities; this discrepancy in dynamics when

H_j is zero or small has important consequences for predicting the outcome of competition. Either herbivore H_j is guaranteed to persist when

$$\alpha_i \gamma_j < \beta_i K_j \quad \text{or} \quad \frac{\delta_i K_j}{\alpha_i \gamma_j - \beta_i K_j} > H_i^*|_{H_i=0} \quad \text{and} \quad \alpha_i \gamma_j > \beta_i K_j \quad (14)$$

These conditions have interpretations that are similar to those for the SPC and SPF models. In contrast with the SPC and SPF models, however, parameter combinations in

the region $\frac{\delta_i K_j}{\alpha_i \gamma_j - \beta_i K_j} < H_i^*|_{H_i=0}$ when $\alpha_i \gamma_j > \beta_i K_j$ do not

always lead to extinction of H_j . Rather, the fate of the herbivore population may be determined by initial conditions in this parameter range. When initial condition dependence is possible, an herbivore H_j will persist if its initial density is high enough to elicit a large enough level of its beneficial phenotype in the face of increases in the detrimental phenotype, $\gamma_j I_j < K_j + \phi_j I_i$. This can occur even when H_i is capable of achieving equilibrium densities that can drive H_j extinct. Because H_j can exhibit negative population growth at low densities and positive growth at higher densities, initial condition dependence manifests as an apparent Allee effect whose strength is dependent on both the initial density of the competing herbivore and the levels of induction already present.

As already stated, the initial condition dependence in competition outcomes occurs when interspecific competition is strong relative to intraspecific density dependence (Fig. 5). This occurs, for example, when effects of inducible changes in plant quality γ or elicitation rates α of these changes are high, or when herbivore carrying capacities K or self-inhibition β or decay δ in induced changes in plant quality are small (results for β and δ not shown). When plant-mediated competition becomes strong, coexistence outcomes are replaced by outcomes determined by initial conditions. Under very strong plant-mediated competition, facilitation can no longer 'rescue' small populations in the face of strong interspecific competition. As a result, initial condition dependent outcomes no longer include coexistence equilibria, meaning that one competitor will always eventually win in competition. Increasing the carry capacities of both herbivores weakens interspecific competition relative to intraspecific processes and increases the potential for coexistence. Unsurprisingly, strong asymmetries in model parameters that translate into strong asymmetries in effects of induced changes in plant quality on interspecific competition tend to promote competitive exclusion of the herbivore more negatively affected by plant quality changes.

The primary effect of facilitation by changes in plant quality ϕ is to promote coexistence. When the results of competition are dependent on initial conditions, facilitation increases the combination of parameters where coexistence outcomes co-occur with exclusion outcomes. This effect occurs even when interspecific competition is otherwise highly asymmetric. Facilitation is not required for initial condition dependence in the outcome of competition, nor is it required for the existence of initial condition dependent outcomes that include both coexistence and exclusion

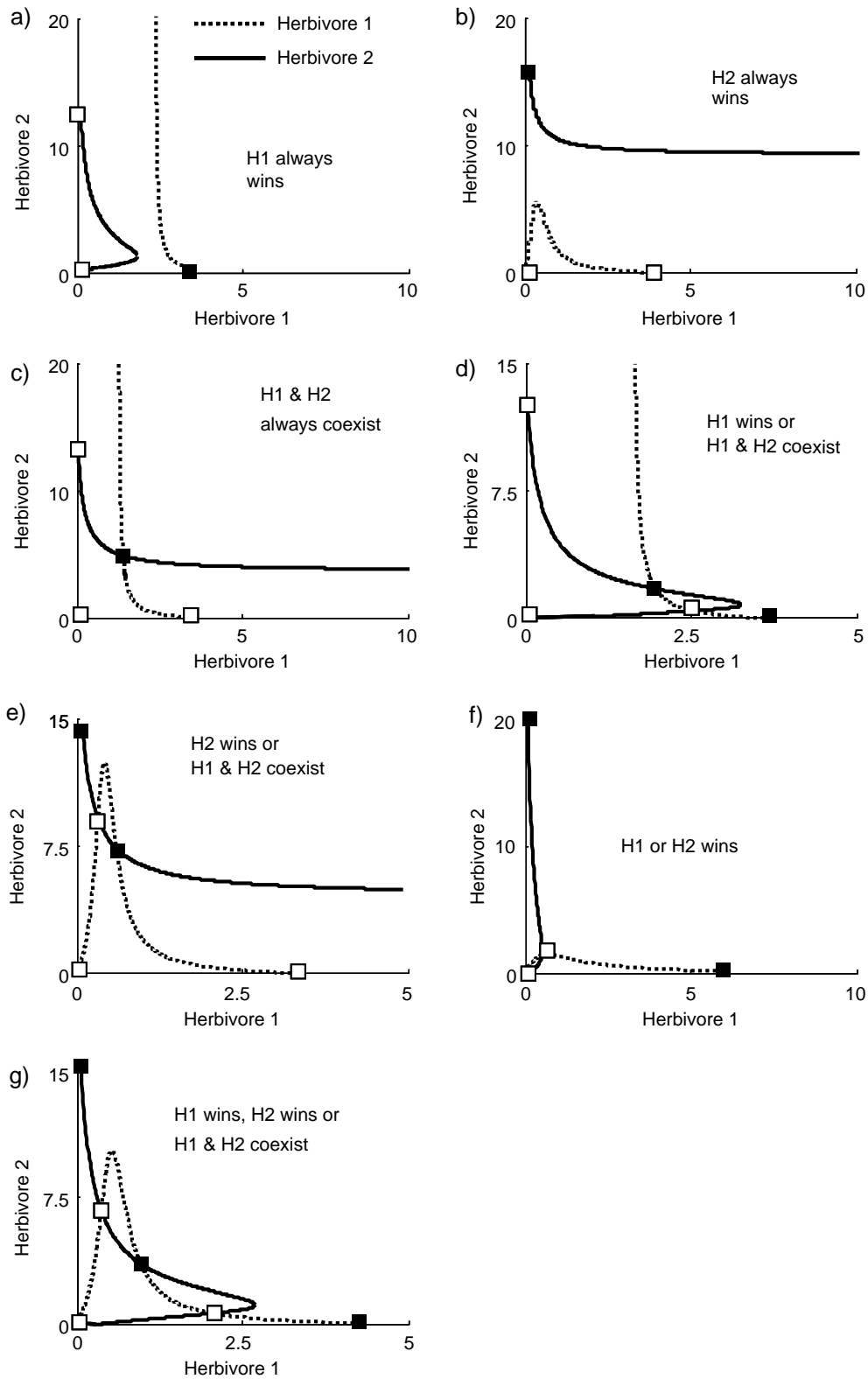


Figure 4. Examples of herbivore isoclines in the MP model. Closed squares (■) indicate stable equilibria while open squares (□) indicate unstable ones. Except where indicated, parameter values are $\alpha_1 = 75$, $\alpha_2 = 100$, $\beta_1 = 5$, $\beta_2 = 3$, $\delta_1 = 1$, $\delta_2 = 1$, $r_1 = 1$, $r_2 = 1$, $K_1 = 2$, $K_2 = 9$, $\gamma_1 = 0.15$, $\gamma_2 = 0.65$, $\varphi_1 = 0.1$, $\varphi_2 = 0.3$. (a) $\alpha_1 = 90$; $\alpha_2 = 30$. (b) $\alpha_1 = 50$, $\alpha_2 = 70$, $K_1 = 3$. (c) $\alpha_1 = 70$, $\alpha_2 = 40$. (d) $\alpha_1 = 90$, $\alpha_2 = 40$. (e) $\alpha_1 = 73$, $\alpha_2 = 53$. (f) $\alpha_1 = 180$, $\alpha_2 = 120$, $K_1 = 2.7$, $K_2 = 8.0$. (g) $\alpha_1 = 105$, $\alpha_2 = 62$.

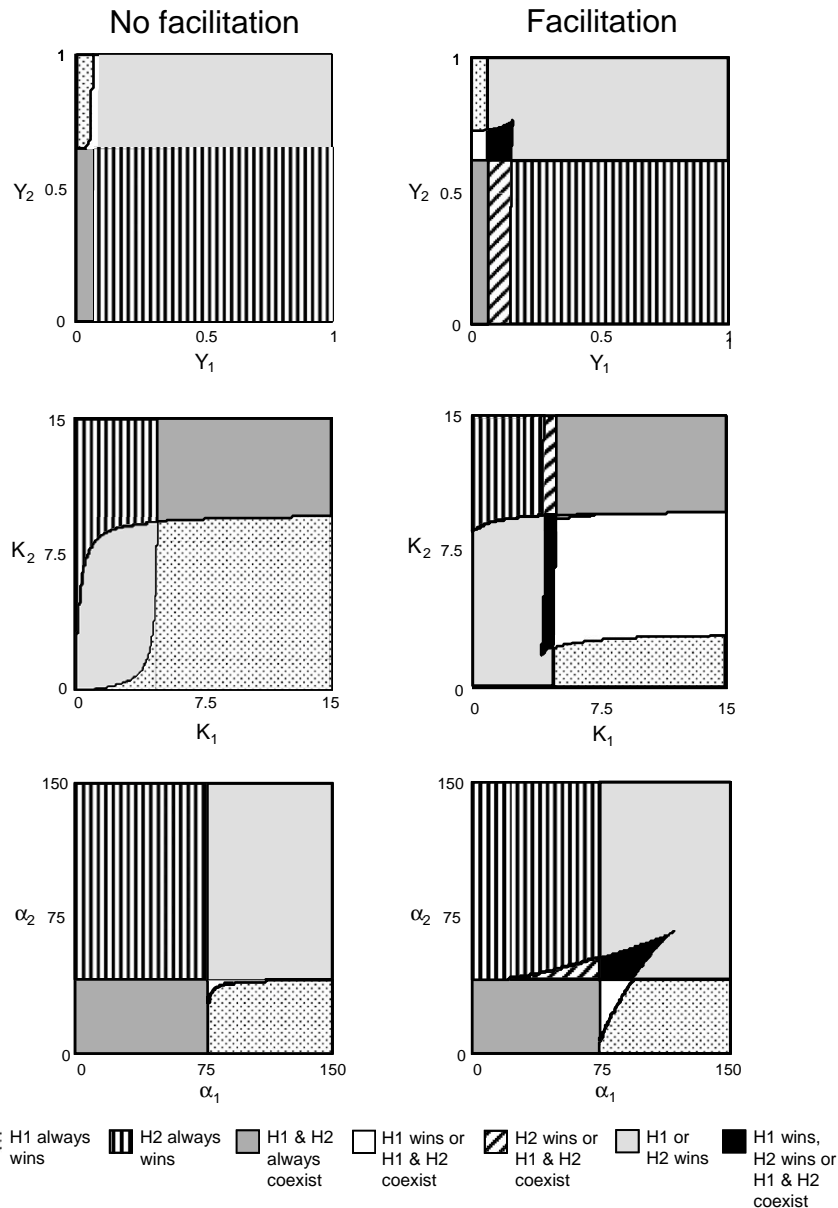


Figure 5. Potential outcomes of competition as functions of model parameters. For results in the ‘No facilitation’ column, $\phi_1 = \phi_2 = 0$, while for those in the ‘Facilitation’ column, $\phi_1 = 0.3$ and $\phi_2 = 0.1$ for variation in γ while $\phi_1 = 0.1$ and $\phi_2 = 0.3$ for variation in K and α . Other parameters are $\alpha_1 = 75$, $\alpha_2 = 100$, $\beta_1 = 5$, $\beta_2 = 3$, $\delta_1 = 1$, $\delta_2 = 1$, $r_1 = 1$, $r_2 = 1$, $K_1 = 2$, $K_2 = 9$, $\gamma_1 = 0.15$, $\gamma_2 = 0.65$, except where indicated.

outcomes (Fig. 5). However, the latter scenario is much more likely when facilitation is present.

Transient dynamics

Transient dynamics of models like ours that contain multiple interacting populations can be highly irregular and depend strongly on initial conditions. Methods for characterizing transient dynamics independent of initial conditions exist (Neubert and Caswell 1997), yet the result is a ‘worst case’ scenario that may only result from unrealistic parameter combinations. Instead, we opt to illustrate transient dynamics using numerical simulations where initial conditions reflect scenarios typically encoun-

tered in empirical settings. Namely, we start all trajectories with plants having expressed no inducible changes in plant quality (i.e. $I = 0$) to mimic dynamics at the beginning of a growing season or experimental introductions on naïve plants. In addition, we present our results unconventionally using two-dimensional phase plots of the herbivores in the SPC, SPF and MP models to mimic empirical scenarios where herbivore densities, but not plant quality levels, are observed or manipulated (Fig. 6).

Induced plant quality levels and herbivore populations in the three models can ‘overshoot’ their equilibria, and these overshoots tend to occur when the dynamics of induced changes in plant quality range from slower to slightly faster than the dynamics of the herbivores (Fig. 6a–c, see also Fig. 2–3). Transient overshoots can lead to a substantial

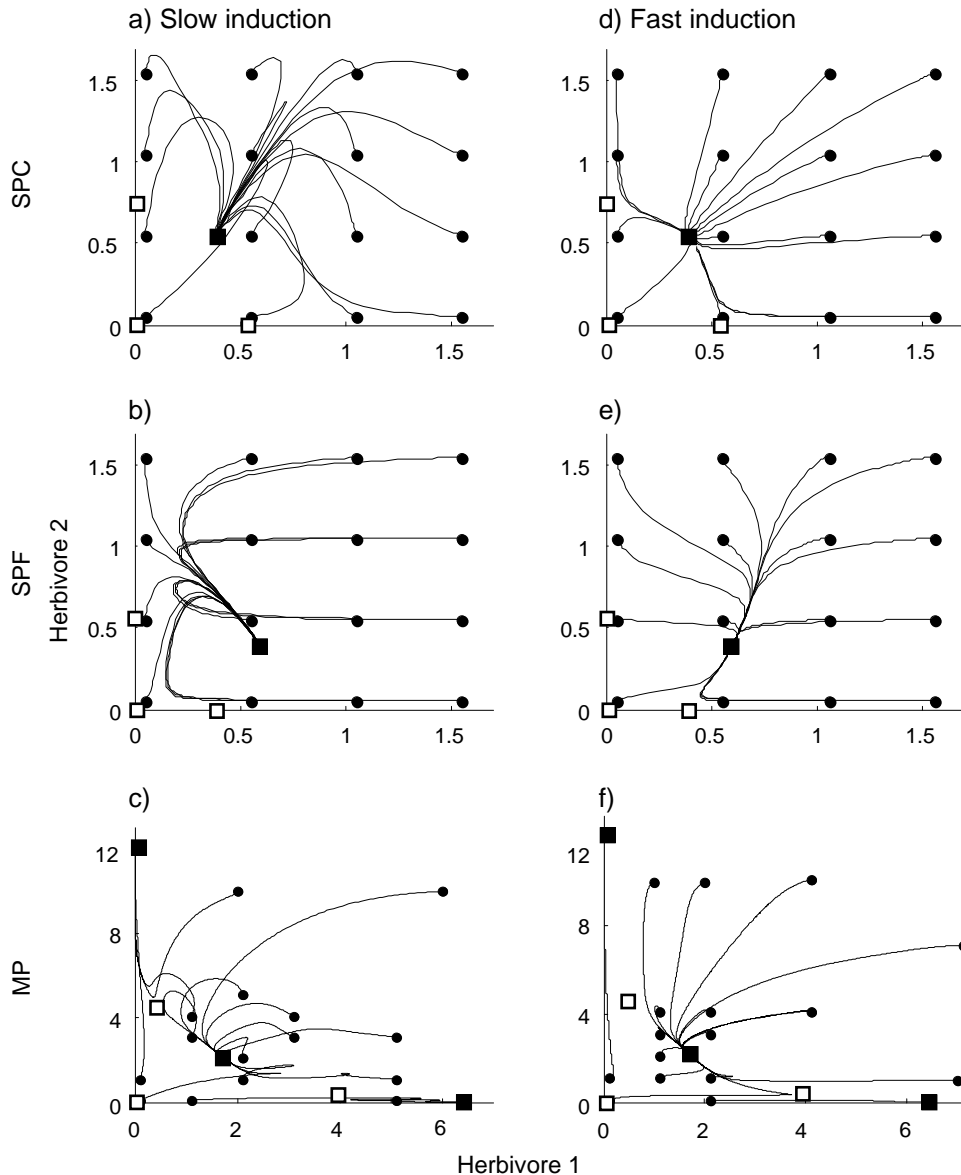


Figure 6. Phase plots illustrating transient dynamics of the herbivores proceeding on plants that possess no initial induced changes in plant quality, $I_{i,j}(0) = 0$; because the system is viewed in two dimensions only, the dynamics of changes in plant quality are not shown. Dots (●) indicate initial herbivore densities, closed squares (■) stable equilibria, and open squares (□) unstable equilibria. (a, b, c) Plant quality and herbivore dynamics proceed at similar time scales. SPC model: $\alpha = 10$, $\beta = 1$, $\delta = 1$, $r_1 = 10$, $r_2 = 10$, $K_1 = 1$, $K_2 = 2$, $\gamma_1 = 0.125$, $\gamma_2 = 0.3$. SPF model: $\alpha = 10$, $\beta = 1$, $\delta = 1$, $r_1 = 10$, $r_2 = 10$, $K_1 = 0.1$, $K_2 = 1$, $\gamma_1 = 0.1$, $\gamma_2 = 0.125$. MP model: $\alpha_1 = 75$, $\alpha_2 = 100$, $\beta_1 = 5$, $\beta_2 = 3$, $\delta_1 = 1$, $\delta_2 = 1$, $r_1 = 10$, $r_2 = 10$, $K_1 = 2$, $K_2 = 9$, $\gamma_1 = 0.15$, $\gamma_2 = 0.72$, $\varphi_1 = 0.3$, $\varphi_2 = 0.1$. (d, e, f) The dynamics of inducible changes in plant quality are much faster than herbivore dynamics. SPC and SPF model: $r_1 = 0.01$, $r_2 = 0.01$, other parameters as in (a) and (b). MP: $r_1 = 1.0$, $r_2 = 1.0$, other parameters as in (c).

mismatch between the initial and near-equilibrium trajectories of the herbivore populations because of a transient ‘escape’ from the slowly increasing effects of induced changes in plant quality; such transient ‘escapes’ are not possible if inducible changes in plant quality are much faster than herbivore dynamics (Fig. 6d–f). Furthermore, trajectories originating from different initial herbivore densities may cross when induction dynamics are slow; these different trajectories proceed from points with similar combinations of herbivore densities but different levels of plant quality. In practice, this could cause the effects of competition on herbivore densities to appear highly variable

if changes in plant quality are unknown: herbivore dynamics may behave differently among observations even when the starting densities in each observation are the same. While these results are not surprising from a dynamical systems perspective, we use them to illustrate the potential for competitive dynamics between herbivores that are mediated indirectly by inducible changes in plant quality to appear variable or unpredictable when plant quality dynamics are not anticipated.

Multiple equilibria in the MP model can elongate the transient phase of dynamics relative to the SPC and SPF models and can cause herbivore densities to be quite

variable before eventually approaching equilibrium (Fig. 6c). Unstable equilibria can attract herbivore population densities to their vicinity before the trajectories proceed on towards their final, stable equilibrium, a result that can also be observed in traditional Lotka–Volterra competition (Hastings 2004). Again, this transient effect is strongest when inducible changes in plant quality are slow. Extensive simulations suggest that unstable equilibria have less effect and initial condition dependence is less frequent when induction responses are fast relative to herbivore dynamics (Fig. 6f), although this pattern is not universal.

Discussion

Interactions among organisms may commonly be trait mediated indirect interactions, i.e. mediated by changes in behavior or other phenotypes rather than density. Recent research has shown that competition between phytophagous insects indirectly mediated by inducible changes in plant quality traits is common and could be an important factor in structuring herbivore communities (Denno et al. 1995, Agrawal 2005, Ohgushi 2005, Kaplan and Denno 2007, Kessler and Halitschke 2007). The majority of relevant studies to date have focused on documenting the occurrence of competition mediated by plant quality traits; explicit connections between short-term effects of trait-mediated indirect competition and the long-term population and community consequences are still lacking in terrestrial plant–herbivore systems (although links between inducible defenses and outcomes of competition have been demonstrated in aquatic systems, van der Stap 2008). As a step towards understanding the long-term consequences of indirect plant-mediated competition, and in hopes of providing guidance for future empirical studies, we have presented a set of models that encapsulate the basic forms of plant-quality mediated competition documented in the literature. Our analyses of these models generate four obvious results: (1) herbivores that compete via one plant quality phenotype exhibit a limited range of outcomes that does not include initial condition dependence; (2) when the outcome of competition is competitive exclusion, the herbivore that persists is the one that can do so under the highest inducible reductions in plant quality; (3) competition via multiple phenotypes can exhibit a wide range of outcomes which includes initial condition dependence when interspecific competition is strong relative to intraspecific density dependence; and (4) transient dynamics may not predict the eventual outcome of competition when changes in plant quality are slow relative to herbivore population growth, especially when multiple equilibria are present.

Our models of plant quality mediated competition share many similarities with more traditional models of consumer–resource interactions in addition to Lotka–Volterra competition theory. In particular, models of apparent competition characterize interactions where prey species have negative reciprocal effects mediated through the densities of a shared natural enemy (Holt et al. 1994). The theory of apparent competition states that shared predation only allows one prey species to persist whose population can grow under the highest predation pressure.

This is similar to our result that the herbivore that persists under the highest levels of negative inducible changes in plant quality wins when the outcome of competition is competitive exclusion. However, herbivore coexistence is possible in our models because of self-limitation of inducible changes in plant quality; such intraspecific density-dependent regulation of the predator is typically not present in models of apparent competition. Our inclusion of plant self-limitation is justified by biological reality, as physiological or morphological limits to inducible changes in plant quality are likely widespread (Baldwin and Callahan 1993). In other contexts, inducible traits that reduce consumption tend to stabilize consumer–resource interactions (Vos et al. 2004, but see Lundberg et al. 1994, Underwood 1999) while, as we show, multiple defensive phenotypes can lead to multiple equilibria and initial condition dependence in the outcome of competition (Ramos-Jiliberto et al. 2008). Facilitation by inducible changes in plant quality strengthens this effect by increasing the region of parameter space corresponding to initial condition dependence and adding the possibility of coexistence and competitive exclusion outcomes co-occurring under the same parameter combinations (Fig. 5). However, it is the presence of multiple induced phenotypes, not facilitation, which leads to initial condition dependence (Fig. 2, 3, 5).

Our results suggest that transient dynamics of herbivores competing via changes in plant quality may often not reflect longer-term dynamics, and thus results of short-term experiments may not reflect the eventual outcome of competition. Transient dynamics are increasingly recognized as important features of ecological interactions (Hastings 2004) because ecological systems may rarely reach equilibrium due to temporal environmental variation such as seasonality. Those mediated by inducible changes in plant quality are likely no exception. Inducible defenses in plants, for example, can take several hours to days to employ (Karban and Baldwin 1997, Underwood 1998). While this is shorter than the typical herbivore generation time, delayed changes spanning several herbivore generations have also been documented (Haukioja 1990), and results from our modeling suggest that competition outcomes in these types of systems may only be evident after multiple generations. Our MP model suggests that competition mediated by multiple independent plant quality traits is particularly likely to show mismatches between short- and long-term dynamics (Fig. 6). Experiments that are too short to capture the full effects of induced changes in plant quality on competing herbivore populations could provide misleading results, especially if herbivore populations initially grow away from equilibrium outcomes that include low densities or exclusion of one of the herbivores. Experiments started with different induction levels could also produce strikingly different short-term outcomes, even if initiated with similar herbivore densities (Fig. 6). This result, as well as the potential for long transients, is a direct consequence of the high dimensionality of the system introduced by including dynamic plant quality traits. While our results pertaining to transient dynamics are not theoretically novel, they do highlight that models of phytophagous insect competition focused solely on density mediated competition, as opposed to including trait

mediated indirect effects, exclude potentially important dynamics.

Field experiments have shown that the outcome of plant-mediated competition can differ dramatically among replicates or years (Van Zandt and Agrawal 2004). Results of our models, particularly the MP model, suggest that this could be partially due to the internal dynamics of plant-mediated competition, which may be particularly sensitive to initial conditions. Sensitivity of plant quality phenotypes can strongly depend on the identity of the initial colonizing herbivore, which in turn strongly effects the subsequent distribution and abundance of other herbivore competitors (Viswanathan et al. 2005, 2007). Thus, for plant responses mediated by multiple phenotypes, relatively small differences in herbivore densities at the beginning of each season could lead to quite different results due to sensitivity to initial conditions. In addition, changes in herbivore growth or plant quality could also change competitive dominance due to shifts in parameter values that change the number of potential outcomes, the effects of which could be exacerbated by environmental variability. Temporal variability affecting plant demography, biomass, or quality could hypothetically work to 'reset' the system with unpredictable starting densities of herbivores in different growing seasons, or cause herbivore growth rates and plant growing conditions to change, while spatial variability in plant quantity or quality could create refuges for inferior competitors (Amarasekare 2003).

Our models have been constructed to explore general features of indirect plant-quality mediated competition in phytophagous insects that have been extensively described in the empirical literature. As such, they do not specify the exact mechanisms by which herbivores are affected by inducible changes in plant quality. Plant quality may affect herbivores in a number of ways (reviewed by Karban and Baldwin 1997, Walling 2000), including changes in fecundity, changes in survival rates reflecting changes in food quality, toxic compounds, or exposure to predators, and changes in development time due to reduced consumption or assimilation of plant biomass. While our models highlight results that are relevant to many systems, generating predictions for any particular system influenced by trait-mediated indirect interactions will require models that include greater mechanistic detail (Bolker et al. 2003). Such detail may potentially include the biochemical and biomass components that compose 'plant quality' as well as the factors responsible for intraspecific density dependence (i.e. the carrying capacity). Physiologically-structured models can be used to quantify the effects of different plant-quality components and on herbivore growth, survival, and reproduction in a way that links with population dynamics (Kooijman 2000). While most studies to date show competition occurs without measurable effects of plant biomass changes (Kaplan and Denno 2007), there are undoubtedly situations where plant biomass does play an important role (Morris 1997). Integrating inducible traits that reduce herbivore consumption of plant biomass into our framework is straightforward, although their effects could be quite substantial if herbivore densities respond strongly to both plant biomass and plant quality (Abbott et al. 2008).

Despite their generality, the structure of our models highlights three basic requirements for empirical experiments to be able to address the longer-term consequences of plant-mediated competition. First, and trivially, experiments must estimate effects of both competitors on each other (reciprocal effects). Many competition experiments focus on effects of one species on another (Kaplan and Denno 2007), but given the potential for feedbacks this is clearly not sufficient for determining long term consequences for either species. Second, experiments should measure the strength of competitive effects, not just the direction of statistically significant differences between competition and no-competition treatments (Inouye 2001). For example, even in the simple case where competition is driven by a single inducible plant phenotype (SPC model), with relatively fast changes in plant quality, competition can lead to one of two outcomes: coexistence or eventual extinction of one of the herbivores, regardless of initial densities (Fig. 2). Experiments that only demonstrate the sign of competitive effects cannot distinguish between these outcomes as competition may lead to both species coexisting but at very low densities. Finally, it is important for experiments to measure intraspecific as well as interspecific effects because intraspecific density dependence in per capita growth rates caused by factors other than plant quality is a necessary condition for coexistence in all the models we have presented here. Very few published studies of plant-mediated competition to date have measured combined intraspecific competition and reciprocal interspecific effects (Kaplan and Denno 2007) and none to our knowledge have included strengths of competition in addition to sign.

We believe that methods are available to allow empiricists to test the importance of plant-quality mediated competition in phytophagous insects for longer-term community structure. Effects of competition – even in systems with initial condition dependence – can be detected using response surface experiments (Inouye 2001) that follow herbivore populations started at several combinations of initial densities. In addition, dissecting the chemical or nutritional pathways underlying plant quality responses to herbivores can determine whether one or multiple plant phenotypes are involved (e.g. testing whether each herbivore induces independent chemical or physical plant changes and the extent to which those changes affect either herbivore). Determining the number of phenotypes mediating competition can identify whether competitive outcomes are likely to be sensitive to the initial experimental conditions. Phenotypes could also be manipulated genetically or chemically (Thaler et al. 1996) to assess the degree to which plant-quality mediated competition is responsible for observed variation in herbivore community structure. Assuming that long-term experiments are not possible, predicting long-term outcomes will require parameterizing models with information from short-term experiments. Doing this requires quantifying functional forms of relationships between herbivore vital rates and plant quality phenotypes. For example, one could relate herbivore growth, mortality, and recruitment rates to different levels of inducible defenses, or, similarly, relate the strength of induction to different densities of herbivores. Given recent advances in our understanding of genetic, chemical, and ecological factors that underlie plant quality phenotypes

(Karban and Baldwin 1997, Walling 2000, Kessler and Halitschke 2007), such mechanistic studies should be increasingly possible.

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Supplementary material (available as Appendix O17437 at <www.oikos.ekol.lu.se/appendix>) Appendix 1 and 2.