



## Plant tolerance and resistance in food webs: community-level predictions and evolutionary implications

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**Abstract.** While evolutionary ecologists emphasize different ways in which plants can evolutionarily respond to herbivory, such as resistance or tolerance, community ecology has lagged in its understanding of how these different plant traits can influence interactions, abundance, composition, and diversity within more complex food webs. In this paper, we present a series of models comparing community level outcomes when plants either resist or tolerate herbivory. We show that resistance and tolerance can lead to very different outcomes. A particularly important result is that resistant species should often coexist locally with other, less resistant competitors, whereas tolerant species should not be able to coexist locally with less tolerant competitors, although priority effects allow them to coexist regionally. We also use these models to suggest some insights into the evolution of these traits within more complex communities. We emphasize how understanding the differential effects of plant tolerance and resistance in food webs provides greater appreciation of a variety of empirical patterns that heretofore have appeared enigmatic.

**Key words:** coexistence, food webs, herbivory, plant resistance, plant tolerance, priority effects, trade-offs

### Introduction

Herbivores often exert strong selective pressures on plant traits (e.g. Ehrlich and Raven, 1964; Coley *et al.*, 1985; Fritz and Simms, 1992), which can directly influence the dynamics and structure of both plant and herbivore populations (e.g. Morris and Dwyer, 1997; Underwood, 1999; Tiffin, 2000). In turn, the impact of herbivores on plant populations often creates indirect effects that influence the abundance, diversity, and composition of the entire plant community (Huntly, 1991; Augustine and McNaughton, 1998; Olf and Ritchie, 1998; Chase *et al.*, 2000). However, the link between the evolution of individual plant traits and the impact on the entire plant community remains elusive, in part due to the difficulty in merging these different scales of investigation.

Ecologists use the 'trophic level' concept (*sensu* Lindeman, 1942; see also Hairston *et al.*, 1960; Slobodkin *et al.*, 1967; Fretwell, 1977; Oksanen *et al.*, 1981; Oksanen, 1991; Oksanen and Oksanen, 2000) to lump species that possess similar traits and perform similar functions. For example, most plant (and algal) species utilize light, water, CO<sub>2</sub> and nutrients in similar ways, and can be lumped into the plant trophic level. Likewise, grazers typically eat more plant than animal material, placing them in the herbivore trophic level. Finally, predators that eat herbivores are lumped into the carnivore trophic level.

Though the trophic level concept is still important for understanding broad-scale community patterns (Hairston and Hairston, 1997; Polis, 1999; Oksanen and Oksanen, 2000), the key assumption underlying the lumping of species into trophic levels – that all species within a level can be considered more-or-less edible and equivalent – has been controversial. While several authors have claimed that the trophic-level concept allows realistic understanding of the patterns of community structure, regardless of slight differences in chemical and structural defenses of plant species (e.g. Slobodkin *et al.*, 1967; Moen *et al.*, 1993; Oksanen and Oksanen, 2000), it is becoming increasingly clear that plant species are not equivalently susceptible to herbivory, and that these differences can often have far-reaching implications for processes and patterns of community structure (Murdoch, 1966; Ehrlich and Birch, 1967; Phillips, 1974; Vance, 1974; Leibold, 1989, 1996; Hunter and Price, 1992; Grover, 1994, 1995; Holt *et al.*, 1994; Polis and Strong, 1996; Leibold *et al.*, 1997; Polis, 1999; Chase *et al.*, 2000).

As evidenced by the papers in this special feature, plants can evolutionarily respond to herbivory by a variety of defensive mechanisms, which are typically placed into two broad categories (Abrahamson and Weis, 1997). *Resistance* reduces or eliminates herbivory through chemical (e.g. secondary compounds), structural (e.g. spines, thorns), and/or other (e.g. crypticity and mimicry) traits (Marquis, 1992). *Tolerance* reduces the fitness impact of herbivory through regrowth of lost tissues (see also Rosenthal and Kotanen, 1994; Strauss and Agrawal, 1999; Stowe *et al.*, 2000; Tiffin, 2000). Both tolerance and resistance traits may be costly (Rosenthal and Kotanen, 1994; Strauss and Agrawal, 1999; Stowe *et al.*, 2000), and plants are likely to face allocation trade-offs among tolerance, resistance, and other fitness enhancing functions, such as competitive ability (e.g. Van der Meijden *et al.*, 1988; Feinblum and Rausher, 1995; Mauricio *et al.*, 1997; Stowe, 1998; De Jong and Van der Meijden, 2000).

While the influence of plant resistance to herbivory on community structure is becoming well understood both theoretically and empirically (e.g. Phillips, 1974; Leibold, 1989, 1996, 1999; Grover, 1994, 1995; Holt *et al.*, 1994; Leibold *et al.*, 1997; Grover and Holt, 1998; Chase *et al.*, 2000), the influence of plant tolerance to herbivory at the community level has received little attention (but

see Augustine and McNaughton, 1998). Yet, given the recent advances in understanding the importance of tolerance at the evolutionary and population level, it is likely that these factors are also important at the community level (see also Strauss and Agrawal, 1999; Stowe *et al.*, 2000). Moreover, community-level interactions may also influence the fitness costs and benefits, and thus the evolutionary dynamics, of these plant traits (Tiffin, 2000).

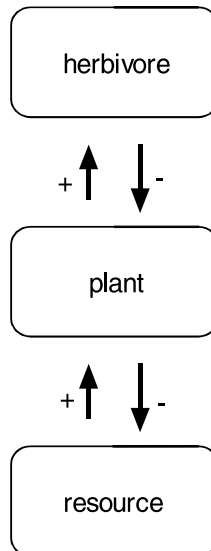
In this paper, we present an initial step toward theoretically understanding both (1) the effects of plant tolerance versus plant resistance on community-level processes and patterns, and (2) the effects of more complex community-level processes on the selective costs and benefits of plant tolerance and resistance.

### **An introduction to the modeling approach**

Evolutionary ecologists define tolerance as a norm of reaction of plant fitness in response to damage intensity. To model the effects of tolerance in a food web, however, it is more effective to define tolerance as the population dynamic (rather than the closely related individual-level) response of a plant species (or genotype) to herbivore density. Thus, rather than incorporating mechanistic realism into our current models, we have chosen to focus on the two paths by which herbivores may influence plant population dynamics. Most obviously, herbivores directly impact plant population dynamics by damaging or killing individual plants. However, herbivores also indirectly influence plant population dynamics via feedback from their indirect effect on resource availability.

The first model represents a food chain consisting of an herbivore species that feeds on a single plant species, which is limited in growth by a single resource (Fig. 1). In the long term, increasing herbivore density has two effects on this simple community. First, increasing the number of herbivores attacking plants directly increases the plant death rate. Second, because it reduces plant density, increasing herbivore density indirectly increases resource availability, which can stimulate plant growth rate, and thus decrease the overall effects of herbivory. This model thus highlights two ways that evolutionary changes in plant traits could reduce their herbivore density dependence. First, plants could evolve resistance, which would decrease the attack rate of herbivores on plants, thereby reducing the density dependence of plant death rate on herbivores. Second, plants could evolve tolerance, which would increase the resource-dependent growth rate that benefits from the indirect effects of herbivory on resource availability.

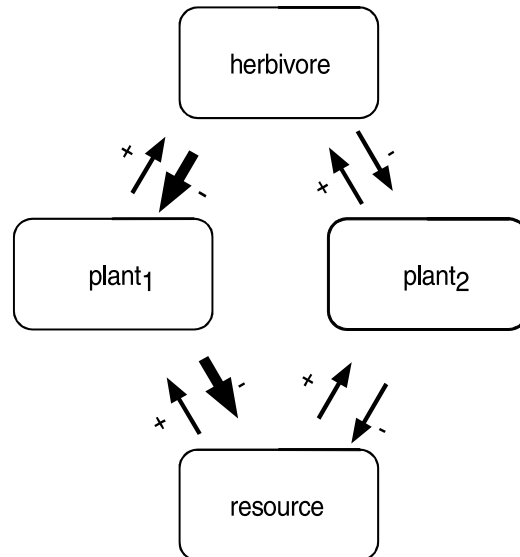
The second model we consider represents a simple food web consisting of a single herbivore species that feeds on two plants species, which in turn



*Figure 1.* A food chain in which a single plant species is limited by one resource and is fed on by one herbivore species. The arrows and symbols indicate directions and signs of direct effects. The magnitudes (and therefore, signs) of indirect effects are equal to the product of their composite direct effects. For example, herbivores negatively impact the plant population, which in turn has a negative effect on the resource; consequently, herbivores have a positive indirect effect on both resources and plants.

are limited by a single resource (Fig. 2). The two plant species may differ in resistance, such that the attack rate of the herbivore is lower on the more resistant plant species, or in tolerance, such that the resource dependent growth rate is higher for the more tolerant plant species. The more resistant plant species, subject to a lower attack rate, will have a lower death rate in the presence of herbivores, and increasing herbivore density will increase the relative difference in death rate between the species. The more tolerant species, with a higher resource dependent growth rate, will increase its relative difference in growth rates between the species as increasing herbivore density increases resource availability.

To more formally model how these two mechanisms contribute to plant–herbivore interactions in food webs, we use a classical theoretical framework based on consumer–resource models (MacArthur, 1972; Tilman, 1982, 1988; Holt *et al.*, 1994; Leibold, 1995, 1996; Grover and Holt, 1998). These models are based on a sound mathematical foundation, but are relatively simple and easily presented using graphical analyses. While these simple models can not substitute for more rigorous mathematical analyses, they are particularly useful



*Figure 2.* A food web in which two plant species are limited by the same resource and fed on by the same herbivore species. The arrows and symbols indicate directions and signs of direct effects, as in Figure 1. The width of the arrows designates the magnitude of the effect of herbivores on plants and plants on resources.

as a first approximation to understanding complicated processes (Leibold, 1995; J.M. Chase and M.A. Leibold, unpublished book).

We first present the mathematical formulation and graphical representation of a simple three trophic-level system consisting of an abiotic nutrient resource ( $R$ ), plant ( $P$ ), and herbivore ( $H$ ). We model abiotic nutrients at the base of the food web, rather than some other factor such as energy, because both plants (Tilman, 1988) and herbivores (e.g. White, 1993; Sterner and Hesson, 1994; Elser and Urabe, 1999) often seem to be nutrient limited rather than energy limited, and because many of the recycling effects of herbivores on these nutrients can be approximated by assuming the system is closed, leading to a mass balance constraint (MBC) (Grover, 1994, 1995; Holt *et al.*, 1994; Grover and Holt, 1998). Furthermore, we assume that herbivores are limited only by plant abundance, and that plants are limited only by nutrient abundance and herbivores, (i.e. the food web is closed), and the interactions within the food web do not vary stochastically. Finally, for ease of graphical representation, we assume that both plants and herbivores remove their food (nutrients or plants, respectively) at a constant rate, that is the functional response is linear (Type I). However, these models are robust to several deviations from these assumptions (Leibold, 1996; Grover and Holt, 1998).

### A model of a simple food chain

Given the above qualifications, a reasonable analytical caricature of the dynamics of a three species food chain consisting of abiotic resources ( $R$ ), plants ( $P$ ), and herbivores ( $H$ ) can take the following form:

$$\begin{aligned} dR/dt &= \frac{c'P}{b'} + \frac{cH}{b_H} + aPH\left(\frac{1}{b'} - \frac{b}{b_H}\right) - d'RP \\ dP/dt &= P(a'b'R - c' - aH) \\ dH/dt &= H(abP - c) \end{aligned} \quad (1)$$

Parameters with primes refer to traits of the plant population ( $P$ ), while parameters without primes refer to traits of the herbivores ( $H$ ). Thus the variable  $c'$  refers to the density-independent loss of the plant, while  $c$  refers to the density-independent loss of the herbivore. Similarly,  $a'$  refers to the uptake rate of  $R$  by plants ( $P$ ), while  $a$  refers to the attack rate of plants ( $P$ ) by herbivores ( $H$ ). Finally,  $b'$  represents the conversion of  $R$  into new plants ( $P$ ),  $b$  refers to the conversion of plants ( $P$ ) into herbivores ( $H$ ), and  $b_H$  represents the conversion factor of  $R$  into herbivores ( $H$ ). Note that  $b_H \neq b'b$  because of transfer inefficiencies. Because  $b'$  and  $b_H$  represent the conversion of  $R$  into  $P$  and  $H$ , the inverse of these,  $P/b'$  and  $H/b_H$  represent the amount of  $R$  tied up in the populations of  $P$  and  $H$ , respectively. The trick with these models that allows an easy algebraic solution to the equilibrium of this system, as well as the presentation of this three-dimensional system into a two-dimensional graphical analysis (Fig. 3), is the assumption that the system is closed according to the MBC. Given this assumption, rather than modeling  $R$  as  $dR/dt$ , it can instead be represented by an equation for mass balance

$$R = S - \frac{P}{b'} - \frac{H}{b_H} \quad (2)$$

Here,  $S$  refers to the total amount of resource that is available to the system (an independent predictor of system productivity).

Solving these equations at equilibrium yields several results. In all cases, we examine the response of the system along axes of  $R$  and  $H$ . To determine the response of plants ( $P$ ) along these axes, we set the dynamics of  $P$  ( $dP/dt$ ) to 0, and solve for  $H$ .

$$H = \frac{a'b'}{a}R - \frac{c'}{a} \quad (3)$$

This equation describes a line, known as the zero net growth isocline (ZNGI) of plants ( $P$ ) relative to resources ( $R$ ) and herbivores ( $H$ ). As its name suggests, this line indicates the combinations of resource and herbivore densities at which plant population growth equals zero. The  $x$ -intercept of this line is

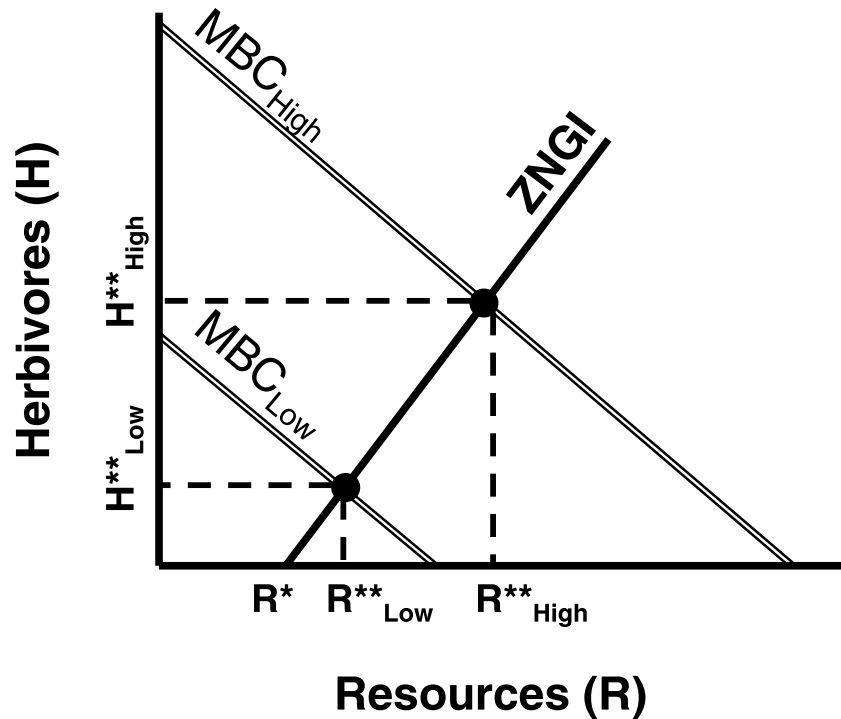


Figure 3. A representative ZNGI (solid line) and MBC (double line), as defined in text. The lower MBC is for a system with low  $S$ , and the upper MBC is for a system with high  $S$ . Filled circles represent stable equilibria at each level of  $S$ . The  $x$ -intercept of the ZNGI, denoted by  $R^*$ , represents the level to which the plant can reduce resources in the absence of herbivores.  $H^{**}$  and  $R^{**}$  represent the predicted equilibrium abundances of herbivores and predators respectively for each resource supply rate.

equivalent to Tilman's (1982)  $R^*$  of the plant for a single resource. The  $R^*$  in our model is the level to which the plant population can deplete the resource, when herbivores are absent. A species with a lower  $R^*$  can exclude any species with a higher  $R^*$ ; hence,  $R^*$  is a measure of plant species' competitive ability. The  $R^*$  is obtained by setting  $H = 0$  and solving for  $R$ , which gives  $R^* = c'/d'b'$ . With  $H > 0$ , the slope of the line, which is given by  $d'b'/a$ , denotes the effect of herbivore density on the amount of resources needed by the plant to maintain zero net growth. The steeper the ZNGI, the less dynamically affected  $P$  is by  $H$  (see Holt *et al.*, 1994; Leibold, 1996).

The other feature that can be predicted from this model when the system is at equilibrium is the MBC. The MBC is obtained by solving Equation (2) for  $H$  after substituting the equilibrium density of plants ( $P^* = c/ab$ ), giving

$$H = b_H \left( S - R - \frac{c/ab}{b'} \right) \quad (4)$$

The slope of the MBC is  $-b_H$ , and its intercepts are determined by the traits of the species ( $a$ 's,  $b$ 's, and  $c$ 's) as well as the total resource supply ( $S$ ) in the system.

The position of the MBC (Equation (4)) can be overlaid on the same axes as the ZNGI (Equation (3)), whose intersection determines the equilibrium abundances of the system at a given resource supply ( $S$ ) (Fig. 3). The equilibrium values of  $R$  and  $H$  at this intersection are denoted by  $R^{**}$  and  $H^{**}$ . Since the MBC is partially determined by the resource supply ( $S$ ), increasing  $S$  increases the level of the MBC (Fig. 3), thereby increasing the equilibrium levels of  $H$  and  $R$ , but not  $P$  (since increased plant production is immediately transformed into herbivore biomass) (Holt *et al.*, 1994).

### Costs and benefits of plant tolerance vs. resistance traits

In this section, we briefly explore how various mechanisms by which plants incur fitness costs and benefits of tolerance and resistance (Van der Meijden *et al.*, 1988; Grover, 1994, 1995; Schmitz, 1994, 1997; Fineblum and Rausher, 1995; Ritchie and Tilman, 1995; Leibold, 1996, 1999; Strauss and Agrawal, 1999; de Jong and Van der Meijden, 2000; Stowe *et al.*, 2000; Tiffin, 2000) can be incorporated into this simple food chain model. In the context of the models discussed here, the ecological costs of traits that reduce dynamical effects of herbivores (including both tolerance and resistance) are manifest in the  $x$ -intercept ( $R^*$ ) of a species, which denotes its ability to reduce resource levels in the absence of herbivory. Similarly, the ecological benefits of tolerance and resistance traits are manifested in the slope of a species' ZNGI; steeper sloped ZNGIs reflect species that are less dynamically affected by herbivory (Fig. 3).

From the equation of a species' ZNGI (Equation (3)), the slope (benefits) and intercept (costs) can be described in terms of the species' traits. The benefit of reducing the dynamical effect of herbivores is reflected by steeper sloped ZNGIs, and the slope of the ZNGI is given by  $d'b'/a$ . A steeper ZNGI can be achieved in two ways. First, the herbivore attack rate ( $a$ ) may be decreased by traits imparting resistance. Second, a higher capacity for regrowth, and thence tolerance, can be achieved by increasing the product of the resource consumption ( $a'$ ) and conversion ( $b'$ ) rates.

When there is a cost to tolerance or resistance, the less affected species (steeper slopes) will be the poorer competitors (higher  $x$ -intercept = higher  $R^*$ s), and there should be a positive correlation between the slopes and intercepts of the ZNGIs. Since  $R^* = c'/d'b'$ , there are two potential (but not mutually exclusive) mechanisms by which a species could incur a cost of herbivore resistance or tolerance. A cost, through an increase in  $R^*$ , will occur

with an increase in the density independent loss rate ( $c'$ ), or a decrease in the product of the resource consumption ( $a'$ ) or conversion ( $b'$ ) rates.

Plant resistance is often thought to confer fitness costs through one of several mechanisms (e.g. Coley *et al.*, 1985; Simms, 1992; Mole, 1994; Agrawal *et al.*, 1999; Tiffin, 2000; other papers in this issue). These mechanisms include: (1) allocational costs of resources used to synthesize chemical or structural defenses which cannot be used for other fitness enhancing functions, such as reproduction (affecting  $c'$  and/or  $b'$ ). (2) increased costs associated with maintaining toxic compounds (affecting  $c'$  and/or  $b'$ ). (3) costs due to reduced uptake ability ( $a'$ ) with resistance traits, particularly resource uptake organs (e.g. leaves and roots) which may be especially vulnerable to herbivory. Further, recent evidence has suggested that even when resistance traits are only induced following the feeding actions of herbivores, rather than constitutive defenses (which are always present), a variety of costs can be incurred (e.g. Agrawal *et al.*, 1999).

Likewise, plant tolerance traits are also envisioned to involve fitness costs (e.g. Rosenthal and Kotanen, 1994; Strauss and Agrawal, 1999; de Jong and Van der Meijden, 2000; Hochwender *et al.*, 2000; Stowe *et al.*, 2000; Tiffin, 2000; other articles in this issue). Simply increasing plant tolerance ( $a'b'$ ) without altering other traits does not lead to a fitness cost. This is because simply increasing plant tolerance will generally decrease  $R^*$  (making the species a better competitor), because  $a'b'$  (tolerance) is in the denominator of  $R^*$  (recall that  $R^* = c'/a'b'$ ). Thus, to incorporate fitness costs,  $R^*$  can decrease when tolerance increases if it also involves a strong increase in density-independent mortality ( $c'$ ). Although somewhat speculative, tolerance may increase  $c'$  through the use of protected storage organs and stored (unused) meristems (Olson and Richards, 1988; Cline, 1994; Marquis, 1996; Hochwender *et al.*, 2000; Stowe *et al.*, 2000), or the ability a plant to up-regulate its metabolic rate in response to herbivory. Finally, tolerance may confer costs through an allocation trade-off with resistance traits (De Jong and Van der Meijden, 2000; Stowe *et al.*, 2000). In this case, resources allocated to storage (tolerance) might not be available for resistance, which would produce a negative correlation between tolerance ( $a'b'$ ) and resistance ( $a$ ).

### **The influence of plant tolerance and plant resistance in food webs**

In this section, we extend our analyses of costs and benefits of plant defensive traits to a more complex situation where there is a second plant species. In theoretical models of interactions within communities, a variety of different assumptions lead to a general prediction: for species to coexist either lo-

cally or regionally, they must differ in some aspects of their ecological traits. That is to say, no two species can occupy the same niche and coexist (e.g. Gause, 1936; MacArthur, 1972; Tilman, 1982; Chesson, 1991; Leibold, 1995). In a simple community with only one limiting resource and relatively linear interactions, a species that is able to maintain the lowest abundance of the limiting resource (i.e. the lowest  $R^*$ ) will always win in competition and exist alone (Tilman, 1982; Grover, 1997). However, if two plant species with one limiting resource are also consumed by a single herbivore, plant coexistence can occur under several conditions (Grover, 1994, 1995; Holt *et al.*, 1994; Leibold, 1996).

Herbivores can mediate the outcome of plant competition and prevent competitive exclusion by one species (facilitate coexistence) when three conditions are met. First, there must be a trade-off between the plant species in their abilities to consume resources versus their abilities to maintain fitness in the presence of herbivores, which causes their ZNGIs to intersect (Holt *et al.*, 1994; Leibold, 1996) (Fig. 4). That is, one species (species 1 in Fig. 4a) must be a superior resource competitor (i.e. lower  $R^*$ ) that is strongly controlled by the herbivores (i.e. shallower ZNGI) while the other species (species 2 in Fig. 4a) must be an inferior resource competitor (higher  $R^*$ ) that is less susceptible to

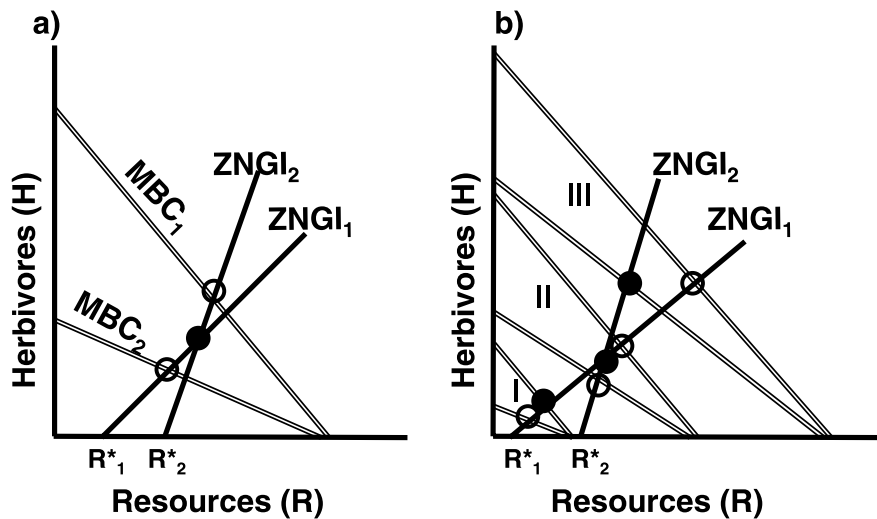


Figure 4. (a) ZNGIs and MBCs for two plant species (labeled 1 and 2) that compete for a common resource and are eaten by a common predator. One species is a superior resource competitor (lower  $R^*$ ) while the other is more resistant to herbivores (steeper ZNGI). In this case, the ZNGIs intersect within the MBCs, and the solid circle represents a stable equilibrium where the two species coexist. The open circles, where each species exists alone, are unstable equilibria. (b) The effects of varying  $S$  on the interaction depicted in (a). Each zone (I, II, and III) represents the situation for a different level of resource supply (low, medium, and high, respectively). Solid and open circles are as in (a).

herbivores (steeper ZNGI). Second, resource availability ( $S$ ) must be at an intermediate level, so that the strategies of both species produce similar net benefits. If instead the resource supply is low, the better resource competitor wins and exists alone at a globally stable equilibrium (Fig. 4b). This is because at low resource availability, the cost associated with maintaining defense against herbivores is high relative to its benefits. In contrast, if the resource supply is high, the better defended species wins and exists alone at a globally stable equilibrium (Fig. 4b). In this case, the benefits gained by defense against herbivores far outweigh the costs of this defense (for proof of these claims, see Holt *et al.*, 1994; Leibold, 1996). Finally, the presence of an ecological equilibrium also depends critically on whether plant species defend themselves through tolerance or resistance mechanisms. Previous analyses of these types of food web models have generally assumed that defended plants utilize a resistance mechanism (e.g. chemical or structural defenses) that decreases the attack rate ( $a$ ) of herbivores (Grover, 1994, 1995; Holt *et al.*, 1994; Leibold, 1989, 1996). Below, we compare and contrast the outcomes when plants defend themselves from herbivory with either tolerance or resistance traits.

### Resistant vs. non-resistant plant species

Plant resistance to herbivory will affect three parameters in the model. First, resistant species will typically have lower herbivore attack rates ( $a$ ), lower rates of conversion of plants into herbivores ( $b$ ), and possibly lower conversion of resource uptake into plant biomass ( $b'$ ). Thus, we expect that the product of these three traits ( $abb'$ ) will typically be lower for a species that possesses more resistance than for a competitor species with less resistance ( $abb'_{\text{less resistant}} < abb'_{\text{more resistant}}$ ). Thus, the MBC line of the more resistant species will fall to the lower left of the MBC of the species with less resistance, regardless of resource supply ( $S$ ) (Holt *et al.*, 1994; Grover and Holt, 1998). In this configuration, the less resistant species provides more nourishment to the herbivore. For a given resource supply, then, a food chain with a less resistant plant species can maintain a higher density of herbivores than can a food chain with a more resistant plant species.

This situation can produce local coexistence when the species whose fitness is more sensitive to the presence of herbivores (shallower sloped ZNGI) is also better food for that herbivore (higher MBC). When the supply rate ( $S$ ) is such that the intersection of the ZNGIs occurs between the two MBCs, there is a stable equilibrium where the two plant species coexist (Fig. 4a). Mathematical proof of this claim can be found elsewhere (Holt *et al.*, 1994; Leibold, 1996; Grover and Holt, 1998), but the stability of this situation can be visualized by recognizing that the system will tend towards ZNGI–MBC intersections that

are higher (maintain higher herbivore density) and to the left (maintain lower resource density).

Figure 4b shows how varying resource supply ( $S$ ), which shifts the absolute (but not relative) position of the two MBCs, influences the dynamics and coexistence of the system. In short, low resource supply ( $S$ ), where the MBCs are fully below the intersection of the ZNGIs, favors dominance by the species with the lowest  $R^*$  and shallowest ZNGI; that is, the less resistant species is favored. At high resource supply the MBCs are fully above the intersection of the ZNGI. The species that is least affected by herbivores (steeper ZNGI), but a poorer resource competitor (higher  $R^*$ ), can exclude the other species and dominate the community. Only at intermediate resource supply, the ZNGIs intersect within the bounds of the two MBCs, and the dynamics are as described above and in Figure 4a.

#### Tolerant vs. non-tolerant plant species

Next, we consider the case of competition between a species highly affected by herbivory and a plant that is tolerant of herbivory (i.e. high product of resource uptake [ $a'$ ] and conversion [ $b'$ ] rates). In this case, we assume that the tolerant species incurs costs (i.e. higher  $R^*$  value) but also receives benefits from being less susceptible to herbivory (i.e. steeper ZNGI). The ZNGIs of the two species consequently intersect, as in Figure 4, but produce a very different equilibrium. Here, although the tolerant plant has a steeper ZNGI due to the smaller dynamical influence of herbivores on its fitness, it also provides food for the herbivore and therefore maintains a higher MBC (i.e.  $abb'_{\text{more tolerant}} > abb'_{\text{less tolerant}}$ ) (Fig. 5). That is, by being tolerant of herbivory, the defended plant species can maintain a higher density of herbivores than can the undefended (superior resource competitor) plant species.

Examining the simple food web model depicted in Figure 5a shows that local coexistence of a more tolerant plant species and less tolerant, superior competitor is not possible. This is despite the fact that the ZNGIs do intersect and, in the case of Figure 5a, the supply rate ( $S$ ) is such that this intersection occurs between the two MBC lines. In this case, however, the MBC of the species that is less dynamically affected by herbivores (steeper ZNGI) is higher than that of the species more affected by herbivores, which makes the intersection between the two ZNGIs an unstable equilibrium (open circle in Fig. 5a). The equilibrium is unstable because it lies below or to the right of the points where each species' MBC intersects with its own ZNGI. As a result, the intersection of each species' ZNGI with its MBC (solid circles in Fig. 5a) represents a locally (but not globally) stable equilibrium. In this case, the realized local equilibrium is determined by the initial conditions from which the system started (see Holt *et al.*,

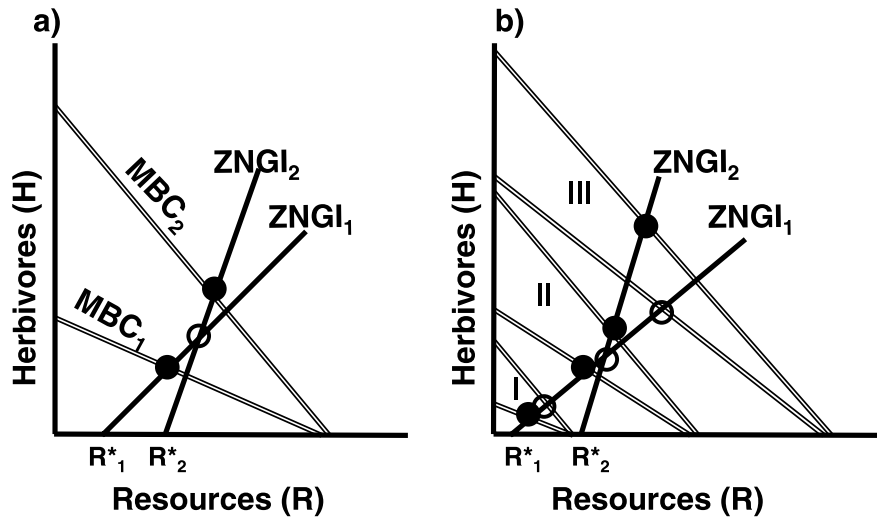


Figure 5. (a) ZNGIs and MBCs for two species of plants as in Figure 2, except here, the species with the steeper ZNGI is tolerant to herbivory (rather than resistant). In this case, the relative positions of the two MBCs are reversed relative to Figure 2, and the two species do not coexist at a locally stable equilibrium (open circle). Instead, the intersection of each species' ZNGI with its MBC represent alternative locally stable equilibria (closed circles). (b) The effects of varying resource supply on the system depicted in (a). Open and closed circles are as in Figure 4.

1994; Chase, 1999a), that is, the system will exhibit priority effects, and create alternative stable states under identical environmental (i.e. resource supply,  $S$ ) and biological (i.e. all species have access to the community) conditions. Thus, with or without herbivores, a tolerant species cannot coexist locally with a superior competitor. However, the presence of herbivores can allow these species to coexist regionally if each species has differential priority in each locality. Furthermore, varying the resource supply rate ( $S$ ) changes the outcome of interaction (Fig. 5b) in a manner similar to that found for species varying in resistance: The less tolerant species exists alone at low  $S$ , priority effects occur at intermediate  $S$ , and the more tolerant species exists alone at high  $S$ .

This graphical/analytical approach points to an important set of predictions and distinguishing characteristics of food webs that support tolerant vs. resistant plant species: Herbivores can facilitate local plant coexistence when plants defend themselves through resistance mechanisms (i.e. reduce the herbivore's attack rate,  $a$ ), but can facilitate regional, but not local coexistence when plants cope with herbivory through tolerance mechanisms (i.e. increase their own resource uptake,  $a'$ , and conversion,  $b'$ , rates). Another way of thinking about this is that when a worse competitor is better food for predators, such as with plant resistance, the average intraspecific effects of each species are greater than interspecific effects; a criterion necessary for local

coexistence in most models of species interactions (e.g. Lotka–Volterra competition models). Alternatively, when the worse competitive species is better food for predators, such as with a tolerant plant species, interspecific effects exceed intraspecific effects (because the tolerant species increases herbivore abundance, and has larger indirect negative effects on the non-tolerant species through apparent competition [Holt *et al.*, 1994]), and local coexistence is not possible. Below, we extend these simple ideas to determine when plant tolerance and/or plant resistance traits are favored in food webs.

### **Tolerant vs. resistant plant species**

Thus far, we have only considered the case of a superior resource competitor interacting with either a resistant or tolerant plant species in the face of herbivory. Now, we briefly consider some potential implications of the interactions between a tolerant and a resistant plant species in a food web. Specifically, we examine several cases with varying costs and benefits of the two anti-herbivore strategies.

We first consider the case in which the costs and benefits of both the resistant and tolerance traits are identical. Although both species will have identical ZNGIs, the MBCs of the tolerant species will be higher than that of the resistant species, because the tolerant species supports a higher density of herbivores. Since the ZNGIs of the two species are identical and completely overlap throughout the range between the MBC lines, there is no single equilibrium. Instead, the species can coexist anywhere within the range between the MBC lines. Because the situation where the ZNGIs completely overlap is quite unlikely, we do not further consider this case.

Next, we consider four cases in which only one plant species is expected to dominate, regardless of resource availability or herbivore pressure. First, if the cost: benefit ratio of either tolerant or resistant plant species is such that the benefit of at least one of the mechanisms always outweighs its cost, then the ZNGIs will not intersect. For example, in Figure 6a, the ZNGI of the resistant species occurs wholly to the left of that of the tolerant species, which indicates that in this environment the cost of resistance is small relative to the cost of tolerance. Such a case might be found when resistance mechanisms are relatively cheap; for example, if secondary metabolites involved in resistance also perform other functions, such as resisting ultraviolet light (Grammatikopoulos *et al.*, 1998). Second, the ZNGI of the tolerant species can occur to the left of that of the resistant species (Fig. 6b). This situation might be expected when tolerance is less costly than resistance, such as when traits conferring tolerance also provide the physiological means to deal with low water availability (Augustine and McNaughton, 1998), or when a single mechanism allows a

species to tolerate both density-independent damage (e.g. from hailstones, fire, or tree falls) and herbivory.

In more specialized cases, tolerance and resistance traits could entail identical costs (i.e. the species have the same  $R^*$ ), but different benefits (different ZNGI slopes) (not shown). For example, when a generalist herbivore prefers the highly edible tolerant species (e.g. Augustine and McNaughton, 1998) over the resistant species, the relative benefits of tolerance may be lower. Alternatively, the benefits afforded a tolerant species could exceed those of a resistant species if, for example, the secondary metabolites that defend a resistant species against generalist herbivores stimulate feeding or oviposition by a specialist herbivore (e.g. Berenbaum and Zangerl, 1999). Similarly, tolerance and resistance traits might confer identical benefits (i.e. by having ZNGIs with the same slope), but have different costs ( $R^*$ s in different positions). In this case, we expect that whichever strategy has the least costs (lowest  $R^*$ ), would always dominate.

Finally, we consider two cases with a trade-off between resistance and tolerance (Van der Meijden *et al.*, 1988; Rosenthal and Kotanen, 1994; Fineblum and Rausher, 1995; Mauricio *et al.*, 1997; Stowe, 1998; de Jong and Van der Meijden, 1999; Strauss and Agrawal, 1999; Stowe *et al.*, 2000). First, consider the situation in which a tolerant species competes better for resources (i.e. lower  $R^*$ ) in the absence of herbivores than does a resistant species, but is more

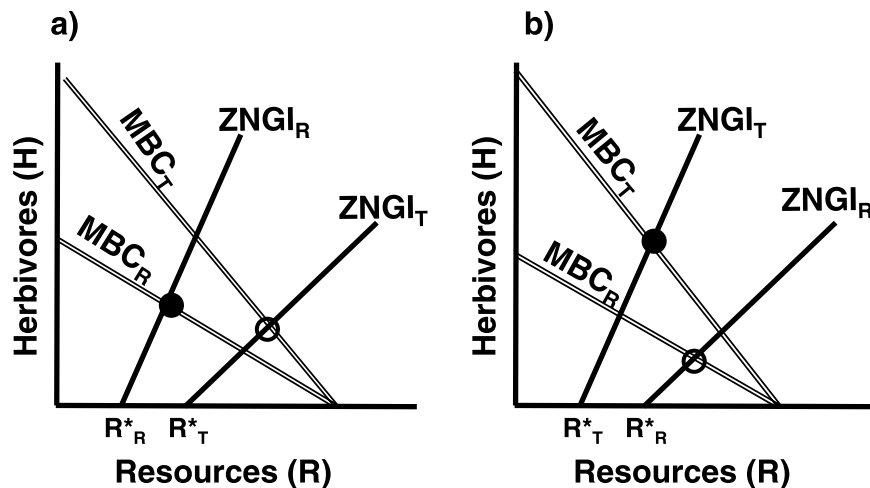


Figure 6. ZNGIs and MBCs of a tolerant (denoted with T subscripts) and a resistant (denoted with R subscripts) plant species that consume the same resource, and are consumed by the same herbivore. (a) The case when the resistant species incurs fewer costs (lower  $R^*$ ), and gains more benefits (steeper ZNGI) than does the tolerant species. (b) The case where the tolerant species incurs fewer costs, and gains more benefits than does the resistant species. Open and closed circles are as in Figure 4.

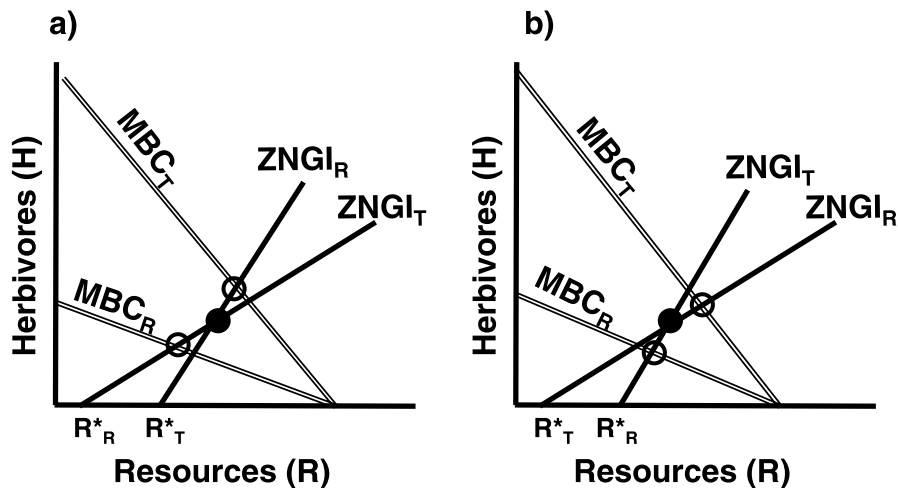


Figure 7. ZNGIs and MBCs of a tolerant and resistant plant species that incur different costs and benefits of those traits. (a) The case where the tolerant species incurs fewer costs (lower  $R^*$ ), but gains less benefit (shallower ZNGI). (b) The case where the resistant species incurs fewer costs, but gains less benefit. Open and closed circles are as in Figure 4.

dynamically affected by herbivory (i.e. shallower ZNGI) than is the resistant species (Fig. 7a). Because the tolerant species provides relatively better food for the herbivore than does the resistant species (i.e. the higher MBC), but is also more dynamically affected by the herbivore (shallower ZNGI), the two species are expected to coexist locally (i.e. the ZNGI intersection is a stable equilibrium) (a result qualitatively similar to Fig. 4a). Thus, when the resistant species incurs more costs, but gets more benefits than does the tolerant species, the two species may coexist locally.

Alternatively, when the tolerant species incurs more costs, but gains more benefits from its defense than does the resistant species (Fig. 7b), the tolerant species still provides better food for the herbivore, and thus has a higher MBC. However, because the tolerant species is now less dynamically affected by herbivores (i.e. a steeper ZNGI) than the resistant species, the criteria for local coexistence of the two species are not met. Instead, priority effects produce two alternative stable states (in a manner similar to Fig. 5a); the two species can coexist regionally, but not locally.

## Discussion

### *The empirical effects of tolerance and resistance at the community level*

Several recent studies have emphasized the importance of variation in plant susceptibility to herbivory for various aspects of community ecology such as

the strengths of species interactions, as well as plant abundance, diversity and composition (reviewed in Leibold *et al.*, 1997; Olff and Ritchie, 1998; Polis, 1999; Chase *et al.*, 2000). Theoretical models predict that under several circumstances, herbivores can facilitate coexistence among plant species by preferentially reducing the abundance of species that are better resource competitors (Vance, 1978; Armstrong, 1979; Leibold, 1989, 1996; Holt *et al.*, 1994; Grover, 1995; Grover and Holt, 1998). Furthermore, these models predict that better defended plant species will dominate in the presence of herbivores and at higher levels of resource supply, whereas species that are susceptible to herbivores, but better resource competitors will dominate in the absence of herbivores and at lower levels of resource supply. A variety of empirical studies at single sites have supported subsets of these predictions in both terrestrial (e.g. Schmitz, 1994, 1997; Ritchie and Tilman, 1995; Ritchie *et al.*, 1998) and aquatic (e.g. Leibold, 1989, 1999; Vanni and Layne, 1997; Murdoch *et al.*, 1998) ecosystems.

However, empirical evidence does not always support these models. In a review of the effects of ungulate herbivory on terrestrial plant communities, Augustine and McNaughton (1998) found many corroborative studies, but also a large proportion of studies showing alternative patterns. In these latter studies, herbivores did not shift species composition towards more resistant plant species. Instead, they drove species composition towards highly edible plant species capable of quick regrowth and tolerance to herbivory. Similarly, in a review of several studies in aquatic ecosystems, Agrawal (1998) found some cases in which herbivores shifted communities to more edible (and perhaps more tolerant) species of algae. In fact, highly edible species often survive and may even dominate under intense herbivory and with high resource availability (see also Moen *et al.*, 1993; Oksanen and Oksanen, 2000). These cases are some of the most difficult to explain with models incorporating differential plant resistance (Leibold *et al.*, 1997; Leibold, 1999; Chase *et al.*, 2000). Our models presented here suggest that these exceptions may represent situations in which plants have evolved more tolerance, rather than resistance to herbivory.

Because models that incorporate species variation in plant defense (e.g. Holt *et al.*, 1994; Leibold, 1996) predict the dominance of less defended species when productivity is low, they also predict that herbivores will have a large relative effects on plant biomass at lower productivity. In contrast, at higher productivity, more defended plants are expected to dominate in the presence of herbivores, and thus the overall effect of herbivores on plant biomass should be lower (Chase *et al.*, 2000). These predictions, too, have been supported by numerous empirical studies, but often with significant outliers.

For example, a review by Chase *et al.* (2000) found that the relative effect of large mammalian herbivores on plant biomass (determined from enclosure

experiments) was negatively correlated with potential primary productivity (i.e. rainfall). Even a cursory inspection of those data (Figs. 2 and 3 in Chase *et al.*, 2000) reveals a significant amount of variation around this relationship (i.e. the correlations only explained 19–21% of the variation in herbivore effect). Further, there was a much higher proportion of unexplained variance at intermediate levels of primary productivity (J.M. Chase, unpublished analyses). Thus, at intermediate productivity herbivores sometimes exerted very strong effects on plant biomass and composition, but at other times these effects were weak. Our analyses here suggest that incorporating plant tolerance into models may begin to explain this variation.

As described above, and as predicted by previous models, in ecosystems dominated by two plant species, one resistant and one a superior resource competitor (Fig. 3), the two species will coexist at intermediate levels of productivity and the relative effect size of herbivores on plants will be intermediate. However, as we also described above, in ecosystems dominated by one tolerant plant species and one superior resource competitor (Fig. 4), the two species are not expected to coexist locally. Instead, the relative effect size of herbivores will either be very small, if priority favors dominance by the tolerant species, or very large, if priority favors dominance by the superior resource competitor that is also more vulnerable to herbivory. Thus, in broad surveys that might include many plant species using both tolerance and resistance mechanisms (e.g. Chase *et al.*, 2000), we should expect large amounts of unexplained variance, especially at intermediate resource levels.

Leibold (1999) also used models that incorporate variation in the resistance of plant species to predict how species diversity, composition, and relative resistance of algae should vary among pond ecosystems arrayed along gradients of potential primary productivity (i.e. nutrients). A particularly interesting pattern predicted by these models is a unimodal (i.e. hump-shaped) relationship between species diversity and primary productivity (Leibold, 1996, 1999). At low productivity, non-resistant species that are superior resource competitors exist alone, at intermediate productivity, the species coexist and richness is highest, and at high productivity, richness again declines as the resistant plant species dominates the system. While Leibold (1999) found significant evidence of such hump-shaped productivity–diversity relationships, there was again a great deal of unexplained variance (see Figs. 4 and 5 in Leibold, 1999). Although species richness was highest at intermediate productivity, there were several ponds with intermediate productivity that did not support more species than found at either high or low productivity. Indeed, several observed unimodal productivity–diversity relationships exhibit similar variability at intermediate levels of productivity (see e.g. Tilman and Pacala, 1993; Rosenzweig, 1995; Waide *et al.*, 1999).

Again, different plant defense mechanisms (tolerance vs. resistance) may be responsible for some of this unexplained variation in productivity–diversity relationships. Our models predict such variation if, at some local sites of intermediate productivity, resistant plant species coexist with superior resource exploiters (causing high local site diversity), whereas at other intermediate productivity sites, tolerant plant species dominate and do not locally coexist with other species. Indeed, while Leibold (1999) found that many resistant algal species occurred in the predicted habitats (e.g. sites with high herbivory and high productivity), this relationship was weak, and many edible (perhaps more tolerant) species also have existed in those types of habitats.

*Some implications for the evolution of resistance and tolerance*

Throughout the above sections, we have used species as the unit with which to examine the community-level effects of differences among plants in tolerance and resistance. Because these niche-based models (*sensu* Leibold, 1995) mechanistically incorporate fitness, however, the characteristics (i.e. ZNGIs and MBCs) that we assigned to species in the above models can also be considered different strategies (i.e. genotypes or phenotypes) within a single species (Leibold, 1998; Chase, 1999b). Hence, these models can also provide insights into the evolution of genotypes or phenotypes differing in resistance and tolerance. In particular, these types of models are useful when attempting to identify likely directions of selection and optimal solutions to given constraints and environmental conditions. They cannot, however, substitute for more rigorous models of evolutionary dynamics, since our models assume static interactions and fixed traits.

Using our approach, we can predict whether tolerance or resistance traits will be favored, given different constraints (i.e. costs and benefits) and environmental conditions (e.g. resource supply), and compare these predictions with others in the literature. For example, Coley *et al.* (1985) predicted that in high resource environments, plants can grow quickly, and should invest less in resistance, whereas in lower resource environments, plants grow more slowly and should therefore invest more in resistance. Superficially, this prediction appears to oppose ours (see also Holt *et al.*, 1994; Leibold, 1996), in that we predict that higher resource environments will favor defended plants (either tolerant or resistant) over plants with no defenses. However, Coley *et al.* (1985) have not simply asked when plants should defend or not defend. Instead, they have explored when plants should allocate resources to resistance (i.e. chemical defenses) vs. tolerance (i.e. higher growth rate). When we make similar assumptions (specifically, that tolerance traits are more costly but confer greater benefits than resistance traits), our model makes predictions that are identical

to those of Coley *et al.* (1985). That is, low resource supply should favor resistance (e.g. chemical or structural defense), and increasing the resource supply should favor tolerance (i.e. regrowth) (Fig. 6b).

In contrast to the model by Coley *et al.* (1985), however, our analysis also allows us to consider interactions among other members of the community, which could prove important to the evolution plant defenses (Adler and Karban, 1994; Tiffin, 2000). Our model demonstrates that, in many cases the fitness of a plant phenotype, which determines whether it can invade a given situation, depends on both direct and indirect ecological effects created by interactions with other species and the environment. Tiffin (2000) also produced a model that explicitly allows for interactions with a dynamic herbivore and competitor plant population. In his model, the frequencies and resulting fitnesses of genotypes in a plant population can evolve at a single locus with alleles for tolerance and resistance traits, which provides an excellent check on our model. Many of the predictions that Tiffin (2000) obtained from his genetical model of the evolution of tolerance and resistance are very similar to the predictions that we make. For example, Tiffin found that when plant populations evolve resistance, a stable dimorphism can be maintained between resistant individuals and undefended individuals that do not incur costs (i.e. superior competitors). This result is directly analogous to our prediction that resistant species can coexist with superior competitors under many circumstances. Alternatively, Tiffin (2000) found that when tolerance is favored, such a dimorphism (i.e. coexistence) is not expected. Again, our analysis corroborates this result, we find that tolerance traits should either become fixed or be eliminated from a given population, depending on priority effects.

We believe that our analyses can extend and complement more detailed evolutionary models, such as that of Tiffin (2000), and suggest avenues for more detailed evolutionary modeling. We propose that both evolutionary ecology and community ecology will benefit by combining these different sorts of modeling approaches in a concerted effort to understand both trait evolution and its community-level implications.

#### *Some possible extensions of the approach*

The modeling approach we have taken here can only begin to address the differential community effects of plant tolerance relative to plant resistance. We do not intend our predictions to close the topic on the influence of plant tolerance and resistance traits on community-level patterns, but rather we hope to stimulate avenues for further exploration. Of course, future directions on this topic are too numerous to list here, but some avenues of investigation that

might prove important as the assumptions of this simple model are relaxed include:

- (1) *Resource subsidies and decoupled herbivore populations.* Many vertebrate herbivores (and even some insects) travel long distances, and in effect decouple their population dynamics from any local plant community (Jeffries, 2000). Agriculture and supplemental feeding of vertebrate herbivores also decouples plant–herbivore interactions (Augustine and McNaughton, 1998). When the dynamics of herbivores are decoupled from their food plants, the costs and benefits of tolerance and resistance will be altered.
- (2) *Dynamic herbivore populations and time-varying herbivory.* When herbivores exhibit cyclic population dynamics (e.g. Krebs *et al.*, 1995; Turchin *et al.*, 2000), or the levels of herbivory vary through time and/or space, the selective pressures on resistance and tolerance traits will also vary.
- (3) *Spatial and temporal variation in environmental conditions.* In the models described above, the parameters (i.e.  $a$ 's,  $b$ 's, and  $c$ 's) that determine the ZNGIs and MBCs are not actual properties of the species themselves, but instead are a product of the species in its environment. In environments where these factors vary spatially or temporally, the selective costs and benefits of tolerance and resistance traits are also likely to be variable.
- (4) *Ecosystems with open nutrient cycling.* Our model explicitly assumes that the ecosystem is closed, and resources are recycled. However, many ecosystems may be more appropriately modeled assuming that the ecosystem is open, which may importantly influence our predictions.
- (5) *Plants that have induced, rather than constitutive resistance traits.* When a plant can induce resistance traits following initial herbivore attack, the relative costs of carrying these traits may be reduced (but not necessarily eliminated), and thus the cost: benefit ratio of being resistant vs. tolerant may change.

## Conclusions

Community ecologists have long recognized the importance of trait differences among species within trophic levels for determining patterns of community structure (e.g. differences in plant susceptibility to herbivory, Phillips, 1974; Leibold, 1989, 1996; Hunter and Price, 1992; Holt *et al.*, 1994; Leibold *et al.*, 1997; Polis, 1999; Chase *et al.*, 2000). However, this work has primarily focused on how plant resistance influences patterns of species interactions and community structure, with comparatively little attention being paid to plant tolerance. Furthermore, the influence of community-level interactions on the

evolution of plant resistance and tolerance traits has rarely been examined theoretically or empirically.

In this paper, we used simple set of models to explore ways in which the effects of plant resistance and tolerance might be manifested differently at the community level, yielding some important predictions. In particular, species with resistance traits are more often predicted to coexist at the local level with undefended species, whereas species with tolerance traits, owing to their ability to support herbivore populations, cannot generally coexist locally, but can coexist regionally. This regional, but not local, coexistence results because tolerant species create two alternative stable equilibria, one dominated by the tolerant species, and the other dominated by a non-defended species that is a superior competitor because it does not incur costs of tolerance. The equilibrium to which a given local site proceeds will depend on initial conditions, or priority effects. Indeed, we suggest that some of the variation frequently seen in natural communities might result from such alternative stable equilibria at local scales. Thus, patterns of coexistence, diversity and trophic dynamics might all depend on whether plants evolve tolerance vs. resistance to herbivory.

Here, we hope to provide an impetus for further investigation into the important differences in community-level responses to plant resistance vs. tolerance in food webs. Future investigations at both the theoretical and empirical level should recognize that tolerance and resistance are both ways in which plants can evolutionarily respond to herbivory, but that their selective pressures, as well as their effects at the community level, can be quite distinct (see also Tiffin, 2000).

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