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VARIANCE AND SKEW OF THE DISTRIBUTION OF PLANT QUALITY INFLUENCE HERBIVORE POPULATION DYNAMICS

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Abstract. Individual genotypes, phenotypes, or species of plants can vary in their effects on herbivore population dynamics. In this study I used a simulation model to explore how the distribution of plant quality in a plant population affects the population dynamics of insect herbivores feeding on those plants. The model considers an herbivore population moving among patches (plants) with differing parameters for growth and carrying capacity. Observed population sizes across all patches were compared to the expectation that, if variance in parameters had no effect, population size should equal the sum of the carrying capacities of all plants. Results showed that variance in K alone, or in r and K together, strongly affected herbivore population size; increasing variance led to progressively stronger effects. The direction of the deviation of herbivore population size from the expectation in the absence of variance could be positive, negative, or both for different combinations of variance in r and K. Increasing skew also increased the deviation of observed population sizes from the expectation. Herbivore mobility increased the effect of variance in patch (plant) quality, whereas herbivore selectivity decreased the effects of variance by decreasing herbivore movement. These results are consistent with observations from agricultural studies that polycultures can either increase or decrease herbivore population sizes relative to monocultures.

Key words: *carrying capacity; herbivore dynamics; insect herbivores; movement; plant–herbivore interactions; plant quality; population growth rate; selectivity; simulation model; skew; variation among patches.*

Introduction

In 1983, the influential book *Variable Plants and Herbivores in Natural and Managed Systems* (Denno and McClure 1983) introduced a new conceptual focus to the field of plant–herbivore interactions by suggesting that variation among individuals and populations might have important ecological and evolutionary consequences. Since 1983, we have learned much about how mean plant quality varies among individual plants and plant populations (Zangerl and Berenbaum 1991, Fritz and Simms 1992), and about effects of host plant quality on individual herbivores (Rausher 1981, Rossiter et al. 1988, Zangerl 1990) and herbivore populations (Hunter and Price 1992, Ylioja et al. 1999, Underwood and Rausher 2000). However, plant populations and communities can differ not only in mean quality but also in the variance in quality around that mean, i.e., the coefficient of variation (CV) of plant quality. Variance in plant quality may be important for herbivore dynamics when herbivores move among plants or plant populations, thus sampling patches with different qualities. A wealth of field studies comparing agricultural monocultures (very low variance) with polycultures of several species or genotypes within a species (higher variance) indicate that herbivores can be either more or less abundant in polycultures than in monocultures (Andow 1991). Although these studies suggest that spatial variation in plant quality can affect herbivore populations in the field, they cannot tell us how different levels of variance affect herbivore populations, and they cannot isolate the many mechanisms that may contribute to these effects.

Our theoretical understanding of the effect of spatial variation on population dynamics, in general, is likewise not fully developed. Chesson (1996) has shown that the dynamics of a population can be affected by heterogeneity of population size among patches, even when patches do not differ in quality. Several other authors have examined models of populations inhabiting patches of different qualities (and thus having some variance in quality), but most of these models address issues other than population size, including the evolution of dispersal (Pulliam 1988, McPeek and Holt 1992), stabilizing effects of dispersal (Hastings 1993), and effects of patch quality on patch occupancy (Gyllenberg and Hanski 1997). Freedman and Waltman (1977) and Holt (1985) focus on the evolution of dispersal, but also show that, when two patches differ in carrying capacity, equilibrium population size can be lower (Freedman and Waltman) or greater (Holt) than the summed carrying capacities of the two patches. This effect is the result of a source–sink interaction

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between high- and low-quality patches. These models suggest that spatial variance in plant quality could be important for population dynamics, matching the observation from field experiments that variance can produce both positive and negative effects. However, previous models have not addressed the question of how different *amounts* of variance among patches might affect populations or how other aspects of the system such as movement rate and selectivity influence the effect of variance. Aspects of the distribution of plant quality besides variance (e.g., skew, or degree of asymmetry) may also affect herbivore dynamics, but have not been examined either theoretically or empirically.

In the study reported here, I used an extension of the two-patch model of Freedman and Waltman (1977) to examine how the distributions of aspects of plant quality (carrying capacity and population growth rate) affect insect herbivore population dynamics (plant population dynamics and vertebrate herbivores are not considered). In considering more than two patches, I chose to sacrifice an analytically exact solution and instead used numerical simulations, but using more patches allowed me to vary the skew in plant quality (undefined for two patches). Using a metapopulation structure with explicit dynamics in each patch, I addressed the following questions:

1) How do variance and skew in plant quality among plant patches affect the size of insect populations? In particular, I compared insect population size across plant patches that vary in quality to an expected population size equal to the average of population sizes in the individual plant patches.

2) How do herbivore mobility and selectivity influence the effects of variance and skew of observed population sizes across patches?

THE MODEL

Consider a population of J plants that differ in their quality as food for herbivores. Each individual plant ($i = 1 \ldots J$) is a patch and has some number of herbivores, $n_{i,t}$, on it at time t, and the total herbivore population (N) is the sum of the herbivores on all plants ($N_t = \Sigma_{i=1}^{J} n_{i,t}$). Likewise, the rate of change of the total herbivore population (dN/dt) is the sum of the rates of change on all of the plants, multiplied by the number on each plant ($dN/dt = \Sigma_{i=1}^{J} (dN_i/dt)\, n_i$). Herbivores move among plants at rate m. The rate of change of the herbivore population on each plant is dictated by the logistic model, adjusted by movement among plants at rate m:

$$\frac{dn_i}{dt} = r_i n_i \left(1 - \frac{n_i}{K_i}\right) - n_i m + \frac{1}{J} \sum_{i=1}^{J} n_i m. \qquad (1)$$

The quality of plant i can affect herbivores in two ways in this model: either through the patch-specific herbivore population growth rate (r_i) or the patch-specific herbivore carrying capacity (K_i).

If herbivores are not selective, the movement rate (m) is a constant. If herbivores are selective, herbivore movement rate becomes a linear decreasing function of plant quality:

$$m_i = \frac{-(pK_i)}{K_{\max}} + p(1 - x) + x \qquad (2)$$

where p (ranging from 0 to 1) is herbivore selectivity, $K_{\max}$ is the highest possible value of K (here $K_{\max} = 100$), and x is the herbivore movement rate in the absence of selectivity (when $p = 0$, $m_i = x$). This expression for selectivity implies that herbivores cannot assess plant quality before they land on a plant and can only exercise host choice by leaving low-quality plants. Studies suggest that many herbivores operate this way (Bernays and Chapman 1994). Movement in this model is spatially implicit. Dispersing herbivores land with equal frequency on all plants. Making the model spatially explicit (a linear array with reflecting boundaries and movement only between neighbors) does not change any of the conclusions (results not shown).

If variance in plant quality has no effect on herbivore dynamics, the expected herbivore population size at any given time (t) on a mixture of plant quality types ($N_{\text{exp},t}$) should be the sum of herbivore population sizes on independent plants of each type in the mixture ($\Sigma_{i=1}^{J} n_{i,t}$, where herbivore movement (m) = 0. At equilibrium, the expected herbivore population size on a mixture (N^*_{exp}) is then the sum of the carrying capacities of all plants in the mixture (at equilibrium, $n_i^* = K_i$): $N^*_{\text{exp}} = \Sigma_{i=1}^{J} K_i$. When this baseline is used for comparison, variance in plant quality is important for herbivore dynamics to the extent that the observed (simulated) herbivore population size on mixtures with movement among plants ($m > 0$) ($N_{\text{obs},t} = \Sigma_{i=1}^{J} n_{i,t}$) differs from the population size expected if each plant is independent ($N_{\text{exp},t} = \Sigma_{i=1}^{J} n_{i,t}$, where $m = 0$). In this model, the effect of variance in plant quality is thus measured as the proportional difference between observed population size and expected population size, $(N_{\text{obs},t} - N_{\text{exp},t})/N_{\text{exp},t}$, or at equilibrium, $(N^*_{\text{obs}} - N^*_{\text{exp}})/N^*_{\text{exp}}$.

For this analysis, variance in plant quality is measured as the coefficient of variation of herbivore carrying capacity ($\text{CV}_K = \text{SD}_k/\bar{K}$) or herbivore population growth rate (CV_r). Because distributions of characters in natural populations are often not perfectly symmetrical, I also considered the effect of the skew of plant quality on herbivore population size. Skew in plant quality was measured as

$$\text{skew}_K = \frac{J}{(J - 1)(J - 2)} \left(\frac{\sum (K_i - \bar{K})^3}{(\sqrt{\sigma_K})^3} \right)$$

where positive values of skew indicate that the tail of the distribution is to the right.

For configurations of the model with variance in both r and K, r is a linear function of K. To allow manip-

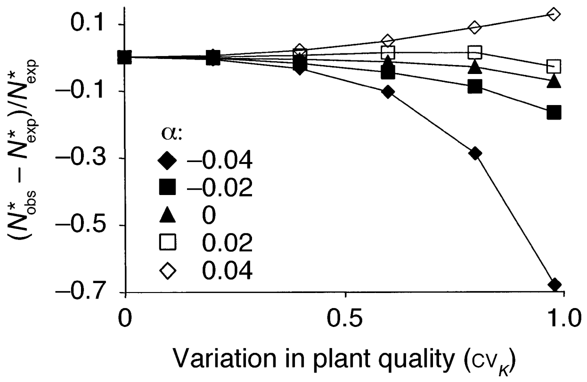

FIG. 1. The effect of the coefficient of variation of plant quality (carrying capacity) on herbivore population size for a range of strength of relationships (α's) between carrying capacity and herbivore growth rate. Positive *y*-axis values indicate herbivore populations larger than expected if there were no effect of variance in plant quality; negative *y*-axis values indicate herbivore populations smaller than expected if there were no effect of variance in plant quality. Here, $\bar{K} = 50$, $\bar{r} = 2$, and herbivore movement rate ($m = x$) = 0.5; N_{obs} and N_{exp} are the observed and expected herbivore population sizes, K is the carrying capcity, r is the population growth rate, and x is the herbivore movement rate in the absence of selectivity. Each point represents equilibrium values for one population after 20 000 iterations.

ulation of average values of both $\bar{r}$ and $\bar{K}$, I considered the case where $r_i = \bar{r} + (K_i - \bar{K})\alpha$, and α is the slope of the relationship between r and K. This expression allows for both negative and positive relationships between r and K (α less than or greater than 0). Holt (1985) showed that when $r_1/K_1 = r_2/K_2$ (proportional difference = 0), there is no effect of variance on population size. For comparison with this condition, I also considered the case where $r_i = K_i c$ (c is a constant), which yields $r_1/K_1 = r_2/K_2 = \cdots = r_J/K_J$. As expected, I found no effect of variance at high movement rates in this case (results not shown).

Simulations

I explored the model with numerical simulation using Visual C++ (Microsoft 1998). Plant population size (J) and initial herbivore population size (N) had no effect on equilibrium conditions. Unless otherwise specified, simulations were begun with populations of five plants and 10 herbivores. For runs using five plants, plant qualities (K's and r's) were assigned to produce a range of CV$_K$'s and CV$_r$'s. To confirm that results were not an artifact of the particular combinations of K's examined or of using a relatively small number of plants, I ran simulations that drew K's from a gamma distribution with specified CV$_K$ and average K ($\bar{K}$) and a plant population size of 200. The mean value of K was held constant at 50 for most runs reported here. Unless otherwise specified, movement rate (m) = 0.5, and herbivores are not selective ($p = 0$). Initial herbivore distribution over plants was even ($n_1 = n_2 \ldots n_j$). Random or aggregated initial distributions of herbivores did not change equilibrium results (results not shown). Population dynamics were approximated using the Euler method (Press et al. 1992) with a time step of 0.001. Smaller time steps did not change the results. Simulations were run long enough for a stable equilibrium to be reached (20 000 iterations).

RESULTS

Variance in K and r

Variance among plants in herbivore population growth rate (r) alone when K was constant had no effect on the equilibrium herbivore population size ($N^*_{exp} = N^*_{obs}$ for all CV$_r$) (results not shown), but variance in carrying capacity (K) alone did affect herbivore population size. Higher CV$_K$ led to smaller than expected herbivore population sizes (Fig. 1; α = 0; see Freedman and Waltman 1977). The relationship between CV$_K$ and the difference between observed and expected population sizes was accelerating, so small changes in CV$_K$ at higher CV$_K$'s led to larger changes in the difference in population size.

When K and r were positively correlated, increasing the variance in r (by increasing α, the slope of the $r - K$ relationship) caused differences between observed and expected herbivore population size to go from negative to positive (Fig. 1). When r and K were negatively correlated ($\alpha < 0$), variance in r increased the effect of variance in K, leading to larger negative deviations of the observed herbivore population size from expected population sizes.

Transient differences between observed and expected population sizes that occurred before equilibrium could be larger than those observed at equilibrium (Fig. 2). Regardless of whether the equilibrium deviation for a population with a given variance in plant quality was negative or positive, transient differences between observed and expected sizes for that population could be negative or positive when both r and K varied.

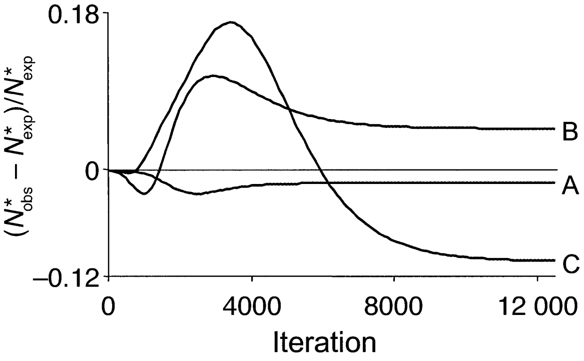

FIG. 2. Transient behavior of herbivore populations on plant populations with variance in K alone (A, CV$_K$ = 0.6, α = 0) or K and r (B, CV$_K$ = 0.6, α = 0.04; C, CV$_K$ = 0.6, α = −0.04). Here, α is the slope of the relationship between r and K.

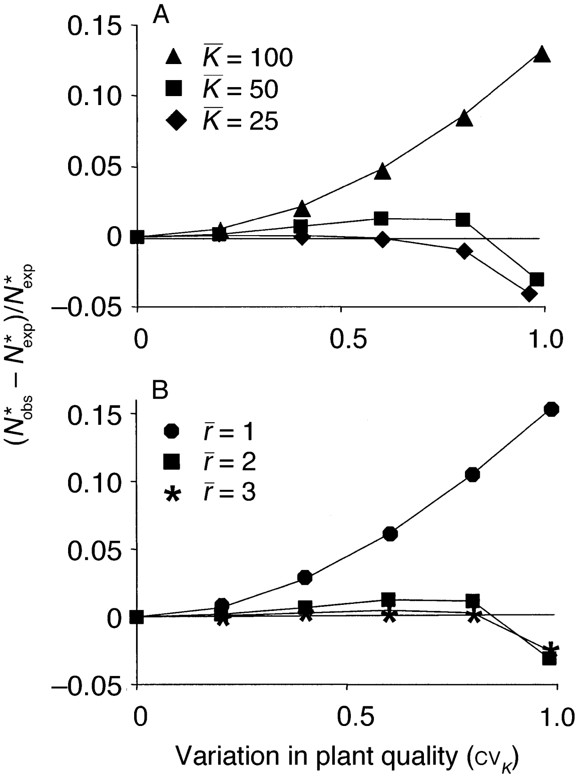

FIG. 3. (A) Increasing the average herbivore carrying capacity ($\bar{K}$) increased deviations of herbivore population sizes from expected (the strength of the relationship between r and K is $\alpha = 0.02$; $\bar{r} = 2$). (B) Increasing the average herbivore population growth rate ($\bar{r}$) decreased the deviations of herbivore population sizes from expected ($\bar{K} = 50$; strength of relationship between r and K is $\alpha = -0.01$). Note for reference that lines indicated by squares in panels (A) and (B) result from the same parameterization of the model.

Average r and K

When population growth rate (r) did not vary, average plant carrying capacity (K) did not affect the relationship between variance in plant quality and herbivore population size (results not shown). When r and K were positively correlated, higher $\bar{K}$'s led to more positive differences between observed and expected population sizes (Fig. 3A); when r and K were negatively correlated, higher $\bar{K}$'s led to more negative differences (result not shown). This effect of $\bar{K}$ resulted because variance in K drives variance in r. As shown in Fig. 1, increasing variance in r (when r and K were positively correlated) led to more positive differences between observed and expected herbivore population sizes. Whether or not herbivore population growth rate (r) varied, higher average rate ($\bar{r}$) caused smaller absolute differences between observed and expected herbivore population sizes (Fig. 3B).

Herbivore movement rate (m) and selectivity (p)

As herbivore movement rate (m) increased, differences between the observed and expected herbivore population sizes increased (Fig. 4). In the absence of movement, the observed and expected herbivore population sizes at equilibrium were equal because each plant type was isolated from the others. When herbivores were more selective, herbivore population sizes were less affected by variance in plant quality (CV_K); this effect was stronger with more variation in plant quality (higher CV_K) (Fig. 5A). When herbivores were selective, the observed movement rate (m) differed from the baseline movement rate x (see Eq. 2; Fig. 5B). Therefore, the effect of selectivity probably arose because increasing selectivity decreased the observed herbivore movement rate.

Nonsymmetrical distributions of plant quality

Asymmetry in the distribution of plant quality also influenced the effect of variance in plant quality on herbivore population size. Positive skew in plant quality (with the tail of the distribution to the right) made differences between observed and expected population sizes more positive, and negative skew made differences more negative (Fig. 6).

Larger models

To confirm that the results reported thus far were not artifacts of using five-plant populations, I also considered a model with a larger plant population size (200 plants) and K's drawn from a gamma distribution. This model showed the same tendency for variance in plant quality to increase deviations of herbivore population sizes (Fig. 7). The gamma did not exactly mirror results from the simple five-plant model because, for most runs of the five-plant model, the distribution of K's was symmetrical ($\text{skew}_K = 0$), whereas for the gamma, the distribution was not completely symmetrical.

DISCUSSION

Results of my study suggest that, for herbivores that move among plants, aspects of the distribution of plant

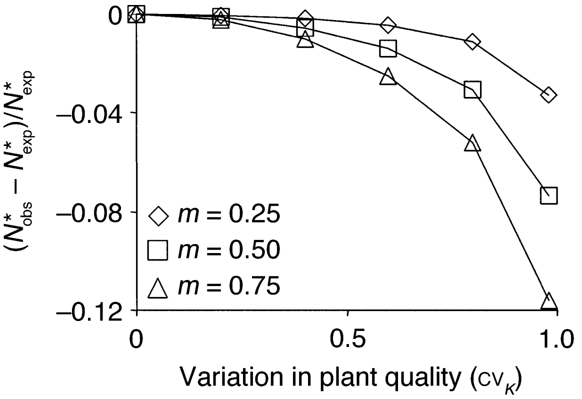

FIG. 4. Higher rates of herbivore movement (m) increased the effect of variation in plant quality on herbivore population size at equilibrium. Here, $\bar{K} = 50$; $\bar{r} = 2$; strength of the relationship between r and K is $\alpha = 0$ (i.e., no variance in r).

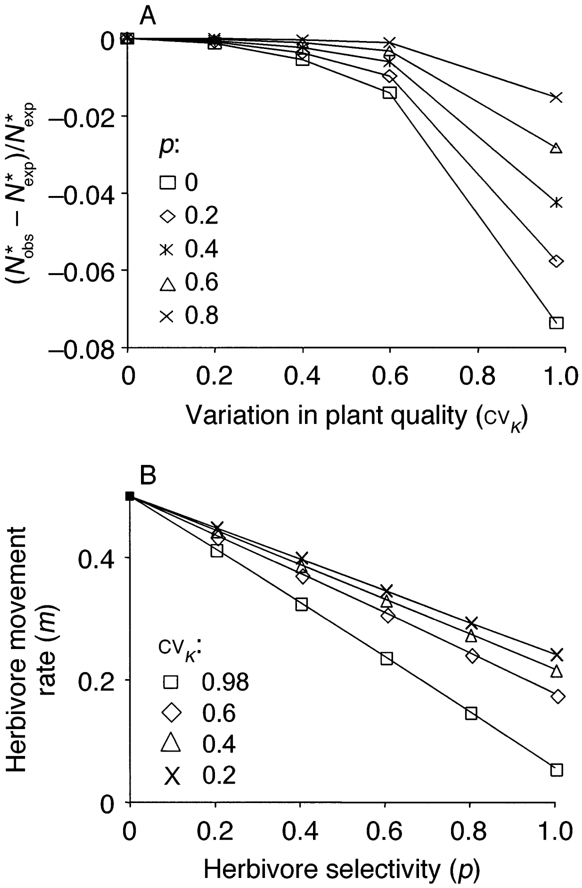

FIG. 5. (A) Herbivore selectivity (p) affects the influence of variance in plant quality on herbivore population size. (B) Greater herbivore selectivity leads to lower herbivore movement rates. For both (A) and (B), $\bar{K} = 50$; $\bar{r} = 2$; strength of the relationship between r and K is $\alpha = 0$ (i.e., no variance in r).

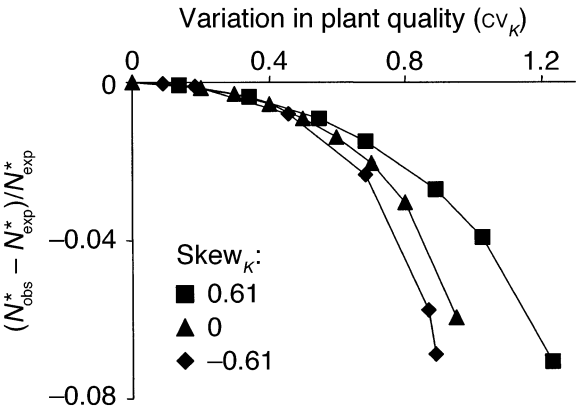

FIG. 6. Asymmetry in the distribution of plant quality affects herbivore population size. Here, $\bar{K} = 200$; strength of relationship between r and K is $\alpha = 0$.

quality other than the mean can influence herbivore population dynamics. Increasing variance in among-plant (patch) quality leads to increasing effects on herbivore population size. The direction and strength of those effects are governed by the interplay between variance in carrying capacity and population growth rate and by a population's proximity to equilibrium. The degree of asymmetry in plant quality also influences herbivore population size. The effects of the distribution of plant quality are modified by herbivore mobility and selectivity, although mobility appears to be more important than selectivity.

The effects of variance are driven by variance in carrying capacity creating sources (plants with $K_i > \bar{K}$) and sinks ($K_i < \bar{K}$) (Pulliam 1988). Sources produce more and sinks produce fewer than the average number of migrants. Because migrants land equally on all plants in this model, sinks are always above carrying capacity (they receive more migrants than they export), and sources are below carrying capacity (they receive fewer migrants than they export) (Fig. 8). The equilibrium size of populations on each plant is determined both by whether the plant is a sink or a source and by the strength of the sink or source (the rate at which that population can grow or shrink). That rate of change is determined jointly by a population's distance from its carrying capacity and by the growth rate (r) of the population. Populations with higher r's are stronger sources or sinks because they tend more strongly toward their carrying capacities. When r and K are positively correlated, high r's are associated with high K's (and vice versa), producing strong sources, weak sinks, and observed populations that are progressively larger than expected as variance in plant quality increases (Fig. 1). When r and K are negatively correlated, the reverse is true, and observed population sizes are smaller than expected population sizes. Although variance in K alone produces smaller than expected population

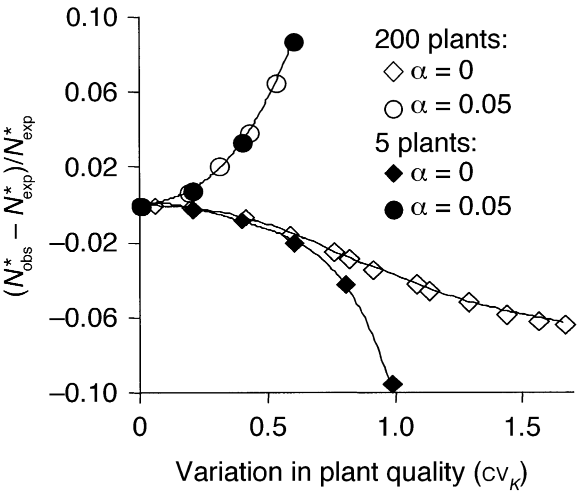

FIG. 7. Comparison of results from the model with five plants ($J = 5$) and a model with 200 plants ($J = 200$). For the larger model, K's were drawn from gamma distributions with specified cv_K's. For both models, $\bar{K} = 50$.

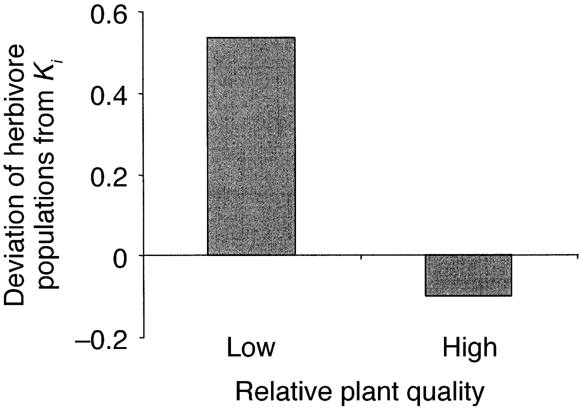

FIG. 8. In plant populations with variance in plant quality, individual plants with relatively low quality ($K_i - \bar{K} = -40$) have herbivore populations greater than carrying capacity ($[n_i^* - K_i]/K_i > 0$), whereas plants of relatively high quality ($K_i - \bar{K} = 40$) have herbivore populations below carrying capacity ($[n_i^* - K_i]/K_i < 0$). The figure shows results for one run of the model, where $\bar{K} = 50$; $\mathrm{CV}_K = 0.8$; $\bar{r} = 2$; and the strength of the relationship between r and K is $\alpha = 0$.

sizes, variance in both r and K can produce populations that are either smaller or larger than expected.

Arguments can be made for a variety of relationships between maximum population growth rate and carrying capacity. For example, one can imagine that a plant trait such as high nitrogen content might increase both herbivore reproduction at low densities and the number of herbivores supported at equilibrium. On the other hand, some theory (see Karban and Baldwin 1997) suggests that plants with high herbivore reproduction at low density (low constitutive resistance) might also have lower carrying capacities (strong induced resistance). Life history theory and some data suggest that r and K (or at least correlates of r and K) should be negatively correlated (Mueller 1997). Derivation of the logistic model (Gotelli 1998) suggests that higher r's are likely to be associated with higher K's (a positive correlation) because both r and K contain terms for birth rate and death rate at low density. I have considered a range of relationships between r and K in this study because, to my knowledge, data do not exist to determine the relative frequency of various relationships between these parameters in real systems.

Results of this model indicate that mean quality and skew (asymmetry) of quality can influence the relationship between variance in plant quality and herbivore population size. Higher mean carrying capacities cause more positive differences between observed and expected population sizes when r and K are positively correlated (Fig. 3A) and more negative differences when r and K are negatively correlated. We might thus expect systems with larger herbivore population sizes to be more sensitive to variance in population-dynamic parameters when r also varies ($\bar{K}$ has no effect on deviations in the absence of variation in r). The effect of $\bar{K}$ on differences between observed and expected population sizes when $\bar{K}$ is correlated with r probably results because higher $\bar{K}$'s cause high variance in r, which in turn causes larger absolute differences in population size. Higher mean herbivore population growth rates (r) cause smaller differences in population size (Fig. 3B), because high r's make all populations tend more strongly toward their carrying capacities. Populations growing very fast might therefore be less sensitive to variance in the quality of their host plants. Positive skew in the distribution of plant quality (skew_K) causes more positive differences between observed and expected population sizes, and negative skew causes more negative differences (Fig. 6). Positive skew (with the tail of the distribution to the right) leads to many sink plants and a few sources with very high K. The many sinks tend to pull the source populations far enough below K that they are in a steep part of their growth curve, making them strong sources and resulting in positive differences between observed and expected population sizes. When skew is negative, the many sources push the few sinks well above K, producing fast-shrinking, strong sinks that cause negative differences. Previous analytical models (Freedman and Waltman 1977, Chesson 1996) that include variance among patches have used the standard technique of ignoring moments higher than 2 in Taylor expansions, and therefore have not looked for effects of higher moments such as skew.

Characteristics of the herbivore affect the relationship of variance in plant quality to herbivore population size in this model; selectivity and mobility have opposite effects on differences between observed and expected population sizes. More selective herbivores show smaller differences between observed and expected populations (Fig. 5A), and more mobile herbivores show greater differences (Fig. 4). In this model, the effect of selectivity seems to be largely due to an effect of selectivity on insect mobility: more selective herbivores move less, and less mobile herbivores experience smaller differences between observed and expected population sizes (Fig. 5B). A wide variety of herbivores have been shown to be selective in their movements from plants (Bernays and Chapman 1994), thus tending to spend more time on preferred plants. It is likely that effects of variance in plant quality in the field would be reduced by herbivore selectivity. Whether generalists or more mobile herbivores are more affected by variance in plant quality in the field has not been addressed directly, although it is known that effects of polyculture on herbivore population size can be mediated by movement (Elmstrom et al. 1988).

The correspondence between the complexity of responses to variance observed in this model and the variety of effects of polyculture observed in experiments suggests that the source–sink mechanism could contribute to herbivore dynamics in the field. Other proposed mechanisms for an effect of variance on herbivores, e.g., effects on immigration or emigration (Power 1987, Elmstrom et al. 1988, Bernays 1999) or on insect physiology (Shelton 2000), tend to predict that observed populations should be smaller than expected populations, whereas both larger and smaller than expected populations are observed in the field. However, experiments isolating only the source–sink mechanism will be logistically difficult if not impossible, and data do not yet exist with which to estimate the effects of this mechanism in the field.

Several mechanisms other than source–sink dynamics have been proposed as ways in which variance in quality might influence herbivore population dynamics. For example, variance in quality has been shown to affect individual herbivore physiology. Insects on diets with higher variance can have lower (Stockhoff 1993) or higher (Bernays et al. 1994) performance than those on diets with lower variance, and these effects on performance could produce effects on herbivore population dynamics. Variation in quality has also been shown to influence herbivore movement, either by causing herbivores to leave high-variance patches more often than low-variance patches or by affecting the rate at which herbivores move within plant populations (Elmstrom et al. 1988, Bernays 1999). The rate of herbivore movement within or among patches might affect herbivore population sizes both because movement will affect which plant qualities herbivores encounter and because movement may be costly to herbivores in time, energy, or predation risk. The importance of the source–sink mechanism in the field will depend, in part, on how the source–sink dynamics described here interact with other mechanisms such as physiological effects or effects mediated by predators.

In the field, differences in the level of variation among plant patches, populations, or communities can occur at the phenotypic, genotypic, or species level. Differences in phenotypic variation might be generated by differences in environmental variation among patches within sites. Population size (Ouborg and Van Treuren 1995, Lammi et al. 1999) and geographically variable selection (Hartl 1988) can influence the level of genotypic variation in a population or community, and species diversity in plant communities might be influenced by factors including environmental heterogeneity and productivity (Stohlgren et al. 1999). Phenotypic, genotypic, and species-level variation in quality have usually been addressed by studies in very different fields (e.g., evolution of plant resistance, community stability, and applied agriculture), but the source–sink effect should apply regardless of the source of the variance. This may also be true for some other mechanisms that may mediate the effect of variance on herbivore populations (such as effects on movement or herbivore physiology). In some cases, it may thus be useful to consider variance in quality as a single phenomenon, regardless of the source of the variation. Thinking about the effect of variance in quality more generally might allow progress on a wider variety of questions at the same time.

To determine the importance of variance in real plant–herbivore systems, we need information on the distribution of plant-quality parameters in natural populations (the natural history of population-dynamic parameters). To my knowledge, variance and skew of r and K in natural populations have not yet been directly measured. Data on variance in plant resistance traits that affect herbivore performance (and thus may affect r and K) provide a measure of potential variance in r and K. For example, Simms and Rausher (1989) found coefficients of variation of resistance to different herbivores in one population of morning glories (*Ipomoea purpurea*) that ranged from <1 to 3.35 (most values well over 1). These data suggest that variation in resistance can be substantial. I found no correlation between r and K in a range of genotypes of wild strawberry (*Fragaria chiloensis*) across a large part of the species range (N. Underwood, *unpublished data*), although nothing is yet known about correlations between r and K within strawberry populations. Clearly, where most systems lie remains to be seen.

The question of how variance in plant quality is related to herbivore population size is not of academic interest only. Understanding the effect of variance is crucial for evaluating the use of polyculture as a pest control measure in agriculture. Despite many studies on the effects of polyculture, progress has been stymied by the observation that polycultures can both reduce and increase herbivore populations (Andow 1991). Results reported here suggest that this range of responses to polyculture should not be surprising. In order to make polyculture a valuable tool for agriculture, we may need to design specific types of polycultures, rather than expecting all polycultures to reduce herbivore abundance.

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LITERATURE CITED

Andow, D. A. 1991. Vegetational diversity and arthropod population response. Annual Review of Entomology **36**: 561–586.

Bernays, E. A. 1999. When host choice is a problem for a generalist herbivore: experiments with the whitefly *Bemisia tabaci*. Ecological Entomology **24**:260–267.

Bernays, E. A., K. L. Bright, N. Gonzalez, and J. Angel. 1994. Dietary mixing in a generalist herbivore: tests of two hypotheses. Ecology **75**:1997–2006.

Bernays, E. A., and R. G. Chapman. 1994. Host-plant selection by phytophagous insects. Chapman and Hall, New York, New York, USA.

Chesson, P. 1996. Matters of scale in the dynamics of populations and communities. Pages 353–368 *in* R. B. Floyd, A. W. Sheppard, and P. J. De Barro, editors. Frontiers of population ecology. CSIRO Publishing, Melbourne, Australia.

Denno, R. F., and M. S. McClure, editors. 1983. Variable plants and herbivores in natural and managed systems. Academic Press, New York, New York, USA.

Elmstrom, K. M., D. A. Andow, and W. W. Barclay. 1988. Flea beetle movement in a broccoli monoculture and diculture. Environmental Entomology **17**:299–305.

Freedman, H. I., and P. Waltman. 1977. Mathematical models of population interactions with dispersal. I: stability of two habitats with and without a predator. SIAM Journal on Applied Mathematics **32**:631–648.

Fritz, R. S., and E. L. Simms. 1992. Plant resistance to herbivores and pathogens: ecology, evolution, and genetics. University of Chicago Press, Chicago, Illinois, USA.

Gotelli, N. J. 1998. A primer of ecology. Sinauer Associates, Sunderland, Massachusetts, USA.

Gyllenberg, M., and I. Hanski. 1997. Habitat deterioration, habitat destruction, and metapopulation persistence in a heterogenous landscape. Theoretical Population Biology **52**:198–215.

Hartl, D. L. 1988. A primer of population genetics. Sinauer Associates, Sunderland, Massachusetts, USA.

Hastings, A. H. 1993. Complex interactions between dispersal and dynamics: lessons from coupled logistic equations. Ecology **74**:1362–1372.

Holt, R. D. 1985. Population dynamics in two-patch environments: some anomalous consequences of an optimal habitat distribution. Theoretical Population Biology **28**: 181–208.

Hunter, M. D., and P. W. Price. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology **73**: 724–732.

Karban, R., and I. T. Baldwin. 1997. Induced responses to herbivory. University of Chicago Press, Chicago, Illinois, USA.

Lammi, A., P. Siikamaki, and K. Mustajarvi. 1999. Genetic diversity, population size, and fitness in central and peripheral populations of a rare plant *Lychnis viscaria*. Conservation Biology **13**:1069–1078.

McPeek, M. A., and R. D. Holt. 1992. The evolution of dispersal in spatially and temporally varying environments. American Naturalist **140**:1010–1027.

Microsoft. 1998. Visual C++. Microsoft Corporation, Seattle, Washington, USA.

Mueller, L. D. 1997. Theoretical and empirical examination of density-dependent selection. Annual Review of Ecology and Systematics **28**:269–288.

Ouborg, N. J., and R. Van Treuren. 1995. Variation in fitness-related characters among small and large populations of *Salvia pratensis*. Journal of Ecology **83**:369–380.

Power, A. G. 1987. Plant community diversity, herbivore movement, and an insect-transmitted disease of maize. Ecology **68**:1658–1669.

Press, W. H., B. P. Flannery, S. A. Teukolsky, and W. T. Vetterling. 1992. Numerical recipes in C: the art of scientific computing. Second edition. Cambridge University Press, New York, New York, USA.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist **132**:652–661.

Rausher, M. D. 1981. Host plant selection by *Battus philenor* butterflies: the roles of predation, nutrition, and plant chemistry. Ecological Monographs **51**:1–20.

Rossiter, M., J. C. Schultz, and I. T. Baldwin. 1988. Relationships among defoliation, red oak phenolics, and gypsy moth growth and reproduction. Ecology **69**:267–277.

Shelton, A. L. 2000. Variable chemical defences in plants and their effects on herbivore behaviour. Evolutionary Ecology Research **2**:231–249.

Simms, E. L., and M. D. Rausher. 1989. The evolution of resistance to herbivory in *Ipomoea purpurea*. II. Natural selection by insects and costs of resistance. Evolution **43**: 573–585.

Stockhoff, B. A. 1993. Diet heterogeneity: implications for growth of a generalist herbivore, the gypsy moth. Ecology **74**:1939–1949.

Stohlgren, T. J., L. D. Schell, and B. V. Heuval. 1999. How grazing and soil quality affect native and exotic plant diversity in Rocky Mountain grasslands. Ecological Applications **9**:45–64.

Underwood, N., and M. D. Rausher. 2000. The effects of host-plant genotype on herbivore population dynamics in a model system. Ecology **81**:1565–1576.

Ylioja, T., H. Roininen, M. P. Ayres, M. Rousi, and P. W. Price. 1999. Host-driven population dynamics in an herbivorous insect. Proceedings of the National Academy of Sciences (USA) **96**:10735–10740.

Zangerl, A. R. 1990. Furanocoumarin induction in wild parsnip: evidence for an induced defense against herbivores. Ecology **71**:1926–1932.

Zangerl, A. R., and M. R. Berenbaum. 1991. Furanocoumarin induction in wild parsnip: genetics and populational variation. Ecology **71**:1933–1940.