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CONDITIONS UNDER WHICH PLANTS HELP HERBIVORES AND BENEFIT FROM PREDATORS THROUGH APPARENT COMPETITION

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Abstract. Leaf domatia are tiny structures in leaf vein axils that are typically inhabited by predatory and fungivorous mites. A recent article reported plant domatia specifically suited for herbivorous mites, which seems paradoxical, since the plant is thus supporting a natural enemy that can harm itself. The authors claimed that domatia are created to promote herbivorous mites as “fodder” for predatory mites that attack another herbivorous mite damaging the plant, and that the relationship among the plant, the fodder mite, and the predatory mite constitute a multiway mutualism because all three species benefit from the interaction. I formulate this system using two simple mathematical models of apparent competition, which differ in how domatia are modeled, and then assess when it is advantageous for the plant to create such space for a natural enemy. As a necessary condition for mutualism, the product of reproductive efficiency and nutritious value of the fodder prey should exceed that of the pest prey. This condition is also sufficient, if the direct costs for making the structure of domatia are negligible. If there are significant costs, however, the condition is broader for predators with lower reproductive efficiency and higher mortality, and for non-fodder prey with high consumption rate and low predation rate. I suggest that creating domatia is more effective when predators are less prolific and non-fodder prey are more severe as pests. Finally, I discuss how this mathematical model can apply to a wider range of tritrophic mutualistic relationships such as those among plants, aphids, and ants.

Key words: *apparent competition; leaf domatia; mite guilds; mutualism; plant strategy; predation.*

INTRODUCTION

Leaf domatia are tiny structures in leaf vein axils that are widespread among plant taxa. Typically, they are inhabited by predatory and fungivorous mites (Walter 1996). Plants with leaf domatia have been considered to have a multiway mutualistic relationship with mites, because predatory or fungivorous mites may benefit from leaf domatia as a refuge, whereas plants may benefit indirectly from reduced herbivory and/or pathogen attack (Agrawal 1997, Sabelis et al. 1999, Norton et al. 2001, Romero and Benson 2004, 2005).

In contrast to this general pattern, recent articles reported a curious system on a camphor tree *Cinnamomum camphora*. Although camphor trees create several leaf domatia types on the same leaf, with each type sheltering a different mite guild (Nishida et al. 2005), Kasai et al. (2002, 2005) paid special attention to smaller domatia, which are inhabited by herbivorous mites that in turn are preyed on by a predatory mite. The entrance into the domatia is narrow enough that the predator

mites cannot pass through, so these domatia protect a natural enemy of the plant. This at first glance seems maladaptive for the plant. However, the authors claimed that the domatia are created to promote herbivorous mites as “fodder” for predatory mites that attack another gall-making herbivorous mite damaging the plant. Thus, the tritrophic relationship among the plant, the fodder mite and the predatory mite constitute a systematic mutualism because each of the three species benefits from the pattern of interaction (Kasai et al. 2005). In effect, the plant facilitates an indirect interaction between alternate prey, mediated by a shared predation leading to apparent competition (Holt and Lawton 1994).

To interpret this relationship as a genuine mutualism, however, the costs to a plant for creating refuge space and for being fed upon by the herbivore should be lower than the benefit from reduction of consumption by another herbivore that presents a serious threat to the plant. To ascertain what is required for mutualism, I formulate this system mathematically, and elucidate conditions describing when it is advantageous for the plant to create such space. Based on these conditions, I discuss what life history parameters of the herbivorous and predatory mites are required for the mutualism to

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TABLE 1. Variables and parameters used in the models.

Symbol	Definition
x_1	density of prey 1
x_2	density of prey 2
y	density of predator
a_1	consumption rate of prey 1
b_1	reproductive efficiency of prey 1
c_1	predation rate on prey 1
g_1	nutritious value of prey 1
a_2	consumption rate of prey 2
b_2	reproductive efficiency of prey 2
c_2	predation rate on prey 2
g_2	nutritious value of prey 2
e	reproductive efficiency of predator
m	density-independent mortality of predator
f	density-dependent mortality of predator
X_1	size of domatia measured by density of prey 1
h	plant's investment in creation of space
h^*	plant's optimal investment

operate. We also ask whether the presented model can apply to a wider range of tritrophic mutualistic relationships, such as those among plants, aphids and ants (Carroll and Janzen 1973).

MODELS

I consider the population dynamics of a predator and two prey species, each exploiting the leaves of an individual plant. We denote the densities of prey 1, prey 2, and predator on the plant as x_1 , x_2 , and y , respectively. I construct two simple mathematical models of apparent competition, which differ in how one envisions the function of domatia. In model 1, domatia are utilized passively, so that a fixed fraction of prey are protected (of one of the two herbivorous species). In other words, domatia provide refuge for a fixed-proportion of prey (Hassell 1978). In model 2, domatia is modeled by providing a refuge for a fixed number of prey. Prey try to enter the refuge, but any excess above the capacity of the refuge are forced to reside on the leaf, exposed to predation. Real patterns of domatia use are doubtless more complex than these idealizations. I formulate the models as simply as possible so that they include neither stage structure, nonlinear functional responses, nor flexible prey preferences of the predator. The two models are analytically tractable. So they permit one to explicitly determine conditions under which creating domatia is advantageous for the plant, which is necessary for the system to be a mutualism.

Model 1: fixed-proportion refuge

Adopting the simplest Lotka-Volterra equation for predation, the changes in x_1 , x_2 , and y are represented as

$$\frac{dx_1}{dt} = b_1 a_1 x_1 - c_1 x_1 y \quad (1a)$$

$$\frac{dx_2}{dt} = b_2 a_2 x_2 - c_2 x_2 y \quad (1b)$$

$$\frac{dy}{dt} = e(g_1 c_1 x_1 + g_2 c_2 x_2) y - [m + f(y)] y \quad (1c)$$

where a_i is the consumption rate on the plant per individual of prey i ($= 1, 2$), b_i is the conversion rate of consumed food to reproduction (reproductive efficiency) of prey i , and c_i is the predation rate on prey i per prey individual and predator individual. Furthermore, g_i is the nutritious value of an individual of prey i , e is the conversion rate of consumed prey to reproduction (reproductive efficiency) of predator, m is density-independent mortality of predator, and $f(y)$ is an increasing function of y , representing direct density-dependent mortality on the predator due to interference. I assume that the prey populations are not involved in direct competition and regulated only by the predator, while the predator population is subject to a density-dependent mortality, acting as a stabilizing mechanism. The definition of variables and parameters in the equations are summarized in Table 1.

In this system (Eq. 1a–c), the two prey species cannot coexist due to “apparent competition” mediated by a common predator (Holt and Lawton 1994), where an increase in either prey increases the predator, which in turn reduces the other prey. The two equilibria for one-predator and one-prey systems are as follows:

$$x_1^* = \frac{1}{e g_1 c_1} \left[m + f \left(\frac{b_1 a_1}{c_1} \right) \right] \quad (2a)$$

$$x_2^* = 0 \quad (2b)$$

$$y_1^* = \frac{b_1 a_1}{c_1} \quad (2c)$$

and

$$x_1^* = 0 \quad (3a)$$

$$x_2^* = \frac{1}{e g_2 c_2} \left[m + f \left(\frac{b_2 a_2}{c_2} \right) \right] \quad (3b)$$

$$y_2^* = \frac{b_2 a_2}{c_2} \quad (3c)$$

When $y_1^* > y_2^*$, that is,

$$\frac{b_1 a_1}{c_1} > \frac{b_2 a_2}{c_2} \quad (4)$$

then equilibrium Eq. 2 with surviving prey 1 is globally stable, implying that (x_1, x_2, y) approaches the equilibrium from any initial states. Otherwise, equilibrium Eq. 3 with surviving prey 2 is globally stable. (Mathematical proof of this claim is given in the Appendix.) In other words, the winner is the prey which sustains the higher equilibrium predator density. This can be

interpreted as a condition where the surviving prey is the one with the higher resistance to predation.

Suppose that from the plant's point of view, prey species 1 is fodder to the predator, and prey species 2 is a plant pest. By creating space for prey 1 to escape from the predator, the plant could reduce predation on prey 1. This increases productivity of prey 1, which can then sustain more predators. I assume simply that the predation rate c_1 in Eq. 1a decreases because of the presence of domatia (see van Rijn et al. [2002] for alternative more complex function that explicitly model refuge space). In effect, a fixed proportion of prey are protected from predation, so this model is a fixed-proportion refuge model (Hassel 1978). I assume that c_1 is a decreasing function of plant's investment h to the creation of space, that is,

$$\frac{dc_1(h)}{dh} < 0.$$

I assumed that $c_1(0)$ is large enough that Eq. 4 is not satisfied.

With these assumptions, prey 1 cannot survive when the plant invests nothing, and the plant suffers consumption by the pest species at a rate $a_2x_2^*$. When the plant increases h , and thus decreases c_1 enough that Eq. 4 is satisfied, it can eradicate the pest species. Note that as the predation rate c_1 decreases, the equilibrium density of the predator actually increases because of the increase in the equilibrium value of the fodder species (see Eq. 2a and 2b). In this case, the total costs for the plant are $h + a_1x_1^*$. (Here, the unit of h is measured as consumption per unit time.) We thus see that the model presented here can simulate the system described by Kasai et al. (2005). To consider the system as a systematic mutualism, the investment by the plant must be as a whole advantageous for the plant, compared to an otherwise similar system where the plant does not create domatia.

The condition for the plant to gain advantage in creating space for the fodder prey is that the costs when making domatia are lower than the costs incurred when not making domatia: $h + a_1x_1^* < a_2x_2^*$. Using Eqs. 2a and 3b, this can be represented as

$$h + \frac{a_1}{eg_1c_1} \left[m + f\left(\frac{b_1a_1}{c_1}\right) \right] < \frac{a_2}{eg_2c_2} \left[m + f\left(\frac{b_2a_2}{c_2}\right) \right]. \quad (5)$$

I assume that the plant invests minimally so that both sides of Eq. 4 are nearly equal because the excess investment gives no further benefit to the plant. Then Eq. 5 can be rewritten as

$$h^* \left(\frac{b_1a_1c_2}{b_2a_2} \right) < (b_1g_1 - b_2g_2) \frac{a_2}{eb_1g_1g_2c_2} \left[m + f\left(\frac{b_2a_2}{c_2}\right) \right] \quad (6)$$

where the left side indicates that h^* is a decreasing

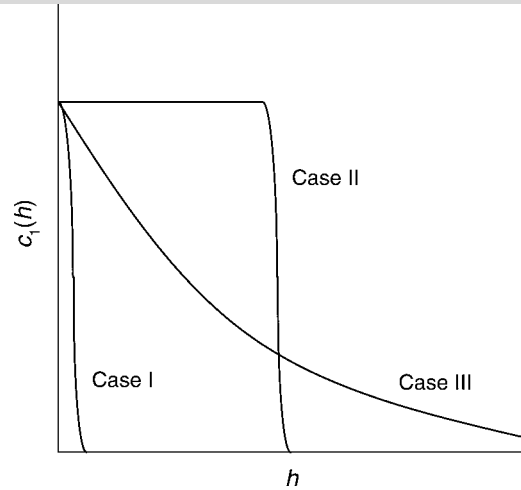


FIG. 1. Three cases in model 1 (with passive refuges) showing how predation rate on the fodder prey (c_1) depends on the cost for the plant to create a refuge (h) and the critical investment (h^*) to eradicate the pest prey. In Case I, $c_1(h)$ decreases to zero at a very small value of h , and h^* is virtually zero. In Case II, $c_1(h)$ decreases rapidly to zero around a positive value of h , and h^* is a positive constant. Finally, in Case III, $c_1(h)$ decreases gradually over a wide range of h , and h^* is a decreasing function of $(b_1a_1c_2)/(b_2a_2)$.

function of the argument, because h^* satisfies

$$\frac{b_1a_1}{c_1(h^*)} = \frac{b_2a_2}{c_2}$$

and $c_1(h^*)$ is a decreasing function of h^* . On the other hand, the density-dependent mortality f at the right-hand side of Eq. 6 is an increasing function of the argument.

The condition in Eq. 6 holds only when

$$b_1g_1 > b_2g_2. \quad (7)$$

This necessary condition means that the product of reproductive efficiency and nutritious value of the fodder prey is larger than the similar product for the pest prey. Thus, compared with the pest species, the ideal fodder species for the plant is one which can efficiently reproduce on a small amount of resource and whose nutritious value for the predator is high. When the plant creates a refuge with a very small cost, such that the left-hand side of Eq. 6 is a negligible value (see Case I in Fig. 1) and can be set to zero, we see that Eq. 7 is also the sufficient condition for the evolution of domatia for herbivores in plants.

When the cost for creating a refuge is not negligible but is approximately constant (see Case II in Fig. 2), additional necessary conditions are implied by expression 6. Naturally, the cost h^* should be small. As the right-hand side of Eq. 6 increases with a_2/c_2 , the condition is broader for a higher consumption rate of, and a lower predation rate on, the pestilent prey. As the right-hand side of Eq. 6 decreases with e , and increases

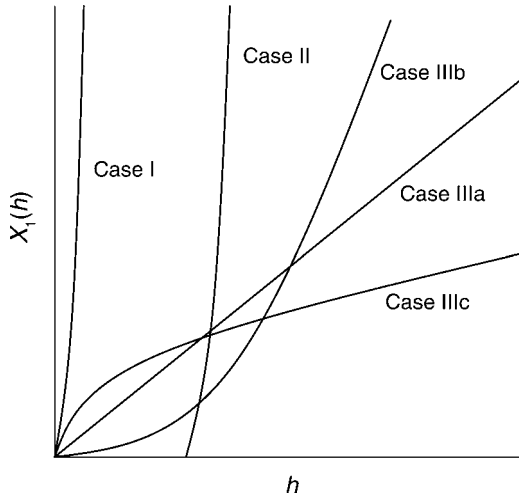


FIG. 2. Five cases in model 2 (with a fixed-number refuge) show how domatia abundance for the fodder prey (X_1) depends on the cost for the plant to create a refuge (h). In Case I, $X_1(h)$ rapidly increases with a very small value of h , and h^* is virtually zero. In Case II, $X_1(h)$ increases rapidly around a positive value of h . In Case III, $X_1(h)$ increases gradually over a wide range of h , linearly (a), acceleratedly (b), or diminishingly (c). In Case IIIc only, the plant should make an intermediate size of domatia smaller than \bar{X}_1 , and both the fodder and pest species coexist. Model 2: Fixed-number refuge describes how these functional forms translate into expectations.

with m , the condition is broader for predators with a lower reproductive rate and a higher mortality. Thus, creating a refuge is more effective for the plant when the pestilent prey is more severe and the predator is less prolific.

When the predation rate c_1 decreases gradually with increasing costs for creating a refuge (see Case III in Fig. 1; thus h^* is a gradually decreasing function of the argument in the left-hand side of Eq. 6), the condition is broader for the fodder prey with a higher consumption rate, a_1 . This is because the plant can eradicate the pestilent prey with a smaller h^* , when it uses fodder prey with a higher consumption rate. Predators with a lower reproductive efficiency e and higher mortality m are also desirable in this case, because creating a refuge is then more effective. As both sides of Eq. 6 are increasing functions of a_2/c_2 , the dependency of the condition on a_2/c_2 is not so straightforward: for the pest species with higher consumption rate and lower predation rate, the costs to eradicate the pest (h^*) become larger when the effect (the difference between $a_2x_2^*$ and $a_1x_1^*$) is larger. When the dependency of h^* on a_2/c_2 is smaller than that of the right-hand side of Eq. 6, the same conclusions as in Case II are obtained.

Model 2: fixed-number refuge

An alternative model for domatia is to assume a fixed number of prey can occupy them (Hassell 1978).

Including a fixed number refuge for species 1 in Eq. 1 leads to

$$\frac{dx_1}{dt} = b_1a_1x_1 - c_1k(x_1 - X_1)y \tag{8a}$$

$$\frac{dx_2}{dt} = b_2a_2x_2 - c_2x_2y \tag{8b}$$

$$\frac{dy}{dt} = e[g_1c_1k(x_1 - X_1) + g_2c_2x_2]y - my \tag{8c}$$

where $k(x_1 - X_1) = 0$ for $x_1 \leq X_1$ and $k(x_1 - X_1) = x_1 - X_1$ for $x_1 > X_1$. The quantity X_1 is the number of prey species 1 guaranteed to be protected in the domatia. Any excess individuals are exposed and suffer a risk of predation. This type of formulation has previously been used for modeling fixed-number refuge for species involved in apparent competition (Holt 1977) and direct competition (Holt 1987). To simplify the model, I further assume that the excess number of prey is immediately eaten. Then, x_1 is maintained to X_1 and the predation rate $c_1k(x_1 - X_1)y$ is equal to the reproduction rate $b_1a_1x_1$ from Eq. 8a. Therefore, Eqs. 8a–c are rewritten as

$$\frac{dx_2}{dt} = b_2a_2x_2 - c_2x_2y \tag{9a}$$

$$\frac{dy}{dt} = e(g_1b_1a_1X_1 + g_2c_2x_2y) - my. \tag{9b}$$

When

$$X_1 < \bar{X}_1 = \frac{mb_2a_2}{eg_1b_1a_1c_2}$$

the system has a globally stable equilibrium

$$x_2^* = \frac{m}{eg_2c_2} - \frac{g_1b_1a_1}{g_2b_2a_2}X_1 \tag{10a}$$

$$y^* = \frac{b_2a_2}{c_2} \tag{10b}$$

where x_2^* is positive. When $X_1 \geq \bar{X}_1$, the system has another globally stable equilibrium where

$$x_2^* = 0$$

and

$$y^* = \frac{eg_1b_1a_1X_1}{m}.$$

Eq. 10a means that x_2^* decreases linearly up to zero as X_1 increases to \bar{X}_1 . (Mathematical proof for global stability is given in the Appendix.)

As before, the cost to the plant of making domatia for X_1 prey is h . The condition for the plant to gain advantage in creating domatia for the fodder prey is that

the costs when making domatia are lower than the costs of not making domatia, or

$$h + a_1X_1 + a_2x_2^* < a_2x_2^*(0). \quad (11)$$

Here, $x_2^*(0)$ is an equilibrium value of pest species when $X_1 = 0$, which equals

$$\frac{m}{eg_2c_2}$$

from Eq. 9a. The plant should not increase X_1 over \bar{X}_1 , because $a_2x_2^*$ does not decrease anymore after reaching zero, while a_1X_1 continues to increase. When $X_1 \leq \bar{X}_1$, using Eq. 10a, the condition in Eq. 11 can be rewritten as

$$h < a_2x_2^*(0) - a_1X_1 - a_2x_2^* = a_1X_1 \left(\frac{g_1b_1}{g_2b_2} - 1 \right). \quad (12)$$

It is necessary that $g_1b_1 > g_2b_2$ for Eq. 12 to be satisfied. In general, the size of domatia X_1 may be an increasing function of costs for making domatia. When the costs are negligible ($h = 0$) as shown as Case I in Fig. 2, however, we can see in Eq. 12 that $g_1b_1 > g_2b_2$ is also the sufficient condition for the plant to make refuge space.

When h is negligible or nearly constant for any size of refuge (Case II in Fig. 2), the plant should attain the maximum value of X_1 , that is, \bar{X}_1 , because the net benefit of the plant is higher as the right hand side of Eq. 12 is larger. In this case, the pest species becomes extinct, and Eq. 12 is changed to

$$h < \frac{mb_2a_2}{eg_1b_1a_1c_2} \left(\frac{g_1b_1}{g_2b_2} - 1 \right). \quad (13)$$

This corresponds to Eq. 6 in model 1 if the term of density-dependent predator mortality is neglected. Therefore, the parameter dependency in the case of constant h holds as previously discussed in model 1.

When X_1 is a virtually increasing function of h , the optimal size of X_1 for the plant depends on the functional form of $X_1[h]$. From Eq. 12, the net benefit is represented as

$$a_1X_1(h) \left(\frac{g_1b_1}{g_2b_2} - 1 \right) - h \quad (14)$$

and the plant should maximize this quantity as a function of h . When $X_1(h)$ is a linearly (Case IIIa in Fig. 2) or an accelerating function of h (Case IIIb in Fig. 2), X_1 should take the maximum value, \bar{X}_1 , for Eq. 14 to be maximized. In these cases, the condition in Eq. 13 holds. However, if \bar{X}_1 is a decelerating function of h (Case IIIc in Fig. 2), Eq. 14 may have a maximum value for a value of X_1 smaller than \bar{X}_1 . In this case, x_2^* is positive as shown in Eq. 10, and therefore, the fodder species and the pest species should be able to coexist.

General results

Although the two models above differ in their representation for domatia as refuges (fixed-proportion

vs. fixed-number refuges), I obtained similar results for conditions for when making domatia is advantageous for plants. First of all, the necessary condition in Eq. 7 holds: the product of reproductive efficiency and nutritious value of the fodder prey is larger than that of the pest prey. This is also the sufficient condition in the two models for mutualism, when costs for making domatia are negligible. Moreover, if the magnitude of density-dependent mortality of predator is negligible in model 2, the condition is commonly represented by Eq. 13 when costs for making domatia are constant (Case II), or even when they are variable (some cases in Case III). In these cases, the condition is satisfied more easily when the predator is less prolific or the pest species is more severe.

The principal difference between the two models is that there is no case where the fodder species and the pest species locally coexist (i.e., on the plant) in model 1, while local coexistence occurs in model 2. I assumed, for simplicity, that predation rate on the pest species, c_2 , is always constant in Eqs. 1b and 8b. However, this rate could become smaller when the density of the pest species becomes low, because the predator can alter its foraging behavior (e.g., switching) or the prey might have an alternate refuge to ensure persistence. Adding such effects, cases where the pest species goes towards extinction in model 1 and 2 may represent coexistence of the fodder species with a low density of the pest species. In these cases, additional costs due to consumption by the pest species remain for the plant, but the necessary conditions discussed in model 1 and 2 are still necessary because these additional costs make the conditions for mutualism more severe.

DISCUSSION

Camphor trees create several leaf domatia types on the same leaf, with each type sheltering a different mite guild, and there may be complex interactions among mites using these domatia and other insects on the leaf (Nishida et al. 2005). Kasai et al. (2005) paid special attention to smaller domatia, which are inhabited by herbivorous mites that are preyed on by a predatory mite, and considered that those domatia ultimately provide the predator with their fodder. The direct effect of creating domatia for a prey species would be to alleviate predation on that prey, and this must have a negative effect on the growth of predator in the short term. It also enhances herbivory on the plant from this particular herbivore. However, the decreasing predation pressure leads to a high equilibrium density of the prey population, and this causes a positive effect on the growth of the predator in the long term. The increased density of the predator ultimately leads to eradication or reduction of the pestilent prey, which is to the advantage of the plant. This fascinating scenario was suggested to be realistic by the data of Kasai et al. (2005). Here I have

explored the conditions for mutualism, using mathematical models of two prey and one predator, involving apparent competition between the two herbivore species. We can say metaphorically that plants may apply the mechanism of apparent competition (Holt and Lawton 1994) for eradication or reduction of their pests.

Our results have described the requirements for the multispecies interaction to be a mutualism, in ecological time. Further analysis will be required to translate this into a model for the evolution of the system. The requirement for it to be advantageous for plants to create a refuge for a prey species against a predator is given by the condition in Eq. 6 for model 1, or Eq. 12 for model 2. These conditions may bear on the requirement for the evolution or maintenance of domatia, because the plant trait could not evolve unless it were advantageous for the plant. Given that such domatia have evolved, the models predict that one might observe either local eradication of the pest species or coexistence of the two prey species. Eradication here means local eradication in the individual plant. For this to be evolutionarily stable of course, requires that the pest persist on alternate plants, and be able to reinvade rapidly were domatia to disappear.

The general necessary condition (Eq. 7) for mutualism implies that the product of reproductive efficiency and nutritious value of the fodder prey is larger than that of the pest prey. Although Kasai et al. (2005) did not present any data on these life history parameters of two prey species in their article, it would be very interesting to examine whether or not the real values satisfy this condition.

In most cases, for the relationships between costs for creating domatia and their effects on reducing mortality in the fodder species in model 1 (or domatia size in model 2), I showed the condition in Eq. 13 holds. The condition was broader for the pestilent prey with a higher consumption rate and lower predation rate, or for the predator with the lower reproductive efficiency and higher mortality. The advantage for the plant to create domatia should be higher when the pestilent prey is more severe or the predator is less prolific. Kasai et al. (2005) showed that the mean areas of leaves with infection by a pest species was less than half that of leaves without infestation. This suggests that the consumption rate is quite high as predicted in our analysis (but note that this alone cannot determine whether the evolutionary condition is satisfied).

Romero and Benson (2005) suggested a different explanation for the benefit of plants from leaf domatia for herbivorous mites. By providing refuges for herbivores, domatia may stabilize otherwise highly unstable predator-prey oscillations and reduce the risk of predator extinction, followed by herbivore outbreaks. This explanation for the plant benefit is not straightforward, and requires theoretical development to provide

parameters for an empirical test. The explanation for the plant benefit by Kasai et al. (2005) is more direct and can be modeled simply as in this paper, predicting necessary conditions for evolution of domatia for herbivorous mites.

The system of plants, prey mites, and predatory mites, taken as a starting point for the analysis presented in this article, may seem to be very special among arthropod communities on plants. However, many similar systems have been shown to exist, for instance involving ants as predators, along with homopteran insects (aphids or scale insects) and other herbivorous insects (Carroll and Janzen 1973, Ito and Higashi 1991, Suzuki et al. 2004). Homopteran insects exploiting plants produce honeydew for ants, and ants exclude herbivores as well as the natural enemies of these homopterans. Therefore, the indirect interaction between homopterans and herbivores mediated by ants may constitute apparent competition as a component of an emergent multispecies mutualism.

If plants can control the density of homopterans, for example, by changing the level of direct chemical or physical defense at the plant part infested by homopterans, the model can potentially be applied, although the detailed structure of the model would doubtless have to be modified, depending on the systems under consideration. The consumption rate of the fodder prey increases, while the predation rate on the fodder prey was decreased in the domatia case. The condition for plants to gain advantage from an increased consumption by the homopterans is that the consumption should be smaller than the potential cost by other pestilent herbivores that would dominate in the absence of homopterans, assuming the frequency of ants visiting the plant then becomes very low. When these conditions hold, the system of plants, homopterans and ants can be regarded as a "systematic mutualism," analogous to the one proposed by Kasai et al. (2005). Whether plants can control the density of homopterans is unknown, but it would definitely be an interesting topic for future study. In general, I suggest that indirect interactions such as apparent competition may be integral in many complex mutualistic interactions.

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APPENDIX

Global stabilities of dynamical systems in Eqs. 1a-c and 9a and b (*Ecological Archives* E088-095-A1).