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## How to analyze long-term insect population dynamics under climate change: 50-year data of three insect pests in paddy fields

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**Abstract** We can precisely predict the future dynamics of populations only if we know the underlying mechanism of population dynamics. Long-term data are important for the elucidation of such mechanisms. In this article we analyze the 50-year dynamics of annual light-trap catches of three insect pest species living in paddy fields in Japan: the rice stem borer, *Chilo suppressalis* (Walker) (Lepidoptera: Pyralidae); the green rice leafhopper, *Nephotettix cincticeps* (Uhler) (Hemiptera: Deltocephalidae); and the small brown planthopper, *Laodelphax striatellus* (Fallén) (Hemiptera: Delphacidae). We separate the long-term dynamics into two components by using locally weighted scatterplot smoothing: (1) the underlying dynamics of populations, and (2) the influence of the past changes in the environment. The former component is analyzed by response surface analysis and vector autoregression to evaluate the nonlinearity of density-dependence and the inter-specific influence of density, respectively. On the basis of these analyses, we perform the state-space model analyses. The state-space model selected by Akaike's information criterion indicates that the observed number of light-trap catches of *C. suppressalis* and *N. cincticeps* in summer increases with increasing temperatures in the previous winter. It also indicates that the influence of temperature is not carried over to the next year. We utilize the selected model to predict the impact of global warming on these species, by

substituting the temperature predicted by a general circulation model.

**Keywords** *Chilo suppressalis* · *Laodelphax striatellus* · Long-term dynamics · *Nephotettix cincticeps* · Paddy field

### Introduction

The study of the mechanism of population regulation has a considerable history. This was most clearly summarized by Turchin (1995, 2003). He wrote that: “time series analysis of population fluctuations can be traced to the famous debate about population regulation, which crystallized at the 1957 meeting in Cold Spring Harbor.” In this debate, Nicholson (1954) claimed that the population density is regulated by density-dependent mechanisms. Elton (1949) supported Nicholson's views. Andrewartha and Birch (1954), however, disagreed with Nicholson. They claimed that a general theory cannot be based on density-dependent factors because they do not describe any substantial body of empirical facts. Recently, this old debate has reappeared, as seen in the controversy between Murray (1999), Turchin (1999) and others (Selås et al. 2001; White 2001; Berryman et al. 2002; Hixon et al. 2002; Berryman 2004; White 2004).

Most analyses of long-term terrestrial dynamics seem to be confined to the study of forest insects and vertebrates (e.g., Royama 1992; Bjørnstad et al. 1995; Turchin 2003; Royama et al. 2005) with a few exceptions such as described in Alyokhin et al. (2005). The dynamics of insect pest populations living in agricultural environments have not been so widely analyzed over the long-term, due partly to the frequent change in agricultural environments; agricultural practices frequently change as agro-technology progresses or due to other economic factors, and the abundance of insects changes accordingly. We generally have a dilemma in this respect. Long-term data are preferable for estimating the mechanism of population dynamics, but environmental conditions change

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over a long period. The resultant population dynamics will be a mixture of two components: (1) exogenous dynamics that are driven by a change of environment, and (2) endogenous dynamics that are driven by the intrinsic mechanism. If we could remove the dynamics caused by exogenous factors by using a smoothing technique, we would be able to clarify the underlying mechanism of population dynamics.

In this paper, we analyze the dynamics over a period of 50 years of three insect pest species in paddy fields: the rice stem borer, *Chilo suppressalis* (Walker) (Lepidoptera: Pyralidae); the green rice leafhopper, *Nephotettix cincticeps* (Uhler) (Hemiptera: Deltocephalidae); and the small brown planthopper, *Laodelphax striatellus* (Fallén) (Hemiptera: Delphacidae). We demonstrate how insect population dynamics can be analyzed from different angles. For convenience, in our explanation we proceed from models that are simple in principle to those which are more complicated. We first discuss the importance of appropriate transformation to enhance additivity and homoscedasticity. We next perform the preliminary test for density-dependence, which is a traditional topic in population ecology. Then, we apply an analysis using the generalized additive model (GAM), which automatically determines the smoothing parameter. After discussing the limitation of such automated analyses, we perform the empirical smoothing where empirical knowledge is used to determine the smoothing parameter. All further analyses are performed using the difference between the observed quantity and the smoothed quantity. Response surface analysis is then performed for each species by considering the possibility that the density-dependent regulation is nonlinear. This analysis indicates that the mechanism causing the dynamics of *C. suppressalis* and *N. cincticeps* is mostly linear. Next, in order to consider the possibility of interspecies interaction in the dynamics, we perform linear vector autoregression analysis (VAR). Measurement errors are ignored in these analyses where the measurement error is defined as a component that influences an observation without influencing the observation of the subsequent year. We next incorporate such measurement errors into VAR to clarify the mechanism generating the influence of temperature. This analysis indicates that temperature most influences measurement errors and that it does not strongly influence the abundance of the next year. It indicates that the fluctuation in the “observed” population is influenced by the climatic fluctuation as was claimed by Andrewartha and Birch (1954) but that the underlying “true” population is regulated in a density-dependent manner across years, as was claimed by Nicholson (1954).

The estimated model for population dynamics can be utilized for various purposes. Predicting outcomes of global warming will be one of the major fields to employ such applications. Future climatic change caused by an increase in the atmospheric concentration of greenhouse gas including CO<sub>2</sub> is usually predicted by using global climate models (GCM), especially atmosphere–ocean GCM, that simulate the substantial circulation of the

atmosphere and oceans. The intergovernmental panel on climate change (IPCC), in its third assessment report published in 2001, used models based upon the latest emissions scenarios from the IPCC special report on emission scenarios (SRES) (IPCC 2001). For the full range of 35 SRES scenarios, based upon a number of climate models, the globally averaged surface temperature was projected to increase by 1.4–5.8°C over the period 1990–2100. We substitute the temperature data that were predicted by GCM into the estimated population models to predict the outcome of global warming; we predict the populations in the period from 2031 to 2050 relative to those in the period from 1980 to 2000. We further predict the amount of relative yield loss caused by *C. suppressalis*.

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## Materials and methods

### Light trap survey

A light-trap survey was carried out at Ibaraki Prefectural Experiment Station at Mito (36°16'N and 140°20'E) in line with the project standards for forecasting pest incidence (Ministry of Agriculture Forestry and Fisheries 1986). We use the annual total catches (May–September) of 1949–2001 for three principal insect pests in paddy fields: *C. suppressalis*, *N. cincticeps*, and *L. striatellus*. The data from 1957 to 2001 are cited from the annual report of the experiment station (Ibaraki Prefecture 1957–2001), and the data from 1949 to 1956 are cited from the data compiled by Ôtake (unpublished data) of annual totals of important rice pest insects caught in light traps in Japan. The data for *L. striatellus* in 1949 are absent. No catch was recorded for *C. suppressalis* in 1987. We omit these data when we use the ordinary least squares (OLS) method for estimating parameters, while missing quantities are automatically interpolated when we use Kalman filter algorithms in later sections. To evaluate the effect of climatic factors on population dynamics, we use the climatic data recorded by the Mito Local Meteorological Observatory (36°23'N, 140°28'E).

### Insect species

The rice stem borer, *C. suppressalis*, is a moth with a length of 12–15 mm. This species has two generations in a year in most areas of Japan. Matured larvae, which overwinter in the dried rice straw in fields (Kojima and Emura 1971), emerge from May to July to lay their egg mass. Hatched larvae enter the stem, sometimes causing the death of the leaf sheath or the death of the growing point. These larvae emerge from August to September. The larvae of the second generation cause the production of sterile grains or the death of young ears. Various studies were conducted during the 1950s to clarify the population dynamics of *C. suppressalis* (Fukaya 1950a, b; Ishikura 1950a, b, 1951; Fukaya et al. 1954; Utida 1954, 1957a, b, 1958; Miyashita

1955; Fukaya and Nakatsuka 1956). The increase in the population density over several successive years, called “gradation”, has been frequently observed in this species (Ishikura 1951). Miyashita (1955) detected a 6-year cycle in the population dynamics of Shimane Prefecture, but no clear cycles have been detected in most prefectures (Itô 1968). Centrifugal spatial spread of infested areas was observed over several years during the gradation period in the Kyushu district of Japan (Kiritani and Oho 1961). Climatic factors such as the low temperatures in July have been thought to responsible for the cause of the initiation of gradation of *C. suppressalis* (Ishikura 1950b; Miyashita and Itô 1961).

The green rice leafhopper, *N. cincticeps*, is a sucking insect with a length of 4.5–6 mm. This species has three or four generations in a year. In winter, the leafhopper lives on grass weeds such as *Poa annua* L. and *Alopecurus aequalis* Sobol. in the overwintering nymphal stage, mainly of the fourth stage. These weeds provide both food and habitat for *N. cincticeps* in late winter. This species has been considered a typical insect, the density of which is regulated by a density-dependent process (Kuno 1968). The density-dependent dispersal of adults of the second generation is one of the mechanisms of negative feedback at work in the Kyushu district in Japan (Hokyo 1972). *N. cincticeps* is a serious pest as it is the vector of the rice dwarf virus in central and western parts of Japan. The fluctuation of the population is relatively large in the Tohoku and Hokuriku districts, occasionally causing a yield loss as a consequence of the direct sucking by the insects, or via the sooty mould that emerges on their excretions (Johraku et al. 1976, 1983; Kidokoro 1979; Johraku 1984; Hirano and Fujii 1995). The length of the snow-covered period and the abundance of weeds in winter is considered to be one of the major factors determining their abundance in the Hokuriku district (Oda 1971; Johraku and Kato 1974; Imai 1976; Johraku 1976; Sekiguchi et al. 1981).

The small brown planthopper, *L. striatellus*, is a sucking insect with a length of 3–4 mm. This species has about five generations in a year in the Ibaraki Prefecture. The abundance of this species is very influenced by the existence of wheat or barley fields. The planthopper enters diapause in the nymphal stage in levees around fallow paddy fields in winter (Murakami and Suzuki 1971). In the Kanto district, brachypterous and macropterous adults emerge from the levees from March to April and enter wheat or barley fields. These adults lay eggs which in turn yield the first-generation macropterous adults from May to June. Wheat is an especially good food for this species. These macropterous adults then emigrate to paddy fields that are transplanted with rice from May to June (Kisimoto and Yamada 1986). Although the rice plant is less preferred as a food by this species, three or four generations of these insects are produced in the paddy fields. Nymphs of the final generation enter diapause, induced by a short-day photoperiod at low temperatures, and move to levees where they overwinter. *L. striatellus* is a serious pest as the vector of the rice

stripe virus (RSV). The occurrence of this disease is determined by a complex interaction between three biological entities: the rice plant, the virus, and the insect. Several epidemiological models have been constructed to predict the disease’s prevalence (Kono 1966; Muramatsu 1979; Kisimoto and Yamada 1986, 1988; Taira et al. 1995; Yamamura 1998).

## Transformation

We first perform transformations to improve the additivity and homoscedasticity of the time-series. Various forms of transformation could be used, including a square root transformation, a logarithmic transformation and, more generally, the Box–Cox transformation (1964). Among these, a logarithmic transformation is usually preferred when analyzing population dynamics for the following reasons. Most populations change by multiplicative factors such as the mortality and birth rates. The logarithmic transformation makes a multiplicative factor into an additive factor. Therefore, if we use logarithmic transformation, we are able to use an additive model, which is analytically more tractable. Simultaneously, homoscedasticity arises in most cases because the multiplicative error factor becomes additive by a logarithmic transformation. Thus, we use a logarithmic transformation in the following analyses. To solve the problem that arises from the discreteness of the number of individuals, we use  $\log(x + 0.5)$  where  $x$  is the number of individuals, although most people traditionally use a transformation of the form  $\log(x + 1)$ , which is less preferable (Yamamura 1999). We use a common logarithm  $\log_{10}(x + 0.5)$  instead of a natural logarithm  $\log_e(x + 0.5)$  so that we are able to easily back-transform the variable using mental calculations.

## Test for density-dependence

Testing density-dependence and testing the hypothesis of random walk are two sides of the same analysis, because a random walk is a situation where there is no density-dependence. We are liable to detect a significant correlation between two time-series, even if they are independent, if they have stochastic trends caused by a random walk. Such a regression is called “spurious regression” in the field of econometrics (Greene 2000). A preliminary test to detect a random walk is required in order to avoid a spurious regression. Various testing procedures collectively referred to as “unit root tests” have been developed for this purpose (Greene 2000; Hayashi 2000; Maddala 2001). Recent versions of statistical software for econometrics such as EViews, LIMDEP, SHAZAM, SAS, Stata, or TSP provide several unit root tests (SAS Institute 1993; Greene 2002; Stata Corp 2003; Quantitative Micro Software 2004; Whistler et al. 2004; Hall and Cummins 2005).

In ecological literature, the difficulty that arises in the detection of density-dependence was first discussed by

Maelzer (1970) and St. Amant (1970). The test statistics calculated from the regression do not follow a standard distribution such as the  $t$ -distribution. Hence, various methods, including those of Bulmer (1975) and Pollard et al. (1987), have been proposed as alternative tests (see Den Boer and Reddingius 1996 for the review of earlier literature in ecological journals). To further complicate matters, measurement errors also yield a bias in the estimation of density-dependence (Kuno 1971; Fuller 1987; Den Boer and Reddingius 1996; Shenk et al. 1998; Solow 1998, 2001). We will discuss the bias caused by measurement errors in estimating parameters in later sections. Initially, however, we ignore measurement errors as we test the null hypothesis of random walk, considering the influence of measurement errors to be relatively small in such extreme cases. Then, we can use several standard procedures such as the Dickey–Fuller test, augmented Dickey–Fuller test, and Phillips–Perron test. Among these, we apply the Dickey–Fuller test that is most widely used in econometrics (Dickey and Fuller 1979; Greene 2000; Maddala 2001). Let  $N_t$  be the transformed quantity, in the form of  $\log_{10}(x+0.5)$ , of the total number of captured individuals of a species in year  $t$ . We first consider the following model:

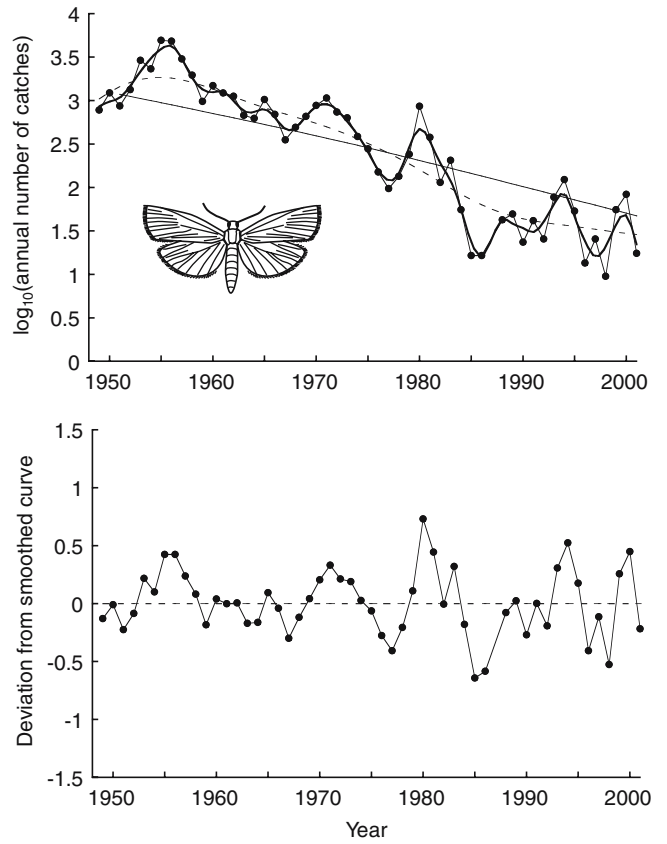
$$N_t = a_0 + a_1 N_{t-1} + e_t, \quad e_t \sim N(0, \sigma^2), \quad (1)$$

where  $a_0$  and  $a_1$  are constants, and  $e_t$  denotes an error that follows a normal distribution. The null hypothesis is  $a_1 = 1$  while the alternative hypothesis is  $a_1 < 1$ .

The  $P$ -value that was evaluated by the approximation described by MacKinnon (1994) was 0.811 for *C. suppressalis*. Thus, no significant density-dependence was detected; we cannot discard the hypothesis that the population dynamics of *C. suppressalis* shown in the upper panel in Fig. 1 were generated by a random walk. In contrast, we found  $P < 0.001$  for *N. cincticeps*, indicating that the dynamics of *N. cincticeps* is regulated by a density-dependent mechanism, and  $P = 0.072$  for *L. striatellus*, indicating that the density-dependence is only marginally significant.

### Additive model

Most techniques for conventional time-series analyses assume that the time-series is stationary. Hence, non-stationary time-series are conventionally converted into stationary time-series by removing the trend before performing an analysis. However, such a procedure is not always appropriate. Many time-series show trends, which are one of two types: stochastic trends that are generated by a random walk and deterministic trends that are generated by a change in exogenous factors. The removal of trends is effective only for deterministic trends. The above unit root test for *C. suppressalis* indicated that the dynamics of this species may have a stochastic trend that was generated by a random walk. If this is true, removing the trend before analysis would



**Fig. 1** Population dynamics of *Chilo suppressalis* (logarithmic scale). *Upper panel* Observed annual number of individuals caught by a light trap,  $\log_{10}(x+0.5)$ . *Thin curve* Locally weighted scatterplot smoothing (LOWESS) selected by generalized cross-validation (GCV) criterion in the full additive model (Eq. 2). *Bold curve* LOWESS selected by GCV criterion in the null model (Eq. 3). *Dotted curve* LOWESS calculated by a normal kernel with a SD of 5 years. *Lower panel* Deviation ( $D_t$ ) between  $\log_{10}(x+0.5)$  and the LOWESS that was calculated by a normal kernel with a SD of 5 years

generate an artificial stationary time-series. However, empirically we consider that the biological components of the dynamics will not be a random walk. There is a long history of pest management practices used against *C. suppressalis*. The population of *C. suppressalis* will rather fluctuate around the potential equilibrium that is determined by the balance between the efficiency of pest management and the reproductive rate of insects. This potential equilibrium may fluctuate continuously by a random walk, but the biological dynamics of *C. suppressalis* around the equilibrium will not be a random walk. Thus, we will be able to assume that the trend is deterministic but not stochastic. Then, we divide the observed dynamics into two components: (1) the dynamics of environmental factors influencing the potential equilibrium of insect pests, and (2) the biological dynamics of insect pests in a given environment. Here we are interested in the influence of temperature, and hence include it in the second component. In the



first component, we include only those environmental factors that are beyond our major interest; these factors can be called “nuisance factors”. For example, the density of insect pests will become much smaller if the area of paddy field is reduced due to changes in land use. Such an artificial reduction is a nuisance factor in the sense that we need not explain the reason for that reduction. In order to isolate those factors that we need to explain, our first concern is to consider how we might automatically remove the influence of nuisance factors.

Two kinds of procedures are usually used to remove these trends (Brockwell and Davis 2002): one is a finite difference procedure, the other is a smoothing procedure. The finite difference procedure, largely derived from Box and Jenkins (1970), uses artificial assumptions in most cases, although they are not always explicitly noted. For example, the time-series may become stationary when a first-order difference such as  $N_t - N_{t-1}$  is used. In this case, we implicitly assume that the difference is not determined by the previous quantities of variables but by the previous difference between variables. However, there would be no clear reason for the difference to become the cause of the next difference. In this respect, smoothing procedures will logically be more appropriate than difference procedures in most cases. We use a smoothing procedure to divide the dynamics between those components that are environmental nuisance factors and those that are biological factors.

We are interested in the influence of a temperature rise on the abundance of these populations. Hence, we additionally include temperatures as exogenous variables in the analysis. It may be preferable to treat the temperature of each month separately because the temperature in different months is likely to influence the dynamics differently. A considerable number of regression analyses were performed before the 1970s to explore the influence of the environmental factors of each month on the abundance of *C. suppressalis* (Ishikura 1950b; Fukaya and Nakatsuka 1956). However, most of these analyses seem unsuccessful, in part due to the multiplicity that arises with multiple testing. In order to avoid such problems, we divide a year into only two seasons: the previous November–April and May–October, referred to as the “winter season” and the “summer season”, respectively. The summer season corresponds to that period during which rice is cultivated, while the winter season corresponds to that period when insects live outside paddy fields. We denote the mean temperature of the previous winter season (W) and summer season (S) in year  $t$  by  $\tau_{Wt}$  and  $\tau_{St}$ , respectively. We use the following model by including lags of up to 2 years:

$$N_t = a_0 + a_1 N_{t-1} + a_2 N_{t-2} + f(t) + b_W \tau_{Wt} + b_S \tau_{St} + e_t, \\ e_t \sim N(0, \sigma^2), \quad (2)$$

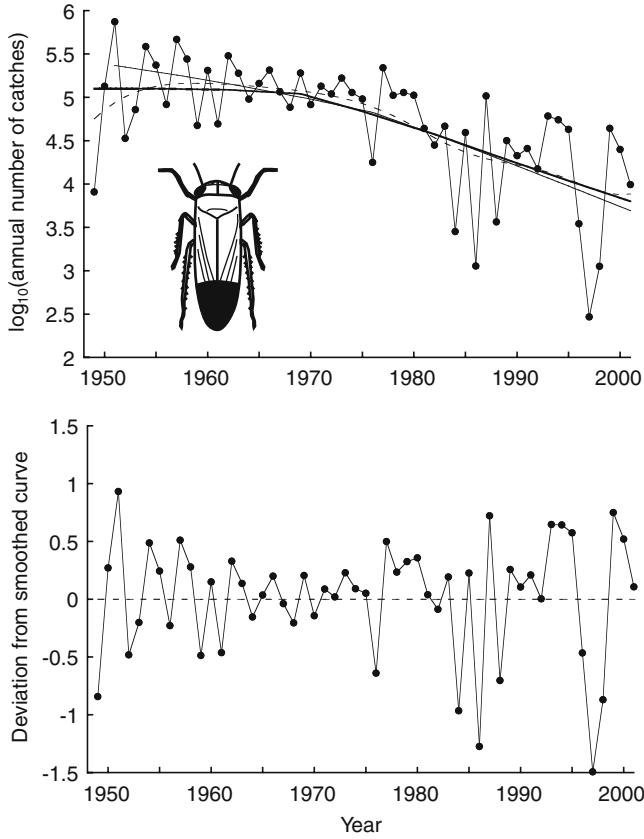
where  $b_W$  and  $b_S$  are constants.  $f(t)$  is a smoothed quantity at year  $t$ . Two categories of smoothing procedures are usually available: (1) smoothing spline, and (2) local

regression. The former procedure assumes a situation where some penalty, such as repulsion force, arises when we bend the curve. The smoothness of the curve becomes large if the repulsion to bending is large, while the smoothness becomes small if the repulsion force is small. The latter procedure, sometimes called locally weighted scatterplot smoothing (LOWESS) after Cleveland (1979) in the broad sense, assumes that the trend consists of local linear components or polynomial components. The smoothness becomes large if the duration of a component is long, while the smoothness becomes small if the duration of a local component is short. As will be discussed later, it is more reasonable to opt for the assumption of LOWESS to remove the dynamics of environmental components from the time-series of populations. Then, we adopt LOWESS as  $f(t)$  in the estimation of the parameters of Eq. 2. We use Proc GAM of the statistical software SAS (SAS Institute 2001). The optimal smoothness is determined by using generalized cross-validation (GCV) that was originally proposed by Craven and Wahba (1979). A tricube weight function is used as the kernel function in Proc GAM. We might alternatively use a Poisson distribution with a logarithmic link in an arithmetic scale, instead of using a normal distribution in a logarithmic scale, by using the framework of GAM (Chambers and Hastie 1991). Fewster et al. (2000) used a quasi-likelihood approach using a Poisson distribution in applying GAM to data from the common bird census of the British Trust for Ornithology. However, we do not use a Poisson distribution in our analysis because the actual distribution will not follow a Poisson distribution with a constant overdispersion as is assumed in the quasi-likelihood approach. This problem will be discussed in more detail later in this paper.

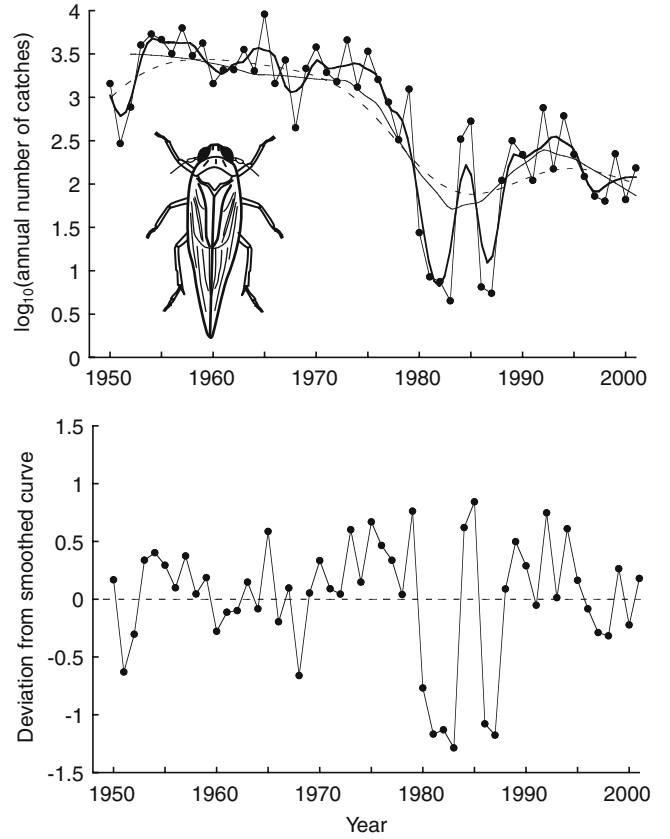
The estimated parameters were quite different among the species (Table 1; thin curves in the upper panels of Figs. 1, 2, and 3). The first-order lagged term was

**Table 1** Estimated parameters in the additive model given by Eq. 2 (where  $a$ , and  $b$  are constants).  $W$  Winter,  $S$  summer

Species	Parameter	Estimate	SE	$P$
<i>Chilo suppressalis</i>	$a_0$	0.247	1.291	0.850
	$a_1$	0.630	0.133	<0.001
	$a_2$	−0.199	0.140	0.164
	$b_W$	0.124	0.059	0.043
	$b_S$	0.016	0.064	0.806
	$\sigma^2$	0.074		
<i>Nephotettix cincticeps</i>	$a_0$	0.647	2.560	0.802
	$a_1$	0.007	0.118	0.955
	$a_2$	0.055	0.121	0.654
	$b_W$	0.148	0.111	0.190
	$b_S$	0.140	0.119	0.245
	$\sigma^2$	0.265		
<i>Laodelphax striatellus</i>	$a_0$	−1.814	1.927	0.352
	$a_1$	0.351	0.111	0.003
	$a_2$	−0.234	0.111	0.041
	$b_W$	−0.165	0.098	0.099
	$b_S$	0.263	0.102	0.014
	$\sigma^2$	0.211		



**Fig. 2** Population dynamics of *Nephrotettix cincticeps* (logarithmic scale). For an explanation of the curves, see Fig. 1



**Fig. 3** Population dynamics of *Laodelphax striatellus* (logarithmic scale). For an explanation of the curves, see Fig. 1

significant for *C. suppressalis* ( $P < 0.001$ ). Both the first and second lagged terms were significant for *L. striatellus* ( $P = 0.003$  and  $0.041$ , respectively). However, no lag term was significant for *N. cincticeps*, indicating that the population abundance of this species does not depend on past dynamics. The influence of temperature is significant for *C. suppressalis* and *L. striatellus*. The population of *C. suppressalis* becomes larger with increasing winter temperature ( $P = 0.043$ ), while that of *L. striatellus* becomes larger with increasing summer temperature ( $P = 0.014$ ).

It should be noted that the smoothed curve achieved by using GAM changes greatly if we do not incorporate appropriate factors into the model. The bold curves in the upper panels of Figs. 1, 2, and 3 indicate the smoothed curves that were estimated under the following null model:

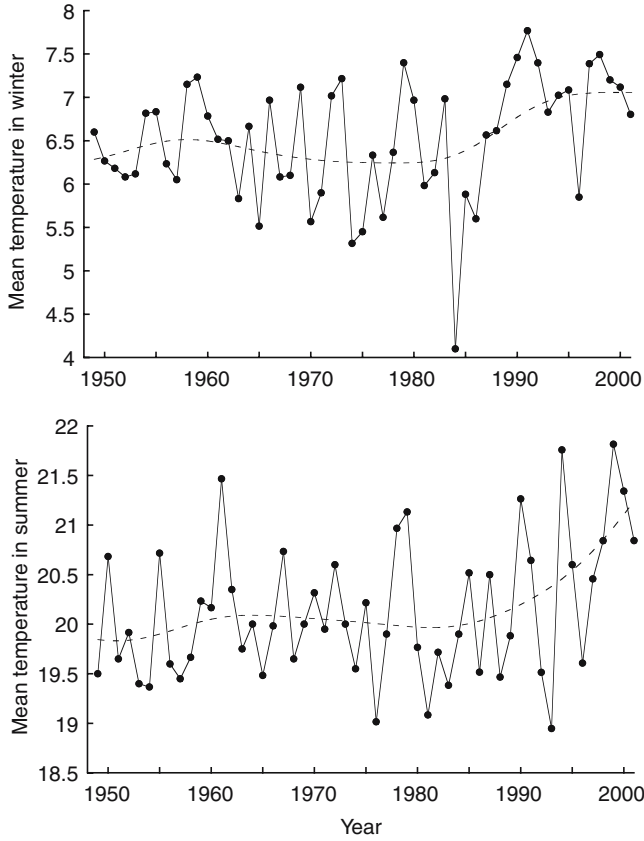
$$N_t = a_0 + f(t) + e_t, \quad e_t \sim N(0, \sigma^2). \quad (3)$$

In the analysis of *C. suppressalis*, the components that should be attributable to factors such as the lagged population are automatically incorporated into the smoothed curve  $f(t)$ . Consequently, the  $f(t)$  curve becomes very variable; the curve is very close to the observed quantity. A similar phenomenon occurs in the analysis of *L. striatellus*. In contrast, in the analysis of

*N. cincticeps*, the smoothed curve that was estimated from the null model was close to the curve that was estimated from Eq. 2, because the null model is eventually the same as that selected by GCV for this species.

### Empirical smoothing

The smoothing procedure using GAM will be useful as indicated above, but it appears to have a shortcoming; we cannot correctly estimate the influence of non- nuisance factors if there is a correlation between the time-series of non-nuisance factors and that of nuisance factors. In our case, the change in temperature correlates with nuisance factors. Actually, the temperature has increased during the past 50 years (Fig. 4). When we perform smoothing to remove the influence of nuisance factors, the influence of a temperature rise is simultaneously partially removed. Hence, the influence of global warming will be underestimated if we use GAM. Let  $\mathbf{N}_t$ ,  $\boldsymbol{\tau}_{wt}$ ,  $\boldsymbol{\tau}_{st}$  be the vectors containing the time-series of  $N_t$ ,  $\tau_{wt}$ , and  $\tau_{st}$ , respectively. Let us denote  $f(t)$  by a more precise expression,  $f(\mathbf{N}_t)$ . Then, if we smooth the factors other than  $\mathbf{N}_{t-1}$ ,  $\mathbf{N}_{t-2}$ ,  $\boldsymbol{\tau}_{wt}$ , and  $\boldsymbol{\tau}_{st}$ , the relation is given by:



**Fig. 4** Change in temperature (°C) during the past 50 years at Mito, Japan. Dotted curve LOWESS that was calculated by a normal kernel with a SD of 5 years. Upper panel Mean temperature from the previous November to April. Lower panel Mean temperature from May to October

$$N_t = a_0 + a_1 N_{t-1} + a_2 N_{t-2} + f(N_t - a_1 N_{t-1} - a_2 N_{t-2} - b_W \tau_{Wt} - b_S \tau_{St}) + b_W \tau_{Wt} + b_S \tau_{St} + e_t. \quad (4)$$

We can use the following relation because LOWESS is additive:

$$f(N_t - a_1 N_{t-1} - a_2 N_{t-2} - b_W \tau_{Wt} - b_S \tau_{St}) = f(N_t) - a_1 f(N_{t-1}) - a_2 f(N_{t-2}) - b_W f(\tau_{Wt}) - b_S f(\tau_{St}). \quad (5)$$

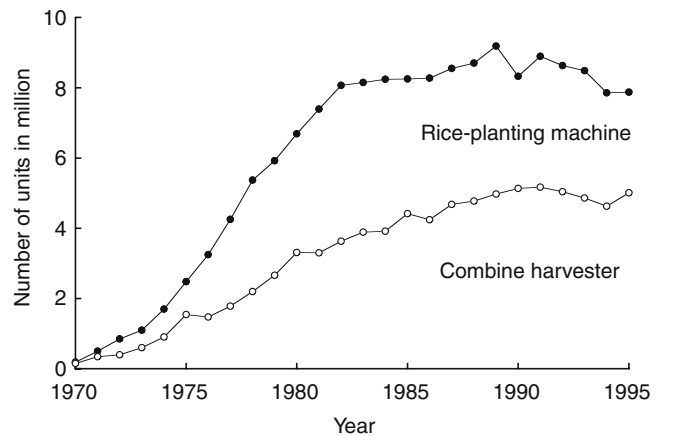
Then, by substituting Eq. 5 into Eq. 4, we obtain the following relation:

$$[N_t - f(N_t)] = a_0 + a_1 [N_{t-1} - f(N_{t-1})] + a_2 [N_{t-2} - f(N_{t-2})] + b_W [\tau_{Wt} - f(\tau_{Wt})] + b_S [\tau_{St} - f(\tau_{St})] + e_t. \quad (6)$$

Thus, we can estimate the parameters by applying smoothing to temperatures as well as logarithmic populations by using the same function for smoothing. Let us denote the difference between the observed and smoothed quantities by  $D_t = N_t - f(N_t)$ ,  $T_{Wt} = \tau_{Wt} - f(\tau_{Wt})$ , and  $T_{St} = \tau_{St} - f(\tau_{St})$ . Then, we can express the above equation by a simpler form:

$$D_t = a_0 + a_1 D_{t-1} + a_2 D_{t-2} + b_W T_{Wt} + b_S T_{St} + e_t. \quad (7)$$

It currently seems difficult to automatically estimate the optimal function  $f$  of the form of Eq. 6. In order to empirically determine the function  $f$ , we should therefore discuss which nuisance factors caused the population decline in these species during the past 50 years. Several changes in cultivation practices are said to be the cause of this decline although the exact reason is not known (Miyashita 1982). Two agricultural machines, the combine harvester and the rice planting machine, are known to be related to the population decline of *C. suppressalis*. The larvae of *C. suppressalis* overwinter in the dried stem of rice plants (Kojima and Emura 1971). A combine harvester kills such larvae when it cuts the stems of rice plants. A rice-planting machine is used for younger seedlings, which are not suitable for the development of larvae (Yuno and Johraku 1975, 1976). Thus, the prevalence of these machines reduces the survival rate of the larvae of *C. suppressalis*. In addition, spraying the seedling plate used in mechanical planting reduced the survival of larvae. Figure 5 shows that the use of these machines took 10 or 15 years to spread among farmers (Ministry of Agriculture Forestry and Fisheries 1970–1990, 1970–1995). The use of industrial chemicals also seems to have taken several years to become popular. For example, the change in how pesticides are applied gradually changed the percentage of egg-parasitism of *C. suppressalis* over 10 years (Nozato and Kiritani 1976); it was about 60% before 1955 but had decreased to a new equilibrium level of about 20% by about 1965. Thus, we can roughly anticipate that the decline of insect pests will be the value generated by the sum of local declines that continued for about 10 years. Some components have large slope while the slope of other components is small. The sum of these slopes gradually changes as it reflects the era. Therefore, we use a normal kernel with the SD of 5 years in applying first-order LOWESS. We use SAS/INSIGHT for the



**Fig. 5** Increase in the use of agricultural machines in Ibaraki Prefecture, Japan, which is a potential cause of the decline of *C. suppressalis*

calculation of the fixed-width LOWESS (SAS Institute 1995). The smoothed curves are shown by broken lines in the upper panels of Figs. 1, 2, and 3. The dynamics of  $D_t$  are shown in the lower panels. We proceed to the analyses using  $D_t$  in the remaining sections.

### Nonlinearity

We previously considered only the linear terms of lagged populations. However, the influence of density may be nonlinear. Several methods have been developed to evaluate the nonlinear dynamics of population in a noisy environment. Among these methods, the response surface method (RSM) that was proposed by Turchin and Taylor (1992) is recommended for data sets of 20–50 points (Hastings et al. 1993; Ellner and Turchin 1995). Turchin and Taylor's original RSM is the generalization of a polynomial regression in which the independent variables, including lagged population, are transformed using the Box–Cox family of power transformation. However, this model can be oversensitive to changes in data (Perry et al. 1993), so we adopt a simpler model proposed by Perry et al. (1993):

$$D_t = a_0 + a_1 D_{t-1} + a_2 D_{t-2} + a_{11} D_{t-1}^2 + a_{22} D_{t-2}^2 + a_{12} D_{t-1} D_{t-2} + b_W T_{Wt} + b_S T_{St} + e_t. \quad (8)$$

The actual form of a nonlinear function is not known in most cases, but we can describe any nonlinear function by using a Taylor series to the infinite order. Then, we can approximately express the function by using the smaller order terms in the Taylor series expansions. In using Eq. 8, we are adopting the second-order polynomials as an approximation of unknown nonlinear functions. The parameters in this equation are estimated by using the OLS method assuming that the distribution of  $e_t$  obeys a normal distribution with consistent variance. The most critical step of RSM analysis is the selection of the appropriate embedding dimension for the model. Turchin (1993) used the cross-validation to select the optimal model. We instead use an information criterion [Akaike's information criterion (AIC); Akaike (1973)] since, currently, AIC seems to be the method most widely used in selecting models (Burnham and Anderson 2002). AIC is defined by:

$$AIC = -2 \log_e(L) + 2p,$$

where  $L$  is the maximum likelihood, and  $p$  is the number of parameters including the intercept. For a regression problem with normal errors, we can use the following formula as an AIC criterion by omitting constant terms:

$$AIC = n \log_e \left( \frac{RSS}{n} \right) + 2p,$$

where  $n$  is the number of data, and RSS is the residual sum of squares. We compare the candidate models and adopt the model that has the smallest AIC. It should be

noted that AIC does not select the true model directly. Instead, AIC selects the model that has the largest expected power of prediction evaluated by the measure of Kullback–Leibler information. A model having the largest predictive power will be close to the true model, where a true model is defined as a model that appropriately summarizes the actual system by ignoring the minor components of the system. Hence, we can utilize AIC to roughly identify the true model in most cases. Before performing the model selection using AIC, we first carefully determine the candidate models. The higher order terms in the Taylor series are included to account for variance that is not explained by the lower order terms. Hence, the higher order terms should be included in the model only if the corresponding lower order terms are included. Such a hierarchical family of models is usually used as the candidates when we select the appropriate model by polynomial regression or log-linear model analysis. By the same principle, we confine our model to the hierarchical family in the comparison of AIC.

For *C. suppressalis*, the linear components of the first and second lagged populations were selected by AIC. Quadratic terms that indicate the nonlinearity were not selected:

$$D_t = 0.572 D_{t-1} - 0.246 D_{t-2} + 0.125 T_{Wt} + e_t, \quad e_t \sim N(0, 0.064). \quad (9)$$

For *N. cincticeps*, only the winter temperature was selected as the explanatory variable:

$$D_t = 0.203 T_{Wt} + e_t, \quad e_t \sim N(0, 0.236). \quad (10)$$

For *L. striatellus*, a slightly complicated equation was selected by AIC:

$$D_t = 0.219 + 0.129 D_{t-1} - 0.666 D_{t-1}^2 - 0.321 D_{t-2} - 0.206 T_{Wt} + 0.166 T_{St} + e_t, \quad e_t \sim N(0, 0.198). \quad (11)$$

The quadratic term of the first-order lagged population was selected, indicating the existence of nonlinearity. Both the winter and summer temperatures were selected in this species.

### Vector autoregression analysis

Three insect pests living in the same paddy field may have some inter-species interactions that modify the population dynamics of each species, although we analyzed the time-series of each species separately in the above analyses. To now include the possibility of inter-species interactions, we use VAR because it automatically analyzes the relation between populations of different times between species as well as within species. We use an approach similar to the one used by Ives et al. (2003) in analyzing the interaction between species in time-series data on the limnological community. For simplicity, when performing VAR, we adopt a linear approximation



of the influence of lagged populations as well as other exogenous factors. We use the subscripts  $C$ ,  $N$ , and  $L$ , to indicate the variable for *C. suppressalis*, *N. cincticeps*, and *L. striatellus*, respectively. Then the vector autoregression model is expressed by:

$$D_{Ct} = a_C + a_{CC1}D_{Ct-1} + a_{CC2}D_{Ct-2} + a_{CN1}D_{Nt-1} + a_{CN2}D_{Nt-2} + a_{CL1}D_{Lt-1} + a_{CL2}D_{Lt-2} + b_{CW}T_{Wt} + b_{CS}T_{St} + e_{Ct}, \quad (12)$$

$$D_{Nt} = a_N + a_{NC1}D_{Ct-1} + a_{NC2}D_{Ct-2} + a_{NN1}D_{Nt-1} + a_{NN2}D_{Nt-2} + a_{NL1}D_{Lt-1} + a_{NL2}D_{Lt-2} + b_{NW}T_{Wt} + b_{NS}T_{St} + e_{Nt}, \quad (13)$$

$$D_{Lt} = a_L + a_{LC1}D_{Ct-1} + a_{LC2}D_{Ct-2} + a_{LN1}D_{Nt-1} + a_{LN2}D_{Nt-2} + a_{LL1}D_{Lt-1} + a_{LL2}D_{Lt-2} + b_{LW}T_{Wt} + b_{LS}T_{St} + e_{Lt}. \quad (14)$$

In Eq. 12, the parameters  $a_C$ ,  $a_{CC1}$ ,  $a_{CC2}$ ,  $a_{CN1}$ ,  $a_{CN2}$ ,  $a_{CL1}$ ,  $a_{CL2}$ ,  $b_{CW}$ , and  $b_{CS}$  are constants,  $e_{Ct}$  is a normal error. The parameters in Eqs. 13 and 14 are defined in a similar manner. We use Stata for the estimation (Stata 2003).

VAR indicates that the influence of the first-order lagged terms was statistically significant within species for *C. suppressalis* and *L. striatellus* ( $a_{CC1}$  and  $a_{LL1}$  in Table 2). The results of these tests, however, indicate trivial phenomena such as the population at time  $t$  tends to be large if the population at time  $t-1$  is large. The first-order lagged terms of *C. suppressalis* and *L. striatellus* have a marginally significant influence on *N. cincticeps* ( $P=0.012$  and  $0.042$ , respectively). The influence of temperature is significant for *C. suppressalis* and *L. striatellus*. The population of *C. suppressalis* increases with increasing winter temperatures ( $P=0.019$ ). The population of *L. striatellus* increases with increasing summer temperatures ( $P=0.003$ ), but decreases with increasing winter temperatures ( $P=0.041$ ).

#### The problem of measurement error

We define “measurement error” as the component that influences the observation without influencing the observation of the subsequent year. The influence of measurement errors was ignored in the above analyses. Although our definition of measurement error is different from common usage, we adopt this term because we can use the same approach, the state-space model that is used for removing the measurement error in common usage. State-space modelling has been used recently in ecological literature when analyzing population dynamics (Zeng et al. 1998; deValpine and Hastings 2002; Calder et al. 2003; Williams et al. 2003; Clark and Bjørnstad. 2004; Viljugrein et al. 2005). We can use the Kalman filter algorithm if we use a linear model and if the errors obey a normal distribution (Harvey 1989; Durbin and Koopman 2001; Brockwell and Davis 2002). Numerical integration or simulation will be required if

**Table 2** Estimated parameters in vector autoregression defined by Eqs. 12, 13, and 14

Species	Parameter	Estimate	SE	P
<i>C. suppressalis</i>	$a_C$	0.009	0.036	0.794
	$a_{CC1}$	0.502	0.152	0.001
	$a_{CC2}$	-0.272	0.160	0.089
	$a_{CN1}$	0.115	0.090	0.202
	$a_{CN2}$	0.002	0.089	0.982
	$a_{CL1}$	-0.005	0.079	0.954
	$a_{CL2}$	-0.073	0.085	0.389
	$b_{CW}$	0.136	0.058	0.019
	$b_{CS}$	-0.017	0.064	0.788
	$\sigma_C^2$	0.071		
<i>N. cincticeps</i>	$a_N$	-0.012	0.061	0.848
	$a_{NC1}$	0.648	0.259	0.012
	$a_{NC2}$	-0.028	0.274	0.918
	$a_{NN1}$	-0.025	0.154	0.869
	$a_{NN2}$	-0.121	0.151	0.426
	$a_{NL1}$	0.274	0.135	0.042
	$a_{NL2}$	-0.129	0.146	0.378
	$b_{NW}$	0.180	0.099	0.067
	$b_{NS}$	0.108	0.109	0.324
	$\sigma_N^2$	0.209		
<i>L. striatellus</i>	$a_L$	0.030	0.064	0.641
	$a_{LC1}$	0.305	0.271	0.260
	$a_{LC2}$	-0.384	0.286	0.179
	$a_{LN1}$	-0.198	0.160	0.216
	$a_{LN2}$	0.283	0.158	0.073
	$a_{LL1}$	0.353	0.141	0.012
	$a_{LL2}$	-0.041	0.152	0.787
	$b_{LW}$	-0.210	0.103	0.041
	$b_{LS}$	0.339	0.114	0.003
	$\sigma_L^2$	0.227		

we incorporate nonlinear terms into the equation (Kitagawa 1987; Durbin and Koopman 2001; deValpine and Hastings 2002). Hence, we consider the linear case where the terms for  $D_t^2$  are omitted for convenience. The above response surface analyses imply that the linear approximations will be reasonable for *C. suppressalis* and *N. cincticeps*. When we assume a distribution other than a normal distribution, such as a Poisson distribution in an arithmetic scale, the calculation also becomes complicated (Durbin and Koopman 2001). Bayesian estimation using the Markov chain Monte Carlo algorithm is especially useful in such cases (Shephard and Pitt 1997; Calder et al. 2003; Saitoh et al. 2003; Stenseth et al. 2003; Clark and Bjørnstad. 2004); however, the assumption of Poisson distribution becomes less likely if the mean fluctuates spatially at random due to some natural or artificial reasons. It seems preferable to use some overdispersed Poisson distributions such as a negative binomial distribution in an arithmetic scale. Actually, the spatial distribution of most populations in the field does not obey a Poisson distribution; the mean-variance relation is instead described by Taylor’s power law where the exponent is relatively closer to 2 than 1 as expected by a Poisson distribution (Taylor et al. 1978, 1979; Yamamura 2000). The quasi-likelihood approach is not appropriate because the dispersion parameter will not be constant. The exponent close to 2 will be partly generated by the multiplicative nature of population

dynamics. In such situations, as discussed above, it is reasonable to assume a normal distribution with a constant variance for the error of  $D_t$  as an approximation. We use normal errors for this reason.

Let  $\mu_{Ct}$ ,  $\mu_{Nt}$ , and  $\mu_{Lt}$  be the “true population” at year  $t$  of *C. suppressalis*, *N. cincticeps*, and *L. striatellus*, respectively. We use the term true population in the sense that it influences the population of the following year. Then, if we ignore the multicollinearity, the full state-space model for *C. suppressalis* is expressed by a form as follows:

$$\begin{aligned} \mu_{Ct} = & a_C + a_{CC1}\mu_{Ct-1} + a_{CC2}\mu_{Ct-2} + a_{CN1}\mu_{Nt-1} \\ & + a_{CN2}\mu_{Nt-2} + a_{CL1}\mu_{Lt-1} + a_{CL2}\mu_{Lt-2} \\ & + b_{C\mu w}\tau_{wt} + b_{C\mu s}\tau_{st} + e_{C\mu t}, \quad e_{C\mu t} \sim N(0, \sigma_{C\mu}^2), \end{aligned} \quad (15)$$

$$\begin{aligned} D_{Ct} = & \mu_{Ct} + a_{CN}\mu_{Nt} + a_{CL}\mu_{Lt} + b_{CDw}\tau_{wt} \\ & + b_{CDs}\tau_{st} + e_{CDt}, \quad e_{CDt} \sim N(0, \sigma_{CD}^2), \end{aligned} \quad (16)$$

where  $e_{C\mu t}$  is a process error, and  $e_{CDt}$  is a signal error. Equations 15 and 16 are a state equation and an observation equation (signal equation), respectively. The notation of parameters is similar to that of Eq. 12. We only show the equations for *C. suppressalis* for convenience, but the corresponding equations are defined for the other two species in a similar manner. The factor of temperature is included in both the state equation and observation equation, because it may influence either or both the true population and the observation. The terms for  $\mu_{Nt}$  and  $\mu_{Lt}$  are included in Eq. 16, because the observed number of individuals may be influenced by the true population of another species of the same year. We use EViews for the estimation by Kalman filter (Quantitative Micro Software 2004). The optimal equation that is suitable for prediction is selected by minimizing AIC. Non-zero covariance is allowed among  $e_{C\mu t}$ ,  $e_{N\mu t}$ , and  $e_{L\mu t}$ , and among  $e_{CDt}$ ,  $e_{NDt}$ , and  $e_{LDt}$ . However, in this application, no covariance was selected by AIC.

For *C. suppressalis*, the following equation was selected:

$$\begin{aligned} \mu_{Ct} = & 0.504\mu_{Ct-1} - 0.276\mu_{Ct-2} + e_{C\mu t}, \\ e_{C\mu t} \sim & N(0, 0.059), \end{aligned} \quad (17)$$

$$D_{Ct} = \mu_{Ct} + 0.087T_{Wt}. \quad (18)$$

That the term  $e_{CDt}$  was not adopted by AIC indicates that the random component of the measurement error is relatively small. The observed number of individuals increases with increasing winter temperature, while the true population is not influenced by the temperature.

For the dynamics of *N. cincticeps*, we obtain:

$$\mu_{Nt} = e_{N\mu t}, \quad e_{N\mu t} \sim N(0, 0.202) \quad (19)$$

$$D_{Nt} = \mu_{Nt} + 0.699\mu_{Ct} + 0.171T_{Wt}, \quad (20)$$

or

$$\mu_{Nt} = 0, \quad (21)$$

$$\begin{aligned} D_{Nt} = & \mu_{Nt} + 0.699\mu_{Ct} + 0.171T_{Wt} + e_{NDt}, \\ e_{NDt} \sim & N(0, 0.202). \end{aligned} \quad (22)$$

These two models have the same log likelihood and AIC. The true population at year  $t-1$  does not influence the population at year  $t$ . Hence, there is logically no discrimination between the measurement error and error of the true population. The influence of temperature is similar to that in *C. suppressalis*; the winter temperature influences the observed number of individuals but does not influence the true population. The above equations also indicate that the true population of *C. suppressalis* positively influences the observed number of *N. cincticeps* but does not influence the true population of *N. cincticeps*.

For the dynamics of *L. striatellus*, we obtain:

$$\begin{aligned} \mu_{Lt} = & 0.430\mu_{Lt-1} - 0.246\mu_{Lt-2} + e_{L\mu t}, \\ e_{L\mu t} \sim & N(0, 0.210), \end{aligned} \quad (23)$$

$$D_{Lt} = \mu_{Lt} - 0.149T_{Wt} + 0.273T_{St}. \quad (24)$$

The term  $e_{LDt}$  was not adopted by AIC, indicating that the random component of measurement error is relatively small, while both winter temperature and summer temperature were adopted in the observation equation.

Both combinations of ( $a_{CC1}$  and  $a_{CC2}$ ) for *C. suppressalis* and ( $a_{LL1}$  and  $a_{LL2}$ ) for *L. striatellus* lie within the stable region, yielding complex roots that cause damping oscillations [see Fig. 2.2 in Harvey (1981), or the equivalent Fig. 2.5 in Royama (1992)]. Such a damping oscillation is observable also intuitively in the lower panel of Fig. 1 for *C. suppressalis*. In contrast, the population dynamics of *N. cincticeps* are non-cyclically stable: the population simply fluctuates around its mean density without any oscillation.

## Abundance of insect pests under global warming

We next utilize the above equations to predict the yield loss that will result from the increase in pest populations under global warming. The outcomes of global warming greatly depend upon the future behavior of human beings. Hence, we should assume a clear scenario of future human action before calculating the prediction. SRES scenarios of IPCC are divided into four families, A1, A2, B1, and B2, each of which contains qualitative storylines (IPCC 2000). The A1 family describes a future world of very rapid economic growth, a global population that peaks in mid-century and declines thereafter, and the rapid introduction of new and more efficient technologies. The A2 family describes a very heterogeneous world. The underlying theme is self-reliance and preservation of local identities. Fertility patterns across regions converge very slowly, which results in a continuously increasing global population unlike in the A1 family. The B1 family resembles the A1 family but the conditions seen with the latter are accompanied by rapid changes in economic structures toward the introduction of clean and resource-efficient technologies. Their emphasis is on “global solutions” to economic, social, and environmental sustainability. The B2 family

resembles the A2 family but describes a world in which the emphasis is on “local solutions” for the sustainability of economic, social, and environmental systems.

The Meteorological Research Institute (MRI) constructed GCM by adopting the A2 family scenario of the SRES, that is, heterogeneous population growth without sustainability. Their GCM called MRI-CGCM2 has a horizontal resolution of 280 km with 30 atmospheric layers (Yukimoto et al. 2001; Yukimoto and Noda 2002). The horizontal resolution is too sparse for actual use. Then, MRI used a regional climate model (RCM) called RCM-20 km having a resolution of 20 km and nested it into MRI-CGCM2 over 2,500×2,500 km around Japan (Kurihara 2004). The predicted climatic data for the 20-year average were given for the present and for two future periods: 1981–2000, 2031–2050, and 2081–2100. Data included measured and predicted temperature, rainfall, wind velocities, and atmospheric pressure. However, the resolution of 20 km adopted by this RCM is different from the standard mesh grids of Japan, which causes problems when we use the predicted climatic data along with existing mesh data. Then, Nishimori et al. (2005) converted the predicted climatic data into standard second-order mesh data by using the same manner as that of Yokozawa et al. (2003). First, the baseline climatic data were calculated with the average from 1981 to 2000 at a resolution of 7.5′ in longitude and 5′ in latitude (approximately 10×10 km) by re-sampling the third-order mesh climatic data (approximately 1×1 km resolution) calculated from automated meteorological data acquisition system (AMeDAS) data, where AMeDAS was constructed by the Meteorological Agency of Japan. For predicting the average climatic data from 2031 to 2050, the climatic difference between the prediction for 1981–2000 and 2031–2050 was calculated for each grid point of RCM. For each second-order mesh, the four grid points of RCM that were nearest the center of the second-order mesh were selected. The climatic differences at these four points were averaged by using a weight that is inversely proportional to the distance. The average climatic data from 2031 to 2050 were then calculated by adding the average difference to the baseline climatic data. The average climatic data from 2081 to 2100 were calculated by a similar manner. The predicted change in the temperature is listed in Table 3. We use only the prediction for 2031–2050 in this article as an illustration.

We predict the average annual trap catches of *C. suppressalis*, *N. cincticeps*, and *L. striatellus* from 2031 to 2050 by using Eqs. 18, 20, and 24, respectively. We ignore the unknown parameters,  $\mu_{Ct}$ ,  $\mu_{Nt}$ , and  $\mu_{Lt}$  that appear in these equations. Hence, we only predict the abundance relative to that expected in a normal year. The temperature rise may also influence the efficiency of traps. For the dynamics of *C. suppressalis* and *N. cincticeps*, however, summer temperature, that is, the temperature during the period of light-trap catches, is not included in Eqs. 18 and 20, indicating that the

**Table 3** Future mean temperature<sup>a</sup> in Japan<sup>b</sup> under global warming predicted by the Meteorological Research Institute’s global climate model (MRI-CGCM2)

Period	Mean winter temperature (°C) <sup>c</sup>	Mean summer temperature (°C) <sup>d</sup>	Mean annual temperature (°C)
1981–2000	3.55	17.92	10.73
2031–2050	5.97	19.71	12.84
2081–2100	6.66	20.30	13.48

<sup>a</sup>Current temperature calculated from automated meteorological data acquisition system is also shown for comparison

<sup>b</sup>Data for Nansei-Shoto are not used

<sup>c</sup>Winter temperature is the average from November to April

<sup>d</sup>Summer temperature is the average from May to October

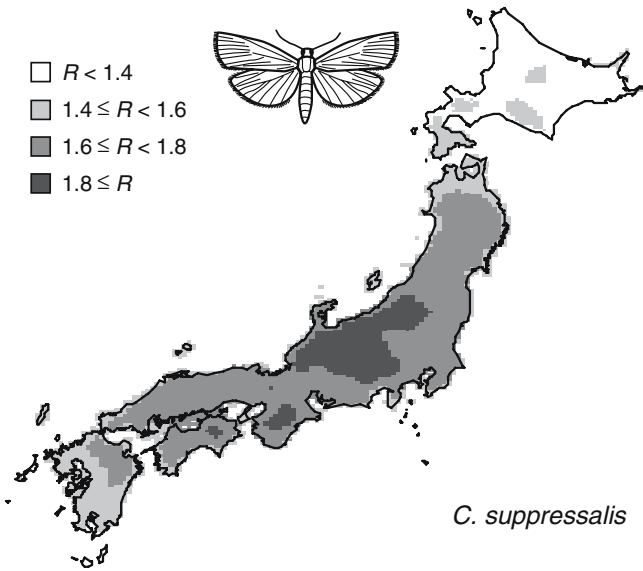
influence of temperature on the trap efficiency is small. Thus, we can consider that Eqs. 18 and 20 indicate the dynamics of the number of individuals that actually exist. Figure 6 shows that the population of *C. suppressalis* will increase by a ratio of from 1.6 to 1.8 in most areas in Japan. Figure 7 shows that the population of *N. cincticeps* will increase by a ratio of from 3 to 4. It is more complicated to determine the increase ratio in *L. striatellus* since it is influenced by both winter and summer temperatures according to Eq. 24. The ratio is larger for the seaboard of the Sea of Japan (Fig. 8).

We should note that the extrapolation that was used in calculating the abundance relies upon the assumption that the future climate change will not modify the structure of the system. Davis et al. (1995, 1998a, 1998b) reported examples which show that the temperature rise may modify the essential interaction between species. Thus, we should carefully interpret the results given in Figs. 6, 7, and 8.

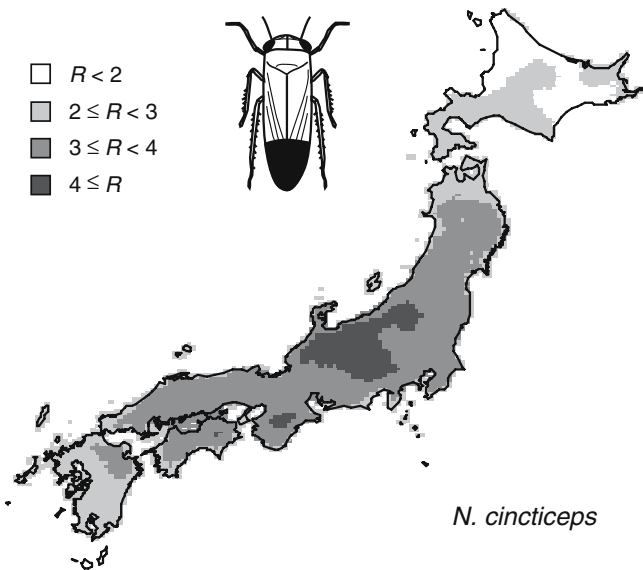
#### Prediction of yield loss caused by *C. suppressalis*

*C. suppressalis* injures the plant directly while the other two species, *N. cincticeps* and *L. striatellus*, cause yield loss by transmitting viral diseases. The occurrence of these diseases is determined by a complex interaction among three biological entities: the rice plant, the virus, and the insect. The sensitivity of rice plants to RSV infection is restricted to the young stages (Shinkai 1962). Hence, the synchronization between the emergence of adult *L. striatellus* and the developmental stage of rice plants susceptible to the virus is one of the major causes for the disease’s prevalence. Yamamura and Yokozawa (2002) predicted the influence of global warming on the prevalence of RSV by calculating the degree of synchronization between the emergence of adult *L. striatellus* and the date of transplantation. In contrast, the yield loss caused by *C. suppressalis* is straightforward. Hence, we focus on *C. suppressalis* in predicting the yield loss in this article.

We first examine the relation between the proportion of injured stems in a plant and the number of larvae in the plant. Kono and Ishikawa (1955) performed experiments

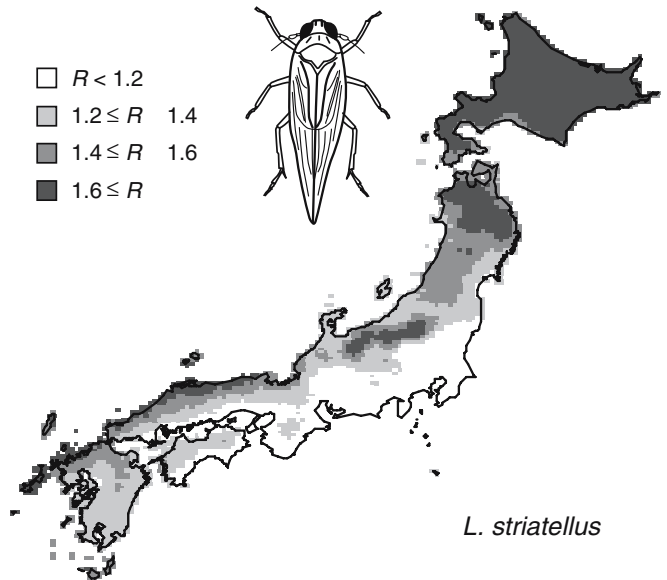


**Fig. 6** Estimated increase in the abundance of *C. suppressalis* under global warming.  $R$  Predicted annual number of individuals caught by a light-trap in the period from 2031 to 2050 divided by that number caught in the period from 1981 to 2000



**Fig. 7** Estimated increase in the abundance of *N. cincticeps* under global warming.  $R$  Predicted annual number of individuals caught by a light-trap in the period from 2031 to 2050 divided by that number caught in the period from 1981 to 2000

where 300 or 1,000 eggs were placed regularly in an experimental wire mesh cage that contained  $10 \times 6$  rice plants ( $1.82 \times 1.82$  m). They reported the proportion of injured stems and the total number of larvae in 60 plants. We use these data to express the relation between the number of larvae in a plant, which is denoted by  $m$ , and the proportion of injured stems in the plant, which is denoted by  $q$ , as an approximation. This is a rough approximation as the larvae are not distributed completely uniformly over the 60 plants. The number of larvae in a plant is treated as continuous variable although it is actually a



**Fig. 8** Estimated increase in the abundance of *L. striatellus* under global warming.  $R$  Predicted annual number of individuals caught by a light-trap in the period from 2031 to 2050 divided by that number caught in the period from 1981 to 2000

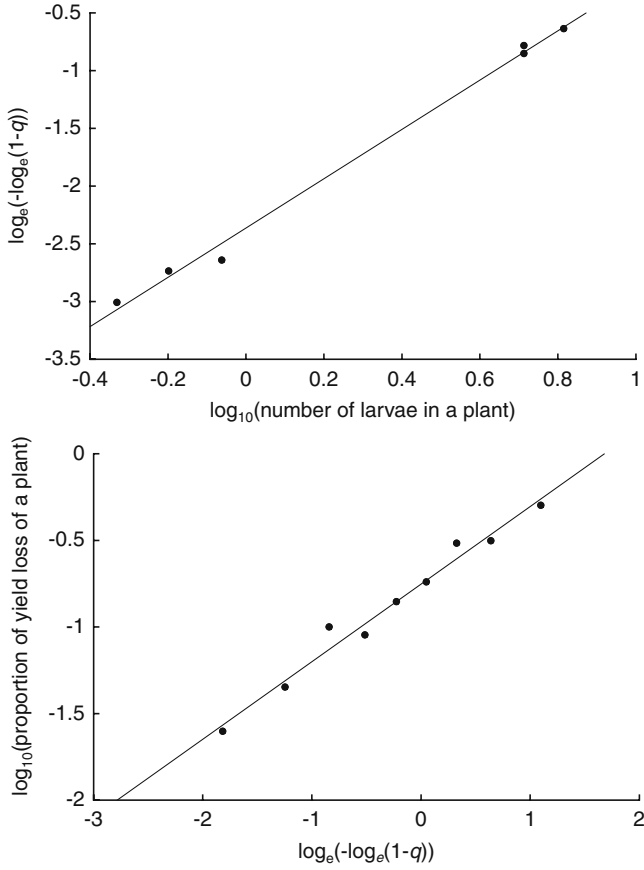
discrete variable. Then, we obtained the following estimate of the linear relation:

$$\log_e[-\log_e(1-q)] = -2.36 + 2.14 \log_{10}(m), \quad (25)$$

where the parameters were estimated by linear regression (upper panel in Fig. 9). The SE of the slope is 0.08. This kind of linear relation, which is called the Kono–Sugino relation (1958), has been used frequently to estimate population density from binomial sampling (Gerrard and Chiang 1970; Nachman 1984; Kuno 1986; Ekbom 1987; Nyrop et al. 1989; Binns and Bostanian 1990; Schaalje et al. 1991; Feng and Nowierski 1992; Roux et al. 1992; Feng et al. 1993). The transformation in the left-hand side of Eq. 25 is called complementary log-log transformation in statistical literature related to generalized linear models or proportional hazard models.

Several authors have examined the relation between the proportion of stems injured by larvae of *C. suppressalis* and the yield loss (Kono and Ishikawa 1955; Okamoto and Sasaki 1957; Takagi et al. 1958; Nitta and Naruse 1985). We use the data of Takagi et al. (1958) in estimating this relation because their report seems the most reliable. Because one cannot directly compare the yields of various fields as yield varies considerably depending upon the variety, the cultivation conditions, and the fertility of the soil, they adopted the following standardization. They first classified the sample plants into strata by varieties and farmers. For each stratum, sample plants were classified into ten classes by the percentage of the injured stems at 10% intervals. The average yield per plant in each class was examined in each stratum. Then the yield index for each class was calculated by the following formula:  $100 \times (\text{average yield})$





**Fig. 9** Upper panel Kono–Sugino relation between the density of larvae of *C. suppressalis* and the proportion of injured stems ( $q$ ). Lower panel Linear relation between the logarithmic proportion of yield loss and  $q$  that was transformed by a complementary log–log link

in a class)/(average yield in the lowest class where the percentage of injured stems is  $< 10\%$ ). The yield index was then averaged over strata for each class of injured stems. We define the proportion of yield loss in a plant, denoted by  $\psi$ , as  $1 - (\text{yield index})/100$ . Then, we found the following linear relation (see lower panel in Fig. 9):

$$\log_{10}(\psi) = -0.75 + 0.448 \log_e[-\log_e(1 - q)], \quad (26)$$

where the parameters were estimated by the linear regression. The SE of the slope is 0.027. We obtain the following relation by substituting Eq. 25 into Eq. 26:

$$\psi = 0.0155m^{0.957}. \quad (27)$$

Knowledge about the spatial distribution of larvae per plant is required to calculate the average proportion of yield loss in a field. As previously stated, we are treating the number of discrete individuals as a continuous variable for convenience. Hence, for the simplest approximation, we use an exponential distribution, which is a continuous distribution with only one parameter. The probability that a plant contains  $m$  larvae in a field where the average number of larvae per plant is  $M$  is given by the probability density function  $g(m)$ ,

$$g(m) = \frac{1}{M} \exp\left(-\frac{m}{M}\right). \quad (28)$$

The average yield loss in a field, which is denoted by  $\bar{\psi}$ , is given by integrating the multiplication of Eqs. 27 and 28.

$$\bar{\psi} = \int_{m=0}^{\infty} 0.0155m^{0.957}g(m)dm = 0.0152M^{0.957}. \quad (29)$$

The expected number of light-trap catches is determined by the multiplication of the number of insects and the probability that an insect is caught by the trap. The second component that is determined by the trap efficiency will be also influenced by the temperature. For *C. suppressalis*, however, only the winter temperature influences the light-trap catches of the summer season; the temperature during the period of the light-trap catches does not influence the number of light-trap catches. Hence, we can assume that the influence of temperature on the trap efficiency is small. Then, let us assume that the annual number of light-trap catches, which is given by (smoothed component)  $\times 10^{D_t}$ , is approximately proportional to the number of larvae in the field ( $M$ ). Then, we have a relation:

$$\bar{\psi} = c_1 \times 10^{0.957D_t}, \quad (30)$$

where  $c_1$  is a constant. By substituting Eq. 18 into Eq. 30, we obtain

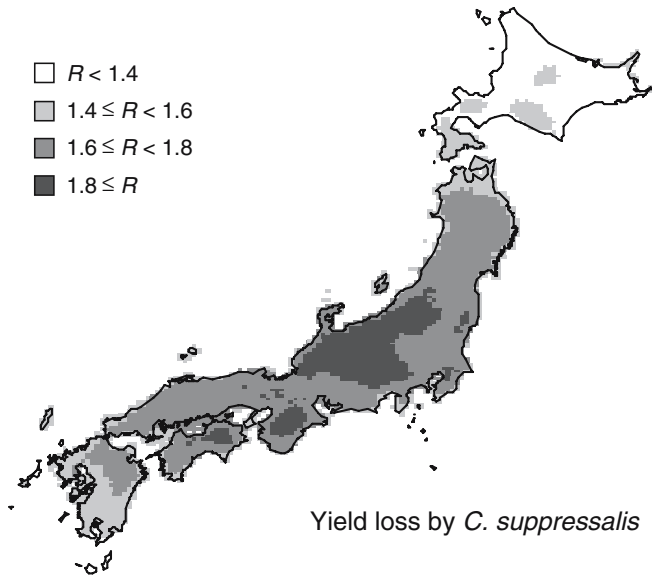
$$\bar{\psi} = c_2 \times 10^{0.0837w_t}, \quad (31)$$

where  $c_2$  is a constant, for a given  $\mu_{Ct}$ . We can calculate the average yield loss relative to that expected in a normal year by substituting the predicted temperature into Eq. 31. Figure 10 indicates that the yield loss in the period from 2031 to 2050 becomes larger than that in the period from 1980 to 2000 by a factor of 1.6 or 1.8 in most areas of Japan.

The actual distribution of *C. suppressalis* will be more complicated than an exponential distribution. The larval distribution is described by a negative binomial distribution (Kono et al. 1952) as well as the distribution of many other organisms. The parameter  $1/k$  of the negative binomial distribution, usually used as the index of aggregation, changes depending on the developmental stage (Kanno 1962; Iwao 1968) and the density (Kono et al. 1952). In applying Eq. 28, we are assuming that the  $1/k$  lies around 1, as for the case reported by Kono et al. (1952). Some biases might be thus suspected in several situations.

## Results and discussion

The analyses conducted by using the state-space model indicated that the “observed population” is influenced by the temperature (Eqs. 18, 20, 24), whereas the “true population” is regulated in a species-specific manner,



**Fig. 10** Estimated increase in the yield loss of rice caused by *C. suppressalis* under global warming.  $R$  Predicted annual yield loss in the period from 2031 to 2050 divided by that loss in the period from 1981 to 2000

which is rather independent of temperature (Eqs. 17, 19, 23). These equations are typically expressed in the following form:

$$\mu_t = h(\mu_{t-1}) + e_{\mu t}, \quad (32)$$

$$D_t = \mu_t + k(T_t), \quad (33)$$

where  $h$  is a function of the vector of past density  $\mu_{t-1}$ ,  $k$  is a function of the vector of environmental variable  $T_t$ . The fluctuation in environmental factors does not influence Eq. 32. Thus, it is indicated that the population dynamics may be a result of multi-level regulation. The deviation in population, which is caused by the fluctuation in environmental factors, is regulated immediately. The regulated populations are further regulated by the function  $h(\mu_{t-1})$ .

The two viewpoints in the classic debate about regulation may correspond to the extreme case of Eqs. 32 and 33. If the function  $k$  is close to zero, the system is most appropriately described according to Nicholson (1954); the population is regulated in a density-dependent manner without suffering the explicit influence of environment. In contrast, if the function  $h$  is close to zero, the system is most appropriately described according to Andrewartha and Birch (1954); the population is determined by the environmental factor without the influence of apparent density-dependent mechanisms as they defined them. The difference in the viewpoints of Nicholson (1954) and Andrewartha and Birch (1954) may have arisen from the difference in the material they studied. Nicholson (1954) used an experimental population, e.g. blowflies, where the function  $k$  may be near zero; such a system may be called a “Nicholson type system”. Andrewartha and Birch (1954) used thrips in fields where the function  $h$  may be near zero; this can be

called the “Andrewartha–Birch type system”. The dynamics of thrips will be expressed by a form similar to that found for *N. cincticeps* (Eqs. 19, 20). The type of system may partly depend on the size or generation time of the organisms. For very small organisms such as fungi, the system may be described as an Andrewartha–Birch type system in most cases. For example, the prevalence of the fungal rice blast disease in a year is predicted from information on climatic conditions without considering the disease prevalence in the previous year. BLASTAM, a system used to predict outbreaks of rice blast disease, only uses weather data from AMEDAS, including data on precipitation, temperature, duration of sunshine, wind force and hourly wind direction (Hayashi and Koshimizu 1988). The BLASTAM system has been used recently in several prefectures in Japan, and its efficacy has been well recognized. In contrast, population dynamics of large mammals seem to be best described as a Nicholson type system. For example, in describing the population dynamics of sika deer, Matsuda et al. (1998, 2002) constructed demographic models including exogenous hunting factors. Insect population may lie in the intermediate position in the continuum from fungi to large mammals; accordingly, both Nicholson type and Andrewartha–Birch type systems arise in the population dynamics of insects, depending on the situation. Such a continuum looks like a classic argument of Pianka (1978) concerning  $r$ - and  $K$ -strategies. The continuum of  $r$ – $K$  strategies is rather ambiguous, but our continuum is clearly defined by Eqs. 32 and 33. Smaller organisms will be generally more sensitive to the environmental change, because they have usually a larger surface–volume ratio. A large surface–volume ratio may enable a large intrinsic rate of increase under their optimal environment. Such a large intrinsic rate of increase will be usually yielded through a shorter generation time rather than a larger number of offspring per individual.

Global warming has seemingly similar influences on the abundance of *C. suppressalis* and *N. cincticeps* (Figs. 6, 7). An increase in winter temperature (defined by the average temperature from the previous November to April) enhances the abundance of both species. However, the increment is much larger for *N. cincticeps* than for *C. suppressalis* as indicated by the difference in scale between Figs. 6 and 7. Such a difference may be related to the difference in the number of generations per year. *N. cincticeps* has twice the number of generations, which may cause a sensitive response to the change in temperature. The prediction for *L. striatellus* (Fig. 8) is very different from that for *C. suppressalis* and *N. cincticeps*. Equation 24 predicts that the higher winter temperature has a negative influence on the abundance of *L. striatellus*. However, the current prediction for *L. striatellus* does not seem that reliable. The dynamics of  $D_t$  shown in the lower panel in Fig. 3 appear somewhat strange for the 20-year period from 1970 to 1990. The  $D_t$  is extremely small for 6 years while in the remaining 14 years, the  $D_t$  is always larger than 0.

It seems that the smoothing procedure using a normal kernel could not successfully remove the influence of nuisance factors for this species. The reliability of the prediction would be enhanced if we could identify the nuisance factor and remove the influence before performing analysis.

No nonlinear component was selected by AIC in the response surface analysis for *C. suppressalis* and *N. cincticeps* (Eqs. 9, 10). A nonlinear component was selected for *L. striatellus* (Eq. 11) but the results for this species may not be reliable, as previously stated. Although a nonlinear relation is widely observed in the laboratory experiments of single species (e.g. Utida 1941), it seems to be rare in field populations except for those in Arctic regions (Ellner and Turchin 1995). A rarity of nonlinear relations in the field seems partly due to the spatial heterogeneity of density. Let us consider a situation where the density at time  $t$  is determined by the density at time  $t-1$  without error. Let  $\lambda_{it}$  be the local density on an arithmetic scale at the  $i$ th spatial position. Let  $\eta(\lambda_{it})$  be the function expressing the local density-dependent relation, that is  $\lambda_{it} = \eta(\lambda_{it-1})$ . Then, by using a Taylor series, we can approximately express the spatial mean density at time  $t$  by:

$$E(\lambda_t) \approx \eta(E(\lambda_{t-1})) + \frac{\eta''(E(\lambda_{t-1}))}{2} V(\lambda_{t-1}), \quad (34)$$

where the double prime (") indicates the second derivative;  $E$  and  $V$  indicate the mean and variance, respectively (Yamamura 1989, 1998). The right hand side of Eq. 34 approaches a linear form with increasing spatial heterogeneity  $V(\lambda_{t-1})$  under several forms of  $\eta$ . The systems tend to enter a stable region simultaneously. Such a linearization in an arithmetic scale is closely related to the classic concept of the "spreading of risks" that was first formulated by Den Boer (1968). He wrote that "the chances of surviving and reproducing must be different in these different places. This means for the population as a whole that the effect of extreme conditions in one place will be damped to some degree by the effect of less extreme conditions in others. In other words: the risk of wide fluctuation in animal numbers is spread unequally over a number of subpopulations living in different micro-environments." Various simulations have been conducted to demonstrate that the spreading of risks can contribute to stabilization (Reddingius and Den Boer 1970; Reddingius 1971; Den Boer and Reddingius 1996). However, Eq. 34 concisely indicates the condition under which stabilization occurs by spreading of risks; the stabilization effect occurs if the function  $\eta$  is sufficiently convex and if there is sufficient heterogeneity  $V(\lambda_{t-1})$ . In this respect, the "linearization effect" and the spreading of risks are almost the same thing. In an ecosystem where the species richness of plants is high, the spatial heterogeneity for herbivores or predators inevitably becomes high. The population dynamics in such systems are inevitably stabilized because of a linearization effect, i.e. the spreading of risks. It seems of

critical importance to understand that the diversity–stability paradigm that was posed by Elton (1958) can be explained by such trivial logic without assuming any special mechanism (Yamamura 2002).

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