
Compensation behaviour by insect herbivores and natural enemies: its influence on community structure

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Insect herbivores feeding on low-quality plants often compensate by increasing their consumption of plant tissue. This usually results in a longer developmental time leading to a higher vulnerability to natural enemies. This has been termed the slow-growth, high-mortality hypothesis. To explore how compensation may shape the species composition of herbivore and natural enemy populations, we present a mathematical model of a tri-trophic system incorporating both the nutritional quality of plants and herbivores, and the compensatory ability of herbivores and their natural enemies. Using this model we predict the abundance of herbivores and natural enemies, and some characteristics of the composition of species of insect communities along a gradient of plant nutritional quality. Specifically, we make the following predictions: 1) In the absence of natural enemies, the abundance of the juvenile herbivores increases with plant quality, and only highly compensating herbivores persist at low plant nutritional quality. 2) If natural enemies are present, the abundance of the juvenile herbivores decreases with increasing plant quality due to more effective suppression by the natural enemies. Poorly compensating herbivores increase while their highly compensating counterparts decrease with lowered plant quality. 3) When the plants have low nutritional quality, natural enemies will only persist when either very highly compensating herbivores are present or if the natural enemy itself is highly compensating. 4) The abundance of adult herbivores in a community with natural enemies can either increase or decrease with increasing plant quality depending on the compensatory abilities of herbivores and natural enemies.

Ecologists have devoted much time in attempting to determine what shapes community trophic structure (e.g. Hairston et al. 1960, Hunter and Price 1992, Power 1992). Two factors that play important roles are believed to be resource availability (i.e., bottom-up effects) and natural enemy attack (i.e., top-down effects) (e.g. Hairston et al. 1960, Rosenzweig 1971, Fretwell 1977, White 1978, Oksanen et al. 1981, Fraser 1998, Hulot et al. 2000). In general, these studies have made predictions on the relationship between resource availability and community trophic structure ignoring any behavioural response to bottom-up factors. Such predictions may not be realistic if the behavioural response of organisms to resource availability has potential to alter the interaction of the organism to its natural enemy. The relative roles of bottom-up and top-down influences may, therefore, not be static and change with varying circumstances and conditions.

One example of a behavioural response to resource levels is found in insect communities. Insect herbivores feeding on plants in environments of low productivity, poor nutritional quality or with sub-lethal defences, often compensate less than adequate ingestion by increasing their consumption of plant tissue (Feeny 1970, Slansky and Feeny 1977, Lindroth et al. 1997; see Stephens and Krebs 1986 for an evolutionary basis for these responses). This frequently results in a longer developmental time. Consequently, herbivores spend longer in the early, more vulnerable, stages of development and often suffer greater mortality from natural enemies – this is termed the slow-growth, high-mortality hypothesis (Feeny 1976, Clancy and Price 1987, Leather and Walsh 1993, Häggström and Larsson 1995, Williams 1999).

Not all herbivores can compensate for poor nutritional quality to the same extent. Empirical studies demonstrating insect herbivore compensation ability have all used Lepidoptera larvae; their relatively high mobility enable rapid compensatory feeding behaviour (Feeny 1970, Slansky and Feeny 1977, Lindroth et al. 1997). Leaf-miners and insect gallers are less likely to be able to compensate as they are constrained to feed within a small area, usually within a single leaf, part of the stem or flower head. In cases where the herbivore cannot compensate, the reduction in plant nutritional quality may strongly influence the herbivore's nutritional quality and hence attractiveness to natural enemies.

Following this argument, it might be expected that a compensating herbivorous insect feeding on a plant with high nutritional quality would itself have a high nutritional quality. Whilst appearing attractive to natural enemies the likelihood of this herbivore being attacked is reduced because the time spent in the vulnerable early stages of development is minimized. Such herbivorous insects feeding in a less nutritional environment might be vulnerable to natural enemy attack for a longer period while a poorly compensating herbivore might not become more vulnerable to natural enemy attack due to its poorer nutritional quality.

Similarly, some natural enemies are more able to compensate for poor nutritional quality of their prey than others. For example, predators normally require a specific mass of prey to complete development and vary the number of prey consumed accordingly (Blackman 1967, Kanika-Kiamfu et al. 1993). Other natural enemies, for example parasitoids, are less able to compensate (Williams 1999), as a single herbivore host has to provide all the nutrients for the development of one or more individuals.

The influence of the varying ability of compensation of insects on community structure has not previously been examined. The aim of this study is to examine how plant nutritional quality influences the interaction between herbivores and their natural enemies, and also how behavioural responses by the herbivore to changes in resource quality determine community structure. More specifically, we examine, mathematically, the interaction between herbivore nutritional quality and development time to determine how this shapes herbivore and natural enemy community structure.

The model

Population dynamics

The model we develop is an extension of Levins' (1979) metapopulation model. The environment consists of a large number of discrete resource patches (i.e. plants). The number of patches occupied by each species (plant, herbivore, natural enemy) changes through time as a consequence of inter-patch colonization occurring via dispersal and within-patch extinction. Juvenile herbivores feed on these resource patches, develop to adults and then disperse to non-occupied patches. During development the juvenile herbivores are exposed to the attack by natural enemies. Natural enemies that successfully disperse to patches occupied by juvenile herbivores produce the next generation of natural enemies. It is assumed that adult herbivore abundance does not influence the dispersal of either juvenile herbivores or natural enemies.

Changes in the number of patches occupied by juvenile herbivores (X_j) and natural enemies (Y), and in the abundance of adult herbivores (X_a) are given by

$$\mathrm{d}X_j/\mathrm{d}t = agX_a(K - X_j) - (X_j/T) - bX_jY \tag{1a}$$

$$\mathrm{d}X_a/\mathrm{d}t = (X_j/T) - d_xX_a \tag{1b}$$

$$\mathrm{d}Y/\mathrm{d}t = ebX_jY - d_yY \tag{1c}$$

where a and b are the colonization rates of herbivores and natural enemies, respectively; K is the number of plant patches; d_x and d_y are the natural-death rates of the herbivore and the natural enemy, respectively; g and e are the reproductive rates of an adult herbivore and natural enemy, respectively; T is the mean length of the juvenile development period, which is inversely proportional to the growth rate from juvenile to adult (Hastings 1983).

Effects of plant nutritional quality on herbivores

In this paper, plant nutritional quality is scaled by its effect on herbivore's reproduction rate: that is, the reproduction rate of an adult herbivore decreases with decreasing plant nutritional quality. The response of a herbivore to plant nutritional quality will be expressed along a continuum between perfect compensation and no compensation. A highly compensating herbivore will consume more plant tissue when plant nutritional quality is low (Feeny 1970, Slansky and Feeny 1977, Lindroth et al. 1997). Although the nutritional quality of an adequately compensating herbivore can be considered independent of the nutritional quality of the plant, its developmental period is frequently found to be inversely proportional to plant nutritional quality. A poorly compensating herbivore, on the other hand, will have a nutritional quality directly dependent on the nutritional quality of the host plant, but its development time will be largely independent of the plant's quality.

In this model we assume that reproductive rate, g, and juvenile development period, T, have constant values, g_0 and T_0, respectively, when plant quality q ($0 \leq q \leq 1$; a larger q for higher quality) is at its maximum ($q = 1$). With decreasing plant nutritional quality, q, the reproductive rate g of an adult herbivore decreases (Fig. 1b). The degree to which reproductive rate decreases is dependent on the herbivore's compensation ability. A herbivore exhibiting high compensation ability may spend a longer period in the juvenile stage at low plant nutritional quality ($T_H(q) > T_L(q)$ for $q < 1$; hereafter, H and L represent herbivores with a high and low compensatory ability, respectively; Fig. 1a). This will result in a smaller decrease in reproductive rate ($g_H > g_L$ for $q < 1$). It is assumed that reproductive rate is proportional to the product of plant nutritional quality and juvenile period: $g = (g_0/T_0)qT(q)$. (Note that as the reproductive rate decreases with lowered plant nutritional quality it must hold that: $\mathrm{d}g/\mathrm{d}q = (g_0/T_0)(T(q) + qT'(q)) \leq 0$.)

The lowered plant quality, q, causes a reduction in herbivore quality, q_x, ($\mathrm{d}q_x/\mathrm{d}q \geq 0$) depending on the herbivore's compensation ability. That is, the more compensatory feeding shown by the herbivore the less quality is reduced by the lowered plant quality ($q_{xH} \geq q_{xL}$ for $q < 1$). Herbivore quality, q_x, for maximum plant quality ($q = 1$) is normalized to one ($q_x(1) = 1$).

Effect of herbivore nutritional quality on natural enemies

The compensation behaviour of natural enemies can be considered similar to that of herbivores. Natural enemies that are poor compensators (e.g. parasitoids) produce a large number of offspring on good quality herbivores (herbivores feeding on plants with a high nutritional quality or highly compensating herbivores), but very few when feeding on poor quality herbivores (Rosenheim and Rosen 1991). Highly compensating natural enemies (e.g. mobile predators) produce offspring independent of herbivore quality; when herbivore quality is poor, compensating natural enemies simply eat more of the herbivore to attain the required amount of resource for development (Blackman 1967, Kanika-Kiamfu et al. 1993). These natural enemies produce only slightly fewer offspring on poor quality herbivores.

In the model we assume that the reproductive rate of a natural enemy, e, decreases with lowered herbivore quality, q_x, depending on their compensation ability, similar to the case for the herbivore ($\partial e/\partial q_x > 0$ and $e_H \geq e_L$ where equation holds for $q_x = 1$). The natural enemy reproductive rate, e, for the maximum herbivore quality, q_x, is set to a constant e_0 ($e(1) = e_0$).

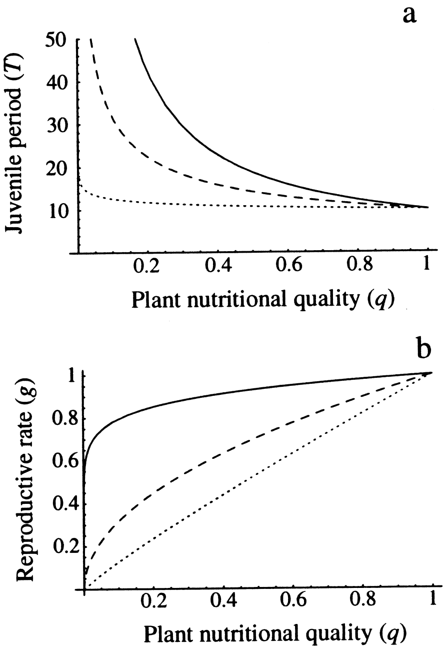


Fig. 1. Examples of changes in (a) the juvenile period (T) and (b) reproductive rate (g) of herbivores along a gradient of plant nutritional quality (q). Solid, broken and dotted lines are for high, intermediate and low compensatory ability, respectively. The following functions are used: $T(q) = T_0q^{-k}$, $g(q) = g_0q^{1-k}$ where $(T_0, g_0) = (10, 1)$; k is set to 0.9, 0.5 and 0.1 for high, intermediate and low compensatory ability, respectively.

Results

Herbivore populations without natural enemies

First, consider a case where herbivores feed on plants in the absence of natural enemies. The number of patches occupied of juvenile herbivore, X_j^*, and the abundance of adult herbivore, X_a^*, at equilibrium are given by

$$X_j^* = K - \frac{d_x}{ag} \tag{2a}$$

$$X_a^* = \frac{1}{T(q)}\left(\frac{K}{d_x} - \frac{1}{ag}\right) \tag{2b}$$

where $g = (g_0/T_0)qT(q)$ (see Appendix for proof of population stability). For herbivores to persist, either the nutritional quality of the plant, q, or the juvenile period, $T(q)$, needs to be high (to hold the condition for $X_j^* > 0$ and $X_a^* > 0$ that $qT(q) > (T_0/g_0)\{d_x/(aK)\}$. Therefore, even at very low plant nutritional quality highly compensating herbivores can persist (Fig. 2).

The sensitivity analysis of X_j^* and X_a^* to q shows that lowered plant nutritional quality results in a lowered abundance of both juvenile and adult herbivore (as confirmed by $\mathrm{d}X_j^*/\mathrm{d}q = (\partial X_j^*/\partial g)(\mathrm{d}g/\mathrm{d}q) > 0$ and $\mathrm{d}X_a^*/\mathrm{d}q = (\partial X_a^*/\partial T)(\mathrm{d}T/\mathrm{d}q) + (\partial X_a^*/\partial g)(\mathrm{d}g/\mathrm{d}q) > 0$). Juvenile herbivores with higher compensatory capability (implying a longer T) decrease less with decreasing plant quality ($\mathrm{d}X_j^*/\mathrm{d}T = (\mathrm{d}X_j^*/\mathrm{d}g)(\partial g/\partial T) > 0$) than those with lower compensatory capabilities. On the other hand, there is a juvenile period T that maximizes the abundance of adult herbivores X_a^* (as derived from the shape of the function that $\mathrm{d}X_a^*/\mathrm{d}T = -(1/T^3)\{(K/d_x)T - 2(T_0/ag_0q)\}$; Fig. 2). If T is higher than a threshold value (T_0d_x/aKg_0q), juvenile growth rate declines to such an extent that adult density decreases. If T is lower than this threshold value, the adult reproduc-

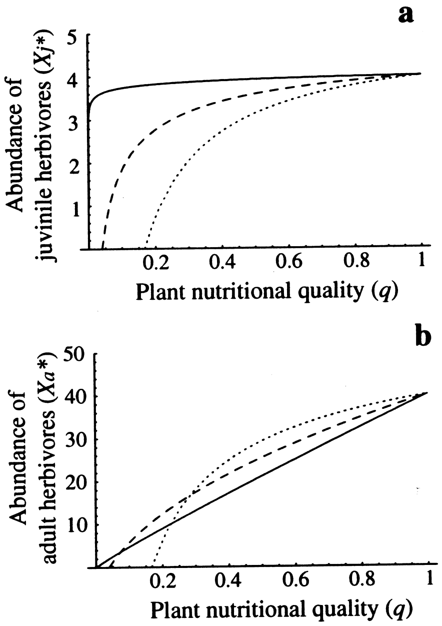


Fig. 2. Effects of plant nutritional quality on the density of (a) juvenile and (b) adult herbivores in the absence of natural enemies. Equilibrium abundances are plotted against plant nutritional quality for high (solid line), intermediate (broken line) and low (dotted line) compensation ability of herbivores. The parameters and functions are the same with those used in Fig. 1. The other parameters are $K = 5$, $a = 0.01$ and $d_x = 0.01$.

tive rate g becomes sufficiently small to result in the adult herbivore density decreasing. The juvenile period ($T = T_0 d_x / aKg_0 q$) that maximizes the adult herbivore abundance increases with decreasing nutritional quality.

Herbivore populations with natural enemies

When both herbivores and natural enemies are present, the population equilibria are given by

$$X_j^* = \frac{d_y}{e(q_x(q))b} \tag{3a}$$

$$X_a^* = \frac{d_y}{e(q_x(q))T(q)bd_x} \tag{3b}$$

$$Y^* = \frac{1}{bT(q)}\left\{\frac{ag}{d_x}\left(K - \frac{d_y}{e(q_x(q))b}\right) - 1\right\} \tag{3c}$$

(see Appendix for proof of population stability). For the system to persist (i.e. $X_j^* > 0$, $X_a^* > 0$, $Y^* > 0$), plant nutritional quality (q), juvenile period of the herbivore (T), nutritional quality of herbivore (q_x), or reproductive rate (e) of the natural enemy should be sufficiently high so that $(ag_0/T_0 d_x)(qT(q))[K - \{d_y/e(q_x(q))b\}] > 1$. This condition implies that natural enemies can exist at lower plant nutrient levels (small q) when attacking highly compensating herbivores (that have large T and high q_x) than when attacking poorly compensating herbivores. Further, even if the compensatory ability of the herbivore is not very high, highly compensating natural enemies (that have large e) can persist while poorly compensating natural enemies cannot (Fig. 3).

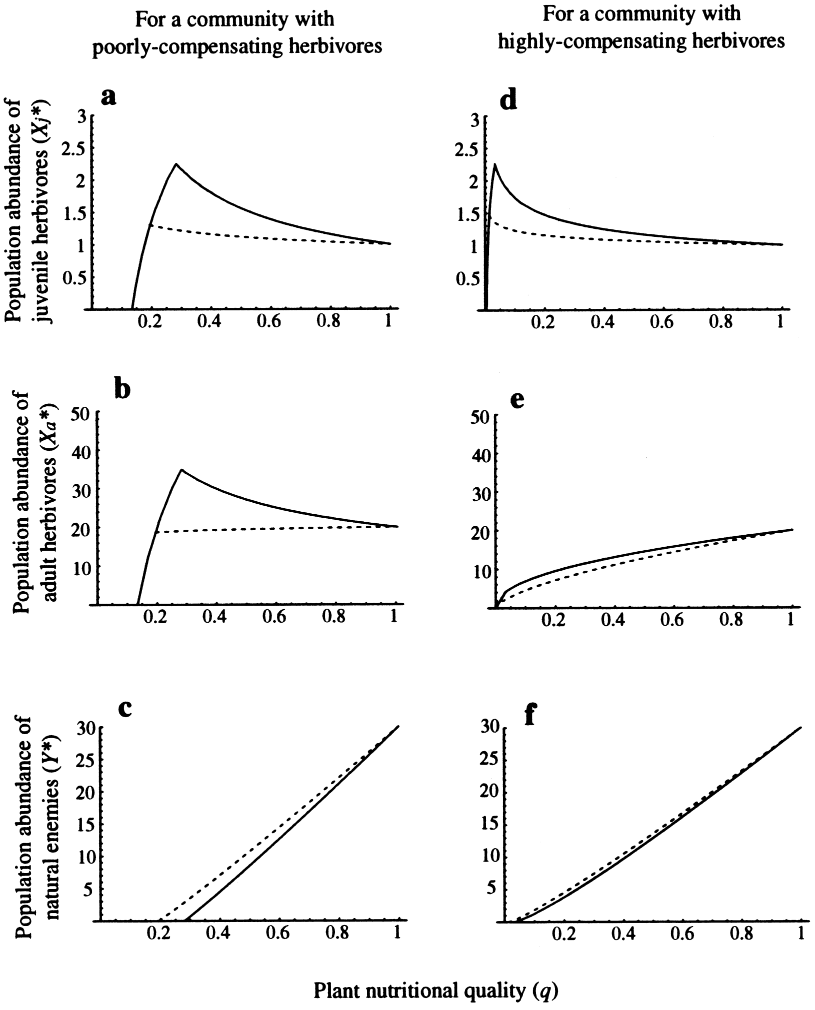
The equilibrium densities, X_j^*, X_a^* and Y^*, derived as functions of q, show the effect of the plant nutritional quality on the respective populations (Fig. 3). Where all interacting species are present, decreased resource quality results in an increasing density of juvenile herbivore whilst that of the natural enemy decreases ($\mathrm{d}X_j^*/\mathrm{d}q = (\mathrm{d}X_j^*/\mathrm{d}e)(\mathrm{d}e/\mathrm{d}q_x)(\mathrm{d}q_x/\mathrm{d}q) < 0$ and $\mathrm{d}Y^*/\mathrm{d}q = \mathrm{d}[(1/b)\{(ag_0 q/\mathrm{d}_x T_0)(K - d_y/eb) - (1/T)\}]/\mathrm{d}q > 0$). At low plant quality, if either the herbivore or natural enemy is compensating, the juvenile herbivore increases ($\mathrm{d}X_j^*/\mathrm{d}T = (\mathrm{d}X_j^*/\mathrm{d}e)(\mathrm{d}e/\mathrm{d}q_x)(\partial q_x/\partial T) < 0$ and $\mathrm{d}X_j^*/\mathrm{d}e < 0$ for $q < 1$), and the natural enemy decreases ($\mathrm{d}Y^*/\mathrm{d}T = (\partial Y^*/\partial T) + (\mathrm{d}X_j^*/\mathrm{d}e)(\mathrm{d}e/\mathrm{d}q_x)(\partial q_x/\partial T) > 0$ and $\mathrm{d}Y^*/\mathrm{d}e > 0$). The effect of plant nutritional quality on adult herbivore abundance can be either positive or negative; the lowered plant quality results in a longer juvenile period (T), which decreases the adult herbivore abundance, and a decreased natural enemy reproduction rate (e), which tends to increase herbivore abundance. If (Te) decreases with plant quality (q), then lowering the plant nutritional quality increases adult herbivore density, if (Te) increases with plant quality, then adult herbivore density will increase with plant quality.

Discussion

We believe this to be the first study that attempts to incorporate both the nutritional quality of plant and herbivore resources and the compensatory abilities of herbivores and natural enemies to examine the response of a multitrophic interaction to changes in productivity. (Note that an alternative assumption that plant abundance (K) is higher when productivity (q) is higher does not change the result qualitatively as confirmed by eqs 2a, 2b, 3a, 3b and 3c). The compensatory ability of both the herbivore and the natural enemy appears to influence the relationship between species composition, species abundance and plant nutritional quality.

The current analysis suggests two mechanisms by which plant quality can affect the interactions between herbivorous prey and their natural enemies. First, through changes in herbivore quality. A lowered plant quality leads to a reduction in the nutritional quality of herbivores, and decreases the growth rate of natural enemies. Secondly, through a change in the juvenile development period of the herbivores. Herbivore juvenile development period increases with lowered plant quality, resulting, over a period of time, in reducing the availability of prey for natural enemies. This second effect was surprising since it might have been expected that a longer juvenile period would result in a higher probability of natural enemy attack. This effect can possibly be explained by the long-term effect of a prolonged juvenile period. In the short term, a longer juvenile period may increase the natural enemy attack, and increase the natural enemy density; however, in the long term, it decreases the prey availability because of the increased vulnerability of juvenile herbivores. This may explain why most insect herbivores on trees (generally regarded as poor quality hosts in terms of nutrition (see Kundu and Dixon, 1995) occur at very low levels.

The model predicts how the compensatory ability of the herbivore and/or natural enemy can shape the interactions between them, and how the abundances of herbivore and natural enemy populations change along a gradient of plant nutritional quality. The effect of plant nutritional quality on herbivores is also dependent on whether or not natural enemies are present. When there are no natural enemies, the population density of both juvenile and adult herbivores increases with plant quality. However, when natural enemies are included in the interaction, populations of juvenile and adult herbivore respond differently to changes in plant quality. In general, the juvenile herbivore population decreases with increasing plant quality. This apparently negative effect of plant nutritional quality can be related to the frequency of natural enemy attack. With increasing plant quality, the nutritional quality of herbivores increases, leading to more effective suppression of juvenile herbivores by their natural enemies. Whether adult herbivores increase or decrease with decreasing plant quality in the presence of natural enemies depends on the compensatory ability of both the herbivores and natural enemies. When the herbivore is highly compensating, the adult herbivore population decreases with decreasing plant quality as a consequence of a prolonged juvenile period. When the herbivore has little compensation ability and is attacked by highly compensating natural enemies, plant quality has


For a community with poorly-compensating herbivores

For a community with highly-compensating herbivores

Fig. 3. The population density of (a and d) juvenile and (b and e) adult herbivores, and (c and f) natural enemies at the equilibrium for the four cases (highly or poorly compensating herbivore and highly or poorly compensating natural enemy). Left (a, b and c) and right (d, e and f) columns are for the low ($k = 0.2$) and high ($k = 0.7$) compensation abilities of the herbivore, respectively. Broken and solid lines are for the high ($l = 0.8$) and low ($l = 0.2$) compensation abilities of natural enemy, respectively. The parameters and functions are as follows: $T(q) = T_0 q^{-k}$, $g(q) = g_0 q^{1-k}$, $q_x(q) = q^{1-k}$, $e(q_x) = e_0 q_x^{1-l}$, $K = 5$, $g_0 = 1$, $a = 0.01$, $e_0 = 1$, $b = 0.02$, $d_x = 0.01$, $d_y = 0.02$ and $T_0 = 5$.

little effect on the adult herbivore population as the reduction in herbivore quality has little influence on highly compensating natural enemies. When poorly compensating natural enemies attack poorly compensating herbivores, the adult herbivore density decreases at higher levels of plant quality, as the natural enemy more frequently attacks herbivores of high nutritional quality.

We can therefore make predictions as to how herbivore and natural enemy species composition may change within an insect community along a gradient of plant nutritional quality. Without natural enemies, only compensating herbivore populations can persist in environments of low plant nutritional quality. Such individuals are likely to be highly mobile and to be able to move from one patch of resource to another to compensate for each patch being of relatively low quality (e.g. mobile Lepidoptera larvae). Such species would be expected to dominate herbivore communities on plants of poor nutritional quality to the exclusion of less mobile herbivores such as leaf-miners and gallers. Conversely, when natural enemies are present, compensating herbivores are more effectively suppressed by natural enemies due to their higher nutritional quality; thus when natural enemy pressure is high, gallers and miners may predominate as they are more capable of escaping attack. In addition, abundances of adult herbivore populations with high compensation ability decrease with lowered plant quality as their growth rate is markedly reduced. Thus, it is predicted that less mobile herbivores would be more predominant in the community than mobile herbivores as plant quality increases in the presence of natural enemies.

Natural enemies will only persist in systems of low plant nutritional quality if the natural enemy either feeds on highly compensating herbivores or is highly compensating itself. In the former situation, natural enemies of highly compensating herbivores would persist at lower resource qualities than those of poorly compensating herbivores as herbivore behaviour would ensure adequate resource availability for the natural enemy. In the latter case, where natural enemy behaviour plays an important role in compensating for the low herbivore nutritional quality, it would be expected that persisting species would have highly mobile larvae (e.g. predators rather than parasitoids).

This model provides a first step in examining the relationship between resource quality and community structure whilst incorporating different strategies within trophic levels. Previous models have either assumed uniform strategies within trophic levels and therefore have not considered the role of behaviour in determining insect community composition (e.g. Oksanen et al. 1981) or have been highly complex and difficult to apply to a broad range of systems (e.g. Gutierrez et al. 1994). Here we have attempted to predict not only the relative population densities of each trophic level but also some of the life strategy characteristics of the organisms within the community. We are unaware of any studies that have investigated the effect of plant quality on herbivore abundance depending on its compensation ability or mobility. Experiments by Fraser (1998) manipulated the ecosystem productivity within communities; such experiments now need to be developed to incorporate taxonomic and life-history details of the herbivores and natural enemies present (Moon et al. 1999).

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Appendix

An equilibrium solution is locally stable if all the eigenvalues of the community matrix are negative (May 1973).

For a one-species (herbivore) system, the community matrix is

$$S = \begin{pmatrix} \mathrm{d}\dot{X}_j/\mathrm{d}X_j & \mathrm{d}\dot{X}_j/\mathrm{d}X_a \\ \mathrm{d}\dot{X}_a/\mathrm{d}X_j & \mathrm{d}\dot{X}_a/\mathrm{d}X_a \end{pmatrix}^*$$

$$= \begin{pmatrix} -agX_a-(1/T) & ag(K-X_j) \\ 1/T & -d_x \end{pmatrix}^*. \tag{A1}$$

Eigenvalues, λ, are given as solutions of $|(S-\lambda E)|=0$ that is rewritten as

$$\lambda^2+\alpha\lambda+\beta=0 \tag{A2}$$

where $\alpha = agX_a^* + (1/T) + d_x$, $\beta = agd_xX_a^*$. Equation (A2) holds a criterion for negative eigenvalues ($\alpha > 0$ and $\beta > 0$; May 1973). This system is locally stable around the equilibrium.

For a two-species (herbivore and natural enemy) system, the community matrix is given by

$$S = \begin{bmatrix} \mathrm{d}\dot{X}_j/\mathrm{d}X_j & \mathrm{d}\dot{X}_j/\mathrm{d}X_a & \mathrm{d}\dot{X}_j/\mathrm{d}Y \\ \mathrm{d}\dot{X}_a/\mathrm{d}X_j & \mathrm{d}\dot{X}_a/\mathrm{d}X_a & \mathrm{d}\dot{X}_a/\mathrm{d}Y \\ \mathrm{d}\dot{Y}/\mathrm{d}X_j & \mathrm{d}\dot{Y}/\mathrm{d}X_a & \mathrm{d}\dot{Y}/\mathrm{d}Y \end{bmatrix}^*$$

$$= \begin{bmatrix} -agX_a-(1/T)-bY & ag(K-X_j) & -bX_j \\ 1/T & -d_x & 0 \\ ebY & 0 & ebX_j-d_y \end{bmatrix}^*. \tag{A3}$$

Similarly, eigenvalues, λ, are given by solving the following equation (derived from $|(S-\lambda E)|=0$):

$$\lambda^3+\alpha\lambda^2+\beta\lambda+\gamma=0 \tag{A4}$$

where $\alpha = d_x + agX_a^* + (1/T) + bY^*$, $\beta = eb^2X_j^*Y^* + (agd_y/ebT)$, $\gamma = eb^2d_xX_j^*Y^*$. Equation (A4) holds a criterion for negative eigenvalues ($\alpha > 0$, $\gamma > 0$ and $\alpha\beta - \gamma = (agd_xd_y/Teb) + \{agX_a^* + (1/T) + bY^*\}\{eb^2X_j^*Y^* + (agd_y/Teb)\} > 0$; May 1973). This system is also locally stable.