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Density dependence and noise determine the long-term dynamics of two species of lady beetle (Coleoptera: Coccinellidae: Epilachninae) in the Indonesian tropics

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Abstract. 1. The long-term dynamics of two beetles (*Epilachna vigintioctopunctata* and *Epilachna enneasticta*) from Indonesia are analysed using descriptive time-series statistics and mechanistic time-series models.

2. Statistical analysis of the time series reveals that the dynamics of *E. vigintioctopunctata* are underpinned by a second order density-dependent [AR(2)] process, which is consistent between sites. Similarly, the dynamics of *E. enneasticta* are also described by a second order density-dependent [AR(2)] process. The predicted dynamics from these statistical models are stable dynamics.

3. Mechanistic models of the density dependence predict that in the absence of noise the dynamics of the populations should also be stable. Inclusion of the stochasticity in the models of density dependence allows a more accurate description of the population dynamics of each species to be determined.

4. Correlation analyses reveal that the fluctuations between species are a function of both the density dependence and the environmental conditions experienced by each species. Under low environmental variance it is predicted that the dynamics could be synchronised but under high variance in environmental noise, the dynamics may not be synchronised and species respond idiosyncratically to the environment.

5. The study highlights the value of long-term population dynamic time series for exploring the structure of population regulation and fluctuations in insect populations.

Key words. Phytophagous insects, population dynamics, synchrony, time series.

Introduction

Population ecologists have long been fascinated with the mechanisms and processes responsible for population fluctuations (Elton, 1924; Nicholson, 1933, 1954; Varley *et al.*, 1973; Hassell *et al.*, 1976; Turchin & Taylor, 1992). Nicholson (1933, 1954) first proposed that population growth was constrained through negative feedback or density-dependent processes. Since then, the concepts in understanding the factors affecting population fluctuations and regulation (the role of density dependence over density independence, whether populations are ever regulated, testing for density dependence) have been overly scrutinised and debated. The emerging consensus is that limitation (i.e. the processes that set the equilibrium by density-dependent and density-independent processes), regulation (through density-dependent processes) and persistence (through regulation) provide the key conceptual cornerstones to population ecology (e.g. Sinclair, 1989).

Although there is a consensus on the conceptual definitions, investigating the structure of population regulation and fluctuations still remains a contemporary topic in population ecology (Bjørnstad *et al.*, 1995; Turchin, 1995; Dennis *et al.*, 1995; Bonsall & Hastings, 2004; Bonsall & Benmayor, 2005). Determining the processes and mechanisms that lead to population regulation requires a combination of experimental and theoretical approaches. The use of field data and laboratory microcosms together with the development of rigorous statistical tests for ecological time series continues to be developed

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(e.g. Dennis *et al.*, 2001; Bonsall & Hastings, 2004). More recently, however, coupling time-series analysis with the development of modern methods of statistical analysis and inference now allows potential mechanisms to be evaluated from time series (Dennis & Taper, 1994; Higgins *et al.*, 1997; Dennis *et al.*, 2001; Turchin & Hanski, 2001). With such quantitative predictions, rival hypothesis on the mechanisms responsible for population fluctuations can be evaluated. For example, although the population cycles of small mammals are well documented (e.g. Krebs *et al.*, 1973), the explanation for these population fluctuations remains unresolved. In fact, a number of different mechanisms such as the role of maternal effects, resources or predators have been proposed to explain these population cycles. By developing a series of parameterised mechanistic models together with time-series analysis, Turchin and Hanski (2001) proposed, based on current evidence, that the predation hypothesis is the most likely cause of cycles in small mammal populations in Fennoscandia.

As part of a long-term study on the insect fauna of Indonesia (Inoue *et al.*, 1993; Nakamura *et al.*, 2001; Sota *et al.*, 2001) the population dynamics and life tables of a number of tropical beetles have been intensively monitored (Abbas & Nakamura, 1985; Nakamura *et al.*, 1988, 1989, 1990; Noerdjito & Nakamura, 1999). With the availability of such long-term population dynamic data, the broad objective in this study therefore is to explore processes and identify the mechanisms leading to the population fluctuations in two lady beetles (*Epilachna vigintioctopunctata* Coleoptera: Coccinellidae: Epilachninae and *Epilachna enneasticta* Coleoptera: Coccinellidae: Epilachninae) from western Indonesia. In particular, the hypothesis that the populations are structured by the interaction between density-dependent (e.g. intra-specific competitive) processes and environmental factors (e.g. rainfall, temperature) is tested using both descriptive and mechanistic approaches of time-series analysis.

More specifically, this is done by asking how is the correlation between the beetle populations influenced by differences in either the type of density dependence and/or the strength of the environmental effect. Is it that the beetle populations are entrained into the same patterns of fluctuation irrespective of the environmental regime? Or, does the environment have an influence on the degree of correlation among the different beetle populations? After presenting the methodology, the patterns observed in the time series are described using descriptive time-series approaches. Based on these results, a series of mechanistic time-series models are then used to understand more fully the density dependence operating on each population. Using correlation analyses the concomitant role of density dependence and environmental effects on the dynamics of epilachnine beetle populations is explored. Accounting for difference in the variability in population fluctuations and correlation between populations is the goal of this study.

Materials and methods

Population data collection

Population surveys of lady beetles have been undertaken in various parts of the Indonesian archipelago (Nakamura *et al.*, 2001). Populations of *E. vigintioctopunctata* have been recorded from two sites in Sumatra: Padang and Sukarami. Concurrent with the population censuses of *E. vigintioctopunctata* at Sukarami, the population fluctuations of *E. enneasticta* have also been recorded. Padang lies close to the Equator (0°53′S, 100°21′E) and has a predominantly humid equatorial climate. Mean monthly temperatures fluctuate between 26.7 °C and 27.5 °C and annual rainfall is 4760 mm. In contrast, Sukarami is a highland region (at an altitude of 930 m) about 40 km north-east of Padang. Average annual rainfall is in excess of 2900 mm and the mean monthly temperatures fluctuate from 20.8 °C to 21.4 °C. Population censuses were undertaken at 3–7 day intervals from 1988 to 1998 for *E. vigintioctopunctata* at Padang and from 1991 to 2000 for *E. vigintioctopunctata* and *E. enneasticta* at Sukarami. The adult beetle population estimates were made using mark–recapture methods (Nakamura *et al.*, 2001) and more detailed procedures are described in Nakamura *et al.* (1990).

Statistical time-series analyses

The population dynamics of *E. vigintioctopunctata* and *E. enneasticta* at Sukarami and the contrasting dynamics of *E. vigintioctopunctata* at Padang are explored using descriptive time-series statistics. Patterns in both the time and the frequency domain (Chatfield, 1996) are used to describe the fluctuations of the lady beetle populations. Each series is regularized using a linear interpolation algorithm in S-Plus 2000 (Insightful Inc., Seattle, WA) in order to obtain equal sampling points and appropriate statistical models for the time series are determined by fitting Box–Cox transforms (Box & Cox, 1964) of lagged explanatory variables (x_t, x_{t-1}) to log changes in population growth (net reproductive rate). In particular, these statistical models take the general form:

$$y = a_0 + a_1 \cdot x_t^{\theta_1} + a_2 \cdot x_{t-1}^{\theta_2} \qquad \text{eqn 1}$$

where y is the log change in population growth ($\ln[x_{t+1}/x_t]$), a_0, a_1, a_2 are coefficients to be estimated from the regression analysis and θ_1 and θ_2 are Box–Cox transforms of log population densities (x_t and x_{t-1}) at time t and $t-1$.

To complement the autocorrelation analyses (eqn 1), power spectra are used to explore the details of the distribution of variance in each of the series as a function of frequency. By decomposing the time series into the variance associated with each frequency allows the effects of different periodic components (e.g. limit or generation cycles) to be evaluated. All these statistical analyses were completed in S-Plus 2000 (Insightful Inc.).

Mechanistic model fitting

Based on this linear statistical analysis of the time and to explore whether the population dynamics are underpinned by direct density-dependent or delayed density-dependent processes, three different density models were fitted to each of the lady-beetle series from Sukarami and Padang. These models reflect differences in the density-dependent structures and natural histories that might affect the population dynamics. The first model describes the simple dependence of population numbers at time $t+1$ on population size at the current time point (t) and is of the form:

$$x_{t+1} = \lambda \times x_t \times x_t^{\alpha} \qquad \text{eqn 2}$$

Here λ is the population growth rate and α is a measure of the strength of the density dependence (Bellows, 1981). A modified version of this model accounts for the possibility that adult beetles might survive between time points and the density-dependent process is modified to include this natural history. This delay-difference process (Quinn & Desiro, 1999) is of the form:

$$x_{t+1} = \gamma \times x_t \times \lambda \times x_t \times x_t^{\alpha} \qquad \text{eqn 3}$$

Here, it is assumed that some individuals simply survive between census points and contribute to numbers at the next time point (t + 1). Again λ is the growth rate and α is the strength of density dependence while γ represents the fraction of individuals surviving between census points. Finally, the delayed density process can be described by:

$$x_{t+1} = \lambda \times x_t + x_t^{\alpha} \times x_{t-1}^{\beta} \qquad \text{eqn 4}$$

Here, it is assumed that individuals in the current and previous time point contribute to population growth and change. Again λ is the growth rate of the population and, α and β are the strengths of the direct and delayed density-dependent process respectively. To fit these models to time series we convert these deterministic difference equations to stochastic difference equations. Variability in the data are assumed to act additively on a log scale so the following generic stochastic model holds:

$$x_{t+1} = f(x) \times \exp(\zeta) \qquad \text{eqn 5}$$

where $f(x)$ is the density-dependent process and ζ is an independent identical distributed random variable assumed to have a normal distribution with mean 0 and standard deviation σ. By assuming that the noise is additive on a log scale, the maximum likelihood estimates of the parameters can be obtained (numerically) by solving a univariate Gaussian negative log-likelihood function (L):

$$L = \sum_{1}^{n} \log(\sigma) + \frac{1}{2}\log(2 \cdot \pi) + \left(\frac{O_t - E_t}{2 \cdot \sigma^2}\right)^2 \qquad \text{eqn 6}$$

where n is the length of the time series, σ is the standard deviation, O_t is the observed beetle abundance at time t and E_t is the expected beetle abundance at time t predicted from the density-dependent model (eqns 2–4). Likelihood estimates were determined using a Nelder–Mead simplex algorithm (Press *et al.*, 1992) implemented in C (e.g. Bonsall & Hastings, 2004).

To explore how coupling environmental variation and density dependence can explain the correlation patterns between and within species, the most parsimonious function for density dependence was coupled with different strengths of the noise term (ζ) (eqn 5). The magnitude of the noise was determined by drawing random numbers from a bivariate normal with a standard deviation ranging from 0 to 4 (representing the environmental noise) and correlation between 0 and 1 representing the similarity (the noise correlation) in the magnitude of the noise acting on the two populations.

Results

Time-series description

The descriptive time-series statistics reveal that the abundance of the epilachnine beetle fauna of Sumatra shows wide variability and fluctuations through time (Fig. 1). Mean abundance of *E. vigintioctopunctata* varies twofold between Padang and Sukarami and the population of *E. vigintioctopunctata* in Padang is more variable than in Sukarami (Table 1). In contrast, *E. enneasticta* at Sukarami is relatively rare with a mean abundance of less that three but fluctuations in abundance indicate that this species is more variable than *E. vigintioctopunctata* in either Sukarami or Padang (Table 1). Correlation analysis shows that the beetle populations are weakly positively correlated within the highland site ($\rho = 0.38$) at Sukarami.

Age structure

Power spectra indicate that fluctuations in the time series at Sukarami are underpinned by low frequency events (Figs 1c,d and 4b). In comparison, intermediate and high frequencies have equal power in affecting the fluctuations in the time series. There is no evidence to suggest that the time series are influenced by a single dominant frequency and as such there is no evidence for generation cycles in either *E. vigintioctopunctata* or the *E. enneasticta* at Sukarami. Similarly at Padang, the power spectra for *E. vigintioctopunctata* indicate that low frequency events underpin the dynamics of the population. Also, and in contrast to, the dynamics of this species at Sukarami, there is evidence for population generation cycles (with a period of about 50 days) in *E. vigintioctopunctata* at Padang. The observation of these generation cycles is clearly stage-dependent. In particular, clear generation cycle effects are seen in the egg and neo-adult stages (Fig. 2a,d) but are not prominent in the larval (Fig. 2b,c) or older adult stages (Fig. 2e).

Regression models

Plots of the changes in population growth rate as a function of log population size at time t and $t - 1$ (Fig. 3a,b) reveal that the populations are regulated through temporal density-dependent processes. There is clear evidence for populations to increase when rare and decline when abundant. Response surfaces (Figs 3c,d and 4d) of the amount of deviance explained for the linear statistical model (eqn 1) suggest that the dynamics of each of the time series can be captured by a second order autoregressive [AR(2)] or delayed density-dependent model. As the parameter estimate for the AR(2) model indicate that $a_2 < -a_1$, then the standard second-order autoregressive models predicted stable population dynamics for each species (Table 2). The difference between species (and sites), however, is primarily influenced by the precise structure of the density dependence (Table 2). At Sukarami, the most parsimonious description of the *E. vigintioctopunctata* dynamics involves population density at time t (x_t) and a 0.1 power transform of the population

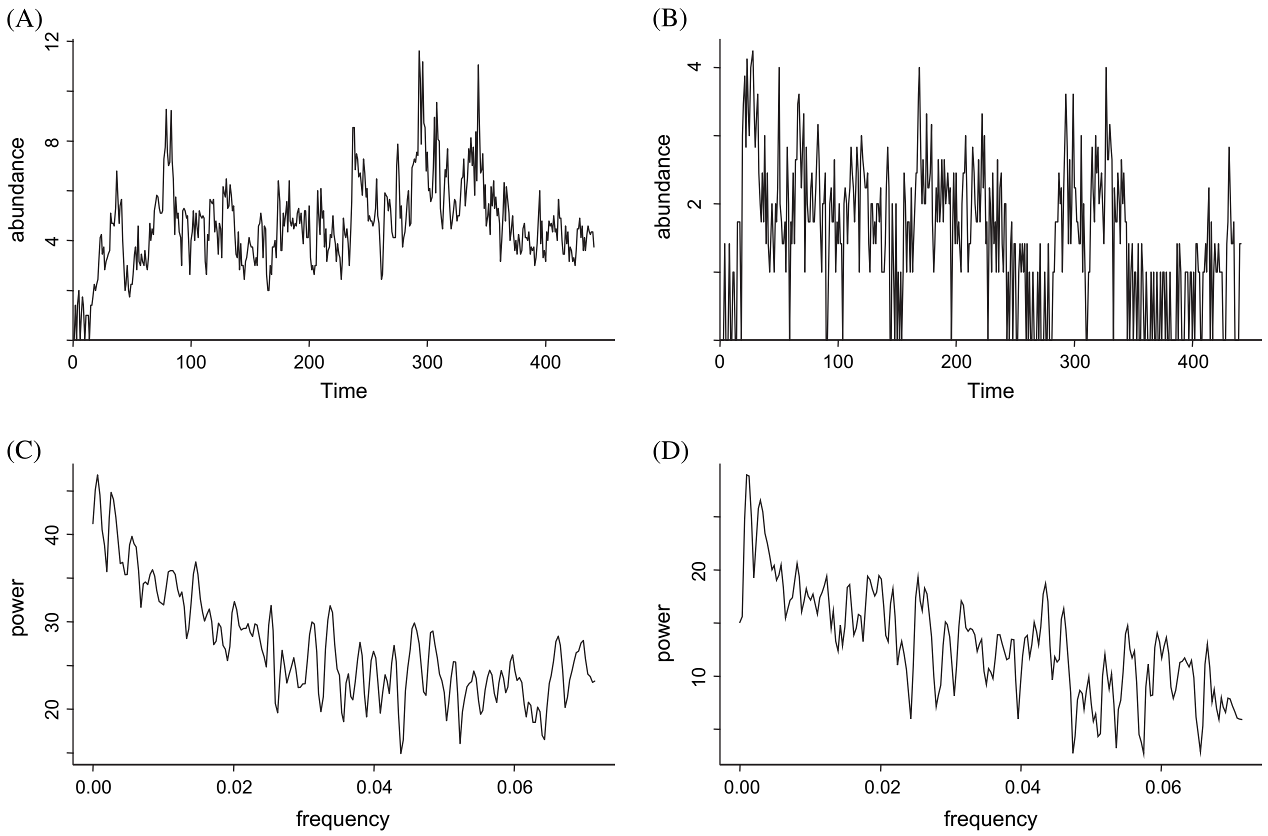

Fig. 1. Time series of *E. vigintioctopunctata* and *E. enneasticta* in Sukarami, Indonesia. (A) Square root adult abundance of *E. vigintioctopunctata*, (B) square root adult abundance of *E. enneasticta*. Power spectra for both EV (C) and *E. enneasticta* (D) suggest that low frequency events dominate the series.

density at time $t - 1$ (x_{t-1}). Similarly, at Padang the dynamics of this species are best described by a –1.9 power transformation of population density at time $t - 1$ (x_{t-1}) and population density at time t (x_t). In contrast, the most parsimonious description of the dynamics for *E. enneasticta* required a Box–Cox transformation of both the explanatory variables x_t and x_{t-1}. These transformations were –0.3 and –0.7 respectively.

Mechanistic model fitting

In this section, the set of mechanistic population models (eqns 2–4) are used to explore the density-dependent processes underpinning the population time series. Using model selection criteria (AIC), the most parsimonious description of the dynamics of *E. vigintioctopunctata* at the two different sites (Sukarami and Padang) is a delayed density model (Table 3). Parameter estimates for the delayed density-dependent processes for *E. vigintioctopunctata* suggest that the fluctuations at the Padang site are likely to be much more variable. This is also observed by a comparison of the *E. vigintioctopunctata* time series from the two sites ($CV_{Sukarami} = 0.7382$, $CV_{Padang} = 0.9878$). In the absence of noise, the parameter estimates also indicate these populations will be regulated to a stable equilibrium at both Sukarami ($x^* = 29.67$) and Padang ($x^* = 126.86$). In contrast, a simple direct density-dependent process, however, describes the population dynamics of *E. enneasticta* (Table 3). Parameter estimates for this lady-beetle population at Sukarami indicate that, in the absence of noise, the population will also be regulated to a stable equilibrium ($x^* = 4.82$). In the next section, we use these models to explore how density-dependent and -independent processes interact to affect the correlation among populations within the same area.

Table 1. Time-series summary statistics [mean, standard deviation (σ) and coefficient of variation and length of the time series (*n*)] for *E. vigintioctopunctata* at Sukarami and Padang and the *E. enneasticta* at Sukarami.

Species	Mean	σ	CV	*n*
E. vigintioctopunctata (Sukarami)	24.918	18.400	0.738	441
E. enneasticta (Sukarami)	3.374	3.426	1.015	441
E. vigintioctopunctata (Padang)	46.018	45.455	0.988	217

Comparative dynamics and synchrony

Using the estimated parsimonious mechanistic model for each of the time series at Sukarami (Table 3), it is possible to

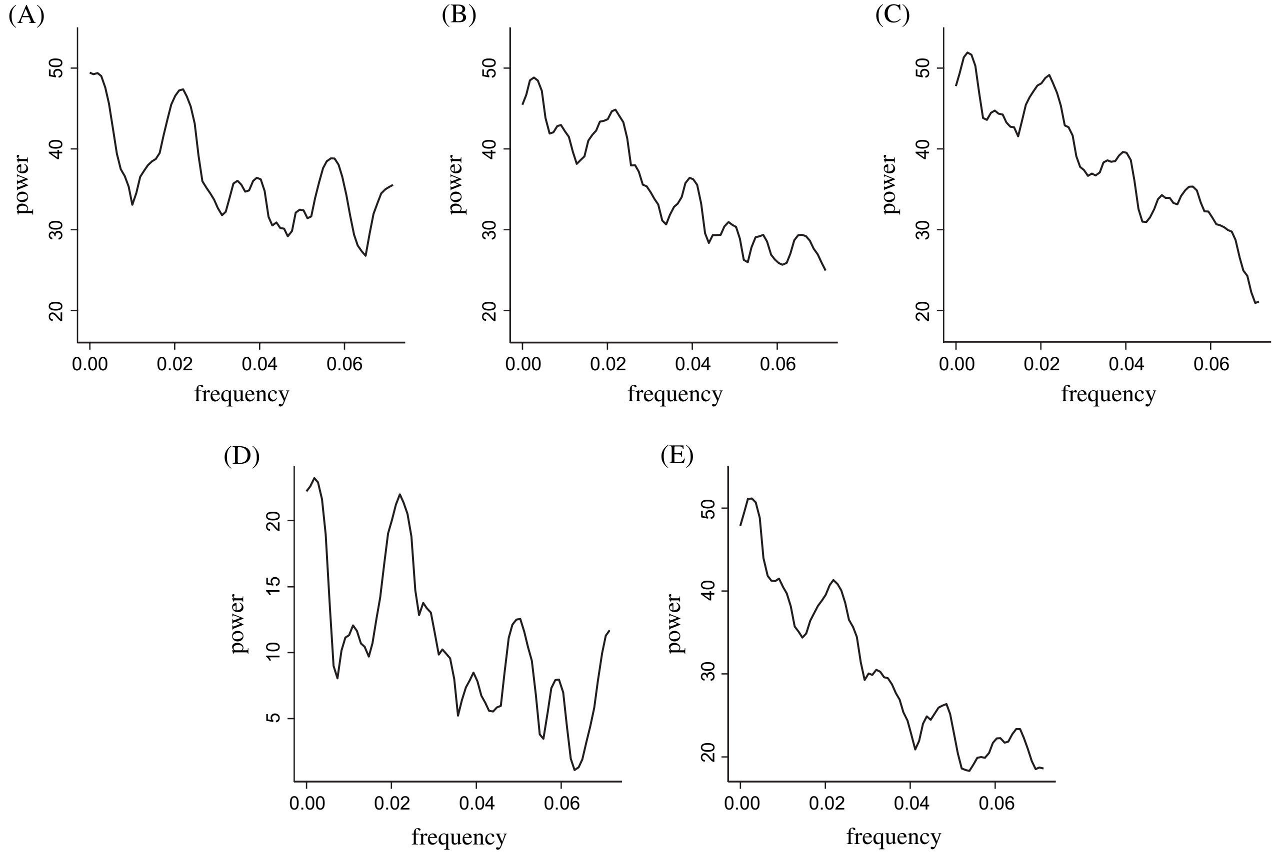

Fig. 2. Power spectra of stage-structure time series for *E. vigintioctopunctata* at Padang for (A) eggs, (B) third larval instar, (C) fourth larval instar, (D) neo-adults, and (E) adults. Generation cycles are prevalent in the egg and neo-adult stages but not in other stages.

compare the dynamics of the two lady-beetle populations under different noise regimes using correlation analyses. This reveals that populations of the similar species are much more likely to be correlated through environmental forcings under low noise conditions. Even under different density-dependent conditions, populations can be synchronised by weak environmental effects (Fig. 5a,c). In contrast, highly variable environments are less likely to lead to population synchrony because of the non-linearities mediated by the density dependence in the system (Fig. 5a,b,d). Specifically, the different density-dependent factors operating on *E. vigintioctopunctata* and *E. enneasticta* under highly fluctuating environments suggest that it is unlikely that the populations will be significantly entrained into the same fluctuating trajectories. The observed correlation (≈ 0.4) between *E. vigintioctopunctata* and *E. enneasticta* at Sukarami is likely to arise through the idiosyncratic responses of each species (*E. vigintioctopunctata* and *E. enneasticta*) to the same highly variable environmental conditions.

Discussion

Here, the density-dependent and -independent processes operating in Indonesian lady beetle populations have been evaluated. Although the density-dependent processes are consistent within species, populations fluctuate widely between sites with evidence for population generation cycles (Gurney & Nisbet, 1985; Godfray & Hassell, 1989; Knell, 1998) at specific sites and particular stages (Nakamura *et al.*, 2004). This suggests that the dynamics of the epilachnine beetles of central Sumatra are underpinned by both density-dependent and density-independent processes.

In the absence of the noise, the populations are predicted, from the statistical and mechanistic models, to be regulated to stable points. In actuality, the observed populations are regulated about some mean level and this leads to a stationary probability distribution of population densities (Turchin, 1995) where the variance of population density is bounded. Haak (2002) has argued that ecological density dependence is not a necessary or required concept and that due to methodological developments only statistical density dependence is of importance. Here, the role of statistical density dependence has been evaluated; this provides evidence that the populations are regulated. It provides no information on the mechanisms that underpin this process, however. To evaluate the potential mechanisms a series of ecological models (and by definition invoking narrow density dependence; *sensu* Royama 1992) have been used to explore how the populations are underpinned by complex non-linear density-dependent

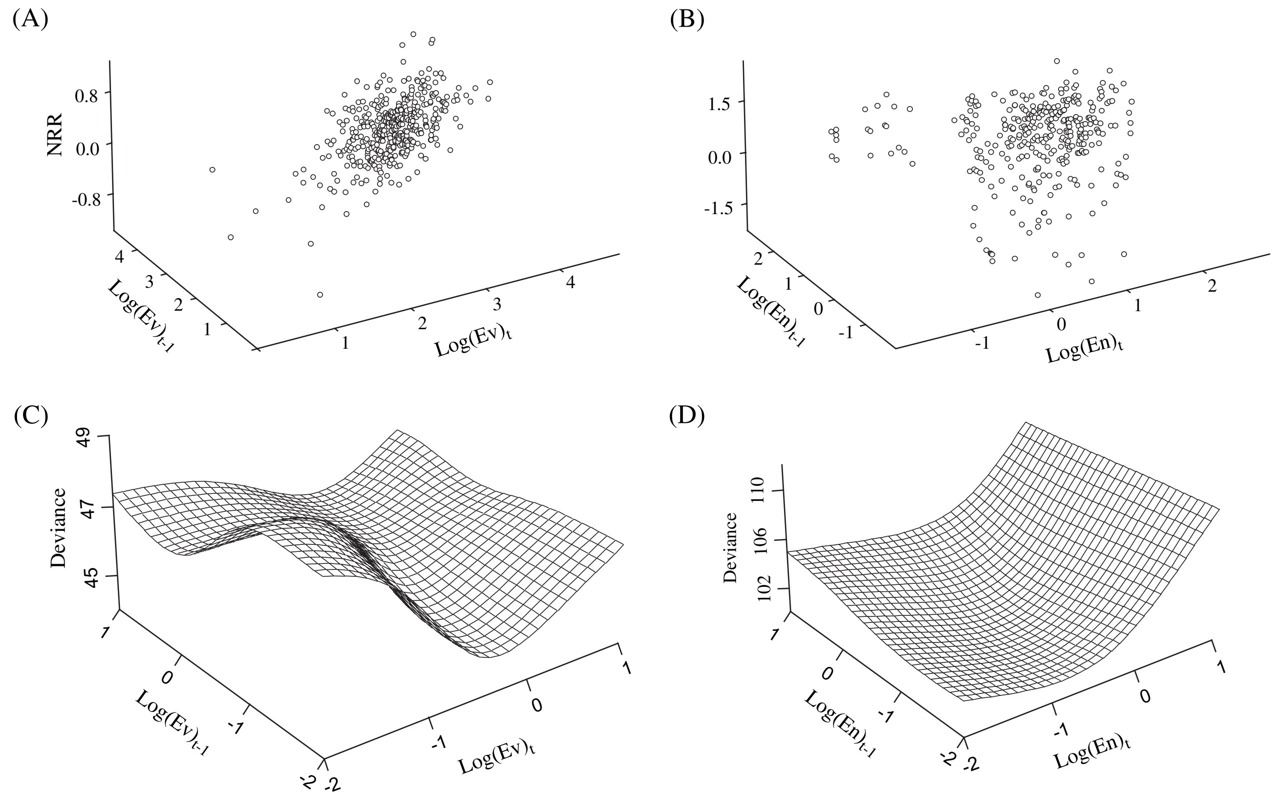

Fig. 3. Dynamics of *E. vigintioctopunctata* and *E. enneasticta* in Sukarami. (A) Change in net population growth rate (NRR) as a function of *E. vigintioctopunctata* density at time *t* and *t*–1, (B) change in net population growth rate (NNR) as a function of *E. enneasticta* density at time *t* and *t*–1, (C) deviance surface from a Box–Cox analysis (eqn 1) for *E. vigintioctopunctata*, and (D) deviance surface from a Box–Cox analysis (eqn 1) for *E. enneasticta*.

mechanisms. In the absence of manipulative experiments the precise density-dependent mechanisms cannot be completely determined. For instance, it may be that density dependence may be enhanced or cancelled by feedback processes acting at different points in the life cycle of the beetles. Notwithstanding, the availability of long time series on the tropical beetle fauna of Indonesia (Nakamura *et al.*, 1990, 2001; Inoue *et al.*, 1993) is essential in accepting or refuting hypotheses on population regulation. Here, using theoretical models and statistical approaches it has been shown that the processes and mechanisms that act to regulate populations can be determined directly from the time-series data. While it is clearly inappropriate to compare the dynamics of *E. vigintioctopunctata* at Sukarami and Padang in any formal way given that they were collected over different time periods, it is reassuring to observe that the same density dependence structure underpins the dynamics of the populations at the two sites. Although encouraging, this is the tacit assumption: the same density-dependent processes drives the population dynamics of a species and the dynamics differ due to quantitative rather than qualitative changes between sites. This is often infelicitous and the same ecological system might show different dynamics due to differences not only in the exogenous processes but also in the endogenous interactions (Bonsall *et al.*, 2003). The results presented here suggests that difference in the dynamics are due to vagaries in the environment rather differences in the underlying density-dependent process.

In contrast to previous studies on population synchrony (Ranta *et al.*, 1995, 1997; Grenfell *et al.*, 1998; Benton *et al.*, 2002), the correlation between different species under the same environmental conditions has been examined. A suitable null model for assessing the population correlation in the presence of environmental noise is the Moran effect (Moran, 1953; Royama, 1992). Under the same environmental conditions and linear density dependence, the Moran effect predicts that fluctuations in populations will be correlated. In fact, the correlation in population fluctuations is expected to be the same as the correlation between random environmental effects (Royama, 1992; Grenfell *et al.*, 1998). Furthermore, it has been suggested that increased variability in environmental noise may cause greater synchrony between populations (Benton *et al.*, 2002). In exploring this theme, Benton *et al.* (2002) showed that in experimental mite systems the degree of synchrony between populations may not be dependent on the variance of the environmental noise. Here, in contrast, the correlation between beetle populations is dependent on the variance of the environmental noise and is coupled with the underlying density-dependent processes. In particular, when different density-dependent processes operate, information on the environmental conditions are essential in

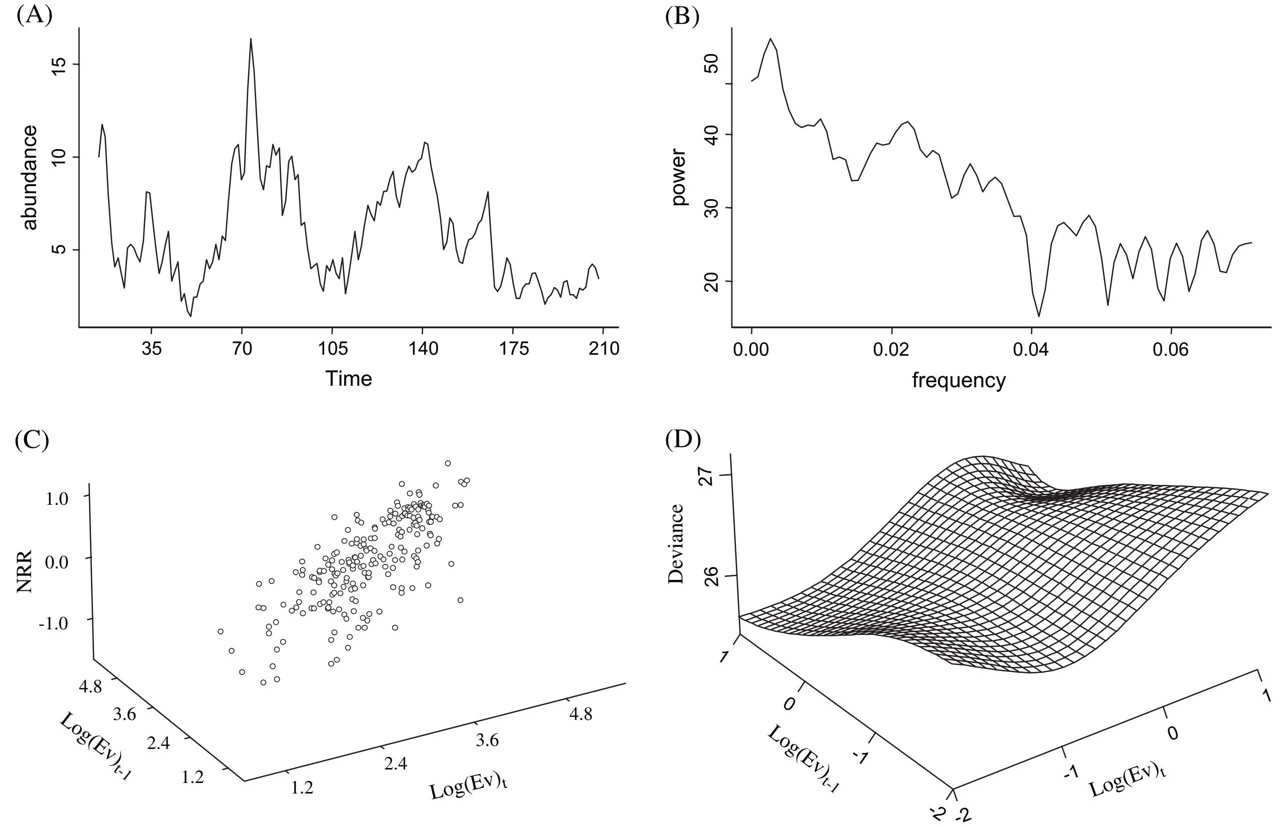

Fig. 4. Dynamics of *E. vigintioctopunctata* in Padang. (A) square root adult abundance of *E. vigintioctopunctata*, (B) power-spectra for *E. vigintioctopunctata*, (C) change in net population growth rate (NRR) as a function of *E. vigintioctopunctata* density at time *t* and *t* – 1, (D) deviance surface from a Box–Cox analysis (eqn 1) for *E. vigintioctopunctata*.

determining whether or not the dynamics are likely to be synchronised. In the absence of noise, the density-dependent structures predict stable population dynamics and as such would be synchronised. In the presence of noise the role of synchrony depends on the type and/or strength of the underlying non-linear density dependence. Under low environmental variability populations with different density-dependent structures are likely to become readily synchronised. In high noise environments, however, the species respond in idiosyncratic ways due to the influence of the density dependence. As Sukarami in central Sumatra is a highly variable environment (Nakamura *et al.*, 2001), the analysis presented here suggests that coupling the environmental effects together with the different density-dependent structures provides a simple explanation for the weak correlation between the *E. vigintioctopunctata* and *E. enneasticta* populations.

Several studies have evaluated population synchrony as a process mediated through the effects of environmental noise and/or dispersal (Ranta *et al.*, 1995, 1997; Sutcliffe *et al.*, 1996; Grenfell *et al.*, 1998; Cattadori *et al.*, 1999, 2000; Benton *et al.*, 2001). The strength and type of environmental variability on the dynamics of populations (Heino, 1998; Greenman & Benton, 2001), however, is also likely to be an important determinant in

Table 2. Parameter values (a_1 and a_2) and deviance estimates for a standard AR(2) and Box–Cox transform AR(2) model. Note that the standard AR(2) model predicts stable dynamics and the Box-Cox model (eqn 1: transformations given in the text) explains more of the variation in thwe time series.

Species	Standard AR(2) model	Deviance	Box–Cox transform AR(2) model	Deviance
E. vigintioctopunctata (Sukarami)	−0.005 (0.002)	46.813	1.468 (0.288)	45.467
	0.002 (0.002)		−0.573 (0.272)	
E. enneasticta (Sukarami)	−0.065 (0.011)	110.022	1.876 (0.210)	101.377
	0.019 (0.011)		−0.531 (0.132)	
E. vigintioctopunctata (Padang)	0.002 (0.002)	26.216	0.702 (0.521)	26.153
	−0.004 (0.002)		0.295 (0.666)	

Table 3. Mechanistic model parameter estimates, log-likelihood and AIC values for three different models applicable to the epilachnine beetle populations in Indonesia. Models are fitted using a numerical likelihood procedure and the AIC value for the most parsimonious model is highlighted in bold. *L* is the negative log-likelihood value and σ is the standard deviation estimated from eqn 6. Other parameter definitions are given in the text.

Model	*E. vigintioctopunctata* (Sukarami)	*E. enneasticta* (Sukarami)	*E. vigintioctopunctata* (Padang)
Direct density-dependent difference model $x_{t+1} = \lambda \times x_t \times x_t^{\alpha}$	σ = 12.434	σ = 3.410	σ = 47.916
	λ = 8.434	λ = 1.980	λ = 1.512
	α = −0.708	α = −0.438	α = −0.117
	L = 784.575	*L* = 524.558	*L* = 1032.207
	AIC = 1575.152	**AIC = 1055.116**	AIC = 2070.414
Delay difference model $x_{t+1} = \gamma \times x_t \times \lambda \times x_t \times x_t^{\alpha}$	σ = 11.865	σ = 3.410	σ = 44.056
	λ = 8.093	λ = 1.879	λ = 1.472
	α = −1.945	α = −0.499	α = −0.632
	γ = 0.979	γ = 0.137	γ = 0.841
	L = 775.244	*L* = 524.567	*L* = 1029.584
	AIC = 1558.488	AIC = 1057.135	AIC = 2067.169
Delayed density-dependent difference model $x_{t+1} = \lambda \times x_t \times x_t^{\alpha} \times x_{t-1}^{\beta}$	σ = 11.834	σ = 3.411	σ = 42.827
	λ = 1.541	λ = 1.913	λ = 1.945
	α = −0.838	α = −0.359	α = 0.0870
	β = 0.698	β = −0.058	β = −0.282
	L = 773.478	*L* = 524.524	*L* = 1029.193
	AIC = 1554.956	AIC = 1057.0482	**AIC = 2066.386**

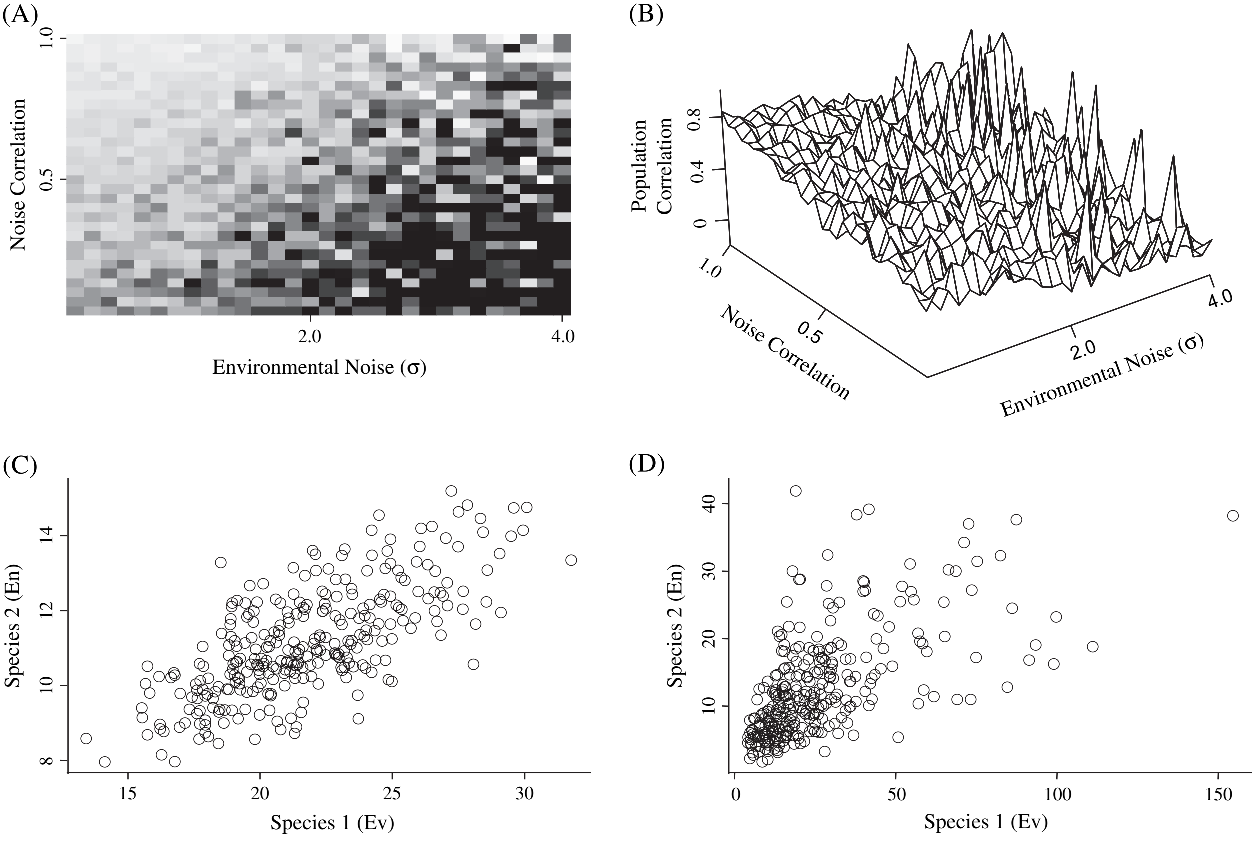

Fig. 5. Simulations of the correlation between lady-beetle populations in Sukarami. (A) Correlation contours from the most parsimonious density-dependent models for *E. vigintioctopunctata* and *E. enneasticta* (light–high population correlation, dark–low population correlation). (B) Population correlation for the parsimonious density-dependent models for *E. vigintioctopunctata* and *E. enneasticta*. (C,D) Representative examples of population correlation under (C) weak environmental noise (σ = 0.1, noise correlation = 0.8, population correlation = 0.71) and (D) strong environmental noise (σ = 1.0, noise correlation = 0.8, population correlation = 0.59).

the synchrony among populations and this warrants further theoretical and empirical investigation.

In summary, the combination of time-series analysis and mechanistic models has allowed the principal processes involved in determining the population fluctuations of two Indonesian lady-beetles to be evaluated. Although a standard postulate is that mechanisms cannot necessarily be inferred from ecological time series, by combining descriptive time-series analysis together with modern methods of analysis (such as fitting and evaluating a series of mechanistic models), it is now feasible to derive the structuring processes and mechanisms that underpin population fluctuations. The stochastic models used in the present study underlines the necessity of a pluralistic approach: adopting a wide range of plausible explanations and mechanisms together with descriptive statistics. Moreover, the availability of long ecological time series allows the density-dependent and independent processes to be identified and this study emphasises the need for long-term data series for testing hypothesis on the dynamics of insect populations.

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