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Detecting spatial interactions in the ragweed (*Ambrosia artemissifolia* L.) and the ragweed beetle (*Ophraella communa* LeSage) populations

Abstract We observed a weed (*Ambrosia artemissifolia*)–beetle herbivore (*Ophraella communa*) system for three years in a spatially continuous field (≈200 ha). We analyzed our field data in the light of two contrasting theories: the *resource-concentration hypothesis* and *reaction–diffusion theory*. For the resource-concentration hypothesis, we calculated the correlation coefficients between weed and beetle abundances for every season in each year. Although we found weak support for resource concentration in some seasons, we could not find any clear relationships in other seasons. We discuss a dispersal-based mechanism to explain the differences observed among seasons in lieu of the resource-concentration hypothesis. For the reaction–diffusion theory, we estimated the nonparametric spatial covariance functions for the spatial autocorrelation of weeds and beetles. Although we could not find any strong spatial structure for the individual species, we found evidence of spatial interactions between weeds and beetles using time lagged cross-correlation functions. Weed abundance enhanced local beetle abundance. Through time, there was evidence of beetle spillover to adjacent locations at roughly the one beetle-generation time scale.

Sites with large number of beetles did not seem to reduce subsequent weed abundance.

Keywords Ambrosia artemissifolia · Ophraella communa · Nonparametric spatial covariance functions (NCF) · Reaction–diffusion · Resource-concentration hypothesis · Spatial statistics

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Introduction

The relationship between plant-patch size and herbivore density has been a central issue in both pest control (Root 1973; Kareiva 1983; Andow 1991; Banks 1998) and conservation biology (Harrison 1991; Thomas and Harrison 1992; Hanski and Ovaskainen 2003). Historically, two theories have been proposed. One is the *resource-concentration hypothesis* originally proposed by Root (1973), which focuses on behavioral processes of herbivores. Although the resource-concentration hypothesis is highly conceptual and has different meanings in different areas of ecology (Kareiva 1983), it essentially predicts that a large patch of plants will contain a higher density of herbivores than smaller ones (Connor et al. 2000). This idea, therefore, has stimulated field research to find a positive relationship between plant-patch size and herbivore density. The literature holds many examples of positive relationships between patch size and *number* of herbivore individuals per patches. However, when the *density* of herbivores (per plants or per biomass) is considered, some herbivores exhibit a positive relationship (Cromartie 1975; Thompson 1978; Macgarvin 1982) while others do not (Macgarvin 1982; Segrra-Carmona and Barbosa 1990) and several species even have negative relationships (Cromartie 1975; Kareiva 1983). Thus, there is no general conclusion as to whether a large patch disproportionately enhances per plant herbivory or not. Empirical and theoretical studies suggest that searching behavior by various herbivores for suitable patches may explain the discrepancy between different studies (Jones 1977;

Banks 1998; Hambäck and Englund 2005). These studies, however, do not generally consider the explicit spatial layout of patches. The herbivores are typically assumed to migrate with equal probability among patches. This is in contrast to many recent theoretical studies of spatial population dynamics, which predict that spatial patterns may arise from distance dependent dispersal (Ranta et al. 1995; Heino et al. 1997).

The second relevant body of theory is *reaction–diffusion theory,* which predicts that the nonlinear interactions among species (e.g., a predator and a prey) together with spatially restricted movement can generate self-organized patterns in space. Its application in population ecology, with particular reference to host–parasitoid interactions, resulted in the rediscovery of several self-organized spatial patterns in theoretically interacting species, such as *spiral waves*, *Turing structures*, and *spatial chaos* (Hassell et al. 1991). Plant–herbivore systems can also be regarded as a reaction–diffusion interaction. Herbivores (= predator) feed on plants produce offspring from the plant biomass. As long as it is not killed through herbivory, the plant (= prey) on the other hand, can recover its biomass after the dissipation of the herbivores. Usually, herbivores disperse much farther and faster than the host plants because the latter generally have to rely on seed dispersal for movement. Because of this, abundant herbivores supported by a dense region of host plant may spill over at the edges of the dense plant region, producing a peripheral zone with a high herbivore:plant ratio that may prevent the plant patch from expanding. Theoretical work has revealed that self-organized pattern formations may arise from a variety of ecological interactions (Solé and Bascompte 1997) and can be robust in the face of stochasticity (Bascompte et al. 1997). These findings have an important implication in nature because they predict that plant–herbivore interactions themselves can result in spatial pattern formation without assuming any a priori spatial heterogeneity. Although 15 years have passed since the initial theoretical work of Hassell et al. (1991), there is not much evidence in nature related to self-organized pattern formation in trophic interactions (but see Maron and Harrison 1997; Bjørnstad et al. 2002).

In the face of the contrasting theories (resource concentration versus reaction–diffusion) for plant–herbivore interactions, we ask several questions. Do herbivores aggregate in larger patches than smaller ones? If so, is the density of herbivores dependent on the patch area? To what extent are the spatial patterns formed by limited dispersal abilities? In short, to what extent are the spatial dynamics of herbivores controlled by resource-concentration theory versus constrained by reaction–diffusion processes? We seek to address these questions with respect to the plant–herbivore system comprised of ragweed (*Ambrosia artemissifolia* L.) and ragweed beetle (*Ophraella communa* LeSage). We have developed a labor-saving method to collect data of plant habitats and herbivore densities in the field (Otuka and Yamanaka 2003). These field survey data were examined with nonparametric spatial covariance functions (NCF) and nonparametric spatial cross-correlation function (SCCF), which have been previously used to analyze the spatio-temporal dynamics of the populations (Bjørnstad et al. 1999, 2002; Bjørnstad and Falck 2001).

Materials and methods

System description

The common ragweed (Ambrosia artemissifolia L.)

The common ragweed (hereafter denoted ''weed'' in this paper) is native in the Nearctic region and became naturalized in Japan more than 100 years ago (Shimizu 2003). It is a summer annual and a major weed in early succession of disturbed habitats such as roadsides, shrub margins and open lots (Bazzaz 1974). It blooms in summer and thereafter gradually starts defoliation until late autumn (Deen and Hunt 2001). In Tsukuba, germination starts in early April, blooming in early August and wilting from mid September (see field survey, below). All weeds die during November.
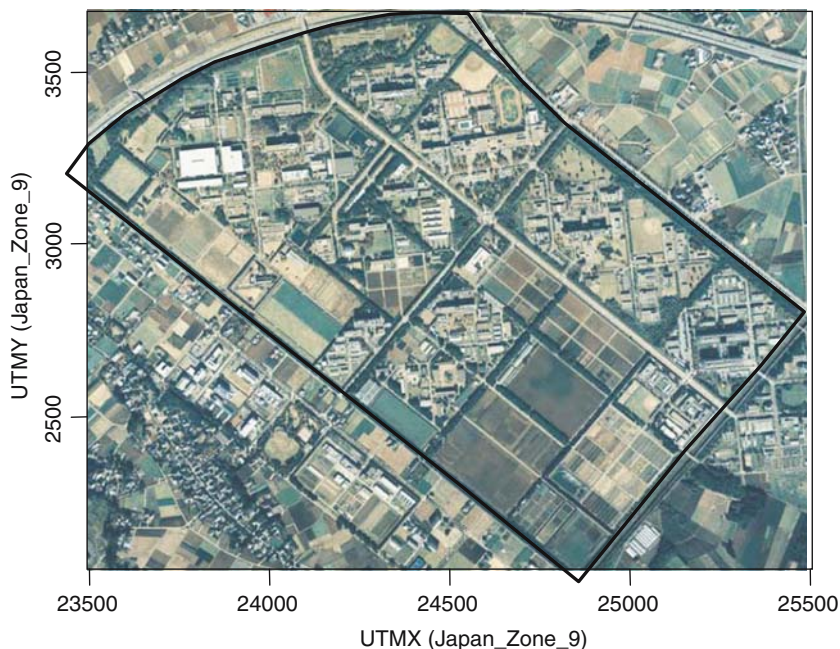
The ragweed beetle (Ophraella communa LeSage, Chrysomelidae)

The ragweed beetle (hereafter the ''beetle''), *O. communa*, was accidentally introduced into Japan from North America in the late 1990s (Emura 1999; Moriya and Shiyake 2001). The larvae and the adult are reported as oligophagous herbivores of asteraceous plants (LeSage 1986; Palmer and Goeden 1991), and the weed is its preferred host plant (Yamazaki et al. 2000). The beetle is multivoltine and has four or five generations a year in Japan (Emura 1999; Yamazaki et al. 2000). Adults diapause reproductively at the end of summer and overwinters as an adult (Watanabe 2000). The beetle has been reported to have great potential to defoliate weed patches (Palmer and Goeden 1991; Teshler et al. 2002). Once a small number of the beetles immigrate to a patch, the weed patch will usually be completely demolished within a few generations not only by the massive appetite of adult beetles but also by their short developing period, high fertility and longevity.

Field survey

The study area is about 200 ha ($\approx 1.8 \times 1.0$ km^2) located in the Agricultural Experimental Institutes Complex in Tsukuba city, Ibaraki prefecture, Japan (Fig. 1; 36°1.27′N, 140°6.49′E). It consists of a heterogeneous landscape of buildings, lawns, playgrounds, and crop fields. The ragweed is the major host plant for the beetle found in the study area, although we did find small numbers of *Xanthium canadense* and *Helianthus tubero-*

Fig. 1 An air photo of the study area (in Tsukuba city, Ibaraki prefecture, Japan). The exact range of the survey is enclosed with the *solid line*. The airphoto was taken by the Geographical Survey Institute in Japan in 1990 and was adjusted to the Japanese plane coordinate system

sus which are regarded as secondary host marginally suitable only for the adult survival (Yamazaki et al. 2000). Application of herbicides and mowing around buildings and in fields to control weeds was conducted irregularly but frequently in the study fields.

We observed the weed patches and the beetle population for three consecutive years from 2003 through 2005, three times a year, in mid June, late July, and early September. These periods correspond to the final instar or the pupal stage of the first generation, the mid instar to pupal stage of the second generation, and the third to fifth overlapping generations toward the end of the year, respectively. Each census was conducted on consecutive days (but avoiding rainy days) and was finished within 10 days. However, the June census of 2003–2005 took 16, 17, and 16 days, respectively, due to frequent rain.

We define a plant patch as a single plant or group of plants separated from any other individuals by at least 10 m. After counting the number of plants in each weed patch, signs of damage by the beetle larvae and adults were thoroughly searched over the patch. Larvae were easy to find around the damaged leaves, but isolated adults were sometimes difficult to find. We counted the number of plants freshly damaged by the beetle and evaluated the percentage of these to the total number of plants in the patch ($P_{Beetle} = 0, 10, 20,...,$ and 100). Then, four of the damaged weeds were randomly selected to count the abundance of the beetle larvae (including pupae) and adults. Abundances and spatial coordinates of the weed and the beetle were recorded in a handheld computer (WorkPad c3®; IBM, San Jose, CA, USA) equipped with GPS (GPS Companion for Palm V®; Magellan, USA; see Otuka and Yamanaka 2003). To minimize survey time and labor, abundance grades were scored corresponding roughly to the log abundance of the weed, adults, and larvae (including

pupae) of the beetle (Table 1). Conversion functions were defined to estimate the abundances of weed and beetle, which roughly correspond to the median number of individuals in each grade (Table 1).

Data compensation and transformation

All data, including the weed score (G_{Weed}), the percentage of plants damaged by the beetle (P_{Beetle}), the beetle adult score (G_{BA}), and the beetle larvae and pupae combined score (G_{BL}) were collected from each weed patch and independently among censuses. We did not track the fate of each patch because they were easily destroyed or disrupted by mowing, herbicides, and displacement by other plants. We sometimes found new patches in later censuses of the year that must have been missed in earlier surveys since the weed does not germinate in the summer. We scrutinized the maps of GPS patch coordinates each year and visually reconstructed the history of the patches in that year. We added missed patches (with the size as recorded in later censuses) when we were convinced that they had been missed in the previous survey. Using this procedure, we could compensate for obvious underestimates of weed abundance, although we must accept the possibility of underestimating the beetle abundance in the early censuses. Thirteen patches were added to 145 patches in June 2003, 17–100 in July 2003, 15–114 in June 2004, 5–94 in July 2004, 8–87 in June 2005, and 7–72 in July 2005.

We estimated the number of beetle adults $(\hat{M}_{BA})$ and larvae including pupae $(\hat{M}_{BL})$ per weed as the product of the estimated mean number of individuals in the four weed plants scored and the percentage of the patches damaged by the beetle (see Table 1) according to:

Table 1 Scores recorded by the handheld computer

Grade (G)	Number (median)	Score	Conversion
Weed			
1	1–3 (2.0)	2.2	Score = exp
2	4–9 (6.5)	6.9	$(G_{Weed}) - 0.5$
3	10–29 (20.0)	19.6	
4	30–100 (65.6)	54.1	
5	101–	147.9	
Beetle (adults in a weed)			
0	0 (0)	0.5	Score = exp
1	1–5 (3.0)	3.2	$(G_{BA}) - 0.5$
2	6–19 (13.0)	13.0	
3	20–99 (60.0)	48.9	
4	100–	180.0	
Beetle (larvae + pupae in a weed)			
0	0 (0)	0.5	Score = exp
1	1–49 (25.0)	11.7	$(2.5 \times G_{BL}) - 0.5$
2	50–299 (174.5)	147.9	
3	300–2,000 (1,150.0)	1,807.5	
4	2,001–	22,026.0	

$$\hat{M}_{BA} = \text{mean}[\exp(1.3 \times G_{BA}) - 0.5] \times P_{Beetle}/100,$$
$$\hat{M}_{BL} = \text{mean}[\exp(2.5 \times G_{BL}) - 0.5] \times P_{Beetle}/100. \quad (1)$$

Then, the number of weeds $(\hat{N}_{Weed})$, beetle adults $(\hat{N}_{BA})$, and larvae $(\hat{N}_{BL})$ per patch can be calculated as

$$\hat{N}_{Weed} = \exp(G_{Weed}) - 0.5,$$
$$\hat{N}_{BA} = \hat{N}_{Weed} \times \hat{M}_{BA}, \quad (2)$$
$$\hat{N}_{BL} = \hat{N}_{Weed} \times \hat{M}_{BL}.$$

Based on these estimates of abundance, we first examined the relationship between the patch size (the number of weeds) and the abundance of beetles per plant. The regression between G_{Weed} and $\log(\hat{M}_{BA} + 0.5)$ or $\log(\hat{M}_{BL} + 0.5)$ were calculated by the following equations

$$\ln(\hat{M}_{BA} + 0.5) = k_{BA} + \psi_{BA} \times G_{Weed},$$
$$\ln(\hat{M}_{BL} + 0.5) = k_{BL} + \psi_{BL} \times G_{Weed}, \quad (3)$$

where k_{BA} and k_{BL} are the y intercepts of the regression line and ψ_{BA} and ψ_{BL} are the regression coefficients. These regressions are equivalent to the log–log plots that are often used to analyze patch–herbivore relationships (e.g., Macgarvin 1982; Otway et al. 2005). Pearson's correlations were used to test for significant relationships.

We found that further spatial analysis (see the next section) was difficult based on individual weed patches because of their high turnover rates and their changing shapes. In addition, a patch-based analysis did not allow us to evaluate vacant spaces that could potentially be suitable for weed growth. For the spatial analysis, we therefore divided our study area into 60×60 m^2 grids, being the minimum size of the cell that can cover almost all patch sizes and that minimizes the misclassification of patches due to GPS precision (which varied and was 30 m at worst). In addition, the number of cells occupied

by beetle adults was too sparse to be analyzed by themselves. Therefore, the number of beetle adults per cells were combined together with those of larvae and treated as our measure of abundance of the beetles. The number of weeds $(\hat{N}_{Weed})$ and the totalized number of beetles $(\hat{N}_{BA} + \hat{N}_{BL})$ were summed within each cell and denoted as $Weed_{t,i}$ and $Beetle_{t,i}$, respectively, for the ith cell at the tth census.

We excluded the cells that had never had any weeds $(Weed_{t,i})$ during any of the nine censuses, assuming that these represented unsuitable habitat for the weed. In this way, 188 cells were extracted from the study area (see, e.g., Fig. 2 for the census in July 2004). The center coordinates of the cells were used as the representative position of the cells.

Spatial correlation functions

Spatial autocorrelation has been used as a measurement of spatial structure in genetic (e.g., Sokal and Oden 1978; Smouse and Peakall 1999) and ecological systems (e.g., Ranta et al. 1995; Heino et al. 1997). The basic idea is simple: many biological processes (such as dispersal) make nearby populations similar in their properties, whether that be with respect to genetic make-up or abundance. Hence the similarity may decrease as the distance between population pairs increase.

Suppose the number of individuals was measured for n points with (x_i, y_i) coordinates $(i = 1, 2,..., n)$ for a single species. Then the sample autocorrelations between points i and j $(i \neq j)$ are calculated by

$$\hat{\rho}_{ij} = \hat{\rho}_{ij}(z_i, z_j) = \frac{(z_i - \bar{z})(z_j - \bar{z})}{\frac{1}{n}\sum_{l=1}^{n}(z_l - \bar{z})^2}. \quad (4)$$

The coefficient $\hat{\rho}_{ij}$ can vary from perfect similarity $(+1)$ to perfect dissimilarity (-1). The average of $\hat{\rho}_{ij}$ for all point combinations, $n, (n-1)/2$, is regarded as the region-wide autocorrelation over populations (Bjørnstad et al. 1999):

$$\underset{i \neq j}{\text{average}}(\rho_{ij}) = \frac{2}{n \times (n-1)} \sum_{i=1}^{n} \sum_{j=i+1}^{n} \rho_{ij}. \quad (5)$$

This average will be zero in the case of single observations at each site, but may be different from zero when we extend the analysis to space-time data (see below).

The nonparametric spline correlogram function (NCF)

Recent advances in computing power enable us to calculate flexible spline correlograms in place of the somewhat awkward stepwise function generated by traditional correlograms, which have been widely employed for ecological data analysis (Cressie 1993). Bjørnstad and co-workers developed this method to fit the nonparametric spatial correlation function (NCF) to the sample autocorrelation (Bjørnstad and Bolker 2000;
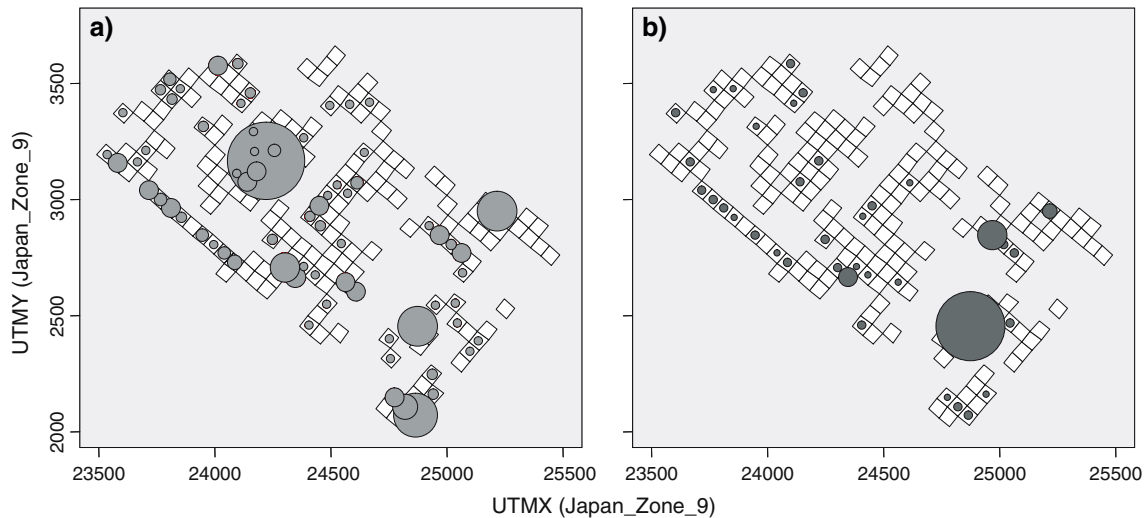
Fig. 2 An example of the study area sliced into lattices (census in July 2004). **a** Number of the weed plants, and **b** number of beetle larvae to adults in the cells were superposed on the map as circles proportional to the abundance (the largest circle corresponds to 315.6 weed plants in **a**, and 23,796 beetle individuals in **b**). *White squares* represent the cells tested which had at least one patch during nine censuses

Bjørnstad and Bascompte 2001; Bjørnstad and Falck 2001). Using a cubic *B*-spline as an equivalent kernel smoother (*K* in Eq. 6), the NCF can be directly fitted to all of the $n(n - 1)/2$ sample autocorrelations themselves (Eq. 4), while the classical correlograms would calculate averages within binned distance classes. The NCF is defined as

$$\tilde{\rho}(\delta) = \frac{\sum_{i=1}^{n} \sum_{j=1}^{n} K(\frac{\delta_{ij}}{h}) \times \hat{\rho}_{ij}}{\sum_{i=1}^{n} \sum_{j=1}^{n} K(\frac{\delta_{ij}}{h})}, \tag{6}$$

where, h (> 0) is the bandwidth that adjusts the smoothness of the fitted curve (Bjørnstad and Falck 2001). There are two notable features to the use of the NCF. First it allows us to estimate the underlying spatial correlation function without assuming any functional form, such as spheral or Gaussian types of functions that are often used in geostatistics (Cressie 1993). This more flexible estimation enables us to discover more complex underlying spatial structure such as U-shaped or periodic correlation functions (Bjørnstad and Bascompte 2001; Seabloom et al. 2005). Second, a bootstrapping algorithm can generate the confidence envelope along the NCF (see Bjørnstad and Falck 2001). Consequently, the zero intersection of the spatial correlogram, which is often interpreted as the length of spatial dependence (Sokal and Wartenberg 1983), can be estimated with confidence limits.

All spatial analyses were executed in *R* (Version 2.2.1; R Development Core Team 2005; URL http://www. R-project.org.) with the ncf-package (ncf is downloadable from the website: http://www.asi23.ent.psu.edu/onb1/ software.html). The NCF was fitted to every census ($t = 1, 2,..., 9$; three census periods for three years) for the weed (Weed$_{t,i}$) and the beetle (Beetle$_{t,i}$) ($i = 1, 2,...,$

188), respectively. We will not show all these individual results because they were very similar among years. We then combined three years for each census period (June, July, and September) of both the weed and the beetle to consider spatio-temporal dynamics (see below).

Spatial correlation for time-series data

When spatio-temporal data of abundance are available, it is possible to study similarities in patterns of fluctuations. This can be achieved by substituting the product moment correlations among time series in place of the sample autocorrelations in Eq. 4 (Bjørnstad et al. 1999; Bjørnstad and Bascompte 2001). Assuming that there are population abundance data $z_{m,i}$ at a time step m ($m = 1, 2,..., t$) and at spatial coordinate (x_i, y_i; $i = 1, 2,..., n$), then the sample correlation between points i and j ($i \neq j$) is calculated as

$$\hat{\rho}_{ij} = \hat{\rho}_{ij}(z_i, z_j) = \frac{\sum_{m=1}^{t} (z_{m,i} - \overline{z_i})(z_{m,j} - \overline{z_j})}{\sigma_i \sigma_j}, \tag{7}$$

where σ_i and σ_j are the standard deviations of the time series and $\overline{z_i} = \frac{1}{t} \sum_{m=1}^{t} z_{m,i}$, $\overline{z_j} = \frac{1}{t} \sum_{m=1}^{t} z_{m,j}$. Again, we use the NCF to extract spatial information from such data. The region-wide correlation (Eq. 5) will reflect common temporal fluctuations in this case. The scale of spatial dependence in such space-time data may be quantified as the intersection between the estimated correlation function and the abscissa represented by the estimated region-wide correlation (Bjørnstad et al. 1999; Koenig 1999), as opposed to the x intercept commonly used in univariate spatial analysis.

The sample correlation and the estimated NCF were calculated for every seasons for the weed (Weed$_{t,i}$) and

the beetle (Beetle$_{t,i}$) with three time series, June ($t = 1$, 4, 7), July ($t = 2, 5, 8$), September ($t = 3, 6, 9$), and for the full time series ($t = 1, 2,..., 9$). We estimated 95% confidence limits for the NCF using the bootstrap with 1,000 resamples.

The cross-correlation between two species and the SCCF

Spatial cross-correlation can detect spatial associations between two species across space. Although this is a statistically trivial extension of standard autocorrelation analysis of single species, patterns of cross-correlation are only slowly gaining recognition as a quantity of theoretical importance in the study of spatially extended inter-specific interactions (e.g., Bolker and Pacala 1999; Keeling et al. 2002). The recent theoretical focus on patterns of spatial cross-correlation has motivated statistical analyses aimed at its quantification on the basis of field data (Tobin and Bjørnstad 2003; Seabloom et al. 2005). Suppose there are abundance data, $z_{m,i}$ for species A and $w_{m,j}$ for species B at time steps m ($m = 1, 2,..., t$) at n spatial locations ($x_i, y_i; x_j, y_j; i, j = 1, 2,..., n$). The sample cross-correlation between points i and j (i can be equal to j) is then calculated as

$$\hat{\omega}_{ij} = \hat{\omega}_{ij}(z_i, w_j) = \frac{\sum_{m=1}^{t} (z_{m,i} - \overline{z}_i) \times (w_{m,j} - \overline{w}_j)}{\sigma_{z_i} \sigma_{w_i}}, \quad (8)$$

where σ_{z_i} and σ_{w_i} are the sample standard deviations of the time series for each species at points i and j, respectively. The sample means are $\overline{z}_i = \frac{1}{t} \sum_{m=1}^{t} z_{m,i}$ and $\overline{w}_j = \frac{1}{t} \sum_{m=1}^{t} w_{m,j}$. The nonparametric SCCF is then estimated by analogy to Eq. 6 according to:

$$\tilde{\omega}(\delta) = \frac{\sum_{i=1}^{n} \sum_{j=1}^{n} K(\frac{\delta_{ij}}{h}) \times \hat{\omega}_{ij}}{\sum_{i=1}^{n} \sum_{j=1}^{n} K(\frac{\delta_{ij}}{h})}. \quad (9)$$

We calculated the sample cross-correlations and the estimated SCCF for every season using the three season-specific time series, June ($t = 1, 4, 7$), July ($t = 2, 5, 8$), September ($t = 3, 6, 9$), and the full series ($t = 1, 2,..., 9$), respectively. Whenever interactions among species are instantaneous (or species respond instantaneously to shared external covariates), we may expect to see significant cross-correlation, as reflected in what we call the lag-0 cross-correlation. If, in contrast, the interaction results in delayed feedback, as would result from delays inherently in numerical responses in predator–prey or plant–herbivore systems, we may expect significant cross-correlations but with a time lag. We calculated lag-1 cross-correlation functions for the beetle, as the correlation between Weed$_{t,i}$ in June ($t = 1, 4, 7$) against Beetle$_{t,i}$ in July ($t = 2, 5, 8$); Weed$_{t,i}$ in July ($t = 2, 5, 8$) against Beetle$_{t,i}$ in September ($t = 3, 6, 9$); and Weed$_{t,i}$ in September ($t = 3, 6$) against Beetle$_{t,i}$ in next June ($t = 4, 7$); and finally Weed$_{t,i}$ in the full time series ($t = 1, 2,..., 8$) against the full series for Beetle$_{t,i}$ ($t = 2$,

3,..., 9). We also calculated lag-1 cross-correlation in the reverse direction: Weed$_{t,i}$ in July ($t = 2, 5, 8$) against Beetle$_{t,i}$ in June ($t = 1, 4, 7$); Weed$_{t,i}$ in September ($t = 3, 6, 9$) against Beetle$_{t,i}$ in July ($t = 2, 5, 8$); Weed$_{t,i}$ in next June ($t = 4, 7$) against Beetle$_{t,i}$ in September ($t = 3, 6$) and finally the lagged cross-correlation for the full time series (Weed$_{t,i}$, $t = 2, 3,..., 9$, against Beetle$_{t,i}$, $t = 1, 2,..., 8$). To our knowledge ours is the first study of the time-lagged SCCF in a trophic system.

Results

Temporal dynamics of the weed and the beetle

The estimated total number of weed plants is shown in Fig. 3a. There is a conspicuous seasonal decline through each year, and an associated decline in weed patch numbers (Fig. 3c). Although the decline of the weed plants was partly caused by herbivory, it likely also reflects human influences such as mowing and herbicide application (unpublished observation). The largest number of weed plants and patches were observed in June 2003 because this was the year of most extensive construction and associated disturbance within the study area. The numbers of patches in early 2004 and early 2005 were comparable. While there were a few locations of semipermanent patches, near dumping grounds and along the edges of field crops, the majority of patches emerged in spatially unpredictable locations in each year.

Beetle abundance fluctuated widely within and among years (Fig. 3b). The number of larvae was relatively low in the June censuses with a conspicuous increase in July (particularly in 2004 and 2005). This increase was associated with significant defoliation by larvae (particularly in 2004). The extensive July defoliation was generally followed by a decline in the number of beetle larvae and adults (reflected in the September census, e.g., in 2004; Fig. 3b), a decline in total number of weed patches, and a decline in the overall patch occupancy by beetle (e.g., as for 2004; Fig. 3c). Curiously, the overall abundance of beetle larvae and adults leveled off but did not decay in the September census of 2005 (Fig. 3b). We believe this anomaly reflects the single large patch located in the north-western end of the study area that and contained 94% of the total beetle abundance yet was not defoliated until late September.

The herbivore dynamics in 2003 were somewhat different from the later two years of study: beetle larval abundances were great in June yet no substantial increase in abundance was observed in subsequent censuses (Fig. 3b; 2003). 2003 saw a very warm spring and cool and rainy summer with temperatures that averaged 0.5°C higher than normal between March and May, yet nearly 1.0°C lower temperatures and about 30% more precipitation between June and July (compared to the yearly average over the past 30 years according to the nearest meteorological station of the Japan Meteorological
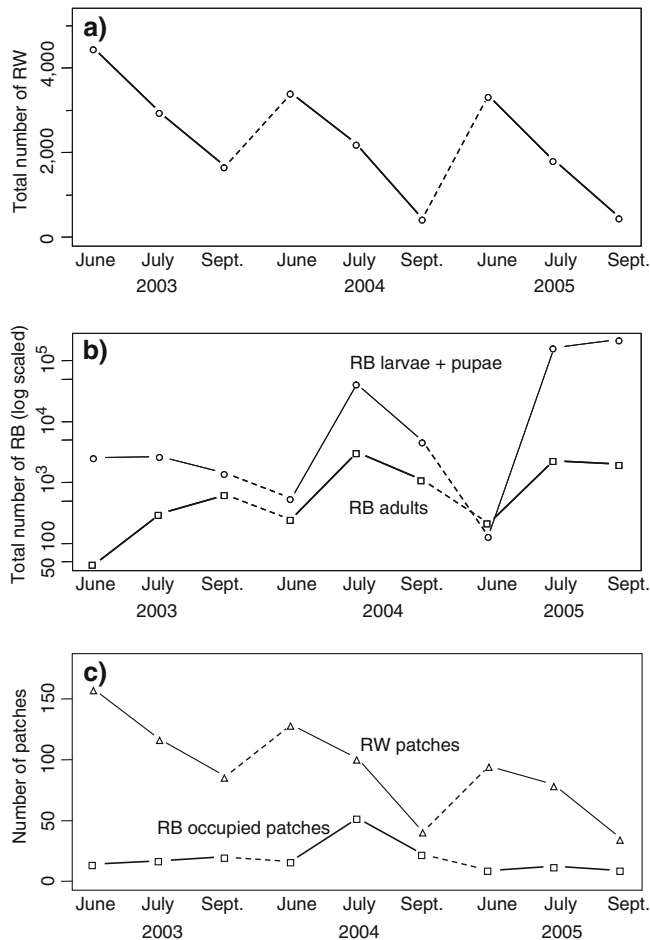
Fig. 3 **a** The total weed plants. **b** The beetle larvae including pupae (*thin lines* with *circles*) and the beetle adults (*thick lines* with *rectangles*). **c** The number of the weed patches (*thin lines* with *triangles*) and those occupied by the beetle (*thick lines* with *rectangles*). Data were collected in the study area (Tsukuba city, Ibaraki prefecture, Japan) for three years from 2003 to 2005

Table 2 Relationships between the number of weed plants in a patch and beetle abundance per patch

	June	July	September
2003			
Adults	−0.0081 (0.0088)	0.0191 (0.0177)	**0.0588*** (0.0670)
Larvae + pupae	**0.0666*** (0.0574)	0.0525 (0.0084)	**0.1213*** (0.0889)
2004			
Adults	0.0110 (0.0066)	**0.0924*** (0.0385)	−0.0542 (0.0022)
Larvae + pupae	0.02632 (0.021)	0.1890 (0.0313)	0.0910 (0.0046)
2005			
Adults	0.0269 (0.0300)	0.0602 (0.0196)	0.1535 (0.0291)
Larvae + pupae	−0.0039 (0.0001)	0.14832 (0.0246)	0.4613 (0.0648)

Values in the tables are the regression coefficients (coefficients of determination) calculated with Eq. 3 (see text for details)
*Bold numbers represent the significant by Pearson's correlation test ($P < 0.05$)

Agency about 3 km east of the study area). These climatic extremes may have affected the dynamics of the beetle.

The estimated densities of the beetle ($\hat{M}_{BA}$ and $\hat{M}_{BL}$) were log-transformed (after adding 0.5) and the regression coefficients were calculated against weed grade (proportional to log patch size; G_{Weed}) for each of the nine censuses. These are listed in Table 2 together with their coefficients of determination. All the regression coefficients were slightly positive or near zero (except for adult beetles in September 2004, which displayed a nonsignificant negative relationship). Our analyses lend weak support to the prediction of the resource-concentration hypothesis: larger patches host a disproportionate number of beetles. However, the regressions have extremely low coefficients of determination (< 0.1) and carry no statistical significance in many cases (Table 2). Some of the ambiguity is likely due to the many zero abundances of the beetle, as only a small proportion of weed patches were occupied by the beetle during any one survey (8.8–25.7%) except in July 2004 (51.5%) and in September 2004 (53.7%). However, we could not eliminate zero patches from the analysis because the empty patches could have been the result of abandonment by the beetle, a component of the resource-concentration hypothesis. Given this at best equivocal support for the resource-concentration hypothesis, we turn our attention to the alternative hypothesis for spatial pattern formation.

Spatial patterns of weed and beetle: autocorrelation

The NCF was fitted to the spatial weed data in each seasonal census across the three years; We did not find any significant localized synchrony in any of the annual transitions (Fig. 4a–c). Our analysis does, however, suggest a distance-dependent effect out to around 100 m. The lack of any significant distance signature in the autocorrelation profile within the weed suggests that the seed dispersals or plants transportation by human activity were not conspicuous beyond the size of the grid cell. Alternatively, this may result from a scenario in which seed dispersal is wide and essentially uniform across the study area. The later scenario seems unlikely, however (Clay et al. 1999). While we did not detect any local spatial signatures, we did uncover significant region-wide synchrony for the analysis of all censuses (Fig. 4d). This region-wide synchrony is likely a reflection of the shared seasonality among all patches (Fig. 3a, c), as patches simultaneously appear, shrink and disappear through the year.

We also did not find any significant distance dependence in the synchrony among the annual transitions in beetle populations (Fig. 5a–c). The region-wide synchrony was slightly positive but not significant (Fig. 5d). These results indicate that the seasonal trend of the beetle population was less clear than that of the weed (Fig. 3). The confidence envelopes are very wide
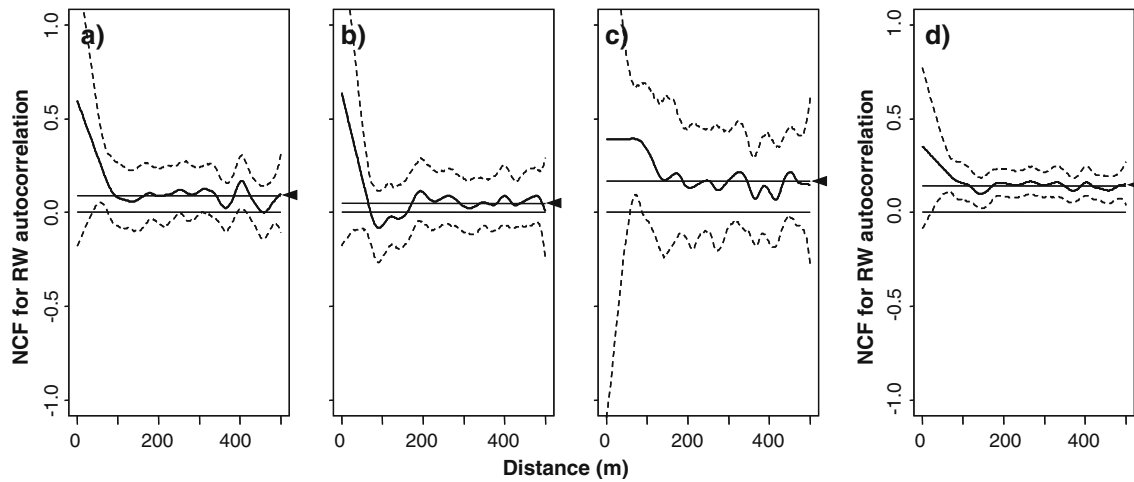
Fig. 4 Spatial synchrony of the weed in each season and total census. The NCFs ($df = 13$) were fitted to the sample autocorrelation **a** in June, **b** in July, **c** in September, and **d** in total. Data were combined as three yearly time series for each season and all nine time series for total. The 95% confidence limits along the NCFs were erected by bootstrapping, resampling 1,000 times
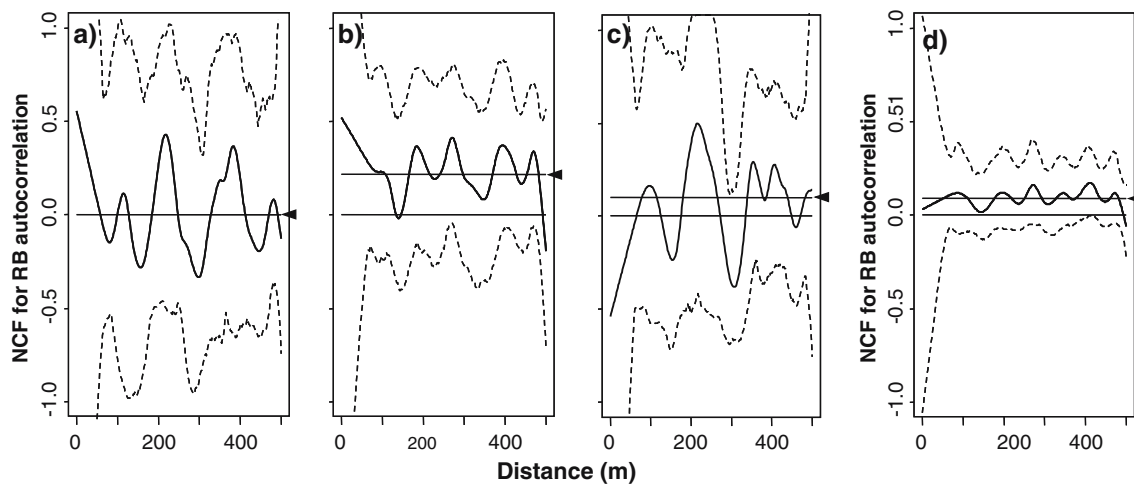

Fig. 5 Spatial synchrony of the beetle in each season and total census. The NCFs ($df = 13$) were fitted to the sample autocorrelation **a** in June, **b** in July, **c** in September, and **d** in total. Data were combined as three yearly time series for each season and all nine time series for total. The 95% confidence limits along the NCFs were erected by bootstrapping, resampling 1,000 times

(Fig. 5a–c). This may, in part, be because there are many zero counts among the beetle population censuses that result in low power of the NCFs.

Cross-correlation between the weed and the beetle

In contrast to the auto-correlation analysis, the cross-correlation reveals strong spatial association between the beetle and its host plat both with respect to annual transitions (Fig. 6a–c) and the full set of censuses (Fig. 6d). The aggregation of beetles on weeds was less clear in June (Fig. 6a) than during the other two sampling periods (Fig. 6a, b) judging by the 0-distance cross-correlation (0.47 in Fig. 6a, 0.71 in Fig. 6b, and 0.69 in Fig. 6c). The spatial extent of the association as judged by where the cross-correlation function intersects with the region-wide cross-correlation, estimated as 60.0 m (95% confidential limit; 38.2–112.9 m) across all censuses. This indicates that the spatial extent of the plant–herbivore association was relatively local and did not extend much beyond the size of the census cells. The region-wide cross-correlation was very close to zero (Fig. 6d). This suggests that there was negligible shared seasonality or shared temporal trends between the weed and the beetle.

Lagged cross-correlation

Numerical responses that result from herbivory may be expected to lead to time-lagged signatures: high plant abundance should lead to enhanced abundance of subsequent herbivory generations, while large herbi-
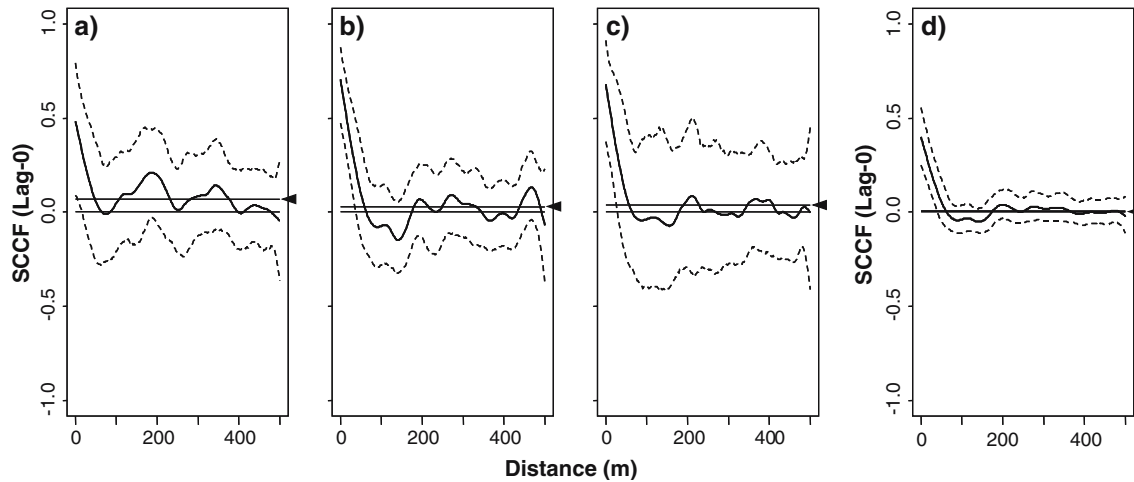
Fig. 6 Lag-0 spatial synchrony between the weed and the beetle in each season and total census. The SCCFs ($df = 13$) were fitted to the sample autocorrelation **a** in June, **b** in July, **c** in September, and **d** in total. Data were combined as three yearly time series for each season and all nine time series for total. The 95% confidence limits along the SCCFs were erected by bootstrapping, resampling 1,000 times
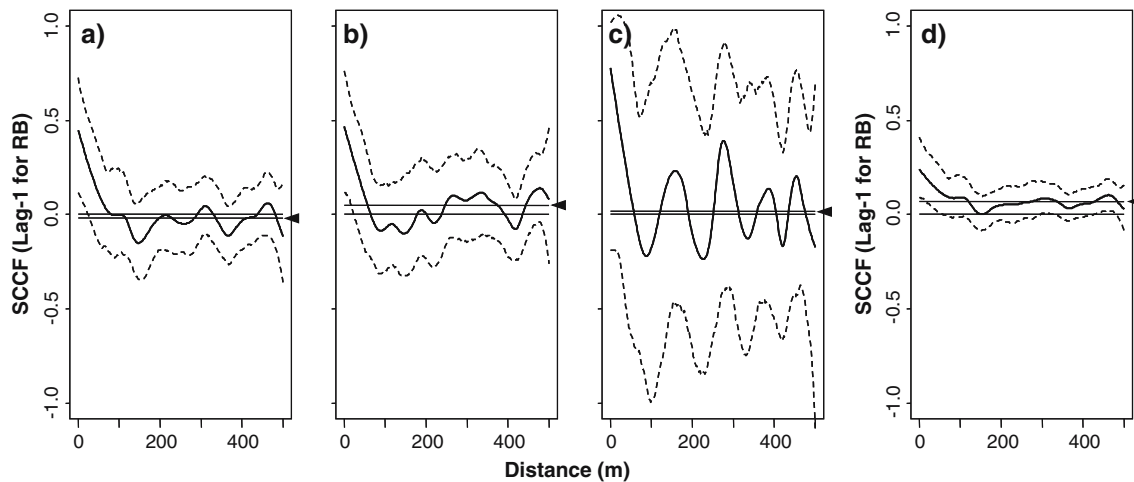

Fig. 7 Spatial synchrony between the weed and the beetle (lag-1 for the beetle) in each season and total census. The SCCFs ($df = 13$) were fitted to the sample autocorrelation between **a** the weed in June and the beetle in July, **b** the weed in July and the beetle in September, **c** the weed in September and the beetle in the next June, and **d** in total. Data were combined as three yearly time series for each season and all eight time series for total. The 95% confidence limits along the SCCFs were erected by bootstrapping, resampling 1,000 times

vore populations should lead to subsequent declines in plant abundance. To look for such signatures we used time-lagged cross-correlation functions. These revealed subtle but significant patterns in the local cross-correlation between weed abundance and the abundance of the beetle in the subsequent census (weed in June and beetle in July: Fig. 7a; weed in July and beetle in September: Fig. 7b; weed in September and beetle in the following June: Fig. 7; and across all censuses: Fig. 7d). The distance of the intersection with the region-wide cross-correlation was estimated as 121.9 m (95% confidential limit; 18.7–192.0 m) for the full time series (Fig. 7d). Thus, cells that previously had a large number of weeds would subsequently generally harbor

a locally high abundance of beetles with a possible spillover to adjoining cells as consistent with reaction–diffusion dynamics. Moreover, the lagged cross-correlation was positive for almost all distances (Fig. 7d). This indicates that high weed abundance had a generally positive effect on the beetle during the subsequent census. The patterns of over-winter cross-correlation are less clear (Fig. 7c).

In contrast, there were no clear patterns in the opposite direction that relates to decreased weed abundance following enhanced beetle populations (Fig. 8a–c). There is no clear spatial signature as the lagged cross-correlation functions are parallel and close to the x-axis (Fig. 8d). We do note, though, that the
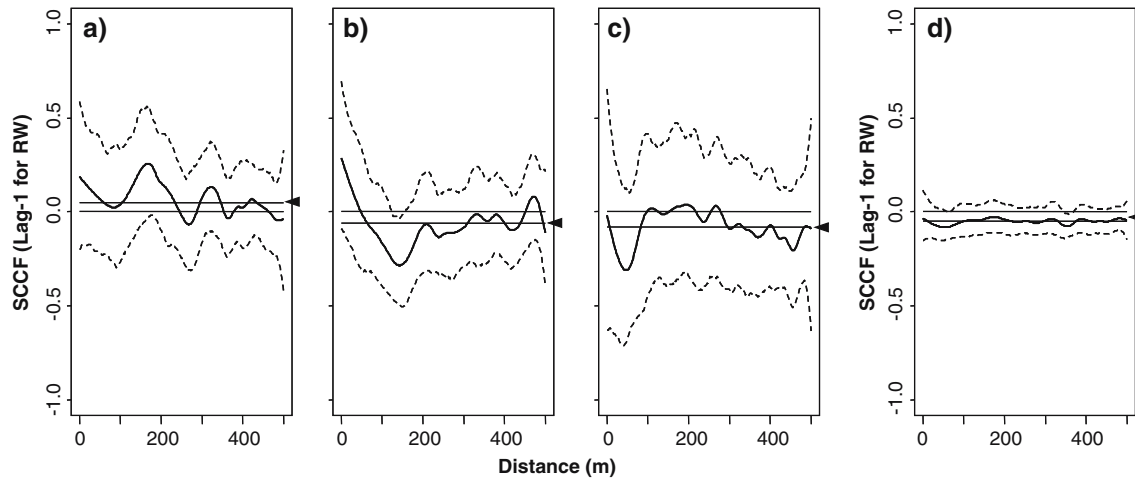
Fig. 8 Spatial synchrony between the weed and the beetle (lag-1 for the weed) in each season and total census. The SCCFs ($df = 13$) were fitted to the sample autocorrelation between **a** the weed in July and the beetle in June, **b** the weed in September and the beetle in July, **c** the weed in the next June and the beetle in the previous September, and **d** in total. Data were combined as three yearly time series for each season and all eight time series for total. The 95% confidence limits along the SCCFs were erected by bootstrapping resampling 1,000 times

region-wide lagged cross-correlation tends to be negative (Fig. 8d). Thus, large beetle populations tend to be followed by reduced weed abundances.

Discussion

Although we found weak support for resource concentration in some seasons in that big weed patches tended to have higher densities of the herbivore (Table 2), we could not find any clear relationships in other seasons. We, therefore, think dispersal-based hypotheses may offer a better explanation. Hambäck and Englund (2005) showed that plant–herbivore relationships may drastically change depending on the conditions of the herbivore population in the patch: when the density of the herbivore is small and the patch receives immigrants rather than effuses emigrants, the correlation between plant patch size and herbivore density will always become more negative. On the other hand, if the density of the herbivore is large, the correlation will be positive. In our study, beetles were distributed sparsely across the study area in the June census (Fig. 3c). These patches must have received immigrants rather than effused emigrants and were regarded as sinks in terms of sink–source dynamics (Pulliam 1988). As the beetle population grew and the weed patches were decreased by human activities, the rate of occupation by the beetle increased and many of them might become source patches. Although we think that such a dynamical change of the patch role is one of the reasons that the on-site relationship between the weed and the beetle was stronger in the latter season than those in June as shown in the lag-0 SCCF (Fig. 6a–c), it will be more pertinent if we try to explain in the context of the reaction–diffusion theory.

The SCCFs revealed evidence of emergent spatial structure of the herbivore–plant interaction across relatively short distances, and subtle temporal dynamics between the ragweed and the beetle, even though there was little evidence of spatial structuring of either the plant or the herbivore. Weed-abundant locations were associated with enhanced beetle populations. Moreover, through time there was evidence of beetle spillover to adjacent locations at roughly the one beetle-generation time scale (Figs. 6 and 7). The results indicate that beetle abundance is strongly dependent on local weed abundance and evidence spatial spillover as consistent with reaction–diffusion dynamics of the herbivore. The cells with large numbers of beetles, however, did not seem to exhibit subsequent reductions in weed abundance (Fig. 8), although on the scale of the study area, beetle population does appear to mildly suppress subsequent weed abundance. Biological control of the ragweed by the beetle, as attempted in Canada (Teshler et al. 2002) and Australia (Palmer and Goeden 1991), seems unlikely to be successful. Reznik et al. (1994) conducted field observations on a different chrysomelid (*Zygogramma suturalis*)–weed system and found that the weed and not the *Z. suturalis* is the driving force in their interacting dynamics. Their result mirrors the findings of our study.

The lack of a prominent spatial structure in the beetle fell short of our anticipation because the beetle is regarded as a strong disperser as judged from its invasion rate (Moriya and Shiyake 2001; Shiyake and Moriya 2005). One reason might be the frequent local perturbations in our weed–beetle system, in particular, in the form of human disturbances such as mowing and herbicide application. In addition, most spatial patterns appeared to collapse at the end of each year (Fig. 7c), to start from weak relationships in every spring (Fig. 6a) and become conspicuous in during summer (Figs. 6b, c, 7a, b). These,

initially unpredictable, patterns may be caused by the variable emergence of the weeds patches in spring.

From a more general point of view, our study illustrates how NCFs are useful tools in the study of spatially extended dynamical systems whether they be theoretical (Bjørnstad and Bolker 2000; Bjørnstad and Bascompte 2001) or empirical (Bjørnstad et al. 2002; Økland and Bjørnstad 2003; Tobin and Bjørnstad 2003; Seabloom et al. 2005). In particular, we show that, whenever there is data on both natural enemies and their hosts, the time-lagged cross-correlation function may be an important tool for describing signatures of reaction–diffusion dynamics. Such dynamics have received much attention in the theoretical literature, but with little empirical verification. Given this statistical tool we urge the collection of more spatially explicit data on herbivore–plant systems at the appropriate spatial scales. This should help disentangle the relative roles of behavioral (resource-concentration hypothesis) versus numerical (reaction–diffusion hypothesis) processes in the spatial ecology of trophic systems.

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