Optimal Control and Cold War Dynamics between Plant and Herbivore

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abstract: Herbivores eat the leaves that a plant needs for photosynthesis. However, the degree of antagonism between plant and herbivore may depend critically on the timing of their interactions and the intrinsic value of a leaf. We present a model that investigates whether and when the timing of plant defense and herbivore feeding activity can be optimized by evolution so that their interactions can move from antagonistic to neutral. We assume that temporal changes in environmental conditions will affect intrinsic leaf value, measured as potential carbon gain. Using optimal-control theory, we model herbivore evolution, first in response to fixed plant strategies and then under coevolutionary dynamics in which the plant also evolves in response to the herbivore. In the latter case, we solve for the evolutionarily stable strategies of plant defense induction and herbivore hatching rate under different ecological conditions. Our results suggest that the optimal strategies for both plant and herbivore are to avoid direct conflict. As long as the plant has the capability for moderately lethal defense, the herbivore will modify its hatching rate to avoid plant defenses, and the plant will never have to use them. Insights from this model offer a possible solution to the paradox of sublethal defenses and provide a mechanism for stable plant-herbivore interactions without the need for natural enemy control.

Keywords: game theory, leaf economics, Nash equilibrium, phenology, photoperiod.

Introduction

An herbivore eats the leaves that a plant needs for photosynthesis. This basic antagonism has been invoked as a driving force for plant-insect coevolution and as a critical aspect of hypotheses related to the role of trophic cascades in ecological systems (Hairston et al. 1960; Ehrlich and Raven 1964; Dawkins and Krebs 1979; Janzen 1980). Decades of research on the adaptive responses of plants to herbivory, such as strategies of inducible defenses, resis-

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tance, and tolerance, have found a highly variable range of responses (Agrawal 2011; Johnson 2011). These can be beneficial, of no consequence, or even detrimental to plant reproductive fitness, despite the expectation that herbivory is costly (Painter 1958; Berenbaum 1983; Maschinski and Whitham 1989; Karban and Baldwin 1997; Stowe et al. 2000; Tiffin 2002; Agrawal et al. 2009).

This basic assumption of conflict between plant and herbivore has generated a large body of research on the adaptive evolution of plant defensive traits, which include the ecological trade-offs between tolerance and resistance, the relative costs of producing and maintaining a particular defensive strategy, and the conditions for facultative versus constitutive defense strategies (Feeny 1976; Price 1991; Fineblum and Rausher 1995; Strauss and Agrawal 1999; Wise and Abrahamson 2007; Agrawal 2011; Fornoni 2011). In particular, inducible defenses may be a solution to the costs of defense because they are expressed only when necessary, if plants can use external cues to predict future conditions (Karban 2011). Many fewer studies, however, have addressed the conditions under which herbivory will have little direct effect on plant fitness in the absence of any compensatory mechanisms (Coley et al. 1985; Trumble et al. 1993). For example, under resource-rich conditions, herbivory becomes relatively inexpensive because the costs of tissue replacement are minimal; hence, investment in defense is unnecessary (Coley et al. 1985).

Here, we propose that the costs of herbivory can sometimes be neutralized through evolutionary optimization of both plant and herbivore strategies, rather than by the balance of external ecological conditions. As a result, leaf consumption by an herbivore may be neutral or minimal in cost to the plant and hence would not require any mechanisms of fitness compensation, such as tolerance (Agrawal 2011; Fornoni 2011).

Specifically, we model strategies of plant defense induction and herbivore hatching, using the economics of their interactions during a single season. We determine

the optimal strategies for the plant and the herbivore by allowing each to adjust its respective strategies by minimizing the cost of defense induction (plant) or the costs of poorly timed hatching and subsequent mortality caused by plant defenses (herbivore). We ask whether and when the timing of both plant defense and herbivory can be optimized by evolution to a point where mutual costs become effectively nil. We develop two models: one that explores herbivore evolution, given a fixed (nonevolving) plant defense strategy, and a second that allows each to (co)evolve in response to the other. Both models lead to stable solutions in which the perceived ecological conflict between a plant and an herbivore is effectively neutral.

Our results suggest that the optimal strategies for both plant and herbivore are to avoid direct conflict; conflict is averted through two basic rules: (1) the herbivore adjusts its hatching strategy to avoid inducing plant defenses and (2) the plant raises its defense threshold when the rate of return from leaf tissue decreases. Consequently, as long as a plant has the capability for moderately lethal defense, it will never have to use that capability. Insights from our model offer a possible solution to the paradox of sublethal defenses (Clancy and Price 1987) and provides a hypothesis for the stability of plant-herbivore systems without the need for natural enemy control (Hairston et al. 1960).

Study System

Our model was inspired by the ecology of the tupelo leafminer *Antispila nysaefoliella* Clemens (Lepidoptera: Heliozelidae) and its host plant, tupelo *Nyssa sylvatica* Marsh (Cornales: Nyssaceae), a deciduous tree that spans most of the eastern United States from New York to Florida. *Antispila nysaefoliella* can be expected to follow the distribution of *N. sylvatica*, but much less is known about the insect's geographic distribution. Supporting information for this article comes from a population located in the northern Shenandoah Valley, Clarke County, Virginia, which has been studied by Low since 2001. Naturalhistory observations of *A. nysaefoliella* suggest that herbivory may not be costly to the plant and that herbivore hatching is timed to occur when the plant will not mount a defense because leaf tissue is already low in value. First, although oviposition occurs during the spring, larvae do not hatch until the end of the summer, typically in August or September, and will persist in high densities until the time of leaf fall (C. Low, personal observation and unpublished experimental data). Second, the consistently high densities at some trees year after year have shown no apparent negative consequences to tree fitness. For example, some trees can have up to 92% of leaves mined and nearly 100% of the leaf mesophyll consumed by the end of the field season (e.g., fig. S1; figs. S1–S5 are available

online; C. Low, unpublished data), yet they continue to grow and thrive (Low 2007, 2008, 2010; Low et al. 2009, 2012). These observations led us to hypothesize that *A. nysaefoliella* and *N. sylvatica* may be coexisting in a nonantagonistic state because leaf mines appear en masse at a time when the plant is predicted to have little net gain from activating its defenses.

The Model

We model a scenario where the intrinsic value of a leaf to a plant varies over the course of the season. The intrinsic value is defined as the photosynthetic potential for carbon gain, which is a function of photoperiod. Therefore, a plant may invest (or not) in mounting defenses against an herbivore, depending on the cost of defense relative to the total payoff, and this is expected to change with time. The herbivore, in turn, adjusts its egg hatching rate to produce a larval density that provides the best fitness payoff, given the plant defense strategy, the background mortality rate, the pupation rate, and expected fecundity over time. We model the defense induction and egg hatching strategy for a single leaf, on the simplifying assumption that all leaves follow the same seasonal pattern of development.

The state variables are leaf area A, herbivore eggs E, and herbivore larvae M. Larvae eat the leaf area at a constant rate b per larva per day, and the plant can respond by upregulating the production of costly chemicals that harm the larvae. We search for the evolutionarily stable strategies by starting the "game" at $t = 0$, when the leaf is fully formed and some number of eggs are present in the leaf, $E(0) > 0$. The game runs until time T, when the leaf is dropped in the fall. The herbivore's strategy variable is $h(t)$, the egg hatching rate. The plant's strategy variable is $u(t)$, the level of defense. We assume that the herbivore has evolved in response to the plant's defense strategy but that their hatching is externally cued (e.g., by photoperiod or temperature) rather than responding to the current state of the leaf.

The objective of the model is to optimize the functions $u(M, t)$ and $h(t)$, for plant defense investment and larval hatch rate, respectively. In the "herbivore evolution model," where only the herbivore evolves, the plant strategy $u(M, t)$ is predetermined and unchanging. We assume that the amount of carbon used for defense $u(\cdot)$ translates into a proportional amount of toxin that is evenly distributed across the leaf. Larval mortality occurs at a background rate μ and can be increased by the lethal effects of plant defense at the egg and larval stages, which are scaled by δ_e and δ_m, respectively. Larvae mature (pupate) at a constant rate π. The dynamic equations are

$$g_1 = \frac{dA}{dt} = -Mb, \tag{1}$$

$$g_2 = \frac{dE}{dt} = -h(t)E - \delta_e u(M, t)E, \tag{2}$$

$$g_3 = \frac{dM}{dt} = h(t)E - (\mu + \pi + \delta_m u(M, t))M. \tag{3}$$

Without loss of generality, units of leaf area and herbivore density are chosen so that $A(0) = E(0) = 1$ and $M(0) = 0$ (the game starts before any eggs have hatched). We assume that $b \le \pi + \mu$, which means that the leaf area is sufficient to support all larvae through to pupation even in the absence of defense-induced mortality. The model is written with plant defenses increasing egg and larval mortality, but it can also apply if defenses disable individuals without killing them. Rather than literally meaning lethality, "killing" may represent a reduction in feeding rate and a reduced chance of pupation due to effects of the plant defense.

Parameters

Values of some parameters are based on *Antispila nysaefoliella* and *Nyssa sylvatica*, but we also extend the parameter range to encompass other systems (table 1). A typical *A. nysaefoliella* larva consumes an average (± 1 SD) of 2.0 ± 0.6 cm^2 of leaf tissue over a life span of 12–24 days ($N = 313$ larvae; Low et al. 2009). Larval consumption is estimated to be ~0.05 of a typical leaf, on the basis of a maximum per capita lifetime consumption of 3 cm^2 and a typical leaf size of 60 cm^2. Mortality rates have ranged from 5% to 13% (parasitism) and from 8% to 25% (unknown), with total observed mortality at 10%–59% (Low et al. 2012; C. Low, unpublished data from 2001, 2002, 2004; 5,374 larvae). Parasitism rates in other leafminer species have been reported to be as high as 60%–80% (Hawkins 1994; Cornell and Hawkins 1995; Hawkins et al. 1997).

Payoffs

We assume that the plant aims to maximize its net carbon gain and that the herbivore aims to maximize the total number of larvae that survive to pupate, weighted by pupal fitness as a function of pupation date, $\omega(t)$. We assume that the leaf will persist throughout the entire season of length T and that its rate of carbon gain is the product of leaf area $A(t)$ and the per unit leaf area photosynthetic rate $p(t)$. We also assume that the cost of defense against herbivores draws directly from the total potential carbon and is paid continuously in proportion to $u(M, t)$. Here, net carbon gain may represent other types of energetic resources that are correlated with plant fitness and similarly limited by $p(t)$ and $A(t)$. The rate of fitness gain for the herbivore is the product of the pupation rate $\pi M(t)$ and their expected fitness $\omega(t)$. Then, the payoff functions are J_c for the plant and J_m for the herbivore:

$$J_c(u) = \int_0^T f_c(t)\, dt = \int_0^T (p(t) - u(M, t))A(t)\, dt, \tag{4}$$

$$J_m(h) = \int_0^T f_m(t)\, dt = \pi \int_0^T M(t)\omega(t)\, dt, \tag{5}$$

with p and ω assumed to be the following functions of time:

$$p(t) = e^{-(t/t^*)^z}, \tag{6}$$

$$\omega(t) = e^{-t/\sigma}. \tag{7}$$

We use $p(t)$ to represent the effect of photoperiod and other correlates of declining within-season conditions. The herbivore fitness payoff $\omega(t)$ also decreases with time and represents the reduction in the number of potential generations that the insect could gain by hatching, feeding, and pupating earlier, as well as any effects of declining

Table 1: Model parameters and their biological interpretations and values

Parameter	Interpretation	Values
b	Herbivore per capita rate of leaf consumption	$.75(\pi + \mu)$
δ_e	Effect of plant defense on egg mortality	.01
δ_m	Effect of plant defense on larval mortality	.1, .5, 1
μ	Natural mortality rate of larvae	.02 (herbivore evolution model)
ρ	Natural mortality of larvae	.25, .5, .75 (coevolution model; see table 2 note)
τ	Larval life span (days to pupation)	10, 25
π	Pupation rate of larvae	.05 (herbivore evolution model); τ^{-1} (coevolution model)
$p(t)$	Photosynthesis rate (per unit of leaf area)	Maximum value scaled to 1
$\omega(t)$	Value (number of offspring) from a larva that pupates on day t	Maximum value scaled to 1
z	Steepness parameter for change of $p(t)$	9
σ	Steepness parameter for $\omega(t)$	200, 1,000

resource quality later in the season. We have assumed that egg mortality is low enough to neglect, but the mortality cost of delayed hatching could also be included in $\omega(t)$.

The objective functions J_m and J_c represent the total fitnesses of the herbivore population and the plant, respectively, from a single leaf. Given the plant's response function u, maximization of the herbivore's objective function J_m is a standard optimal-control problem (Lenhart and Workman 2007). The optimal control $h(t)$ is found by forming the Hamiltonian function H_m for the herbivore,

$$H_m = f_m + \sum_{j=1}^{3} \lambda_j g_j, \tag{9}$$

where the three adjoint variables $\lambda_i(t)$ represent the marginal benefit to the herbivore of an increase in each state variable and are the solutions of the three differential equations $d\lambda/dt = -\partial H_m/\partial x$ for $x = A$, E, and M, with $\lambda_i(T) = 0$. The optimal hatching rate $h^*(t)$ maximizes H_m with respect to h, and we find that

$$\frac{\partial H_m}{\partial h} = (\lambda_3 - \lambda_2)E. \tag{10}$$

The optimal control for the herbivore $h^*(t)$ therefore takes the maximum possible value at times when $\lambda_3(t) - \lambda_2(t) > 0$, the minimal possible value (0) when $\lambda_3(t) - \lambda_2(t) < 0$, or an intermediate value (called a "singular control") that results in $\lambda_3(t) - \lambda_2(t) \equiv 0$ over an interval of time (Lenhart and Workman 2007).

For the herbivore evolution model, we specified 16 different plant defense strategies, using a sigmoid function (eq. [11]) and various coefficient values to form a series of plant strategies that spanned the spectrum of biological possibilities (fig. 1; table B1),

$$u(M, t) = \frac{a(t)M^{b(t)}}{M_h(t)^{b(t)} + M^{b(t)}}, \tag{11}$$

where $a(t) = a_0 e^{-t/1,000}$, $b(t) = b_0 e^{-t/200}$, and the "half-saturation constant" for plant defense was

$$M_h = M_0 \left(1 + \max\left(\frac{t - t_{crit}}{t_c}, 0\right)^3\right). \tag{12}$$

Here, $M_h(t)$ specifies the time-varying "threshold" larval density at which plants turn on defense; when the value of b is large this is a steep threshold, and for smaller values of b it is more gradual.

Because the herbivore objective function J_m is the total fitness of the herbivore population, it appears that we are assuming group selection on the herbivores. In fact, for a large herbivore population, the optimal strategy for this payoff function is an evolutionarily stable strategy under individual selection at the egg level, for the following reasons. Suppose that the timing of herbivore egg hatching maximizes J_m, given the plant's defense strategy. The payoff to an egg that hatches on a given day is its probability of survival to pupation times the value of ω on its pupation date. If this product is not constant, then an egg that hatches on a low-payoff day could benefit by switching to a higher-payoff day, because a change in behavior by one egg (in a very large population) will not affect the defense level u by enough to change the relative payoff values (lower vs. higher on the two days). But the switch by that egg would also increase the total population fitness, contradicting the assumption that J_m is maximized. The hatching schedule that maximizes J_m is thus an ideal free distribution in hatching time, at which an egg cannot gain by "cheating."

For the coevolutionary model, we explored 18 different scenarios (table 2). Each had a particular combination of larval life span ($\tau = 10$ or 25 days), the fraction of eggs that would die from background mortality (parasitism) before pupating in the absence of plant defense (0.25, 0.5, or 0.75), and the lethality of plant defense ($\delta_m = 0.1$, 0.5, or 1).

Numerical Methods

Our numerical methods to find the optimal plant defense and herbivore hatching strategies are described briefly in this section and in more detail in appendix A. In the herbivore evolution model, the plant response function $u(M, t)$ is fixed, and we seek the optimal herbivore hatching function $h(t)$. Although optimization of $h(t)$ is a standard optimal-control problem, standard numerical methods were not successful, because we found numerically that the optimal control was singular (Lenhart and Workman 2007) over long time intervals rather than being the "bang-bang" control that is generally expected in models, such as ours, with a Hamiltonian that is linear in the control variable. We therefore found the optimal $h(t)$ by an iterative hill-climbing method similar to steepest-ascent function maximization.

Solving the coevolutionary model is more complicated. We seek a Nash equilibrium, meaning that each player's strategy is the best response to what the other is doing. In some cases, Nash equilibria can be found by a simple iteration: pick some initial strategy for player A; find the best response by player B; find player A's best response to player B's new strategy; continue until the strategies both converge to a limit (Alonzo et al. 2003*a*, 2003*b*). As in many other models, we found that this iteration did not lead to convergence because the best-response functions were nonsmooth or too strongly nonlinear (McNamara et al. 1997). We therefore used a combination of the approaches suggested by McNamara et al. (1997), "damping" and "introducing errors." Iteration with damping and errors converged to a stationary pattern in which extended
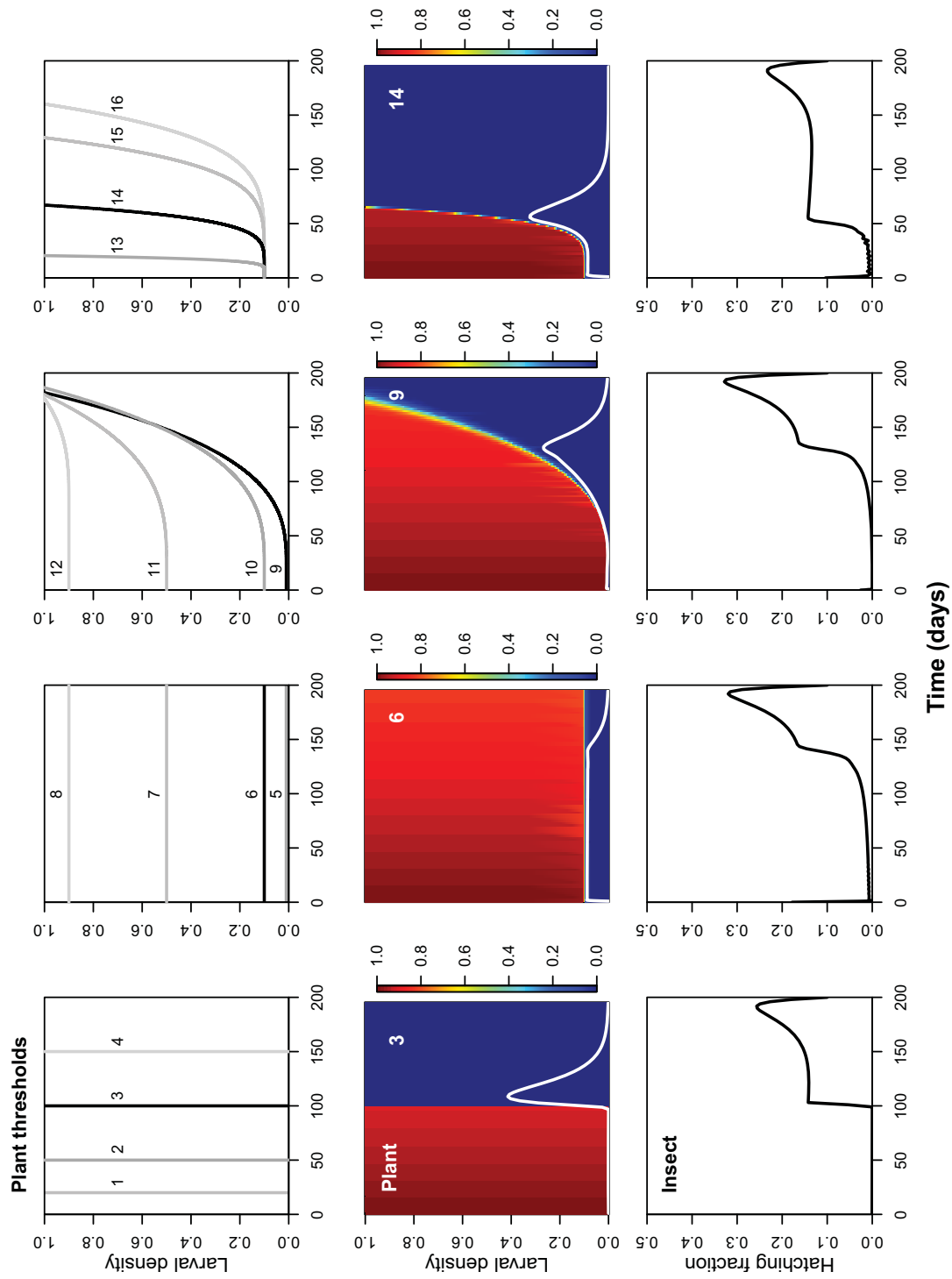
periods of mutual adaptation were interrupted by briefer transient periods when one player or the other temporarily got ahead of the other (high fitness for one, low fitness for the other). We allowed at least 500 rounds of "coevolution" (continuing longer, if needed, until a stationary pattern was reached) and then identified the periods of mutual adaptation as times when the payoff to each player was within 2.5% of the median payoff for that player. The results that we report are based on the average strategy of each player during the periods of mutual adaptation.

These numerical calculations were all programmed in R (R Core Development Team 2012), with the deSolve package (Soetaert et al. 2010) for numerical solution of differential equations and the subplex package (Rowan 1990; King 2008) for numerical optimization; the code is available on request. All fitness payoffs are scaled relative to the maximum potential fitness that a plant would receive in the absence of herbivores or that an herbivore would receive in the absence of plant defenses.

Results

Herbivore Evolution Model

Nearly all scenarios in the herbivore evolution model led to a strategy of conflict avoidance, except when the plant strategy offered few opportunities for avoiding defenses or when plant defenses were too ineffective to deter the herbivore (figs. 1, S2). In nearly all cases, herbivore hatching began ($h^*(t) > 0$) as soon as plant defense switched off and remained positive as long as $u(M, t) = 0$. There were, however, two exceptions to this rule. The first was when $u(M, t) > 0$ at most times even for very low herbivore density, so that the herbivores had no opportunities to hatch without encountering plant defenses (strategies 4 and 5; fig. S2). The second was when the effect of plant defense was too weak to make the payoff worth the wait for delaying hatching until $u(M, t) = 0$ (e.g., plant strategies 3 and 9 when $\delta_m = 0.1$; fig. S2).

Whenever defenses were at least moderately lethal ($\delta_m = 0.5$ or 1) and the plant strategy offered some times at which herbivores could hatch without inducing plant defenses, the herbivore's optimal hatching function always tracked the plant's threshold larval density (M_h), such that larval density never became high enough to induce plant defenses. Hence, the herbivore's response to nearly all

Table 2: Parameter values for 18 different scenarios simulated in the coevolutionary model

Scenario	Lethality (δ_m)	Fraction parasitized (ρ)	Larval life span (τ)
1	.1	.25	10
2	.1	.50	10
3	.1	.75	10
4	.1	.25	25
5	.1	.50	25
6	.1	.75	25
7	.5	.25	10
8	.5	.50	10
9	.5	.75	10
10	.5	.25	25
11	.5	.50	25
12	.5	.75	25
13	1	.25	10
14	1	.50	10
15	1	.75	10
16	1	.25	25
17	1	.50	25
18	1	.75	25

Note: These scenarios are shown graphically in figure S4, available online. "Larval life span" τ is defined as the mean time to pupation in the absence of larval mortality, so $\tau = 1/\pi$, where π is the instantaneous pupation rate. "Fraction parasitized" ρ is defined as the fraction of larvae that would die from the background mortality rate μ rather than surviving to complete the larval stage, in the absence of additional mortality due to plant defenses. Thus, $\rho = \mu/(\mu + \pi)$, and therefore the background mortality rate used in the model was $\mu = \rho\pi/(1 - \rho)$.

plant strategies (except for strategies 4 and 5, as described above) was to keep $M(t) < M_h$ so that $u(M, t)$ was always nearly 0 (figs. 1, S2).

Plant fitness was highest if defenses protected the leaf when it was most valuable. Plant strategies with the lowest fitness payoffs were those to which the herbivores responded by feeding early in the season, when leaf tissue had the highest potential for present and future carbon gain (figs. S2, S3; strategies 1, 7, 8, and 11–13). This occurred if the larval density threshold for inducing plant defenses was fairly high ($M_h \geq 0.5$; strategies 7, 8, 11, and 12) or if there was only a short period when defenses could be induced (strategies 1 and 13; figs. S2, S3). Interestingly, despite resulting in defense for relatively short time periods, strategies 1 and 13 were still effective in keeping

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Figure 1: Plant strategies and solutions of the herbivore evolution model. Plant strategies were fixed in this model and were determined with equation (11). *Top*, threshold larval densities for each plant strategy at which plants will defend against herbivores. For strategies 5–8, defense is active above the plotted curve and inactive below it; for all other strategies, defense is active to the left of the curve and inactive to the right of the curve. *Middle*, solutions of optimal insect hatching strategy $h^*(t)$ for four exemplar plant strategies (defense thresholds shown by the black curve in the corresponding top panel). The white line overlaid onto the plant strategy represents the number of larvae $M(t)$. *Bottom*, optimal herbivore hatching strategies $h^*(t)$ for the given plant strategies (directly above, middle row). The entire suite of strategies used for the evolution model simulations is shown in figure S2, available online. Parameter values are in table B1.

larval density below the level that would induce defenses, even with weak lethality ($\delta_m = 0.1$; figs. 1, S2).

Defense lethality had a small to negligible effect on herbivore fitness in all cases where the plant strategy provided an option between direct conflict and delayed hatching (and subsequent conflict avoidance). This is because the herbivore's optimal strategy was to avoid inducing plant defenses. Plant fitness was affected by lethality when the plant strategy was highly intolerant of larvae ($M_h \leq 0.01$) and less than 50% of the latter half of the season was available for the herbivore to hatch without inducing plant defenses (strategies 3–5 and 9; fig. S2). In these cases, however, lethality affected plant fitness in two different ways, depending on the form of the plant strategy. First, lethality had a direct effect on herbivore fitness if the herbivore was given no choice but to hatch early, as in strategies 4 and 5 (figs. 1, S2). Here, moderate to high lethality levels increased the plant's payoff and decreased the herbivore payoff, relative to a weak lethality level, because of direct effects on herbivore survival ($\delta_m = 0.1$; figs. 2, S2). Given the declining fitness function $\omega(t)$, there was no incentive for the herbivore to delay hatching. Second, lethality had an indirect effect in less pervasive but still highly defensive strategies (i.e., $M_h \leq 0.01$), such as strategies 3 and 9, that presented an option for the herbivore to either hatch early and battle against plant defenses directly or delay hatching to a time when plant defenses were no longer a threat (fig. 1). Here, lethality level presented a penalty for the herbivore and hence enforced the avoidance of plant defenses. The difference in the herbivore's response between the weak-lethality ($\delta_m = 0.1$) condition and moderate- ($\delta_m = 0.5$) or high- ($\delta_m = 1$) lethality conditions for strategies 3 and 9 demonstrates the importance of the indirect effects of lethality (figs. 2, S2). Here, increasing lethality led to a substantial increase in the fitness payoff for the plant and a comparatively small effect on the payoff for the herbivore (<10%; fig. 2).

Plant-Herbivore Coevolution Model

In all scenarios, the coevolution model predicted that (1) plants should be highly defended early in the season, but with some very low level of larval density permitted, and (2) herbivore hatching should be delayed so as to avoid plant defenses completely. Because of the stochastic algorithm used to find Nash equilibria in the coevolution model (see "Numerical Methods"), rather than converging to single strategy, solutions eventually oscillated within a narrow range of payoff values (e.g., scenario 11; fig. 3). To characterize this outcome, we used the average strategy for each player during periods when the payoff was within 2.5% of the median payoff for both plant and herbivore (figs. 4, S4). Throughout all 18 coevolutionary scenarios (table 2), the optimal hatching functions (including all those within the 5% range around the median payoff) were, without exception, delayed toward the end of the season, so that $h^*(t) > 0$ when $u(M, t) = 0$ (figs. 4, S4). The direct-conflict situations of the herbivore evolution model, as illustrated by strategies 4 and 5 (all δ_m values) and 3 and 9 ($\delta_m = 0.1$ only), were not a Nash solution in any of the coevolutionary-model simulations. The herbivore strategy also included a very brief, intense pulse of hatching in which a few larvae "sneaked" in at the very start of the season, to get ahead of plant defenses (figs. 4, S4 at $t = 0$).

Once there are no eggs left to hatch, selection on the plant strategy is effectively neutral. This explains the large variation in the plant strategies at the end of the season (figs. 4, S4). To confirm this interpretation, we added to the plant's payoff function a small (arbitrary) cost for having a low defense induction threshold that was independent of whether defenses were activated and then reran a subset of the coevolutionary scenarios (results not shown). As expected, the only effect of this cost was that the plant's threshold for defense induction remained high even after all herbivore eggs had hatched and pupated.

Defense lethality increases plant fitness as a result of more complete deterrence of herbivores from feeding during times of high intrinsic leaf value. Therefore, herbivore fitness decreased in association with increasing lethality. However, this reduction in herbivore fitness was a consequence of delaying egg hatch to a time when the reproductive potential was lower and not of a direct encounter with plant defenses (figs. 4, 5, S4).

To determine the importance of defense lethality, background mortality rates, and larval life span (or feeding rate) on plant and herbivore optimal strategies, we analyzed the fitness values of the median solutions for each coevolutionary scenario (e.g., table 2; figs. 5, S4; data in fig. 5), using multiple linear regression. The analysis indicated that defense lethality (δ_m), parasitism or background mortality rate (μ), and larval life span (τ) are all significant predictors of fitness (fig. 5). First, as defense lethality (δ_m) increased, the relative fitness of both the plant and the herbivore increased. Second, as the background mortality rate (μ) increased, plant fitness decreased and herbivore fitness increased. However, the absolute value of potential fitness payoff decreased as well, as a result of the increase in the fraction lost to background mortality (for interpreting relative payoffs in fig. 5). Finally, increased larval life span (τ) led to a slight increase in plant fitness and a slight decrease in herbivore fitness. Linear functions of these variables explained 90% of the variance of plant relative fitness (y_1; model: $y_1 = 0.5 + 0.35\delta_m - 0.23\mu + 0.006\tau$) and 89% of the variance of herbivore relative fitness (y_2; model: $y_2 = 0.77 + 0.25\delta_m - 0.12\mu + 0.003\tau$; fig. 5).
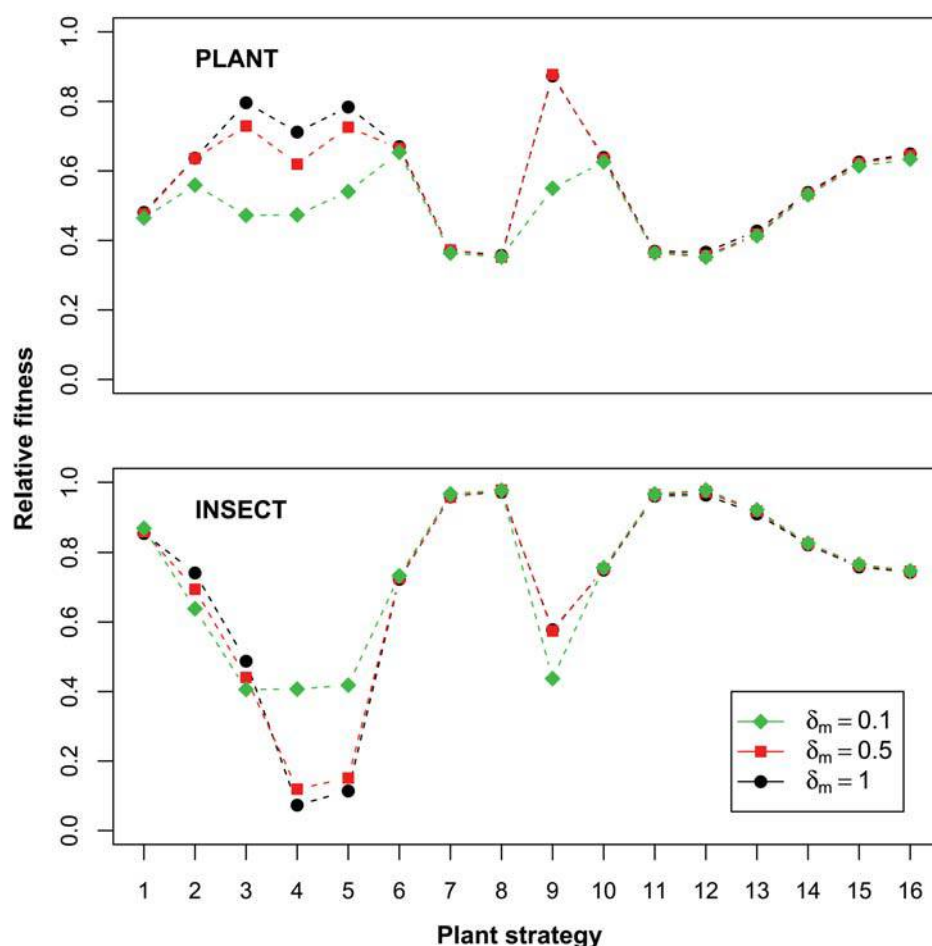
Figure 2: Fitness payoffs for the plant and the insect herbivore resulting from the herbivore evolution model for three values of plant lethality δ_m. Payoffs are scaled relative to the maximum potential fitness payoff without herbivory (*top*) or without plant defenses (*bottom*).

Discussion

Our model predicts reduction of conflict between plant and herbivore via coevolution of their respective strategies of defense induction and egg hatch. We arrived at these results by using two models. In the herbivore evolution model, we allowed only the herbivore to evolve and asked, "What is the best hatching strategy for the herbivore, given the plant's strategy?" Then, in the coevolutionary model, we allowed both plant and herbivore to evolve and asked, "What are the mutually optimal solutions for both players?"

The predicted optimal strategy for the plant is to tolerate only a low level of herbivory early in the season, when leaf value is high, followed by a relaxation of defense as a leaf's marginal return diminishes. Herbivore hatching rates were generally optimized so that larval densities were low enough to avoid induction of plant defenses, that is, $u(M, t)$ was 0 or close to 0. Two exceptions were found in the herbivore evolution model, and both occurred when

the plant defense was active throughout more than 50% of the range of larval densities and time of year, so that the herbivore had no better option than to face plant defenses head-on (strategies 4 and 5; figs. 1, S2). These defense strategies were suboptimal for the plant (fig. 2) and never surfaced as a solution in the coevolutionary model (fig. S4). In the coevolutionary model, defense induction was avoided under all conditions that we examined. Moreover, the plant's strategy converged to the general form of the best strategy of the herbivore evolutionary model (strategy 9; fig. 1), in which defense was reduced and eventually dropped as leaf value declined (figs. 4, S4). This allowed some small proportion of herbivores to hatch early in the season and then full hatching much later (figs. 1, 2, S3). Because the herbivore avoided plant defenses, its fitness depended more on the loss of reproductive potential due to late hatching than on the direct effects of plant defenses.
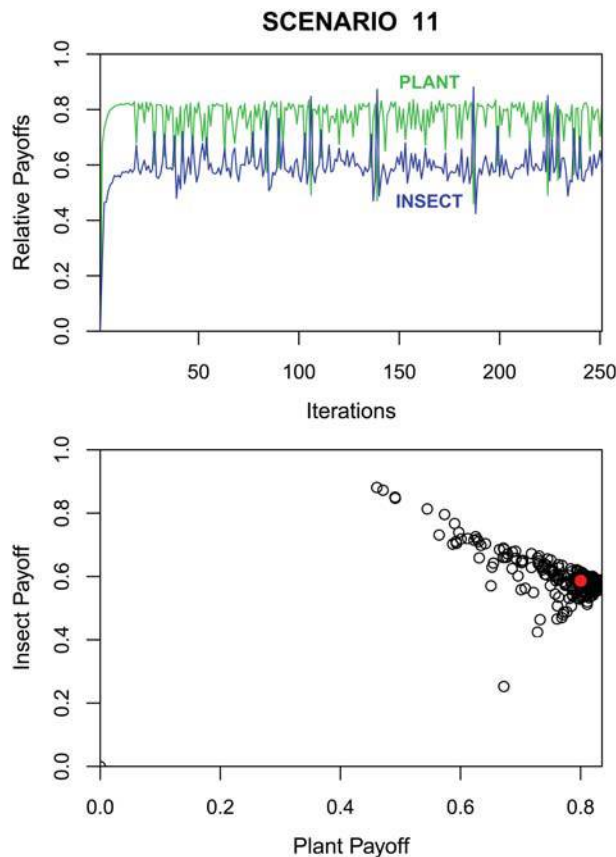
Figure 3: Relative fitness payoffs for scenario 11 of the coevolutionary model over 250 iterations (*top*) and the same data plotted in the phase plane (*bottom*). In the phase plane plot, the red dot indicates the median solution.

Role of Lethality

Our results suggest that one important function of plant defenses may be to minimize herbivory when leaf tissue is most valuable to the plant. Being highly defensive when leaf tissue was most valuable (but later raising the threshold for defense induction) led to higher fitness for both plant and herbivore. This is best illustrated by comparing the herbivore's responses to plant strategies 3 and 9 with those to strategies 4 and 5 (figs. 1, 2, S2). A low-lethality defense ($\delta_m = 0.1$) was insufficient incentive for the herbivore to delay hatching in plant strategies 3–5 and 9. However, because strategy 3 provides an earlier defense-free feeding zone (at $t = 100$ days), compared to strategies 4 and 5, a moderately effective defense was sufficient to tip the balance for the herbivore, giving it a higher payoff for hatching later in the season (figs. 1, 2, S2). Because defense induction is pervasive in strategies 4 and 5, late hatching was not a better choice for the herbivore (fig. S2).

Paradox of Sublethal Defenses

The paradox of sublethal plant defenses (Clancy and Price 1987) is that although sublethal plant defenses can retard larval growth, evidence suggests that larvae often compensate by consuming more of the plant before they pupate. How, then, could sublethal plant defenses be good for the plant? Because slower growth is expected to increase the herbivore's exposure to natural enemies, natural enemies have been invoked as a potential solution to the paradox: killing the herbivores before they reach their maximum consumption. However, empirical evidence of a higher risk of natural-enemy attack on slower-growing larvae is highly equivocal and tends to suggest that in fact it is the faster-growing larvae that suffer higher attack rates (Clancy and Price 1987; Lill and Marquis 2001; Thaler 2002; Walker et al. 2008).

Our results offer a possible solution to this paradox by suggesting that prolonging larval development, despite the potential for greater consumption, may in fact be less costly to the plant because a greater proportion of herbivory (when larvae are larger and feeding more) is shifted to a time when the costs of herbivory are lower. Our results indicate that plant strategies resulting in delayed herbivory can provide higher payoffs to both plant and herbivore and can be mutually evolutionarily stable. Therefore, the result from our model provides a different hypothesis for sublethal plant defenses: that they evolved not to march herbivores toward natural enemies but to nudge them along in time so that the bulk of their consumption occurs when leaf tissue is intrinsically lower in value.

Herbivore Density and Trophic Effects

Our model suggests that the plant may be more important than natural enemies for shaping and stabilizing the density of herbivores within a patch or group. The observation that the world is green fuels the notion that natural enemies limit herbivore effects on plants (Hairston et al. 1960; Lawton and McNeil 1970). However, the evidence for the response of natural enemies to herbivore density and their ability to regulate the population has been equivocal (Walde and Murdoch 1988; Auerbach et al. 1995; Lill 2001). Although many studies have been conducted to examine the effect of parasitoids on insect herbivores, few have detected a significant effect in regulating patches of high host density (Walde and Murdoch 1988). Instead, evidence from a review of leaf-mining systems suggests that horizontal and bottom-up forces may have greater regulatory effects on populations than do top-down forces (Auerbach et al. 1995; Lill 2001). This is in line with our results, which showed that the top trophic level (represented by the background larval mortality rate) does in-
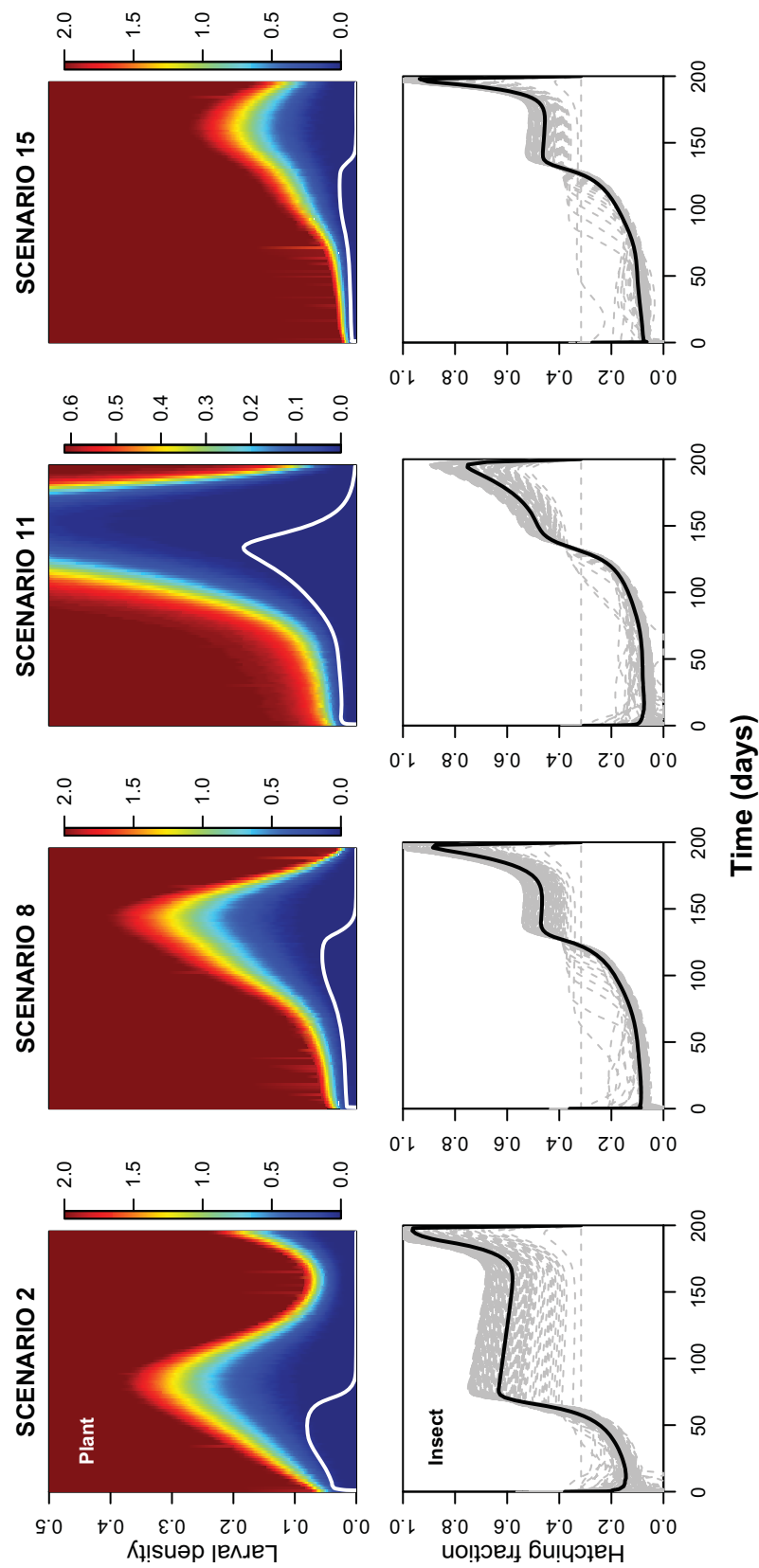
Figure 4: Results of the coevolutionary model for four exemplar scenarios plotting median Nash solutions for $u*(M, t)$ and $h*(t)$. Values of $u*(M, t)$ are shown by the color gradient. The solid black line indicates the median solution of $h*(t)$ and dashed gray lines 5% of the surrounding solutions. The full suite of scenarios and their solutions are found in figure S4, available online. Parameter values are in table 2.
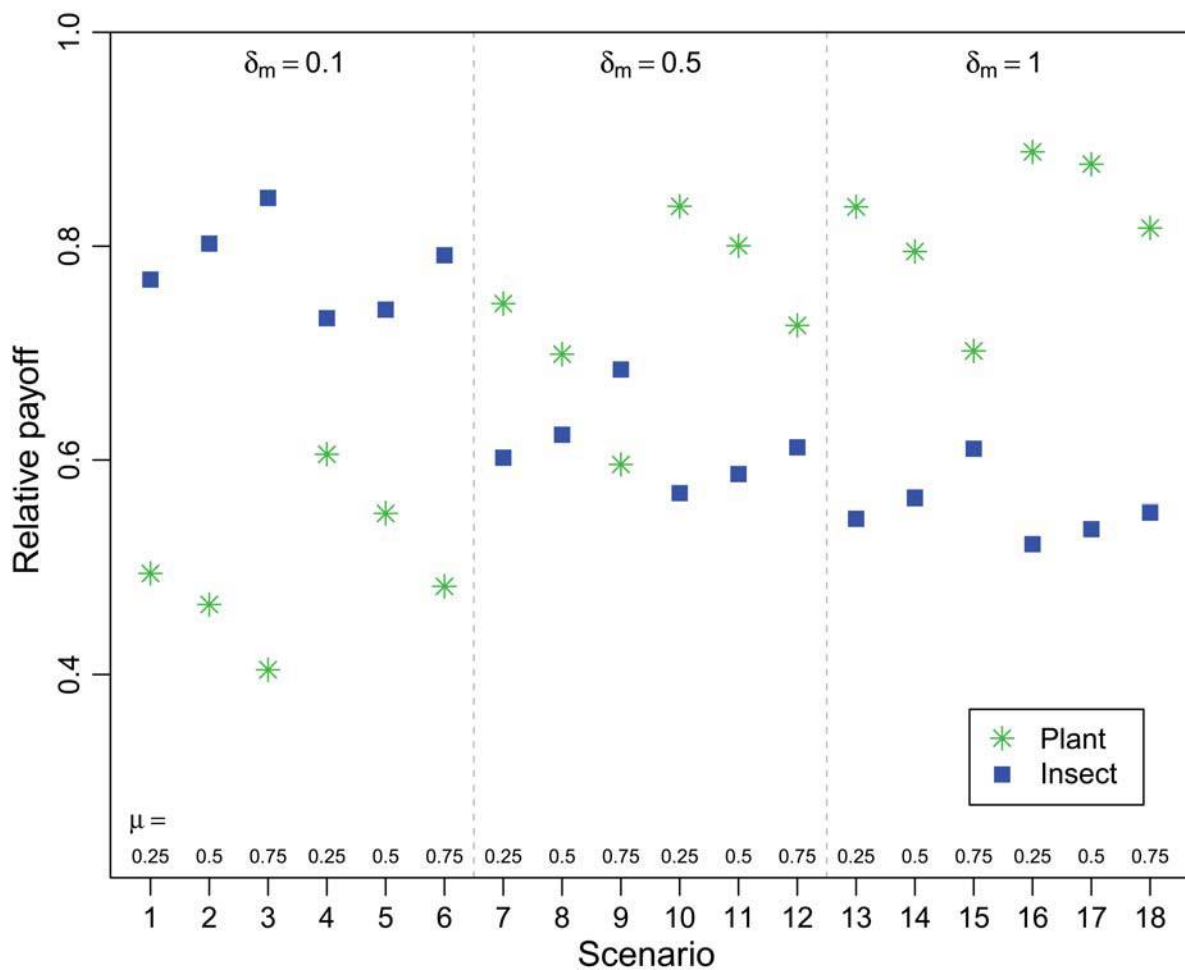
Figure 5: Relative payoffs for plant and herbivore (insect) from median solutions of each coevolutionary scenario (table 2; fig. S4, available online). Three parameters were varied across scenarios: plant lethality (δ_m), background mortality (μ), and time to pupation (τ). See text for model statistics.

deed affect herbivore density but that it is secondary to the effects of the bottom trophic level.

What Drives an Herbivore to Engage with Plant Defenses?

In our models, antagonistic plant strategies were generally less advantageous than ones that allowed the herbivore to avoid plant defenses. However, we did find conditions in which the plant did initiate defenses and the herbivore did not avoid these defenses, a situation that is known to occur in many natural systems (Agrawal and Fishbein 2006; Karban 2011). So under what conditions would it be optimal for the herbivore to behave in a way that evoked damaging defenses by the plant?

In our models, conflict resulted from herbivore behavior when the effects of defense were mild compared to the cost of delayed hatching, represented by the larval fitness

function $\omega(t)$. Environmental conditions could increase the cost of delayed hatching if abiotic conditions (e.g., temperature) or resources required by later stages in the life cycle were not available late in the plant's growing season or if the egg mortality rate was not low enough to neglect, as we have assumed in our model. Alternatively, the herbivore might evolve a way to circumvent plant defenses or gain an advantage from feeding on defended plant tissue. However, the benefits would have to outweigh the costs, which could be reinforced by changes in external conditions and developmental trade-offs (Fordyce and Nice 2008; Lindstedt et al. 2010; Laurentz et al. 2012). For example, a high rate of natural-enemy attack and the evolution of aposematism (warning signal plus toxicity) could reinforce the benefits of feeding on chemically defended plant tissues (Ruxton et al. 2004). Feeding on toxic plant material then could provide a fitness benefit through de-

Table 3: Emergence dates of *Antispila nysaefoliella* recorded for six field seasons at C. Low's study site

Date of mass emergence	Total larvae	Leaves with larvae	Total leaves	Julian date	Model day	% completed larval stage	% newly emerged
2001[a]	755	175	485				
August 14				226	106	.1	58.3
August 20				232	112	...	41.6
2003[b]	390	135	362				
August 26				238	118	.3	99.7
2004[a]	1,138	211	357				
August 19				231	111	.2	69.1
August 27				239	119	...	30.7
2005[b]	910	179	263				
August 30				242	122	.3	99.7
2008[a]	1,281	146	146				
August 16				228	108	.0	69.3
September 4				247	127	...	30.7
2009[c]	2,176	395	893				
August 23				235	115	.05	17.7
September 2				245	125	...	82.3

Note: "Model day" is the number of days since May 1, the earliest recorded date in spring when adults (which had overwintered as pupae) were observed in the field. Actively feeding larvae with very small mines (1–3 mm^2) were classified as "newly emerged." Data sets listed here were collected for several different studies, and therefore leaves and larvae were sampled according to several different protocols described in the footnotes. Depending on the data set, leaves were selected from 4–10 different trees.

[a] Leaves with larvae were tagged and monitored nondestructively throughout the season, so the hatching of new larvae on monitored leaves was apparent. The second date is a rough estimate of the emergence of a second cohort of larvae on the monitored leaves (Low 2010). In 2008, only leaves with mines were selected.

[b] Randomly chosen leaves within a tree canopy were destructively sampled at the time of first mass emergence, so "total larvae" does not include larvae that emerged later in the season.

[c] Leaves were sampled destructively on the second date. On the basis of mine size, larvae were classified as newly emerged (82.3%), older larvae (17.7%) assumed to have emerged on the observed date of the first mass emergence in 2009, or individuals that had already completed the larval stage (0.05%).

creased mortality from natural enemies. It would be worthwhile to identify the conditions in which an herbivore would actually benefit from inducing the defense response of its host plant.

Conflict avoidance was possible in our models because there were times when it was optimal for the plant to accept herbivory rather than pay the costs for defense. At some point before leaf drop, the potential gain from a leaf over its remaining life span becomes too low to justify defending it. When this occurs will depend on the cost of defense, which could depend on extrinsic factors such resource availability and the fitness consequences of allocating resources to defense (Coley et al. 1985). If defense is so cheap that a leaf is always (or almost always) worth defending, conflict avoidance becomes impossible.

Empirical Support for Model Predictions

The question of whether plant and herbivore could coevolve to avoid conflict was motivated by natural-history observations of the tupelo leafminer *Antispila nysaefoliella*, a specialist of tupelo trees *Nyssa sylvatica*, over a 10-year period. Our model successfully predicted the observed pat-

terns of emergence in *A. nysaefoliella*, specifically the lengthy delay between oviposition in May and mass larval emergence in August. Using May 1 as "day 1" (the first date on which adults that overwintered as larvae were observed in the field) for comparison with the model, mass hatching of larvae was estimated to occur on days 106–127, which correspond to August 14–September 4 of each year (2001–2009; table 3).

The model also successfully predicted the bimodal distribution of larval hatching times: a small burst of early hatchers followed by mass emergence much later. Although the vast majority of *A. nysaefoliella* larvae emerge in August and September of each year, a few singly occurring individuals ("sneakers") emerge much earlier and complete the larval stage before the mass emergence of the rest of the population (table 3; fig. S5). Because the mines on each leaf provide a complete record of all leaf-mining activity up to that point, we were able to score the frequency of sneakers by using images of leaves that were taken at the time of mass emergence from multiple years of study (2001–2009; table 3). Image scanning of leaves was part of a standard protocol (by C. Low) to assess the distribution of leaf mine sizes and numbers across leaves at different times or the consumption rates of

individual larvae (e.g., Low et al. 2009, 2012). The presence of a completed mine among a group of newly emerged mines at the time of mass emergence was a clear indication that one larva had hatched much earlier than the others (fig. S5 shows an example). A small burst of hatching at the start of the season was also a very common outcome in our model, because the plant's optimal strategy is to tolerate a low density of larvae early in the season (figs. 4, S4).

A low-cost, nonantagonistic state is likely to characterize other specialized plant-herbivore systems as well. However, whether a system would have dynamics similar to those of *A. nysaefoliella* may depend on the cost function, external resource conditions, and species-specific adaptations for efficient resource use. Some studies have categorized high-density emergence as a characteristic of some insect species, and in many of these, there is consistent late-season emergence (Hunter 1991; Auerbach et al. 1995), when leaf value would be lowest. Our predictions are also in line with the results from a meta-analysis by McCall and Fordyce (2010) testing the prediction that chemical defenses would be optimized according to the potential value of a particular plant tissue ("optimal-defense theory"). They found that putatively more valuable tissues, such as young leaves, had higher levels of defensive chemistry, compared to tissues that were less valuable. Together with our theoretical results, this evidence supports the general importance of the economics of defense as a predictor of the response of plants.

Our model predicts possible outcomes of coevolution when the background resource conditions (photosynthesis rate $p(t)$ and larval fitness $\omega(t)$) are defined explicitly as declining functions of time. In general, these functions may depend on specific adaptations of the species and on local differences in ecological conditions. Our model is also specific to one component of plant fitness, photosynthesis by leaf tissue during a single growing season in a highly seasonal environment. Herbivory and plant defenses on other plant parts cannot be explained with our models. Nevertheless, our models demonstrate the usefulness of delineating the basic economics of interspecific interactions and using evolutionary game theory to understand the evolution of phenologies, and this general approach can be applied to a wide range of systems (e.g., pollinator-exploiter systems [e.g., Law et al. 2001]).

Conclusion

Antagonism is typically expected of plant-herbivore interactions, with plants on constant alert against herbivores and herbivores under the constant threat of plant toxicity. Instead, we found that the plant should allow some low level of herbivory, with an eventual full relaxation of defense when the value of a leaf declines with the approach-

ing end of the period when carbon gain occurs. Because the plant is more likely to mount a defensive response when leaf value is high, the herbivore does not hatch during these times and avoids contact with plant defenses. Therefore, as long as a plant is capable of at least moderately lethal defense, sufficient to outweigh the costs of delayed hatching for the herbivore, the plant will not have to use those defenses.

APPENDIX A

Numerical Methods Details

As suggested by Lenhart and Workman (2007), we approximated $h(t)$ by specifying its values $h(t_i) \geq 0$ at a closely spaced grid of time points t_i, with linear interpolation between grid points. For given values of $h(t_i)$, our algorithm began by solving the state equations forward in time from their initial conditions and then solving the adjoint equations backward in time from their terminal conditions, $\lambda_j(T) = 0$. This "forward-backward sweep" (Lenhart and Workman 2007) gives the values of the state and adjoint variables at the grid points. We used those values to compute the herbivore's Hamiltonian at each grid point, which gives the derivative of the herbivore payoff with respect to the control variable at that moment. The values of $h(t_i)$ at each grid point were then adjusted slightly in the direction that gave an increase in fitness, unless this was impossible (e.g., a zero value for h was not decreased below 0). In the herbivore evolution model, this entire process was repeated until the values of $h(t_i)$ were such that no further increase in the herbivore fitness payoff was possible, implying that h^* had been reached.

In the coevolution model, numerical convergence to a mutual evolutionarily stable strategy required the use of damping and errors, as noted in the main text. The herbivore response was damped: rather than adopting the best response to the plant's current strategy, it took a few small hill-climbing steps (as in the herbivore evolution model)

in the direction of increased payoff. The plant then adopted the best response to the new herbivore strategy, but with errors introduced in its payoff function.

Specifically, for any defense strategy $u(M, t)$, the payoff to the plant was computed for three randomly chosen small perturbations to the initial herbivore density and then averaged. Numerical optimization was then used to find the plant response that gave the highest value of this imprecise payoff. The entire process, starting with updating of the herbivore strategy, was then repeated. This way of updating strategies gives a quasi-"coevolutionary" dynamic in which strategies never converge to constant values, because of the random errors in the plant's best-response function. Instead, strategies settled (generally within 100 or so iterations) into a stationary pattern in which periods of mutual adaptation were interrupted by transient periods when one player temporarily got ahead of the other (high fitness for one, low fitness for the other). Results presented in the main text are based on the strategies during the periods of mutual adaptation.

APPENDIX B

Parameter Values

Table B1: Parameter values for the 16 different plant strategies simulated for the herbivore evolution model

Strategy	t_{crit}	t_c	M_0	a_0	b_0
1	20	1	.001	1	50
2	50	1	.001	1	50
3	100	1	.001	1	50
4	150	1	.001	1	50
5	200	1,000	.01	1	50
6	200	1,000	.1	1	50
7	200	1,000	.5	1	50
8	200	1,000	.9	1	50
9	20	35	.01	1	50
10	20	80	.1	1	50
11	20	160	.5	1	50
12	80	200	.9	1	50
13	5	10	.1	1	50
14	5	40	.1	1	50
15	5	80	.1	1	50
16	5	100	.1	1	50

Note: These strategies and corresponding herbivore solutions are shown graphically in figure S2, available online.

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