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Biodiversity and stability of herbivore populations: influences of the spatial sparseness of food plants

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Abstract Returning to the classical diversity–stability problem about population densities, we propose a hypothesis that the spatial sparseness of food plants of herbivores, which is frequently observed in diversified communities such as those in the tropics, may be a potential source of the low variability in herbivore densities. The hypothesis consists of the following components: (1) sparseness of food plants of several herbivores increases with increasing number of plant species in a given amount of area, (2) spatial sparseness of food plants reduces the dispersal rate of herbivores between food plants, (3) such a decrease in dispersal rate causes a larger spatial variance in the consumption rate of food plants, (4) such a large spatial variance in the consumption rate of food plants reduces the temporal variance in the amount of food plants, and (5) the reduced temporal variance in the amount of food plants yields a smaller variance in the temporal dynamics of herbivores. A simple mathematical model was constructed to show a theoretical basis of the fourth component of the hypothesis. To exemplify the second, third, and fourth components of the hypothesis in fields, we conducted field experiments on the interaction between butterfly larvae and cabbages, in which cabbage seedlings were planted by two levels of sparseness: 1 m apart and 0.2 m apart. The spatial variance in the amount of leaf dry weight that escaped from larval feeding was larger in sparsely planted fields, which was in accordance with the third component of the hypothesis. The variability in the mean amount of leaf dry weight was smaller in sparsely planted fields, which was in accordance with the fourth component of the hypothesis.

Key words Community · Spatial variance · Synchrony · Temporal variance

Introduction

The relationship between species diversity and ecosystem function has emerged as a central topic in ecology today (Schläpfer and Schmid 1999; Tilman 1999; Loreau 2000). Recent experiments have shown that biodiversity sometimes increases the magnitude of total ecosystem processes, such as total plant biomass production, total nutrient retention, and total CO_2 flux (Naeem et al. 1994, 1996; Tilman et al. 1996; Hooper and Vitousek 1997; Jolliffe 1997; Tilman et al. 1997; van der Heijden et al. 1998; Hector et al. 1999). Several other experiments have shown that biodiversity enhances the stability of total ecosystem processes in the face of perturbations (Tilman and Downing 1994; Tilman 1996; McGrady-Steed et al. 1997; Naeem and Li 1997). These recent arguments are quite different from the classical diversity–stability arguments posed by MacArthur (1955) and Elton (1958). MacArthur (1955) defined the stability of a community as a state in which one species in the community does not change markedly in abundance when another species has an abnormal abundance. Elton (1958) presented several kinds of "evidence" about the diversity–stability relationship, such as (1) insect population outbreaks frequently occur in arctic regions but rarely occur in tropical regions where the number of species is large, and (2) insect population outbreaks most often happen on cultivated or planted land, that is, in habitats and communities very much simplified by humans. Thus, both authors mainly considered the population stability of individual species, instead of the stability of total ecosystem processes, and hence recent arguments do not contribute much to solving the classical diversity–stability problem.

In an environment with a small number of species, such as an arctic community, food plants of an herbivorous species are rather continuously distributed. In an environment with many species, such as a tropical community, the food plants are rather sparsely distributed as compared to those in an environment with a small number of species because the range of food plant species is more or less restricted in most herbivores. Such sparseness in the spatial distribution

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of food plants seems to be an inevitable consequence of biodiversity (species richness) of plant species.

In this article, we propose a new hypothesis: the population variability of herbivorous species in a diversified community will be reduced by the sparseness of their food plants. We constructed a simple mathematical model to indicate a theoretical basis of this hypothesis. To exemplify several components of the hypothesis in fields, we conducted field experiments on the interaction between cabbages, *Brassica oleracea* Linnaeus, and larvae of the small white butterfly, *Pieris rapae crucivora* Boisduval (Lepidoptera, Pieridae), by planting cabbage seedlings by two levels of sparseness. It is shown that the variability in the mean amount of food plants that escapes from larval feeding is smaller in sparsely planted fields than in densely planted fields, which is in accordance with our hypothesis.

Model

Our hypothesis consists of the following components: (1) sparseness of food plants of several herbivores increases with increasing number of plant species in a given amount of area, (2) spatial sparseness of food plants reduces the dispersal rate of herbivores between food plants, (3) such a decrease in dispersal rate causes a larger spatial variance in the consumption rate of food plants, (4) such a large spatial variance in the consumption rate of food plants reduces the temporal variance in the amount of food plants, and (5) the reduced temporal variance in the amount of food plants yields a smaller variance in the temporal dynamics of herbivores.

Several conditions are necessary to validate each of the components. For the first component to become valid, each herbivore must eat, more or less, a limited range of plants. For the second component to become valid, the herbivores must have dispersal ability that is more or less limited. For the third component to become valid, when the generation is discrete, for example, the number of juvenile herbivores per food plant in the beginning of a generation must fluctuate by chance, and herbivores must try to move to the next food plant, at least when they exhausted one food plant. Concerning the fourth component, several authors have discussed the stabilization effects of spatial aggregation of organisms (May 1978; Yamamura 1989; Pacala et al. 1990; Hassell et al. 1991; Pacala and Hassell 1991; Yamamura 1998). Most of the previous results are derived from several restrictive assumptions in spatial variance and in the form of density dependence. However, we are able to show the general applicability of the fourth component by the following simple model. We first restrict our discussion to plant–herbivore systems, although a similar mechanism is expected for prey–predator systems.

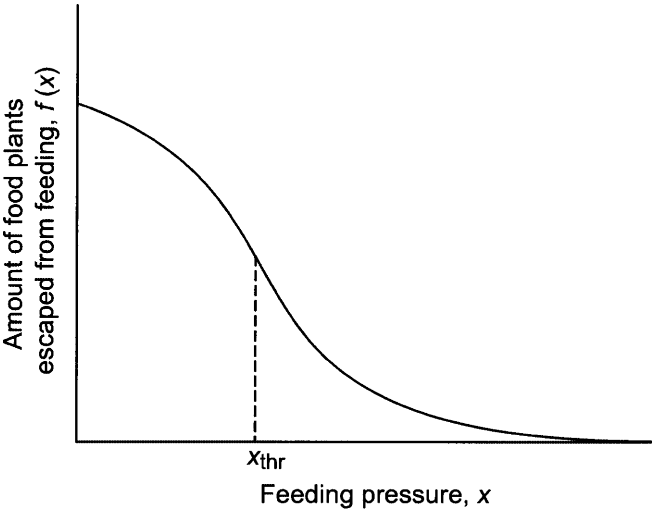

Fig. 1. Schematic illustration of the form of $f(x)$. x_{thr} indicates the feeding pressure at which the curvature is zero

Let x be the amount of feeding pressure on a plant ($x \geq 0$). Let $f(x)$ be a smooth decreasing function describing the amount of food plants escaped from feeding under a feeding pressure of x ($f(0) > 0, f(\infty) = 0, f'(x) \leq 0$, and $f'(\infty) = 0$). We approximate that $f(x)$ linearly decrease with increasing x around $x = 0$, that is, $f''(0) = 0$. Then, there exists a threshold amount of feeding x_{thr} (≥ 0) where $f''(x_{\mathrm{thr}}) = 0$ and $f'''(x_{\mathrm{thr}}) > 0$. The general form of the $f(x)$ curve is illustrated in Fig. 1. Let $\bar{x}$ be the mean of x within a field. Let $V_1(\bar{x})$ be the spatial variance of x in a field in which food plants are sparsely planted, and $V_2(\bar{x})$ is that in a densely planted field. We consider a general case where the variance may change with increasing $\bar{x}$, because it is known that the variance usually increases with increasing mean (Taylor 1961; Iwao 1968; Iwao and Kuno 1971; Taylor et al. 1978, 1979; Yamamura 1990, 2000). Then, we have a relation under the second and third component of the hypothesis:

$$V_1(\bar{x}) \geq V_2(\bar{x}) \tag{1}$$

We can approximately express the mean amount of $f(x)$ that is denoted by $M_i(\bar{x})$ by the following equation, by using Taylor series expansions around $\bar{x}$ (see Yamamura 1998, for example):

$$M_i(\bar{x}) \approx f(\bar{x}) + \frac{1}{2} f''(\bar{x}) V_i(\bar{x}) \quad (i = 1, 2) \tag{2}$$

where $i = 1$ and 2 correspond to sparsely planted fields and densely planted fields, respectively. Let $\bar{\bar{x}}$ and σ^2 be the mean and variance of a given probability distribution of $\bar{x}$. Let H_i be the resultant variance of $M_i(\bar{x})$. Then, σ^2 and H_i can be interpreted as input variance and output variance, respectively. By using the delta method (Stuart and Ord 1994) and by using Eq. 2, we obtain an approximation:

$$\begin{aligned} H_i &\approx \left[M_i'(\bar{\bar{x}})\right]^2 \sigma^2 \\ &\approx \left[f'(\bar{\bar{x}}) + \frac{1}{2} f''(\bar{\bar{x}}) V_i'(\bar{\bar{x}}) + \frac{1}{2} f'''(\bar{\bar{x}}) V_i(\bar{\bar{x}})\right]^2 \sigma^2 \quad (i = 1, 2) \end{aligned} \tag{3}$$

Around $\bar{\bar{x}} = x_{\mathrm{thr}}$, we obtain:

$$H_i \approx \left[f'\left(\bar{\bar{x}}\right) + \frac{1}{2} f'''\left(\bar{\bar{x}}\right) V_i\left(\bar{\bar{x}}\right) \right]^2 \sigma^2 \tag{4}$$

as we have $f''(x_{\mathrm{thr}}) = 0$, as mentioned before. Let us first imagine that feeding pressure is spatially uniform for both sparsely planted fields and densely planted fields, i.e., $V_1(\bar{x}) = V_2(\bar{x}) = 0$. In this case, Eq. 3 becomes

$$H_i \approx \left[f'\left(\bar{\bar{x}}\right) \right]^2 \sigma^2 \tag{5}$$

If the feeding pressure becomes slightly aggregated, i.e., $V_1(\bar{x}) \geq V_2(\bar{x}) > 0$, we obtain the following inequality from Eq. 4 around $\bar{\bar{x}} = x_{\mathrm{thr}}$, as we have $f'(x_{\mathrm{thr}}) < 0$ and $f'''(x_{\mathrm{thr}}) > 0$, as mentioned before:

$$H_1 \leq H_2 \tag{6}$$

Inequality (Eq. 6) indicates that the output variance of the amount of food escaped from feeding, under a same input variance of $\bar{x}$, is smaller in sparsely planted fields than in densely planted fields. In a plant–herbivore system where the herbivore population is much influenced by the amount of food, a smaller output variance in food quantity (H_i) will cause a smaller input variance in the herbivore population (σ^2) of the next generation. Hence, the variability will be damped if H_i is small. Conversely, a larger output variance will cause a larger input variance of the next generation in this system. Hence, the variability will be sometimes amplified if H_i is large.

To exemplify the foregoing arguments, let us examine the simplest case where the mean feeding pressure in the ($t + 1$) generation is given deterministically by the mean amount of food that escaped from feeding in the t generation: $\bar{x}_{t+1} = M_i(\bar{x}_t)$, where $\bar{x}_t$ is the mean feeding pressure in the tth generation. Let $\bar{\bar{x}}_t$ and σ_t^2 be the input mean and input variance of $\bar{x}_t$, respectively. When the spatial distribution of feeding pressure is uniform, we obtain $\sigma_{t+1}^2 \approx [f'(\bar{\bar{x}}_t)]^2 \sigma_t^2$ from Eq. 5. Hence, the variance converges to 0 if $-1 < f'(\bar{\bar{x}}_t) < 1$ around the equilibrium density. This criterion is identical to the well-known local stability criterion (e.g., Clark 1976). Two-point cyclicity will be yielded if $f'(\bar{\bar{x}}_t) = -1$. The behavior of this system is more complex if $f'(\bar{\bar{x}}_t) < -1$; a cyclical dynamics with a longer period is yielded in several cases, whereas chaotic dynamics is yielded in other cases depending on the form of $f(x)$, as first indicated by May (1974, 1975, 1976). The mean feeding pressure ($\bar{x}_t$) will fluctuate widely around x_{thr} in these unstable situations. Therefore, Eq. 4 indicates that these unstable systems will become locally stable if $V_i(\bar{x}_t)$ is sufficiently large.

Field experiment

We are able to exemplify some of the components of the hypothesis in field experiments. However, the following complexities will arise in actual fields.

First, it is known that the sparseness of food plants influences the mean of herbivore populations, although we are considering the variance (and local stability) of herbivore populations in the fourth component of our hypothesis. Root (1973) proposed the resource concentration hypothesis whereby "many herbivores, especially those with a narrow host range, are more likely to find hosts that are concentrated." This hypothesis predicts that the density of herbivores per host plant is higher in dense stands of their host plants. However, most of the experimental results examining the effect of plant density contradict the resource concentration hypothesis if the size of the experimental plots is kept constant. The density of herbivores per plant decreased with increasing density of host plants in most cases (Luginbill and McNeal 1958; Pimentel 1961; Way and Heathcote 1966; A'Brook 1968; Farrell 1976; Solomon 1981; Latheef and Ortiz 1983; Root and Kareiva 1984; Power 1987; Segarra-Carmona and Barbosa 1990; Thompson and Quisenberry 1995; Yamamura 1999). Only a few experiments supported the resource concentration hypothesis (Ralph 1977; Turchin 1988) and several experiments did not detect consistent results (Mayse 1978; Bach 1980; Boiteau 1984; Power 1989; Coll and Bottrell 1994). Therefore, Yamamura and Yano (1999) adopted the opposite hypothesis, which may be called the resource diffusion hypothesis: herbivores more efficiently use hosts that are diffused (i.e., sparsely distributed). One of the causes of such phenomena is the dilution effect of dense planting; the potential amount of total immigration is limited, and hence immigrated herbivores are diluted in a densely planted plot where the total number of plants in a plot is large (Yamamura 2002).

Second, other plant species that are planted adjacent to the main food plants of herbivores yield various influences on the herbivores. For example, several other plant species may generate habitats for predatory ground beetles that reduce the herbivore density (Theunissen et al. 1995). Such an influence of other plant species was called the enemies hypothesis by Root (1973). If the herbivore can eat other plant species as well as the main food plants, the sparseness of their food does not occur. Thus, the influence of other plant species on the sparseness of food changes depending on whether the herbivore species is polyphagous or monophagous. Risch et al. (1983) and Andow (1991) used the comparison between polyphagous or monophagous species to evaluate the relative liability of the enemies hypothesis and the resource concentration hypothesis.

We adopted several simplifications to reduce the influence of the aforementioned problems in field experiments. We regulated only the sparseness of plants, without using other plant species, because other plant species may cause various influences such as those already indicated. Thus, we designed the experiments to exemplify the second, third, and fourth components of the hypothesis. We must compare the output variance (H_i) between sparsely planted plots and densely planted plots under the same $\bar{\bar{x}}$. However, the quantity of $\bar{\bar{x}}$ is liable to become smaller in densely planted plots as a result of the dilution effect. Hence, we kept the total number of plants in a plot constant, to avoid the dilution effect of dense planting, by changing the planted area in a plot. In this experimental design, however, we cannot eliminate the influence of spatial heterogeneity. The probability of immigration to a plant from outside the plot will be different between adjacent plants within the same plot due to unknown spatial heterogeneity. Such difference between adjacent plants inevitably increases with increasing distance between plants. Therefore, the spatial distribution of immigrants within a plot might be more aggregative in a sparsely planted plot than in a densely planted plot.

Materials and methods

Four 1-month-old cabbage seedlings were planted squarely at two distances at the center of each experimental plot: in sparsely planted plots, 1 m apart; and in densely planted plots, 0.2 m apart. The size of each experimental plot was 5 × 5 m. Experiments were performed with two blocks, each containing eight sparsely planted plots and eight densely planted plots, in July of 1994 and 1996 (Fig. 2). Wild adult females of the small white butterfly, *P. rapae crucivora*, freely entered these experimental plots to lay their eggs. Arthropods on cabbages, except for larvae of *P. rapae crucivora*, were removed by hand twice every week during the experimental period. Larvae of *P. rapae crucivora* were left to eat cabbages freely. Although we could not avoid the attack by the parasitoid *Cotesia glomerata* (Linnaeus), we could not find any significant influence of this parasitoid, because this parasitoid killed larvae only after they were fully grown. The dry weight of leaves that escaped from larval feeding was measured after the completion of one generation of *P. rapae crucivora*. Variance of dry weight was estimated by the maximum likelihood method, and the difference was tested by the likelihood ratio test by using PROC MIXED of SAS (SAS Institute 1997). Another experiment of a similar design was performed to estimate the probability of successful movement of larvae between cabbages. One of the four cabbages was replaced by a wood stick (3 mm in diameter, 50 mm in height), and a fourth-instar larva was released on the stick. The larva was observed until it successfully moved to the neighboring plants or died.

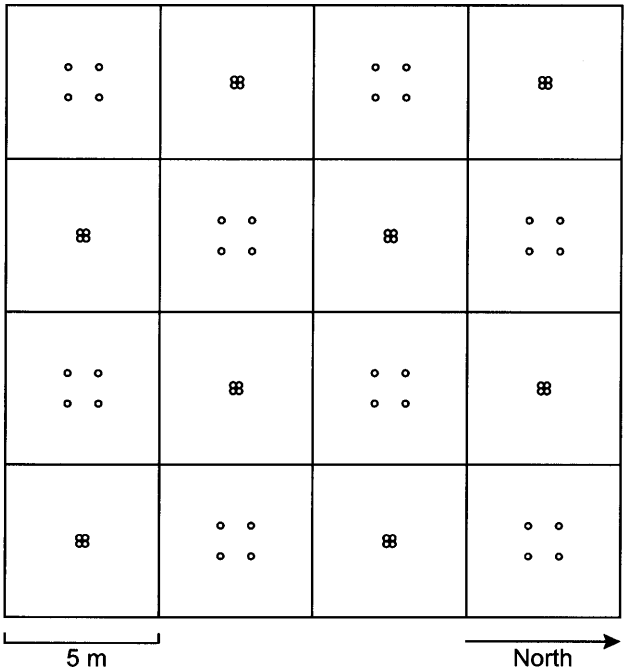

Fig. 2. Map of an experimental block in field. Each circle indicates a cabbage seedling. One block consists of 8 sparsely planted plots (1 × 1 m in plant spacing) and 8 densely planted plots (0.2 × 0.2 m in plant spacing). *Line* indicates the division of plots

Results

Plots in each block are independent replicates because larvae rarely move across plots. Hence, the variance between plots, that is, the variance of mean dry weight of four cabbages between plots, indicates the output variance, H_i. The variance within a plot, that is, the variance of leaf dry weight between four cabbages within a plot, indicates the spatial variance, $V_i(\bar{x})$. The variance within a plot was larger in sparsely planted plots than in densely planted plots in three blocks (*B*, *C*, *D* in top graphs in Fig. 3). These results correspond to the inequality $V_1(\bar{x}) \geq V_2(\bar{x})$ (Eq. 1). In contrast, the variance between plots was smaller in sparsely planted plots than in densely planted plots in three blocks (*B*, *C*, *D* in middle graphs in Fig. 3). These results correspond to the predicted inequality $H_1 \leq H_2$ (Eq. 6). In these blocks, several cabbage seedlings were completely destroyed by feeding of larvae. In block 1 in 1994, however, no cabbage seedlings were completely destroyed, probably because the number of eggs laid by female adults was unexpectedly small. No difference in variance was observed in this block (Fig. 3, *A*). The mean amount of dry weight of leaves that escaped from larval feeding was not much different between sparsely planted plots and densely planted plots (bottom graphs in Fig. 3).

The estimated probability of successful movement of larvae was 1.00 for densely planted plots and 0.31 for sparsely planted plots (sample size, 59 and 58, respectively). Hence, we can consider that the smaller within-plot variance in densely planted plots is the result of the free movement of larvae among four plants, at least to some extent, because larvae try to move to other plants when they have completely eaten the leaves of a plant. However, the spatial heterogeneity in the number of eggs within a sparsely planted plot may be one of the causes of the larger within-plot variance. Difference in the effect of predators may be also suspected; there is a possibility that the smaller within-plot variance in densely planted plots was caused by the uniform predation pressure, because predators will also move freely among four plants in a densely planted plot as well as herbivores. However, such influence of predation might not be large in our experiment because we removed the possible predators twice every week.

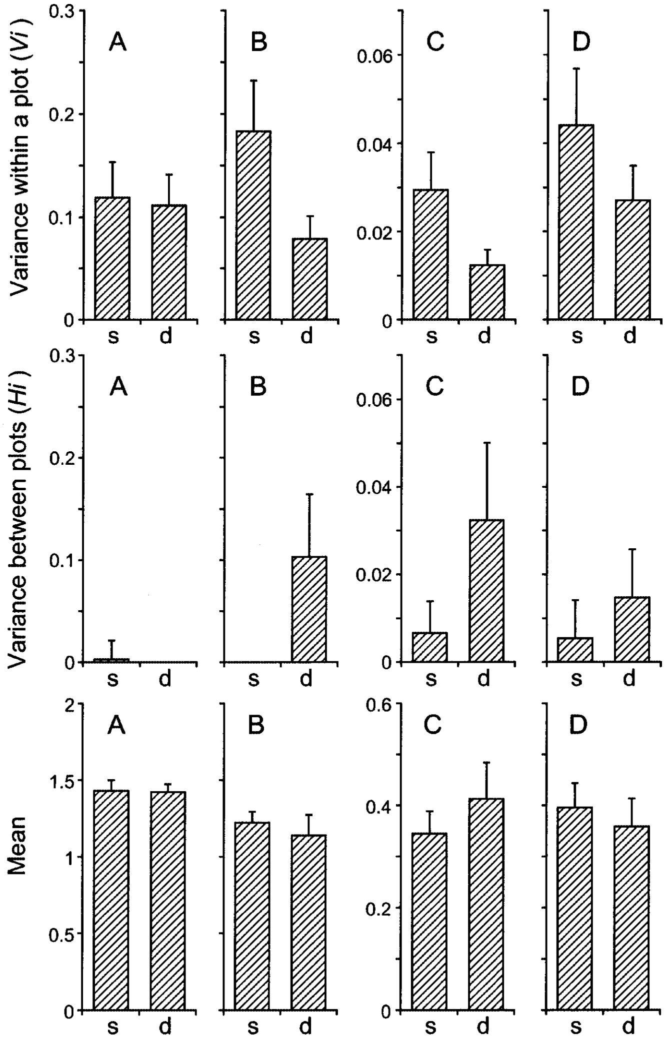

Fig. 3. Influence of spatial sparseness of food plants (cabbage seedlings) on the dry weight of leaves escaped from larval feeding of the small white butterfly (*Pieris rapae crucivora*). The square root transformation of dry weight (g) was used to stabilize the variance. *s*, sparsely planted plots (1 × 1 m in plant spacing); *d*, densely planted plots (0.2 × 0.2 m in plant spacing). *A*, block 1 in 1994; *B*, block 2 in 1994; *C*, block 1 in 1996; *D* block 2 in 1996. *Top graphs*, variance within an experimental plot (maximum likelihood estimate ± asymptotic SE). *A*, $\chi_1^2 = 0.030, P = 0.864$; *B*, $\chi_1^2 = 4.422, P = 0.035$; *C*, $\chi_1^2 = 4.434, P = 0.035$; *D*, $\chi_1^2 = 1.398, P = 0.237$. *Middle graphs*, variance between experimental plots (maximum likelihood estimate ± asymptotic SE). *A*, $\chi_1^2 = 0.026$, $P = 0.872$; *B*, $\chi_1^2 = 3.938, P = 0.047$; *C*, $\chi_1^2 = 2.269, P = 0.132$; *D*, $\chi_1^2 = 0.448$, $P = 0.503$. *Bottom graphs*, mean dry weight in each plot (mean ± SE). *A*, $F_{1,13} = 0.01, P = 0.921$; *B*, $F_{1,13} = 0.31, P = 0.586$; *C*, $F_{1,14} = 0.76, P = 0.397$; *D*, $F_{1,14} = 0.30, P = 0.590$. Error degrees of freedom were 13 in 1994, because one plot was destroyed by ants

Discussion

We focused on the stability of population dynamics of individual species instead of the stability of total ecosystem processes. Relatively few arguments have ever been conducted for the diversity–stability question at the population level (Sankaran and McNaughton 1999). Tilman (1996) showed that stability at the population level is quite different from that at the ecosystem level by analyzing the 13-year data of plant species abundance, diversity, and production in 207 grassland plots in Minnesota. The year-to-year variability in total aboveground plant community biomass was significantly lower in plots with greater plant richness, whereas the year-to-year variability in population abundance of each species was rather larger in plots with greater plant richness. In this sense, biodiversity stabilized ecosystem processes, but simultaneously destabilized the population dynamics of individual species. Such experimental results seemed to coincide with the current theoretical framework; the stabilization effects of biodiversity on total ecosystem processes can be explained by several mechanisms, such as the insurance hypothesis and the portfolio effect that is an inevitable effect from the point of view of traditional sampling theory (Doak et al. 1998; Tilman et al. 1998; Yachi and Loreau 1999; Hughes and Roughgarden 2000), whereas the destabilization effect of biodiversity on population dynamics of individual species is consistent with the mathematical results of May (1972, 1973), who found that greater diversity led to lower local stability of multispecies equilibrium in a Lotka–Voltera competitive model. These results contradicted Elton's evidence, such as frequent outbreaks of herbivores in simplified arctic communities.

May's results were supported by Wolda (1978), who showed that insect populations in the tropics have the same annual variability as those in temperate zones. However, the empirical evidence posed by Elton seems to be partially valid, because cyclicity in population dynamics has been mostly reported in arctic or temperate regions (Turchin and Taylor 1992). Therefore, we should explore another mechanism, one that was not considered by May (1972, 1973) and Tilman (1996), to explain such evidence. A possible mechanism was indicated by McCann et al. (1998). They showed that the population oscillation might be damped by the increase in biodiversity within a restricted range of parameters (i.e., under weak interactions). We proposed a hypothesis about another possible mechanism for the biodiversity–stability relationship at the population level: spatial sparseness of food plants reduces variability in the mean amount of food that escapes from herbivorous feeding, and hence the population variability of herbivores will be smaller in diversified communities where their food plants are sparsely distributed. Although we focused on the plant–herbivore systems in this article, we can expect a similar stabilization mechanism in prey–predator systems in diversified communities. The predation pressure on prey may become spatially uniform in simplified communities where predators can move freely. In such communities, the temporal variance of the number of prey may become larger. A series of spatial prey–predator models have indicated the importance of spatial aggregation of predation pressures on the local stability of population dynamics (Hassell 1978; Pacala et al. 1990; Hassell et al. 1991; Pacala and Hassell 1991).

Equations 1 and 6 indicated a close relationship between spatial synchrony and cyclicity, because spatially uniform consumption of food plants (i.e., small V_i) means that the consumption is spatially synchronous. Spatial synchrony is often observed in the cyclic dynamics of forest insects and mammals (Williams and Liebhold 1995; Ranta et al. 1997; Bjørnstad et al. 1999; Koenig 1999; Kamata 2000). Two possible mechanisms of such synchrony have been identified: (1) dispersal and (2) the Moran effect (Jansen 1999; Lloyd and May 1999; Ranta et al. 1999a). The Moran effect, which was named after Moran (1953), occurs when there are some density-independent factors (such as climatic factors) that are correlated between wide regions (Royama 1992). Much attention has been paid as to which of the two is the principal cause of synchrony (Grenfell et al. 1998; Lande et al. 1999; Ranta et al. 1999b; Cattadori et al. 2000). Kendall et al. (2000) discussed the interaction of these two factors by using a simple model.

In contrast, we suggested the possibility that dispersal is the principal cause of both synchrony and cyclicity. Dispersal creates the synchrony (small V_i), and the synchrony creates large H_i. If V_i is very small, H_i approaches its maximum quantity, as given by Eq. 5. Such a system will show cyclic dynamics depending on both the form of $f(x)$ and how $f(x)$ determines the population of the next generation. If V_i is large, however, H_i is given by Eq. 4, and hence the population dynamics will become locally stable even if the dynamics is cyclic under Eq. 5. In this mechanism of outbreaks, therefore, outbreaks do not happen without spatial synchrony. Bjørnstad (2000) reanalyzed the time series of rodent peaks reported by Steen et al. (1990) and found that the degree of synchrony was high when the population was cyclic but that it was low when the population was noncyclic. Such a close relationship between synchrony and cyclicity is seemingly consistent with our hypothesis.

Our hypothesis may further imply the importance of the size of a nature reserve in maintaining the populations at locally stable situations. The difference in plant spacing in our experiment (0.2 m and 1 m) can be interpreted as the difference in the size of microecosystems at 0.2 × 0.2 m and 1 × 1 m. Then, the middle graphs in Fig. 3 indicate that the variability in the mean food amount (H_i) is larger in a smaller microecosystem than in a larger microecosystem. Thus, the experimental results indicate that the size of ecosystems may be one of the principal components determining the local stability of population densities. In this context, the model can be interpreted in the following way. If the size of a nature reserve is too small, herbivores can freely move around the nature reserve, causing the uniform utilization of food plants (small V_i). Then, Eq. 6 indicates that the population dynamics of herbivores in such a small nature reserve will not be locally stable. Extrapolating from a small-scale experiment to the size of a nature reserve is unwarranted, but such a possibility may be worth noting.

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