Keystone Predation and Plant Species Coexistence: The Role of Carnivore Hunting Mode

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ABSTRACT: Plant communities are shaped by bottom-up processes such as competition for nutrients and top-down processes such as herbivory. Although much theoretical work has studied how herbivores can mediate plant species coexistence, indirect effects caused by the carnivores that consume herbivores have been largely ignored. These carnivores can have significant indirect effects on plants by altering herbivore density (density-mediated effects) and behavior (trait-mediated effects). Carnivores that differ in traits, particularly in their hunting mode, cause different indirect effects on plants and, ultimately, different plant community compositions. We analyze a food-web model to determine how plant coexistence is affected by herbivore-consuming carnivores, contrasting those causing only density-mediated effects with those causing trait-mediated effects as well. In the latter case, herbivores can adjust their consumption of a refuge plant species. We derive a general graphical model to study the interplay of density- and trait-mediated effects. We show that carnivores eliciting both effects can sustain plant species coexistence, given intermediate intensities of behavioral adjustments. Coexistence is more likely, and more stable, if the refuge plant is competitively dominant. These results extend our understanding of carnivore indirect effects in food webs and show that behavioral effects can have major consequences on plant community structure, stressing the need for theoretical approaches that incorporate dynamical traits.

Keywords: apparent competition, behavior, dynamical traits, indirect effects, herbivory, top-down.

Introduction

A perennial interest in ecology is resolving the degree to which the structure and dynamics of plant communities are controlled by bottom-up processes such as competition for nutrients (Tilman 1982; Goldberg and Barton 1992) and top-down processes such as selective herbivory (Holt and Lawton 1994; de Mazancourt et al. 1998; Olff and

Ritchie 1998). Resource competition and predation by herbivores have been shown to have intricate connections (Olff and Ritchie 1998; Chase et al. 2002; Hillebrand et al. 2007; Chesson and Kuang 2008). In particular, herbivory can mediate the coexistence of plant species with different competitive abilities, so that predation is "keystone" for species diversity (keystone predation; Leibold 1996). Nevertheless, it is increasingly apparent that our understanding of the interplay of bottom-up and top-down processes will be incomplete without consideration of an additional top-down factor: carnivore indirect effects mediated by herbivores (Grover 1997; Hulot and Loreau 2006). Indirect effects caused by the predators of herbivores can indeed be an important determinant of total plant biomass (Borer et al. 2005), plant productivity (Paine 2002; Duffy et al. 2003; Schmitz 2003), plant diversity (Lubchenco 1978; Wootton 1995; Paine 2002; Tessier and Woodruff 2002; Schmitz et al. 2003; Duffy et al. 2005), and nutrient cycling (Schmitz et al. 2010). The challenge remains, however, to explain the basis for differences in carnivore indirect effects on plant community composition and dynamics (Duffy et al. 2007; Schmitz et al. 2008).

There are generally two ways that carnivore indirect effects may propagate to plants (Schmitz et al. 2004). Carnivores could cause numerical reductions in herbivore populations directly by killing them. Fewer herbivores then translate into lower impacts on plants. In this case, the indirect effect of carnivores on plants is mediated by changes in herbivore population density and is therefore called a density-mediated indirect interaction, or DMII (Abrams 1995; Werner and Peacor 2003). Alternatively, the mere presence of predators in a community can force herbivores to make behavioral choices between vital activities such as feeding and avoiding contact with predators (Sih 1982; Brown et al. 1999). Avoiding carnivores detracts from foraging, which also causes reductions in herbivore impacts on plants (Schmitz et al. 2004). In this situation, however, the indirect effect of carnivores on plants derives

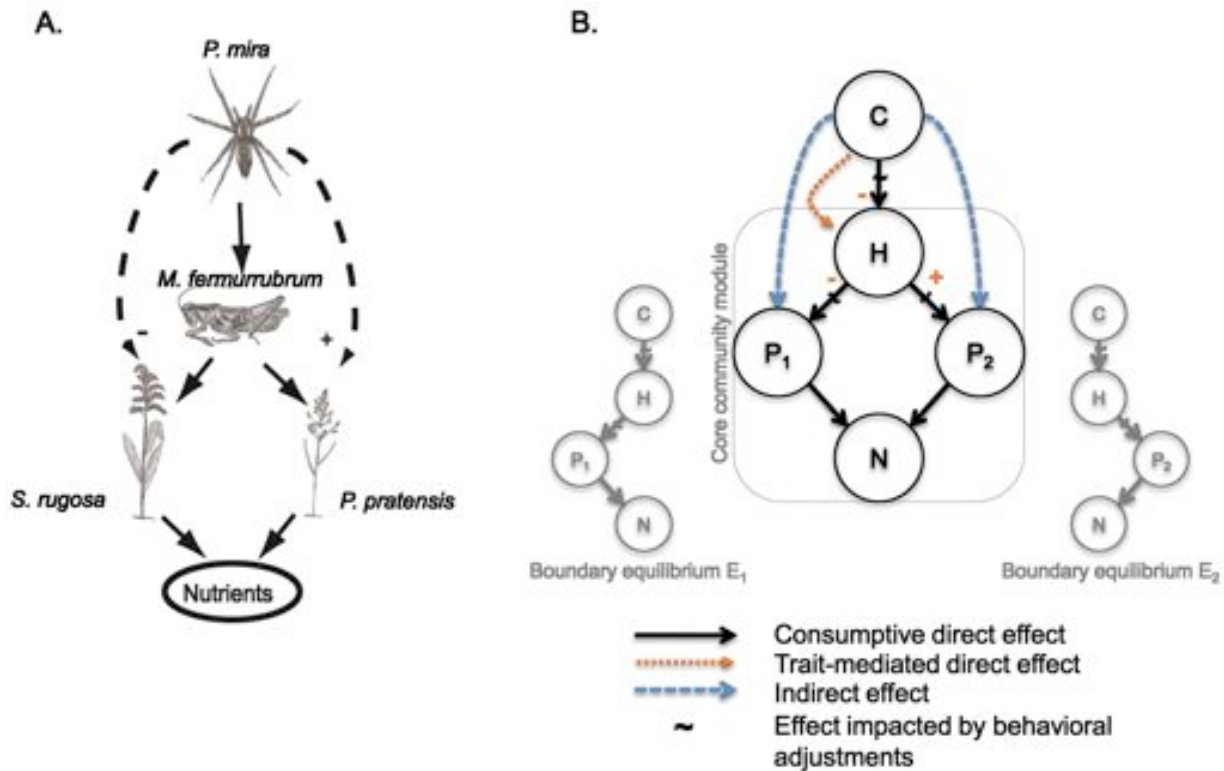* Corresponding author; e-mail: vincent.calcagno@mcgill.ca.

A.

B.

Figure 1: Community module. *A*, The grassland ecosystem inspiring the model and the specific function in equation (3). The spider genus is *Pisaurina*, the grasshopper is *Melanoplus*, and the plants are *Solidago* and *Poa*. *Pisaurina mira* is a sit-and-wait hunter, causing opposite indirect effects on the two plant species. Schematic by O. Schmitz. *B*, Model. N = amount of nutrients available, P_1 = biomass of plant species 1, P_2 = biomass of plant species 2, H = biomass of the herbivore, C = biomass of the carnivore. The two boundary equilibria, E_1 and E_2, are also shown.

from evasive behavior of herbivores (an individual trait). This kind of indirect effect belongs to a broader class known as behavioral- or trait-mediated indirect interactions (TMIIs; Abrams 1995; Werner and Peacor 2003).

Different carnivore species often exert different types of indirect effects (McPeek 1998; Bernot and Turner 2001; Finke and Denno 2005; Straub and Snyder 2006; Peckarsky et al. 2008). One important determinant of these differences is carnivore hunting mode (Preisser et al. 2007). Widely roaming, actively hunting carnivores such as weasels or ladybird beetles typically propagate positive density-mediated indirect effects on plants, by lowering the population density of herbivores. In contrast, sit-and-wait or sit-and-pursue ambush predators such as web spiders more readily propagate trait-mediated indirect effects, by causing behavioral adjustments in the herbivores. These differences in indirect effects appear to come about because of the risk cues associated with hunting modes. Whereas active hunters exert highly variable predation risk cues and are thus unlikely to cause chronic, energetically costly behavioral responses in their prey, ambush carni-

vores provide persistent, point-source cues of their presence that favor prey behavioral responses (Schmitz 2005).

Whereas density-mediated effects generally affect all plants, nonconsumptive effects often cause herbivores to change their relative use of different parts of their habitat (e.g., Magalhães et al. 2002; Valeix et al. 2009). This can lead to a redistribution of herbivore damage on different plant species, for example, when phytophagous insects shift from preferred but risky plant species to less nutritious plants that offer refuge. A well-documented example involves grasshoppers consumed by spiders in a grassland ecosystem (Schmitz and Suttle 2001; Schmitz 2008; see fig. 1A). In this system actively hunting spiders are found throughout the habitat, whereas sit-and-wait spiders, such as *Pisaurina mira*, are restricted to specific habitat portions (e.g., upper canopy on grass). The latter cause the herbivore to shift its feeding activity toward ground level, thereby increasing the relative consumption of *Solidago rugosa* over the grass *Poa pratensis*.

Even though a number of theoretical studies have explored the consequences of optimal or adaptive foraging

Table 1: Model parameters and notation

Symbol[a]	Friendly definition[b]
I	Total nutrient input to the community
d_0	Nutrient leaching from the system
r_i	Nutrient uptake by plant P_i
k_i	Conversion efficiency of nutrients by plant P_i
$\tilde{e}_i$	Feeding rate by H on plant P_i (dynamical)
d_i	Natural mortality rate of plant P_i
k_{Hi}	Conversion efficiency of plant P_i by H
$\tilde{e}_H$	Attack rate by C on H (dynamical)
d_H	Natural mortality rate of H
k_C	Conversion efficiency of H by C
d_C	Natural mortality rate of C
e_i	Maximum feeding rate by H on plant P_i
e_H	Maximum attack rate by C on H
p_0	Fraction of time spent in nonrefuge habitat without carnivores
ν	Intensity of behavioral adjustments by herbivore
$x^{(i)}$	Quantity x measured when species P_j is rare
ΔR^*	Difference in R^* value between species P_1 and P_2
$\Delta R_i^{H(j)}$	Advantage at herbivory-mediated competition of species P_i when rare

[a] By order of appearance in the text; i can be 1 or 2, and $i \neq j$.

[b] C = carnivore; H = herbivore.

behaviors in predators and/or prey (Sih 1987; Abrams and Matsuda 1993, 2004; Křivan and Schmitz 2003; Kondoh and Ninomiya 2009), flexible behaviors are still largely omitted in the modeling of food webs (Lima 2002; Abrams 2010). The graphical models commonly used to conceptualize plant competition and herbivory rely solely on consumptive effects (Holt et al. 1994; Leibold 1996; Grover and Holt 1998). In addition, many models are bitrophic and hence do not include predators of herbivores. In this context, it is not surprising that indirect effects of carnivores, especially trait-mediated effects, have received very little theoretical attention (but see Abrams 1991; Křivan and Schmitz 2004).

Our goal here is to explore how carnivore indirect effects, both density and trait mediated, affect plant species coexistence. We focus on contrasting carnivores that cause density-mediated effects only (such as actively hunting carnivores) and those that also cause trait-mediated effects (such as sit-and-wait carnivores; Preisser et al. 2007). To this end, we build on previous analyses (Grover 1997; Hulot and Loreau 2006) that describe trophic interactions among carnivores, herbivores, plants, and a limiting nutrient, with the added possibility of behavioral adjustments by the herbivore. We keep our results general through the use of graphical arguments and link them to earlier studies of predation-mediated plant coexistence.

Model Construction

We conceptualize a community as a set of tightly interacting species (community modules; Holt 1995) in which

consumers of resources are themselves resources for higher-level consumers. The core of the model combines resource (exploitative) competition and herbivore-mediated (apparent) competition between two plant species (fig. 1B). This "diamond" module has been used repeatedly in analyses of consumer-mediated resource-species interactions (Levin 1970; Holt et al. 1994; Leibold 1996; McPeek 1996; McCann et al. 1998). Unlike most previous analyses, we do not treat all parameters as constant but let the herbivore have dynamical traits that can change with the state of the community. Specifically, the herbivore may change its feeding rates on the two plant species. These behavioral changes are assumed to occur very rapidly (instantaneously) but then have chronic effects, on the timescale of ecological dynamics (Ma et al. 2003; Křivan and Schmitz 2004). Feeding rates are therefore arbitrary (monotonic) functions of community variables. The equations for the core community model (soil nutrient N and plant P_i dynamics mediated by herbivores) are

$$\frac{dN}{dt} = I - d_0 N - r_1 N P_1 - r_2 N P_2, \tag{1a}$$

$$\frac{dP_1}{dt} = P_1(r_1 k_1 N - \tilde{e}_1 H - d_1), \tag{1b}$$

$$\frac{dP_2}{dt} = P_2(r_2 k_2 N - \tilde{e}_2 H - d_2). \tag{1c}$$

Parameter definitions are presented in table 1 and figure 1. The herbivore feeding rates on plants ($\tilde{e}_1$ and $\tilde{e}_2$) are

dynamical, as indicated by the tilde. At this stage, the dynamics of herbivore abundance (H) are left unspecified. This core model provides a basic framework to understand plant coexistence mediated by keystone predation.

To study the extent of carnivore indirect effects on plant species coexistence, we add an explicit equation for the dynamics of H and, following Hulot and Loreau (2006), a carnivore trophic level (fig. 1B). The two additional equations are

$$\frac{dH}{dt} = H(\tilde{e}_1 k_{H1} P_1 + \tilde{e}_2 k_{H2} P_2 - \tilde{e}_H C - d_H), \qquad (2a)$$

$$\frac{dC}{dt} = C(\tilde{e}_H k_C H - d_C). \qquad (2b)$$

Parameters are, as above, defined in table 1 and figure 1. A third dynamical parameter has been introduced: the attack rate of the carnivore on the herbivore ($\tilde{e}_H$). The resulting community module (fig. 1B) is general and plausible because many plant communities harbor a combination of competitive dominant and subordinate plant species (Chalcraft and Resetarits 2003; Wilsey et al. 2005; Hulot and Loreau 2006; Hillebrand et al. 2008), both nutrient supply and herbivory can mediate competitive outcome (Hillebrand et al. 2007), and carnivores often affect plants by inducing changes in herbivory (Wootton 1995; Tessier and Woodruff 2002; Schmitz 2003, 2008).

Since we are interested in herbivore reactions to predation risk, we let dynamical traits be functions of carnivore abundance (C) only. Our model thus ignores optimal foraging decisions, which would make the dynamical parameters functions of plant relative abundances (Murdoch 1969; Pyke et al. 1977). It also ignores predator handling times and satiation; herbivores and carnivores thus have linear functional responses. This is a useful starting point and is adequate for communities in which prey abundance is low enough for satiation not to be a concern. Saturating functional responses could be included, at the expense of tractability (see "Discussion").

We contrast two scenarios below. In the first, the carnivore is actively hunting the herbivore, so that the herbivore cannot efficiently react to the abundance of carnivores or reduce its vulnerability to predation. The dynamical traits are thus effectively constant, that is, $\tilde{e}_1 = e_1$, $\tilde{e}_2 = e_2$, and $\tilde{e}_H = e_H$. In the second scenario, the carnivore has a sit-and-wait hunting mode. This allows the herbivore to assess carnivore abundance and respond accordingly. The exact functions linking dynamical parameters to carnivore abundance obviously depend on the detailed mechanisms involved in predator avoidance, on how these affect foraging time, and on the trade-off in plant exploitation. When necessary, we use specific func-

tions inspired by the system presented in figure 1A (Schmitz 2001, 2008). We model two habitat compartments: one in which the herbivore feeds on plant P_1 and is vulnerable to predation, and one in which it feeds on plant P_2 but is carnivore free (i.e., a refuge compartment). Plant P_2 is considered the refuge plant by convention. Herbivores forage in the two compartments, spending a fraction p of the time in the first and a fraction $1 - p$ in the second. This fraction is adjusted in response to predation risk, thus decreasing with C. Mathematically, this means $\tilde{e}_1 = e_1 p(C)$, $\tilde{e}_2 = e_2[1 - p(C)]$, and $\tilde{e}_H = e_H p(C)$, where e_1, e_2, and e_H are the maximum feeding rates achievable. We use the following form for $p(C)$:

$$p(C) = \frac{p_0}{1 + \nu C}. \qquad (3)$$

Positive parameter ν governs the degree of behavioral adjustment by the herbivore, whereas p_0 is the fraction of time spent in the nonrefuge habitat in the absence of any predation risk (table 1). Equation (3) is similar to functions used in the related literature (e.g., Křivan and Schmitz 2004) but is more tractable.

A Graphical Model of Plant Species Coexistence

In the core community module (fig. 1B), exploitative competition tends to maintain the plant species with lower nutrient demands at equilibrium (the R^* rule; Tilman 1982). Competition mediated by herbivory (often called apparent competition) can counteract this effect and enable coexistence. Several works have analyzed this keystone predation scenario, offering graphical models of mixed competition (Holt et al. 1994; Leibold 1996; Grover and Holt 1998; Hulot and Loreau 2006; Chesson and Kuang 2008). Nevertheless, these ignore the flexibility of herbivore traits, so we first derive a new graphical model appropriate for dynamical traits.

We are interested in nontransient coexistence of species that increase in abundance when rare and are thus protected from extinction (Chesson 2000; Leibold and McPeek 2006). Such coexistence occurs if both plant species have positive growth rates when rare, that is, can invade the boundary equilibrium set by the other plant species alone (fig. 1B; app. A in the online edition of the *American Naturalist*). Let E_1 be the boundary equilibrium with only species P_1 and E_2 that with only species P_2. At E_1 and E_2, let feeding rates take values $\tilde{e}_1^{(1)}$, $\tilde{e}_2^{(1)}$ and $\tilde{e}_1^{(2)}$, $\tilde{e}_2^{(2)}$, with herbivore abundances $H^{(1)}$ and $H^{(2)}$, respectively (superscripts indicate the corresponding boundary equilibrium). All these quantities are left unspecified at this stage, that is, they could result from arbitrary dynamics. The graphical model we derive is therefore not tied to

equation (2) or (3); its assumptions are contained in equation (1).

From equation (1), coexistence conditions are

$$\frac{1}{P_i}\frac{dP_i}{dt}\bigg|_{E_j} = r_i k_i \frac{d_j + H^{(j)}\tilde{e}_j^{(j)}}{r_j k_j} - H^{(j)}\tilde{e}_i^{(j)} - d_i > 0, \quad (4)$$

for $i, j = \{1, 2\}$ and $i \neq j$. The left-hand side of the equation quantifies the per capita growth rate of plant species i when rare. It includes two sources of mortality: background mortality (d_i) and loss to herbivory (at rate $H^{(j)}\tilde{e}_i^{(j)}$). Dissociating these two components yields

$$\underbrace{\left(\frac{d_j}{r_j k_j} - \frac{d_i}{r_i k_i}\right)}_{\widetilde{R_j^*} \quad \widetilde{R_i^*}} + \underbrace{\left(\frac{H^{(j)}\tilde{e}_j^{(j)}}{r_j k_j} - \frac{H^{(j)}\tilde{e}_i^{(j)}}{r_i k_i}\right)}_{\widetilde{R_j^{H(j)}} \quad \widetilde{R_i^{H(j)}}} > 0, \quad (5)$$

for $i, j = \{1, 2\}$ and $i \neq j$.

The four quantities introduced in equation (5) are all ratios of mortality rates to nutrient uptake efficiencies. Therefore, they have the dimension of nutrient amounts. The first term in parentheses is the difference between the traditional R^* values of species j and i (i.e., the amounts of nutrient they let at equilibrium when grown alone in the absence of herbivory; Tilman 1982). The second term in parentheses is the equivalent quantity when herbivory is the sole source of mortality (as could be measured after background mortality is experimentally suppressed or compensated for). We call these values R^H, by analogy with R^*.

The quantity R^* is independent of the boundary equilibrium considered, but R^H is not, because it involves $\tilde{e}$ and H values (eq. [5]). It follows that the first term in parentheses will have the same magnitude but the opposite sign when switching from one species ($i = 1$) to the other ($i = 2$). Indeed, $R_j^* - R_i^* = -(R_i^* - R_j^*)$. This reflects the fact that one or the other species is the superior resource competitor, that is, has the lower R^* value. Without loss of generality, we will take $\Delta R^* := R_1^* - R_2^*$, so that ΔR^* is positive when the second plant species (the refuge) is superior and negative otherwise. The magnitude of ΔR^* quantifies the imbalance in exploitative competition, that is, the difference in resource drawdown between plant species.

We now do the same for R^H values. The imbalance measure now depends on the boundary equilibrium considered,

$$\Delta R_i^{H(j)} := R_j^{H(j)} - R_i^{H(j)} = H^{(j)}\left(\frac{\tilde{e}_j^{(j)}}{r_j k_j} - \frac{\tilde{e}_i^{(j)}}{r_i k_i}\right). \quad (6)$$

This quantifies the advantage of species i at herbivory-mediated competition, as measured at boundary equilibrium E_j. It is positive when species i is favored and negative otherwise. Note that the herbivore abundance $H^{(j)}$, contained in the expression of R^H, is what has been called the P^* value in earlier theory (Holt et al. 1994). Unlike P^*, R^H has the same dimension as Tilman's R^*, which allows combination and comparison of the two quantities.

The coexistence criteria in equation (5) can then be expressed as

$$\Delta R_1^{H(2)} > \Delta R^*, \quad (7a)$$

$$\Delta R_2^{H(1)} > -\Delta R^*. \quad (7b)$$

These criteria state that each plant species, when rare, must have relative performance at herbivory-mediated competition (ΔR^H) good enough compared to performance at exploitative competition ($\mp\Delta R^*$). Specifically, the species inferior at exploitative competition must compensate with a sufficient (positive enough) ΔR^H, whereas the other species can withstand some disadvantage (negative ΔR^H), provided that it is not too strong.

These conditions can be represented on a graph whose main axes plot the values of $\Delta R_1^{H(2)}$ (the advantage at herbivory-mediated competition of species 1 when rare) and $\Delta R_2^{H(1)}$ (the advantage of species 2 when rare; fig. 2). Equation (7) partitions the graph into four regions in which competition outcomes differ (fig. 2): exclusion of one or the other plant species (*lower right*, *upper left*), founder control (*lower left*), or plant coexistence (*upper-right shaded area*). The location of these regions is determined by the vertex ($\Delta R^*, -\Delta R^*$). When $\Delta R^* = 0$, this is just the origin and the four regions match the four quadrants of the plane (fig. 2B). In this case, each plant species simply needs to have some advantage at herbivory-mediated competition when rare for coexistence to occur. Imbalance in exploitative competition ($\Delta R^* \neq 0$) shifts the vertex down and to the right (when species 2 is superior, as illustrated in fig. 2A) or up and to the left (when species 1 is superior; fig. 2C). Consequently, conditions for the inferior species to persist become more stringent, whereas those for the superior species are relaxed.

Since ΔR^* systematically favors one species over the other, it has an unequalizing effect on coexistence (Chesson 2000). In contrast, ΔR^H can vary in a density-dependent manner, thereby providing the stabilizing mechanism required for coexistence. The stabilizing effect of ΔR^H can stem from two sources (see eq. [6]): (i) variations in herbivore abundance (H) and (ii) variations in feeding rates ($\tilde{e}$) between boundary equilibria, corresponding to density- and trait-mediated effects, respectively.

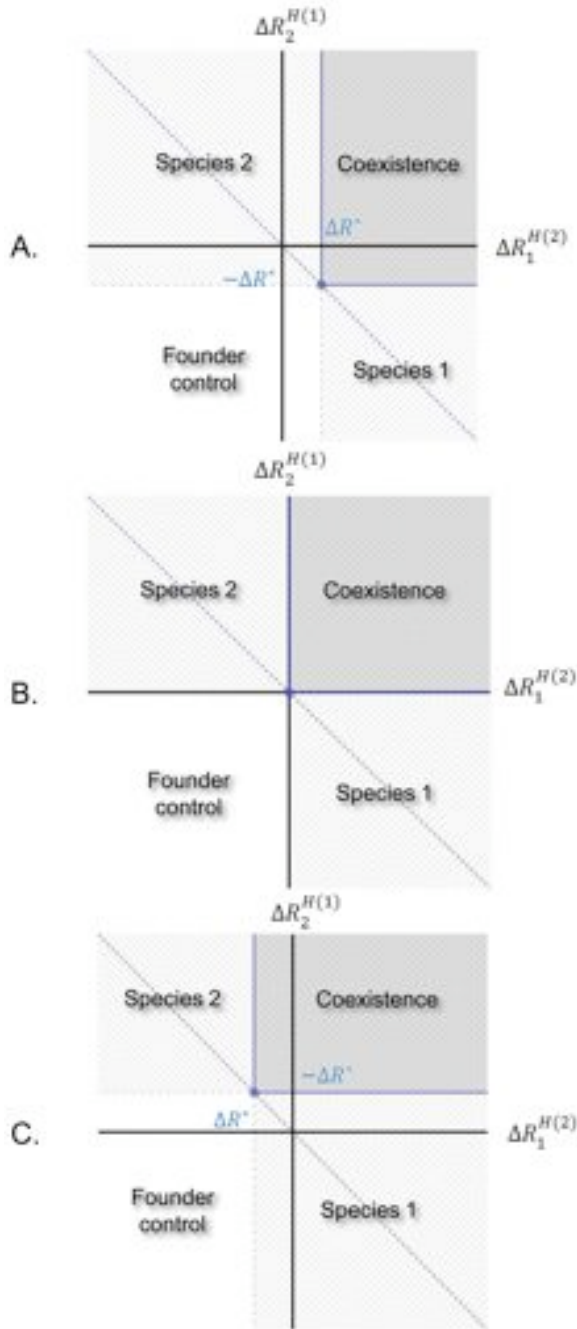Interestingly, these two stabilizing effects correspond to

Figure 2: Graphical model of plant species coexistence. Axes represent the relative advantage at herbivory-mediated competition (ΔR^H) of each species when rare: species 1 on the X-axis and species 2 on the Y-axis. In this plane, the vertex (ΔR^*, $-\Delta R^*$), shown as a blue point, separates four quadrants with different competition outcomes. Coexistence occurs only in the upper-right quadrant (*shaded area*). Depending on the value of ΔR^* (the imbalance at exploitative competition), the vertex moves along the $y = -x$ line. Three different cases are illustrated: *A*, species 2 superior ($\Delta R^* > 0$); *B*, two equivalent species ($\Delta R^* = 0$); *C*, species 1 superior ($\Delta R^* < 0$).

the models of keystone predation most studied in ecological literature, namely, the mixed-competition model (Holt et al. 1994) and the "switching-predator" model (Murdoch 1969). The graphical model presented in figure 2 applies to these classical bitrophic scenarios (see app. B in the online edition of the *American Naturalist*), but we focus here on the tritrophic scenario with a carnivore trophic level.

Application to Carnivore Hunting Modes

We now turn to the full model described by equations (1) and (2) (fig. 1*B*). The herbivore has explicit dynamics governed by equation (2a), resulting in the following abundances at the boundary equilibria (app. A):

$$H^{(i)} = \frac{d_C}{k_C \tilde{e}_H^{(i)}}. \tag{8}$$

In the case of an actively hunting carnivore, no trait adjustments occur. From equation (6), this implies that $\Delta R_2^{H(1)} = -\Delta R_1^{H(2)}(H^{(1)}/H^{(2)})$. In addition, since $\tilde{e}_H^{(1)} = \tilde{e}_H^{(2)}$, $H^{(1)} = H^{(2)}$ (eq. [8]). Overall, $\Delta R_2^{H(1)} = -\Delta R_1^{H(2)}$, so that for any parameter set the system lies along the $y = -x$ line in figure 2, where coexistence is impossible. One or the other plant species prevails, depending on the combined performances at exploitative and herbivory-mediated competition (see Hulot and Loreau 2006). In the absence of trait dynamics, only herbivore abundance could vary and act as a stabilizing mechanism. The addition of the carnivore, by generating top-down control of herbivore abundance, therefore suppresses the only possible stabilizing effect. Differences in carnivore abundances between boundary equilibria cannot be transmitted to the plant trophic level.

If the carnivore has a sit-and-wait hunting strategy, trait adjustments become possible. The herbivore may react behaviorally to increased carnivore abundance. This has two consequences. First, $H^{(1)}$ and $H^{(2)}$ can differ, since the possibility for the herbivore to adjust its vulnerability to predation ($\tilde{e}_H$) partly relaxes top-down control by the carnivore. Second, changes in the feeding rates on the two plant species ($\tilde{e}_1$ and $\tilde{e}_2$) allow departures from the relation $\Delta R_2^{H(1)} = -\Delta R_1^{H(2)}(H^{(1)}/H^{(2)})$. Both effects have the potential to sustain plant species coexistence.

Let us start by studying the first effect alone. Assume that herbivores make behavioral adjustments that reduce vulnerability to predation but do not affect plant exploitation. This leaves $\tilde{e}_H$ as the only dynamical trait in our model. In such conditions, the relation $\Delta R_2^{H(1)} = -\Delta R_1^{H(2)}(H^{(1)}/H^{(2)})$ still holds, but since the herbivore is no longer perfectly top-down controlled, $H^{(1)}$ and $H^{(2)}$ need not be equal. From equation (8), the higher $C^{(i)}$, the lower

$\tilde{e}_H^{(i)}$, and hence the higher $H^{(i)}$. Differences in carnivore abundances at the boundary equilibria thus translate, to some extent, into differences in herbivore abundances, creating a positive association between $H^{(i)}$ and $C^{(i)}$ values (fig. 3A). This changes the slope of the relation between $\Delta R_2^{H(1)}$ and $\Delta R_2^{H(2)}$: increasing $C^{(1)}$ makes the relation steeper, and vice versa. This can push the system into the area of coexistence, provided that the species superior at resource exploitation maintains a greater abundance of carnivores (and hence herbivores; fig. 3B). The superior plant should thus be preferred by the herbivore. Note that two equally competitive plant species ($\Delta R^* = 0$) cannot coexist. Since carnivore indirect effects on plants are transmitted through variations in herbivore density, this mode of coexistence is analogous to the classical mixed-competition model in bitrophic models (app. B), except that variations in herbivore abundance are driven by variations in carnivore abundance.

Let us now consider the opposite situation, in which the herbivore alters its diet in response to predation risk but fails to reduce predation risk significantly. This would be the case, for instance, if herbivores were confronted by an alien carnivore and reacted with inappropriate strategies. It amounts to setting $\tilde{e}_1$ and $\tilde{e}_2$ as the sole dynamical traits in our model. Since $\tilde{e}_H$ is constant, $H^{(1)} = H^{(2)} = \overline{H}$. The coexistence conditions expressed in equation (7) are then

$$\frac{\tilde{e}_2^{(2)}}{r_2 k_2} - \frac{\tilde{e}_1^{(2)}}{r_1 k_1} > \frac{\Delta R^*}{\overline{H}}, \tag{9a}$$

$$\frac{\tilde{e}_1^{(1)}}{r_1 k_1} - \frac{\tilde{e}_2^{(1)}}{r_2 k_2} > -\frac{\Delta R^*}{\overline{H}}. \tag{9b}$$

The left-hand sides of equations (9) are measures of herbivore diet preference at each boundary equilibrium, with feeding rates scaled on plant nutrient uptake performance (rk). These measures are, of course, functions of the carnivore abundance maintained at the boundary equilibria. Let us make this explicit by calling the left-hand side of equation (9a) $F(C)$ and that of equation (9b) $G(C)$. Under our convention that plant P_2 is a refuge from predation, $\tilde{e}_1$ decreases monotonically with C and $\tilde{e}_2$ increases monotonically with C (fig. 4A). This implies that $F(C)$ increases with C whereas $G(C)$ decreases with C. We may thus rewrite equation (9a) as $C^{(2)} < C_{\lim}^{(2)}$, where $C_{\lim}^{(2)}$ is the carnivore density at which $F(C_{\lim}^{(2)}) = \Delta R^*/\overline{H}$. Similarly, we may rewrite equation (9b) as $C^{(1)} < C_{\lim}^{(1)}$, where $G(C_{\lim}^{(1)}) = -\Delta R^*/\overline{H}$. Since for any given C we have $F(C) = -G(C)$, it follows that $C_{\lim}^{(1)} = C_{\lim}^{(2)} = C_{\lim}$ and that the coexistence conditions are simply

$$C^{(1)} < C_{\lim} < C^{(2)}. \tag{10}$$

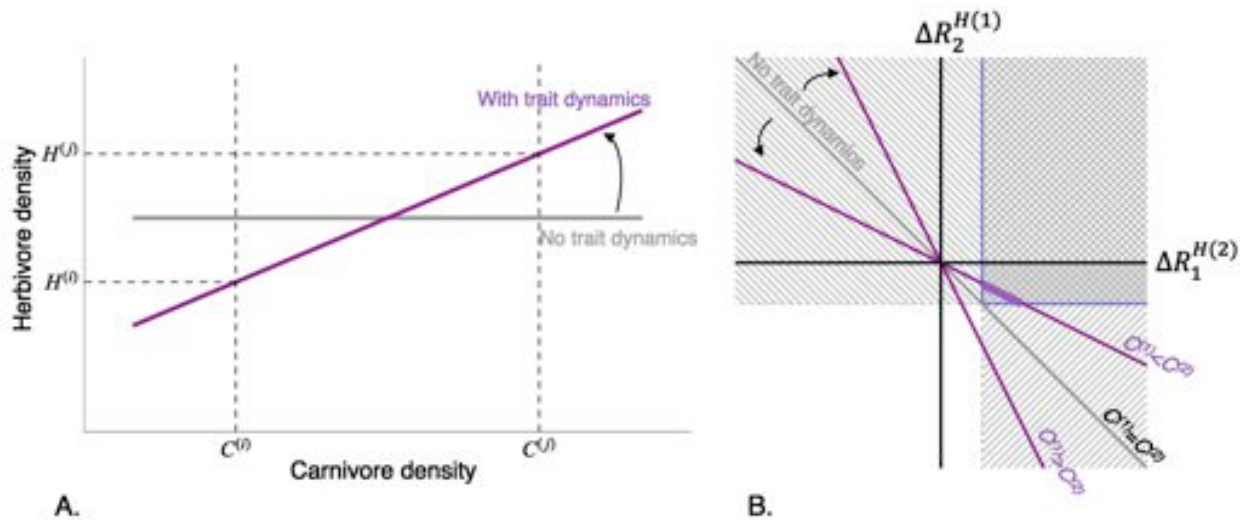This means that the refuge plant species should sustain

Figure 3: First coexistence mechanism: dynamical $\tilde{e}_H$ trait. *A*, In the absence of behavioral adjustments, herbivore density stays constant even if carnivore densities vary between boundary equilibria (*horizontal gray line*). With a dynamical $\tilde{e}_H$, herbivore densities become positively associated with carnivore densities (*purple line*). *B*, Variations in herbivore density between boundary equilibria change the slope of the relation between the two ΔR^H values (-1 in the absence of behavioral adjustments; *gray line*). This makes coexistence possible only if the dominant species (species 2 in the illustrated example; i.e., $\Delta R^* > 0$) sustains the higher density of carnivores (and hence herbivores) when alone (*thickened purple segment*). The system can enter only a fraction of the coexistence area (*cross-hatched area*).
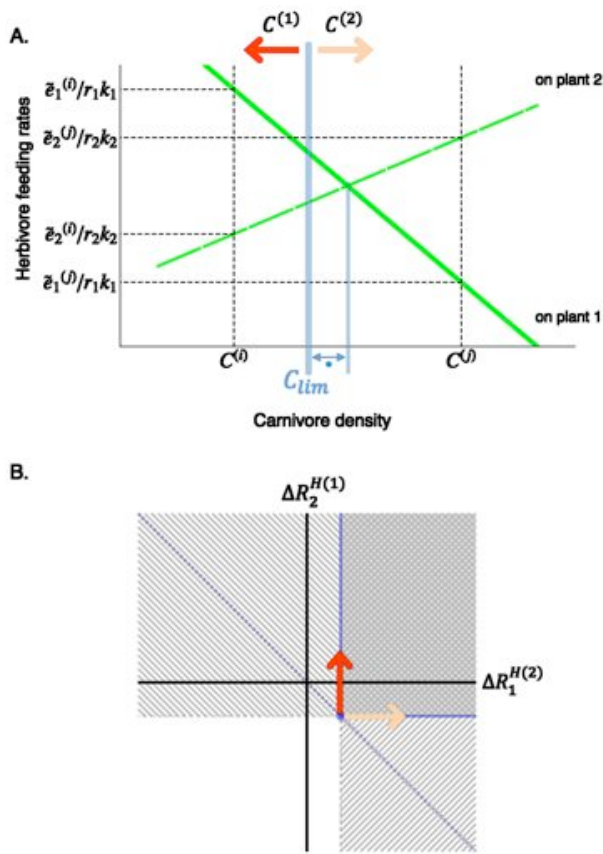
Figure 4: Second coexistence mechanism: dynamical $\tilde{e}_i$ traits. *A*, Herbivore feeding rates change with carnivore density: $\tilde{e}_1$ monotonically decreases (*dashed green line*), and $\tilde{e}_2$ monotonically increases (*solid green line*). These trends are taken to be linear for illustrative purposes, but they could have arbitrary shapes (such as those resulting from eq. [3]). When $C^{(1)} = C^{(2)} = C_{\text{lim}}$ (*thick vertical blue line*), the system lies on the vertex in the coexistence diagram (fig. 2). The origin of axes in figure 2 corresponds to the crossing of the two lines (*thin vertical blue line*), from which the vertex is distinct if $\Delta R^* \neq 0$ (*asterisk*). From the vertex, increasing $C^{(2)}$ (*orange arrow*) and decreasing $C^{(1)}$ (*red arrow*) make coexistence possible. *B*, Increasing $C^{(2)}$ above and decreasing $C^{(1)}$ below C_{lim} (*orange and red arrows*, respectively) both push the system from the separating vertex into the coexistence area. Any part of the latter can potentially be accessed.

higher carnivore density $(C^{(2)})$ than does the nonrefuge plant species $(C^{(1)})$ and that the two densities should lie on different sides of some threshold value C_{lim}. Graphically (see fig. 2), the threshold value corresponds to the carnivore density such that if $C^{(1)} = C^{(2)} = C_{\text{lim}}$, the system lies exactly on the vertex $(\Delta R^*, -\Delta R^*)$. From this vertex, increasing $C^{(1)}$ and decreasing $C^{(2)}$ increases $\Delta R_2^{H(1)}$ and $\Delta R_1^{H(2)}$, respectively, pushing the system into the area of coexistence (fig. 4*B*). The value of C_{lim} increases with ΔR^* (eq. [9]).

Note that unlike the previous case where $\tilde{e}_{\text{H}}$ was dynamical, both species may have positive ΔR^H values. This occurs when variations in carnivore abundance between boundary equilibria generate sufficient preference switching in the herbivore, so that both plants are relatively favored when rare (see fig. 4*A*). An important consequence is that differences in R^* values are not required for coexistence (i.e., the two plant species can be competitively equivalent). This mechanism of coexistence is analogous to the switching-predator model of keystone predation (Murdoch 1969; Abrams and Matsuda 2004), with the difference that switching is triggered by the fear of predation rather than by optimal foraging (app. B).

Clearly, conditions (10) can be satisfied only if the trait functions have suitable shapes. With our particular trait functions (eq. [3]), we can determine C_{lim} analytically as

$$C_{\text{lim}} = \tag{11}$$

$$\frac{k_C e_{\text{H}}(d_2 k_1 r_1 - d_1 k_2 r_2) + e_2 k_1 p_0 r_1 d_C - e_1 k_2 (1 - p_0) r_2 d_C}{e_1 k_2 r_2 d_C \nu}.$$

The first term in the numerator represents the deviation from $\Delta R^* = 0$ (fig. 4*A*). As expected, coexistence is impossible in the absence of behavioral adjustments ($\nu = 0$), because C_{lim} is infinite. Increasing the intensity of behavioral adjustments asymptotically decreases C_{lim} to 0, implying that coexistence requires intermediate values of ν.

We now consider the general case in which the two previous mechanisms operate at the same time, that is, with the three dynamical traits included. How will they interact? The answer depends critically on the value of ΔR^*. By combining figures 3 and 4, we can see that if the refuge plant is not the better exploitative competitor ($\Delta R^* < 0$), then the two coexistence mechanisms actually work in opposite directions (fig. 5*A*). If the refuge plant is superior at resource competition ($\Delta R^* > 0$), they work in the same direction (fig. 5*B*). Of course, when $\Delta R^* = 0$, only the second mechanism can operate. Overall, plant coexistence is much more likely if the refuge plant is superior at resource competition.

These conclusions are illustrated in figure 6. Using our specific functions and contrasting parameter sets, we numerically determined when coexistence was possible and the type of steady state dynamics that resulted (app. A). In a first scenario (fig. 6*A*), the refuge species is superior at resource competition and coexistence is primarily driven by the first coexistence mechanism (herbivore abundance). In a second (fig. 6*B*), the two species are equivalent competitors and preference switching is the sole coexistence mechanism. In a third scenario (fig. 6*C*), the refuge species is an inferior competitor.
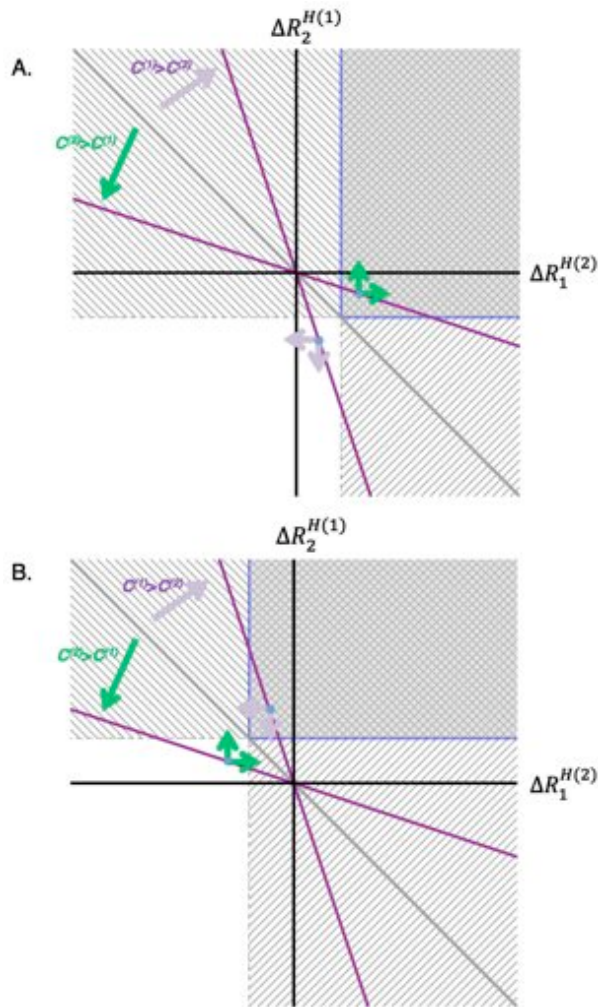
Our coexistence criterion (eq. [7]) was derived to guar-

Figure 5: General case: all three dynamical traits. *A,* The refuge plant (species 2) is dominant at exploitative competition ($\Delta R^* > 0$). Depending on the relative values of $C^{(1)}$ and $C^{(2)}$, both coexistence mechanisms push the system either away from (*lavender*) or into (*green*) the area of coexistence; they work synergistically. *B,* The nonrefuge plant (species 1) is dominant at exploitative competition ($\Delta R^* < 0$): the two coexistence mechanisms now work in opposite directions.

antee persistence of all species (i.e., absence of extinction) as long as all boundary equilibria are feasible (which covers most biological situations of interest). It can be seen that, indeed, coexistence always occurs inside and never occurs outside the area of coexistence we defined (fig. 6). In all cases, coexistence is possible only for a window of intermediate ν values. It is also much more likely when the refuge plant is superior (fig. 6*A*) rather than inferior (fig. 6*C*) at exploitative competition.

Coexistence does not always result in stable dynamics, however (Anderson et al. 1992). In the second and third

scenarios (fig. 6*B*, 6*C*), stable coexistence was observed for low- or high-enough intensities of behavioral adjustments, but sustained oscillations (limit cycles) were typically observed for intermediate values of ν. As shown in figure 7*A*, the system therefore undergoes two supercritical Hopf bifurcations as ν is increased. This is similar to what is observed in some predator-prey models (e.g., Takeuchi and Adachi 1983; Fussmann et al. 2000). The limit cycles can be quite complex, especially for the refuge plant species, with up to three local maxima per period (fig. 7*B*). Increasing the intensity of behavioral adjustments results in the general transitions species 1 $\rightarrow$ coexistence at stable equilibrium $\rightarrow$ coexistence with cycles $\rightarrow$ coexistence at stable equilibrium $\rightarrow$ species 2. Making the refuge plant competitively superior ($\Delta R^* > 0$) always tends to stabilize the system, reducing the scope for oscillations and possibly suppressing them completely (as in the first scenario; fig. 6*A*).

Discussion

It is becoming increasingly apparent that the structure of plant communities, such as patterns of dominance and species coexistence, should be considered in a broader food-web context that includes the predators of herbivores (Grover 1997; Hulot and Loreau 2006). Carnivores can affect plant species indirectly through their effects on herbivores, be they consumptive (e.g., reduced abundance) or trait based (e.g., altered foraging activity). Depending on their identity, particularly their hunting mode, different carnivores will have different indirect effects on plants (Schmitz 2005).

In this article, we studied the effect on plant coexistence of a carnivore feeding on a generalist herbivore. The herbivore may adjust its behavior to alleviate predation pressure, concomitantly changing its relative consumption of the two plant species. Carnivores can therefore have both density- and trait-mediated indirect effects on plants. This general scenario is observed, for instance, when herbivores must allocate their foraging effort between two plant species, one of which offers refuge from predation. We contrasted two kinds of carnivores: those that cause density-mediated effects only (such as active hunters) and those that also cause this sort of trait-mediated effect (such as sit-and-wait predators). We found that plant coexistence is possible in the second case but not in the first. In the absence of behavioral adjustments, it is well known that a generalist herbivore can prevent competitive exclusion of two plant species limited by the same resource, provided that there is a suitable trade-off between competitive dominance and vulnerability to the herbivore (Holt et al. 1994). Adding a carnivore generates top-down control of the herbivore, buffering the variation in herbivore abundance that
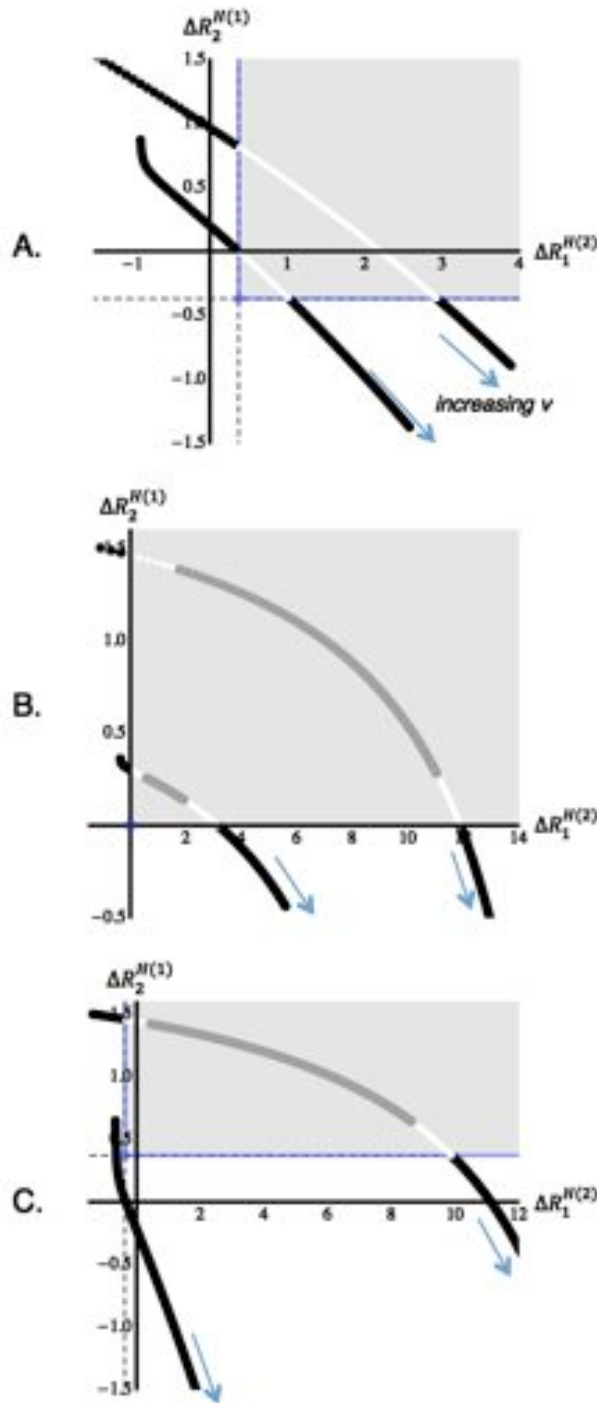
Figure 6: Effect of increasing the intensity of behavioral adjustments (ν) with our specific functions (eq. [3]). *A*, The refuge plant is superior at resource competition ($\Delta R^* = 10/27$). *B*, The two plant species are equivalent at resource competition ($\Delta R^* = 0$). *C*, The refuge plant is inferior at resource competition ($\Delta R^* = -10/27$). The value of ν was steadily increased from 0 (*top left dots*) to 5. Equilibrium feasibility and local stability were assessed numerically, and dots were painted accordingly:

results from changes in relative plant abundances. This effectively suppresses the only stabilizing mechanism that makes coexistence possible.

This is no longer true in the presence of behavioral adjustments. Flexible antipredation strategies in the herbivore, by relaxing top-down control, restore the previous stabilizing mechanism. In addition, they introduce a second stabilizing mechanism: variations in carnivore abundance can trigger an analog of adaptive switching in the herbivore (switching to the most abundant prey; Murdoch 1969). This occurs when the refuge plant sustains higher carnivore abundance than the nonrefuge species and the two carnivore abundances lie on different sides of some critical value. Unlike the first, this second stabilizing mechanism does not require the two plant species to differ in competitive abilities (R^* values).

Plant coexistence results in either stable temporal dynamics or sustained oscillations. The magnitude of behavioral adjustments (ν) acts as a bifurcation parameter controlling the type of steady state dynamics. Coexistence requires that behavioral adjustments have intermediate intensity, but within the range of suitable values, coexistence is more stable for low or high intensities. Lotka-Volterra food-chain models do not produce limit cycles; nonlinear functional responses and/or time delays are required (e.g., Fussmann et al. 2000). Oscillations can nonetheless be obtained in Lotka-Volterra food-web models with two plant species and a generalist herbivore, but under very specific conditions: one plant species must be unable to persist with the herbivore in the absence of the other, so that coexistence does not occur for all initial conditions (Takeuchi and Adachi 1983). Hence, in cases of robust coexistence like those we are interested in, limit cycles cannot occur. The introduction of behavioral adjustments in our model is thus the cause of oscillations. Making feeding rates functions of C obviously makes per capita rates nonlinear, but the nonlinearity is qualitatively different from that introduced by more complex (e.g., saturating) functional responses. The occurrence of limit cycles is robust to the shape of the functions governing behavioral flexibility: replacing equation (3) with simple linear functions of C does not suppress them (not shown).

The two stabilizing mechanisms described above make plant species coexistence possible in the presence of flexible behaviors, provided that behavioral adjustments have suitable magnitude. Nevertheless, they operate synergistically only when the refuge plant is also superior at resource

black for no coexistence, white for stable coexistence, and gray for oscillatory coexistence. Two different parameter combinations are shown in each panel. See table C1 in the online edition of the *American Naturalist* for a full list of parameter values.
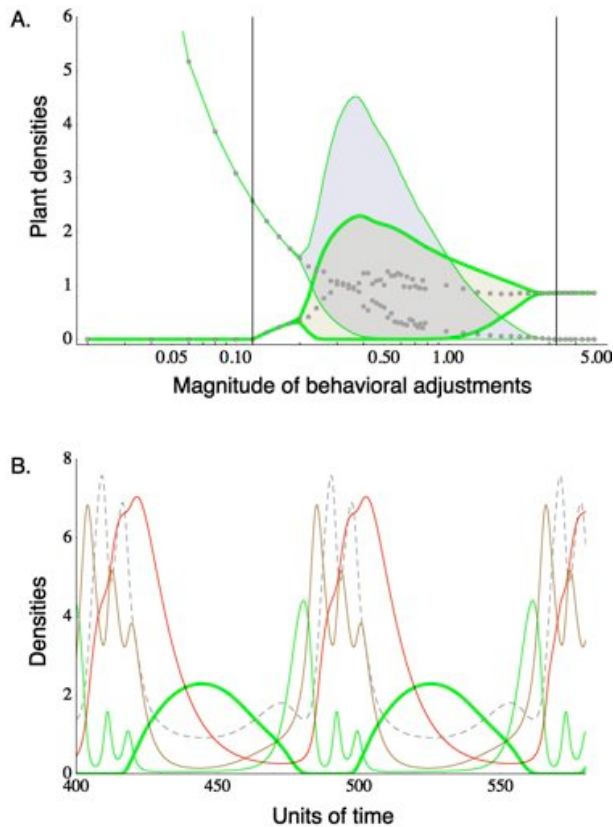
responses) and (ii) mortality rates were density independent within trophic levels. The first assumption is very common in the literature, but its validity is debated and difficult to assess from available data (Morgan et al. 1997; Skalski and Gilliam 2001). Saturating (Type II) or even sigmoid (Type III) responses are often preferred (Skalski and Gilliam 2001). These are destabilizing at high prey densities, potentially causing limit cycles. As long as the boundary equilibria remain stable, our results would not be much affected: nonlinear functional responses would not suppress top-down control of herbivore abundance, although they may buffer variations in carnivore abundance. The latter effect, all else equal, could somehow reduce the scope for coexistence, since variations in carnivore abundance are the drivers of behavioral adjustments. If limit cycles are observed at the boundary equilibria, their interaction with dynamical traits might lead to even more complex dynamics and possibly chaos, which remains to be explored. Our general argument would still apply, although determining the invasibility of the boundary equilibria would be more involved mathematically. The first stabilizing mechanism would still operate to promote plant coexistence but could itself cause sustained oscillations (Yoshida et al. 2007). The second would not be significantly affected. Overall, oscillations would be more prevalent, and differences in R^* values would probably no longer have the stabilizing effect we observed.

The assumption of predator density-independent mortality is reasonable in several natural systems, but it may be violated if individuals engage in interference competition or other intraguild interactions, such as predation (Schmitz 2007). Density-dependent mortality in the herbivore is not expected to change conclusions, but its addition in the carnivore trophic level would relax to some extent the top-down control of herbivore abundance. In the latter case, plant coexistence could occur even in the absence of behavioral adjustments (by restoration of the first coexistence mechanism). Behaviorally dynamical traits would nevertheless greatly increase the scope for coexistence, for the same reasons we have presented here.

This work contributes to extending our understanding of top-down effects on plant communities, specifically that of carnivore indirect effects. It also underlines the importance of trait-mediated effects and their interaction with density-mediated effects. Despite empirical evidence of their importance, trait-mediated indirect effects have so far received too little theoretical attention. Traditional graphical approaches to competition in trophic systems have focused on isocline analysis (Holt et al. 1994; Leibold 1996; Hulot and Loreau 2006). These methods, derived from the R^* rule, are most useful for studying the effect of productivity on the outcome of competition. In contrast, the graphical model we have used here focuses on

Figure 7: Steady state dynamics. *A*, Bifurcation diagram. For increasing magnitudes of behavioral adjustments (*v*; *horizontal axis*), the graph shows the minimum and maximum abundances of plant species (*thick line*, species 1; *thin line*, species 2). Time averages are also shown (*dots*). Coexistence occurs between the two vertical bars (as determined from eq. [7]). *B*, Example of a limit cycle, for $v = 0.4$. The curves correspond to the values of *N* (*dashed line*), P_1 (*thick green line*), P_2 (*thin green line*), *H* (*solid brown line*), and *C* (*red line*). Parameters are the same as in the upper scenario of figure 6*B*.

exploitation (i.e., has a lower R^*). In addition, the first mechanism tends to make plant coexistence more stable, that is, it reduces the scope for oscillatory coexistence. Overall, plant coexistence appears to be a more likely outcome when (i) the carnivore has attributes, such as hunting mode, that can elicit behavioral adjustments in the herbivore; (ii) the intensity of behavioral adjustments lies within a range of intermediate values but is as low or as high as possible within this range; and (iii) the plant more consumed in the presence of high predation risk (e.g., the refuge plant) is superior at resource competition.

Although the graphical arguments we used possess some degree of generality, they are constrained by the assumptions we made when constructing our model (eqq. [1], [2]). Importantly, we assumed that (i) functional responses were linear in the abundance of prey (Type I functional

invasion analysis (Chesson 2000). We believe that this kind of approach has great potential both to aid understanding of how different indirect effects interact to determine plant species diversity and to address complex processes such as trait-mediated indirect effects. We hope this work will stimulate further theoretical studies of the role of flexible behaviors in determining ecosystem structure.

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