

From complex spatial dynamics to simple Markov chain models: do predators and prey leave footprints?

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In this paper we present a concept for using presence–absence data to recover information on the population dynamics of predator–prey systems. We use a highly complex and spatially explicit simulation model of a predator–prey mite system to generate simple presence–absence data: the number of patches with both prey and predators, with prey only, with predators only, and with neither species, along with the number of patches that change from one state to another in each time step. The average number of patches in the four states, as well as the average transition probabilities from one state to another, are then depicted in a state transition diagram, constituting the “footprints” of the underlying population dynamics. We investigate to what extent changes in the population processes modeled in the complex simulation (i.e. the predator’s functional response and the dispersal rates of both species) are reflected by different footprints.

The transition probabilities can be used to forecast the expected fate of a system given its current state. However, the transition probabilities in the modeled system depend on the number of patches in each state. We develop a model for the dependence of transition probabilities on state variables, and combine this information in a Markov chain transition matrix model. Finally, we use this extended model to predict the long-term dynamics of the system and to reveal its asymptotic steady state properties.

The simplest models of predator–prey systems, such as the Lotka–Volterra model (cf. Lotka 1925), describe population dynamics by means of only two variables: the mean densities of prey and predators. Changes in the density of one species are linked to changes in the other through the functional response (Solomon 1949), which predicts how many prey individuals a predator consumes per time unit at a given mean prey density. However, if prey and predators are not evenly distributed in space, mean densities alone are likely to be poor predictors of predation rates, because they provide no information about the actual degree of spatial overlap between the species (Nachman 2006a, b).

Spatially explicit population models (Gurney et al. 1998), on the other hand, apply information about the numbers of prey and predators occupying every spatial unit (called patches) within a system. The changes in population sizes within each patch due to births, deaths, immigrations and emigrations can then be computed for each small time step. These models are powerful strategic tools for understanding predator–prey dynamics, because they generate detailed predictions of the system’s trajectory through time. However, spatially explicit models need to be fed by high resolution data about the current distributions of the species, which limits their practical application for e.g. pest management or conservation. A solution in these cases is to develop spatially implicit models that only need low

resolution data easily obtainable from field samples, as e.g. proportion of plants or leaves with or without prey and predators, but still retain enough complexity to generate realistic predictions.

In this paper, we model the dynamics of an acarine predator–prey system consisting of the two-spotted spider mite *Tetranychus urticae* and its phytoseiid predator *Phytoseiulus persimilis*. The spider mite is a serious pest in many crops, including greenhouse cucumbers. The predator species is known as a very efficient predator of *T. urticae* and therefore widely used as a biocontrol agent against it (Helle and Sabelis 1985).

We use a spatially explicit stochastic simulation model of the above system to produce spatio-temporal patterns of prey and predators. The output of these simulations forms the basis for developing a spatially implicit matrix model. The advantage of using model-simulated data instead of field-collected data is that we are in control of the processes that produce the observed predator–prey dynamics. This means that we can test the hypothesis that these underlying processes are revealed by the parameters of the matrix model. Specifically, we address the hypothesis that the transition probabilities reflect the dispersal ability of both species and the efficacy of the predators. If this hypothesis is confirmed, transition probabilities and steady state distributions, which can be combined and depicted graphically as a

“footprint” diagram, may serve as a diagnostic tool under field conditions, with application for e.g. pest control.

The spatially implicit model is based on a model by Maynard Smith (1974), who simplified predator–prey dynamics by dividing patches into a set of categories: empty, inhabited by few individuals (of prey and/or predators), or inhabited by many individuals. Gurney and Nisbet (1978) simplified this classification further to just four groups: patches with both prey and predators, with prey only, with predators only, and empty patches. Over a certain time interval patches are likely to change from one state to another. The likelihood of such discrete events can be expressed through transition probabilities, which are elements of a finite Markov chain model and are defined by a transition matrix (Dharmadhikari 1963). Once the elements of the transition matrix and the current state of the system are known, it is straightforward to calculate the expected state of the system after one time step, and to do this recurrently for any desired number of time steps. Matrix transition models (also called population projection matrices) are useful as analytical and predictive tools in e.g. conservation (Lusseau 2003), landscape management (Yemshanov and Perera 2002) and pest control strategies (Woolhouse and Harmsen 1991).

A challenge for applying matrix models to predator–prey systems is that the transition probabilities are likely to be non-stationary, i.e. to depend on the number of patches in each state; e.g. if there are many patches already containing prey, it is more likely that an empty patch will be occupied by prey in the next time step (Gurney and Nisbet 1978, Woolhouse and Harmsen 1987a, b). We apply a correlation-based approach to identify simple functional relationships between the state variables and the transition probabilities and use simulated data to parameterize these relationships. The resulting projection matrix can be used to predict the system’s asymptotic behaviour in order to investigate emergent properties such as stability, bifurcations, sensitivity etc. (Caswell 2001).

Methods

The biological system

As the biological background for modeling, we used a series of experiments conducted in 500 m² commercial greenhouses (Nachman 1981). Each greenhouse hosted 720 cucumber plants arranged in 8 rows. Early in the growing season every second plant in the greenhouses were inoculated with five or six adult female spider mites and two days later two, three or four adult female predators were released onto the same plants. The plants were sampled every week during the following 23 weeks. At each sampling occasion 36 plants were randomly selected and three leaves were picked from each. All mites occurring on their lower leaf surface were counted. Details on the biology of the involved species can be found elsewhere (Helle and Sabelis 1985).

The simulation model

The complex simulation model used to simulate the greenhouse system and to parameterize the transition matrices

is described in Nachman (2001). Basically the model applies a metapopulation concept where each plant in a greenhouse is considered as a patch with its own local dynamics. In contrast to the classic metapopulation approach (Levins 1969), the model is spatially explicit with respect to patch location. Furthermore, patches are characterized by their size/quality and the numbers of individuals present. Finally, dispersal from a patch is condition-dependent and the likelihood that an individual succeeds to move from one patch to another depends on the distance between them. The model incorporates demographic stochasticity to cope with discrete events as births, deaths, immigrations and emigrations; this stochasticity plays an important role in creating patch asynchrony (Nachman 1987a, b). Sex and age structure of the populations are modeled implicitly by using weighted parameter values. The model is implemented in Delphi 7 (Borland).

The model described in Nachman (2001) applied Holling’s (1959) disc equation to model the functional response of *P. persimilis*. Since this model assumes that the predators search for prey at random, it is unrealistic when the prey is patchily distributed and the predators exert non-random search (Nachman 2006a). The problem was partly alleviated in Nachman (2001) by increasing the parameter expressing the predator’s attack efficiency, but since then a more mechanistic functional response model has been proposed (Nachman 2006b). It incorporates the spatial distribution of the prey among leaves within plants, the aggregative response of the predators to the prey distribution and mutual interference among searching predators. This new model was chosen to represent the functional response of *P. persimilis* in the simulations.

The simulations

The model simulated a greenhouse system consisting of 400 fully grown plants arranged in 8 rows. The distances between plants and the physical conditions were assumed to be the same as those described in Nachman (2001). At day 0, every second plant was inoculated with 60 spider mites, and two days later the same plants were inoculated with 3 predatory mites. The duration of a simulation was set to 3000 d. Provided both mite species were still present in the system at the end of a simulation, the last 2000 d were used for the subsequent analyses. For each of the 2000 d, the following information was recorded: average number of prey and predators per plant, the number of plants without mites, with both species, with prey only and with predators only, and the number of transitions from one state to another during the preceding day. The growing season for greenhouse cucumbers is normally ca 200 d, but since we were interested in the long term dynamics of prey and predators, it was necessary to assume that the plants do not deteriorate for reasons other than exploitation by the spider mites, and that they are able to recover from any level of damage; though the time to recover completely increases with the severity of the damage. This assumption also facilitates generalization to other multi-patch systems, where the level of biological patch deterioration is often negligible.

The model was used to simulate six different scenarios: Scenario 1: the prey is patchily distributed among leaves

within plants and the predators search non-randomly. This scenario served as the standard case against which the other five scenarios were compared. The simulations were based on the default parameter values in Nachman (2001, 2006b). Scenario 2: the prey is distributed as in Scenario 1, but the predators exhibit random search. Since it turned out that a randomly searching predator performed so poorly that it could not obtain sufficient prey for its survival, we assumed that low predation efficiency is partly compensated by a better ability to exploit consumed prey. This was achieved by doubling the per capita birth rate and halving the per capita death rate compared with the predator in Scenario 1. Scenario 3: as Scenario 1 except that the prey is evenly distributed among leaves within plants. Scenario 4: as Scenario 1 except that the dispersal rate of the prey is reduced by a factor 10. Scenario 5: as Scenario 1 except that the dispersal rate of the predator is increased by a factor 10. Scenario 6: as Scenario 1 except that the dispersal rate of the prey is reduced by a factor 10 and the dispersal rate of the predator is increased by a factor 10.

In order to compare the state transition diagrams (called “footprints”) originating from different scenarios, it is necessary to compare them with the variation among replicates within the same scenario; this ensures that the differences are not just due to the inherent stochasticity associated with the simulations. We therefore also ran six replicates of Scenario 1 and calculated the standard deviation of the state variables and the transition probabilities after subjecting the data to an arcsine square root transformation. 95% confidence limits for the variables were obtained after a back transformation (Sokal and Rohlf 1995).

The matrix model

The full transition matrix can be described by considering that at any given time t a patch (plant) can be in one of the four states: occupied by neither species (State 1); occupied by prey only (State 2), occupied by both species (State 3), and occupied by predators only (State 4). The distribution of the N plants in each of the four states at time t can be expressed as a vector with four elements $\mathbf{Q}(t) = \{Q_1(t) \ Q_2(t) \ Q_3(t) \ Q_4(t)\}$ where $Q_i(t)$ denotes the number of plants in state i ($i=1, 2, 3, 4$). Note that $\sum_{i=1}^4 Q_i(t) = N$ and that $\sum_{i=1}^4 q_i(t) = 1$, where q_i is the proportion of plants in state i , i.e. $q_i = Q_i/N$. The probability that a plant will be in state i at time $t+1$ given it is in state j at time t ($j=1, 2, 3, 4$) is denoted a_{ij} . Hence, the index j represents the donor state and index i the recipient state (Caswell 2001).

The state vector \mathbf{Q} at time $t+1$ can therefore be found as

$$\mathbf{Q}(t+1) = \begin{Bmatrix} Q_1(t+1) \\ Q_2(t+1) \\ Q_3(t+1) \\ Q_4(t+1) \end{Bmatrix} = \begin{Bmatrix} a_{11} & a_{12} & a_{13} & a_{14} \\ a_{21} & a_{22} & a_{23} & a_{24} \\ a_{31} & a_{32} & a_{33} & a_{34} \\ a_{41} & a_{42} & a_{43} & a_{44} \end{Bmatrix} \begin{Bmatrix} Q_1(t) \\ Q_2(t) \\ Q_3(t) \\ Q_4(t) \end{Bmatrix} = \mathbf{A}\mathbf{Q}(t) \quad (1)$$

where \mathbf{A} is a non-negative transition matrix. The values of a_{ij} are constrained by $a_{ij} \geq 0$ and $\sum_{i=1}^4 a_{ij} = 1$ for $j=1, 2, 3, 4$.

The transition probabilities for the time interval $(t, t+1)$ are estimated from sampling data as

$$\hat{a}_{ij}(t) = \frac{n_{ij}}{Q_j(t)} \quad (2)$$

where n_{ij} denotes the number of transitions from state j to state i .

Transition probabilities depend on the time intervals between successive samplings. The shorter the intervals, the less likely it will be that a patch changes to another state, and in particular that a patch passes through more than a single state. Ideally, the system should be sampled at intervals that are so short that the likelihood that a patch undergoes more than a single transition can be ignored. This reduces the 16 elements of the full 4 times 4 transition matrix to (maximally) 12 non-zero elements: the probabilities for each of the four patch types to remain the same type, change to the next type in the sequence, or revert to the immediately preceding type. Because a patch is allowed to revert to the preceding type, the matrix includes more than the eight non-zero elements employed when a unidirectional cyclic sequence is assumed. A unidirectional cyclic sequence from state 1 through state 4 and back to state 1 was suggested by Gurney and Nisbet (1978) as sufficient to model Huffaker (1958) and Huffaker et al.’s (1963) experiments with acarine prey and predators in a patchy system composed of oranges; however, as pointed out by Woolhouse and Harmsen (1987a), at least some of the transitions are likely to be reversible. For instance, predators may leave a patch before all prey individuals have been consumed or new prey individuals may move to patches where only predators remain after having eradicated prey individuals from the patch.

Test for stationarity

Time-homogeneity of the transition matrix was tested by means of log-linear analyses; this method is recommended by Caswell (2001) as an alternative to the procedure proposed by Anderson and Goodman (1957). Matrices that fail to be time-homogenous because one or more of its transition probabilities vary with time are said to be non-stationary (Anderson and Goodman 1957). Log-linear analysis was also applied to check the similarity of matrices obtained from replicated runs of the same model and to test whether matrices obtained from different models differ significantly. The log-linear analyses were carried out by means of PROC CATMOD in SAS Enterprise guide 4.1 (SAS Inst.).

State transition diagrams

The average values of $q_i(t)$ and $a_{ij}(t)$, recorded on a daily basis for the last 2000 d in a simulation, were visualized graphically as a state transition diagram, where states are represented by circles with an area proportional to the average value of q_i , and transitions are represented by arrows

connecting state j with state i . By discarding the first 1000 d of a simulation we achieved convergence of the average values of $q_i(t)$ and $a_{ij}(t)$ to values that are insensitive to short-term variations and thus reflect properties (or “footprints”) of the underlying processes.

Modeling transition probabilities

If tests for time-homogeneity show that transition probabilities vary with time, the next step is to investigate whether the variation can be related to the current state of the system.

Since we had no a priori assumptions concerning the quantitative relationships between transition probabilities and state variables, we first formulated a fairly simple and general model for such a relationship, namely

$$a_{ij} = c_{ij} L_{ij}(\mathbf{q})^{b_{ij}} \quad (0 \leq a_{ij} \leq 1; 0 \leq c_{ij} \leq 1) \quad (3)$$

where $L_{ij}(\mathbf{q})$ is a linear combination of the four state variables q_1, q_2, q_3 , and q_4 ($0 \leq L_{ij}(\mathbf{q}) \leq 1$), while b_{ij} and c_{ij} are non-negative constants. Thus, $b_{ij}=0$ implies that a_{ij} is independent of the current state of the system and equal to c_{ij} , whereas $b_{ij}>0$ means that a_{ij} increases with $L_{ij}(\mathbf{q})$ provided $c_{ij}>0$. The relationship between $L_{ij}(\mathbf{q})$ and a_{ij} is downward accelerating for $0 < b_{ij} < 1$, linear for $b_{ij}=1$ and upward accelerating for $b_{ij}>1$.

For each of the 12 non-zero matrix elements (a_{ij}) we screened all 14 linear combinations of q_1, q_2, q_3 , and q_4 (except the sum of all four) to find the linear combination that yielded the highest positive Spearman correlation coefficient between a_{ij} and $L_{ij}(\mathbf{q})$. This linear combination was then chosen as candidate for estimating the parameters of eq. 3. The Solver tool in Excel was used to maximize the log likelihood function (Supplementary material) by means of iteration. Once the best set of parameter values had been identified, we used Akaike’s information criterion (AIC) to test whether a state-dependent model performed significantly better than the concomitant state-independent model derived by setting $b_{ij}=0$. The difference between the models was tested by means of a χ^2 -test, because twice the difference in AIC between the full and the reduced model, nested within the former, is distributed approximately as χ^2 with ν degrees of freedom, where ν is the difference in DF between the two models (Hilborn and Mangel 1997).

Matrix modeling

When the transition probabilities of the projection matrix (eq. 1) have been parameterized based on eq. 3, the model can be reiterated to reveal the system’s dynamics. In particular we are interested in finding the long-term (asymptotic) steady state distribution of \mathbf{Q} or \mathbf{q} , because this tells us whether the system is inherently stable with respect to coexistence of prey and predators, i.e. the system returns to equilibrium after a small perturbation. Since the system may possess more than a single steady state, the stability domain was explored by varying the initial state distribution (denoted $\mathbf{Q}(0)$ or $\mathbf{q}(0)$).

We examined the effect of the initial state distribution on the asymptotic behavior of the model by varying $q_1(0), q_2(0), q_3(0)$, and $q_4(0)$ in steps of 0.1 under the constraint that the four state variables should sum to unity. This gives 286 different combinations.

Results

The simulations and their footprints

Figure 1 shows the predator-prey fluctuations of the six scenarios while Fig. 2 shows the concomitant footprints. Table 1 summarizes the outcome of all simulations including the replicated runs of Scenario 1.

In Scenario 1 both species exhibited violent and irregular fluctuations. As seen from Fig. 2, on average, 95.9% of the plants were occupied by mites. 67.1% of the plants hosted both species, 27.1% only prey and 1.6% only predators. Clean plants had on average 4.9% chance per day of being colonized by prey and 4.1% chance of being colonized by predators. Once a plant was inhabited by prey, its chance of also being colonized by predators was 7.2% per day, which means that the average time elapsing from being invaded by prey to being colonized by predators can be found as

$$\frac{1}{-\ln(1 - 0.072)} = 13.4 \text{ d.}$$

In Scenarios 2 and 3, the predators were assumed to forage less efficiently than in Scenario 1. As a consequence they were unable to eradicate the prey from a plant, so plants in state 4 were absent and the same applies to plants in State 1. Occasionally predators went extinct on a plant but the likelihood of such an event was 0.3 and 1.1% d^{-1} for Scenarios 2 and 3, respectively. Plants with only prey were almost immediately colonized by predators, so that plants on average remained unprotected for only two days. Thus, the lower efficiency of the predators was compensated by their ubiquitous presence. Both scenarios were significantly different from Scenario 1 with respect to state variables and transition probabilities (log-linear analysis: $p < 0.001$); accordingly, the footprints (Fig. 2b, c) look very different.

The reduced dispersal rate of the prey in Scenario 4 caused a significant reduction in the percentage of plants with prey only (from 27.1% in Scenario 1 to 14.8% in Scenario 4), partly because the transition probability from clean to prey infested plants declined from 4.9% in Scenario 1 to 3.9% in Scenario 4, and partly because plants with prey alone were more quickly infested with predators in the latter scenario. The proportions of plants with both species and with predators alone were significantly higher in Scenario 4 than in Scenario 1 (Table 1).

The increased dispersal rate of the predators in Scenario 5 significantly increased the transition probability from State 1 to State 4 and vice versa, and from State 2 to State 3 and vice versa in comparison with Scenario 1 (Table 1). This shows that the highly mobile predators more quickly colonize new plants but on the other hand also leave them

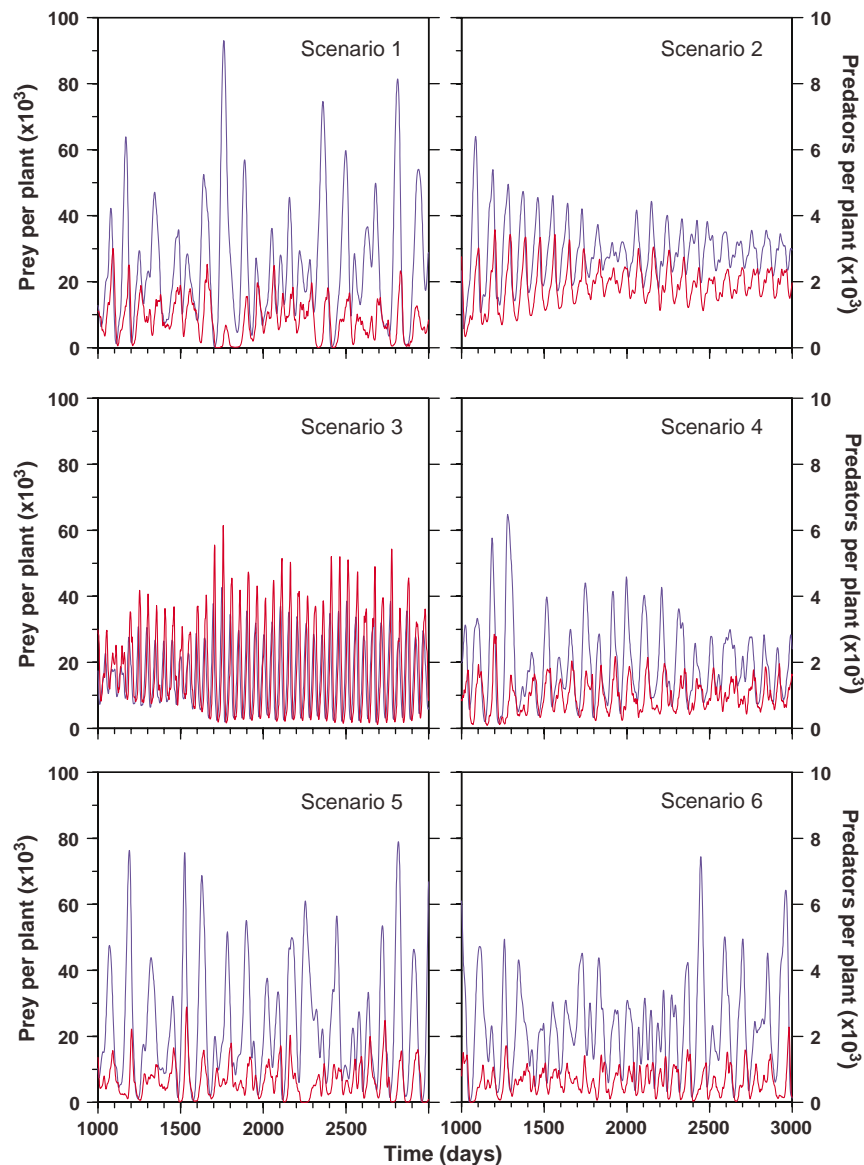


Figure 1. Temporal dynamics of prey (blue line) and predators (red line) during the last 2000 d of a simulation. Scenario 1 (the standard case); prey is patchily distributed within plants and the predators exhibit non-random search; Scenario 2: the prey is patchily distributed within plants, but the predators exhibit random search; Scenario 3: the prey is evenly distributed within plants; Scenario 4: like Scenario 1 except that prey dispersal is reduced; Scenario 5: like Scenario 1 except that predator dispersal is increased; Scenario 6: like Scenario 1 except that prey dispersal is reduced and predator dispersal is increased.

again more rapidly. Plants colonized by prey alone are found by predators within 7.4 d on average.

Finally, in Scenario 6 when the dispersal rate was reduced for the prey and increased for the predator, the chance that a clean plant was colonized by prey decreased to 3.4% and the chance that it was colonized by predators increased to 14.9% d^{-1} (Table 1). The chance that a plant with prey alone is colonized by predators increased to 18% d^{-1} , which means that a plant on average is left unprotected for only five days.

Overall, there are consistent differences between the footprints of the six scenarios. This is especially clear for Scenarios 2 and 3 versus all other scenarios, indicating a strong effect of the predator's functional response on the resultant state distributions.

Dynamics of state distributions

The upper panel of Fig. 3 shows the temporal variation in state distribution obtained from the simulation of Scenario 1 (Fig. 1), while the lower panel shows the development in state distribution averaged over time. The latter can be interpreted as the expected distribution of plants at time t when the initial distribution is known. The expected distribution gradually approaches a stable state distribution, which after 3000 d is found to be 5.3% empty plants, 29.5% plants with prey alone, 63.5% with both prey and predators, and 1.7% with predators only. This distribution is close to the one shown in the footprint diagram (Fig. 2), The latter, however, discards the transient period, which arbitrarily was set to the first 1000 d of a simulation.

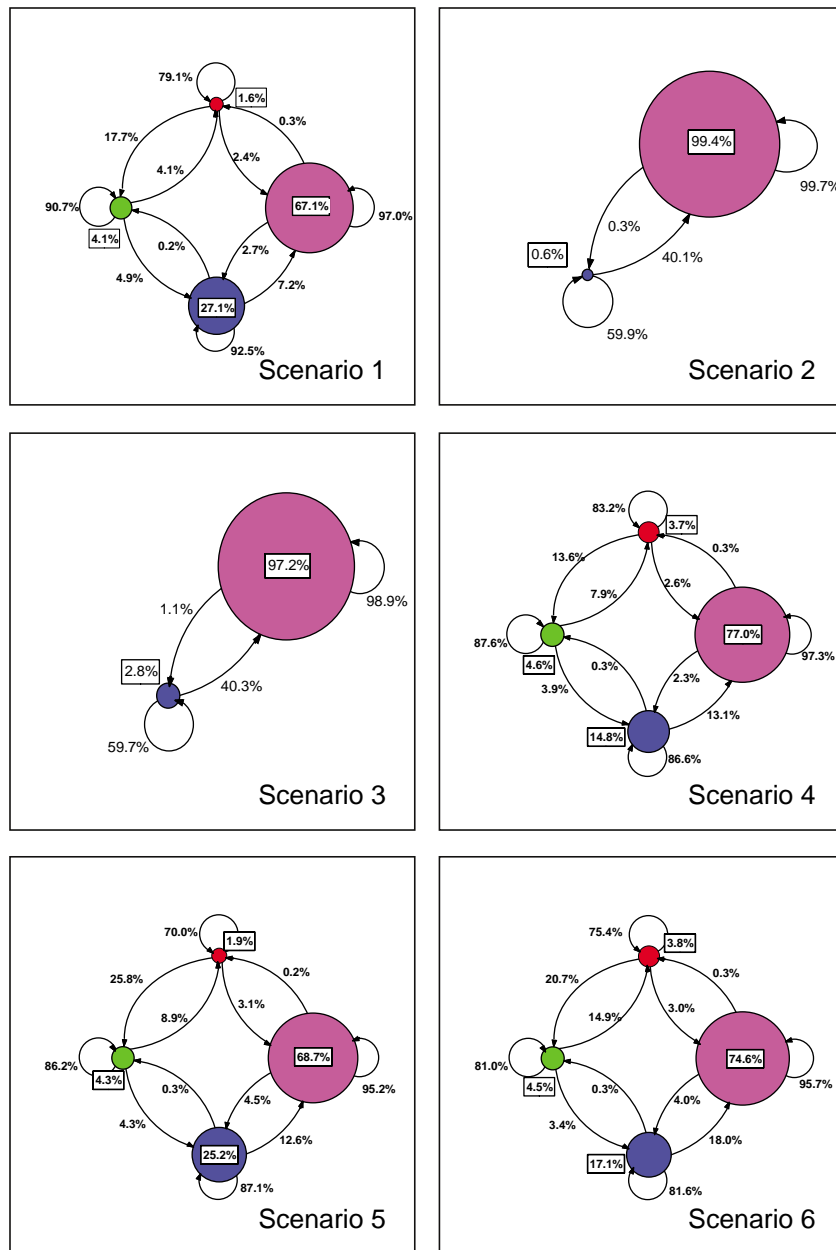


Figure 2. Transition diagrams (also called “footprints”) of the six scenarios. The framed values show the proportion of total time plants on average spend in the various states (also indicated by the circle’s area). The arrows connecting the states mark the transitions with the associated transition probabilities annotated. Note that the transition probabilities from a state may not necessarily sum to unity because rare transitions involving more than a single event are omitted. State 1 (green) is empty, State 2 (blue) is with prey alone, State 3 (purple) is with both species and State 4 (red) is with predators alone.

Variation among scenarios

The six replicates of Scenario 1 showed little variation among the individual replicates. Thus, the coefficient of variation (CV) ranged from 0.05 to 1.2% for the state variables, and from 0.002 to 1.9% for the transition probabilities. The variation among scenarios was considerably larger than the within-scenario variation, both with respect to state variables and transition probabilities (Table 1) which is a prerequisite for comparing footprints obtained from scenarios with different population dynamics. Thus, Scenario 1 could be separated from the five other scenarios on at least one, but in most cases several, parameters.

Test for stationarity

The log-linear analyses of the transition matrices clearly showed for all scenarios that the transition probabilities were non-stationary ($p < 0.0001$). Consequently, at least some of the transition probabilities are likely to be state-dependent.

Modeling transition probabilities

Table 2 gives an overview of those linear combinations of q_i ($i = 1, 2, 3, 4$) that correlated best with the transitions

Table 1. Comparisons between Scenario 1 and the five other scenarios. Values in bold fall outside the 95% confidence limits for Scenario 1 obtained from six replicated runs. q_1 = per cent of plants in State 1 (neither prey nor predators), q_2 = per cent of plants in State 2 (only prey), q_3 = per cent of plants in State 3 (both prey and predators), q_4 = per cent of plants in State 4 (only predators). a_{ij} is the estimated probability that a plant in state j at day t will be in state i ($i, j = 1, 2, 3, 4$) at day $t+1$.

Scenario	States (%)				Transition probabilities (%)															
	q_1	q_2	q_3	q_4	a_{11}	a_{21}	a_{31}	a_{41}	a_{12}	a_{22}	a_{32}	a_{42}	a_{13}	a_{23}	a_{33}	a_{43}	a_{14}	a_{24}	a_{34}	a_{44}
Scenario 1 (avg)	4.05	27.09	67.12	1.63	90.72	4.87	0.27	4.10	0.25	92.52	7.20	0.02	0.02	2.70	97.02	0.26	17.73	0.73	2.43	79.08
lower limit	2.07	21.80	59.70	1.29	87.69	3.81	0.11	2.46	0.15	90.70	5.46	0.01	0.01	2.43	96.71	0.18	15.71	0.40	1.60	77.33
upper limit	6.69	32.96	74.97	2.00	93.80	6.06	0.49	6.15	0.36	94.36	9.17	0.03	0.04	2.97	97.34	0.35	19.89	1.16	3.43	80.84
Scenario 2	0.00	0.65	99.35	0.00	0.00	0.00	0.00	100.00	0.00	40.13	40.30	0.00	0.00	0.26	99.74	0.00	8.33	0.00	25.00	66.67
Scenario 3	0.00	2.76	97.24	0.00	0.00	0.00	0.00	0.00	0.00	59.70	40.30	0.00	0.00	1.15	98.85	0.00	0.00	0.00	16.67	83.33
Scenario 4	4.55	14.76	76.99	3.70	87.65	3.92	0.58	7.85	0.29	86.59	13.08	0.03	0.02	2.31	97.34	0.33	13.62	0.51	2.63	83.24
Scenario 5	4.30	25.15	68.66	1.89	86.23	4.32	0.52	8.94	0.31	87.05	12.59	0.05	0.04	4.48	95.23	0.25	25.76	1.21	3.05	69.98
Scenario 6	4.51	17.08	74.65	3.77	80.97	3.37	0.81	14.86	0.34	81.57	18.00	0.08	0.04	3.97	95.67	0.33	20.68	0.88	3.01	75.43

obtained from Scenario 1. All relationships are highly significant and confirm the a priori assumption that colonization probabilities of plants without prey (a_{21} and a_{34}) correlate with the proportion of plants already occupied by prey ($q_2 + q_3$) and that the probabilities of plants without predators being colonized by predators (a_{41} and a_{32}) correlate best with the proportion of plants already occupied by predators ($q_3 + q_4$). The probabilities that prey goes extinct depend on whether predators are present on the plant. In the absence of predators, the extinction probability (a_{12}) declines with an increase in q_2 , whereas a_{43} declines with an increase in q_3 in the presence of predators. Similarly, the probabilities that predators go extinct depend on whether prey is present. When prey is present, a_{23} decreases as q_3 increases; when there is no prey a_{14} decreases as q_4 increases.

The remaining transitions occurred with low frequencies and the probabilities of these transitions were all set to 0. Hence, the eight transition probabilities listed in Table 2 require estimation of 16 parameters.

Table 3 summarizes the results of the maximum likelihood analyses. All analyses except for a_{14} yielded positive values of both b_{ij} and c_{ij} (eq. 3), though b_{34} was not significantly different from 0 and was therefore replaced by 0. In the remaining six cases, setting b_{ij} equal to 0 resulted in a significant increase in AIC , which confirms that these transitions are indeed state-dependent.

The model for a_{21} indicates that empty plants will be colonized by prey with an increasing probability as the proportion of plants occupied by prey increases and will approach a maximum of ca 9% d^{-1} . Likewise, the probability that an empty plant becomes occupied by predators increases with the proportion of plants already occupied by predators up to a maximum of ca 13% d^{-1} .

The models for a_{12} and a_{32} show that transitions from plants inhabited by prey to empty plants occur with decreasing probability the higher the proportion of prey plants is, while the probability of transitions from plants with only prey to plants with both species increases with the proportion of plants already occupied by predators. The former transition is a much slower process than the latter, which has a maximum of $>16\%$ d^{-1} .

The models for a_{23} and a_{43} show that the transition probabilities accelerate as the proportion of plants occupied by both prey and predators approaches 0. However, the maximum probabilities for both processes are low, especially for the rate at which plants become devoid of prey (a_{43}), indicating that once a plant is inhabited by both species it takes rather long time before the predators have eradicated the prey, partly due to the fact that both prey and predators continuously immigrate to such plants.

Finally, the models for a_{34} and a_{14} show that these two probabilities can be regarded as state-independent. The parameters indicate that predators quickly disappear from plants without prey ($a_{14} = 0.19$), whereas plants occupied by only predators are rather unlikely to be (re)colonized by prey ($a_{34} = 0.0058$).

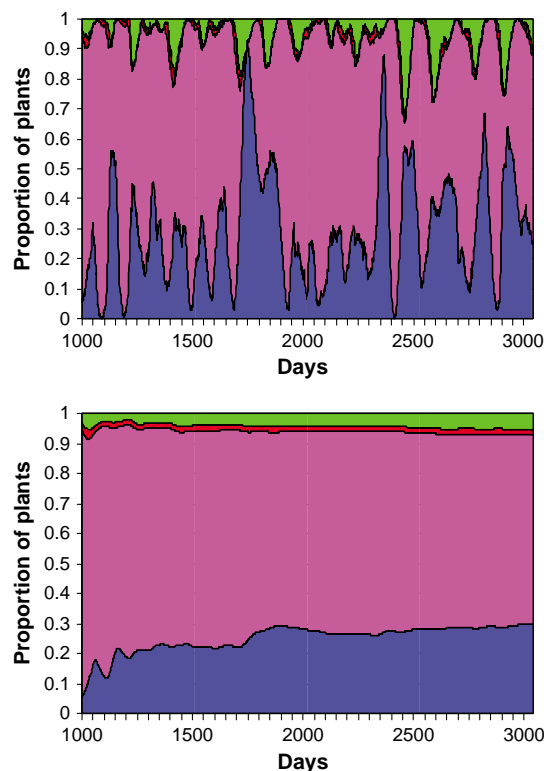


Figure 3. Upper panel: temporal variation in the distribution of plants based on Scenario 1. Lower panel: expected state distribution at time t obtained by cumulating the distributions in the upper panel and then averaging over time. Colours as in Fig. 2.

Matrix modeling

The exploration of the asymptotic behavior of the matrix model parameterized by means of data from Scenario 1 revealed that the long-term state distribution (denoted q_i^*) depends on the initial conditions. Hence, the model is non-ergodic (Caswell 2001). Three of the asymptotic state distributions are identical to the initial state distributions and occur when the systems starts in a completely synchronized state, i.e. $q_1^* = q_1(0) = 1$ (all plants are clean), $q_2^* = q_2(0) = 1$ (all plants are occupied by prey) or $q_3^* = q_3(0) = 1$ (all plants are occupied by both prey and predators). The fourth synchronized state with all plants occupied by predators alone (i.e. $q_4^* = q_4(0) = 1$) of course quickly leads to an equilibrium where all plants are clean (i.e. $q_1^* = 1$). However, if the initial distribution is

asynchronous, i.e. $q_i(0) < 1$ for all i , the system will converge toward one of three asymptotic states (Fig. 4): a) extinction of both species, b) extinction of predators and a very high (99.95%) frequency of prey-infested plants, and c) coexistence of both species with 4.46% of the plants in State 1, 21.67% in State 2, 71.26% in State 3, and 2.61% in State 4. Outcome (a) occurred in 44% of the cases and was associated with combinations where the initial proportion of plants with prey was low relative to the proportion of plants with predators. Outcome (b) occurred in 35% of the cases and was associated with combinations where the initial proportion of plants with prey was high and the proportion with predators low. Finally, outcome (c) occurred in 21% of the cases and was associated with combinations where the initial proportions of plants with prey ($q_2(0) + q_3(0)$) and with predators ($q_3(0) + q_4(0)$) were both high. In particular, all cases where $0.64 \leq q_3(0) < 1$ lead to outcome (c) irrespective of the three other states. Outcome (c) agrees well with that obtained from the simulation model (Fig. 3 lower panel), although 3000 d of simulation is not sufficient for the system to attain a steady-state distribution.

Discussion

Our preliminary study, based on a single specific model and a few characteristic scenarios, has demonstrated that complex population dynamics can be summarized by means of simple state transition diagrams which are likely to represent “footprints” of the underlying population processes. Thus, the footprints of predator–prey dynamics are composed by merely four state variables, each representing presence/absence of prey and predators, as well as the connections between these states. Connectivity is expressed in terms of transition probabilities which provide information about the turn-over rates of the states. This may serve as a diagnostic tool in biological control programmes, because the time elapsing from a plant becomes infested with a pest organism to it is found by a natural enemy is often crucial (Huffaker and Messenger 1964). Likewise, turn-over rates can be used to forecast the risk of local extinctions, a factor that may influence the persistence of species living in fragmented habitats (Burkey 1989). In fact, many metapopulation (Hanski 1999) and biogeographical studies (Soberón 2010) rely on incidence data only, and in such cases it can be valuable if a link from this type of data

Table 2. List of functions yielding the highest positive Spearman correlation coefficient between state variables (q_i) and transition probabilities (a_{ij}) obtained from Scenario 1. The functions tested comprise all linear combinations of q_i (i.e. $q_1, q_2, q_3, q_4, q_1 + q_2, q_1 + q_3, q_1 + q_4, q_2 + q_3, q_2 + q_4, q_3 + q_4, 1 - q_1, 1 - q_2, 1 - q_3$, and $1 - q_4$) except $q_1 + q_2 + q_3 + q_4 = 1$.

Transition probability (a_{ij})	Function ($L_{ij}(q)$)	Corr. coeff. (r_s)	Sample size (n)	p
a_{21}	$c_{21}(q_2 + q_3)^{b_{21}}$	0.809	964	<0.0001
a_{41}	$c_{41}(q_3 + q_4)^{b_{41}}$	0.627	824	<0.0001
a_{12}	$c_{12}(1 - q_2)^{b_{12}}$	0.716	448	<0.0001
a_{32}	$c_{32}(q_3 + q_4)^{b_{32}}$	0.775	1979	<0.0001
a_{23}	$c_{23}(1 - q_3)^{b_{23}}$	0.474	1869	<0.0001
a_{43}	$c_{43}(1 - q_3)^{b_{43}}$	0.546	817	<0.0001
a_{34}	$c_{34}(q_2 + q_3)^{b_{34}}$	0.475	255	<0.0001
a_{14}	$c_{14}(1 - q_4)^{b_{14}}$	0.462	1040	<0.0001

Table 3. Maximum likelihood estimates of the parameters used to model the state-dependent transition probabilities in Table 2 obtained from Scenario 1. b_{ij} is either estimated to be 0 (as for \hat{a}_{14}) or to be so close to 0 (as for \hat{a}_{34}) that it can be set to 0 (i.e. the transition probability is state-independent). p is the probability that a state-dependent and a state-independent model are equally good to fit data. State-dependent probabilities are only used if $p < 0.05$.

Transition probability (a_{ij})	b_{ij}	c_{ij}	ΔAIC	χ^2_1	p
\hat{a}_{21}	4.542	0.088	242.2	483.7	<0.0001
\hat{a}_{41}	2.378	0.134	445.2	967.4	<0.0001
\hat{a}_{12}	0.596	0.0041	18.4	36.8	<0.0001
\hat{a}_{32}	1.477	0.163	2818.3	5636.5	<0.0001
\hat{a}_{23}	0.627	0.063	1288.8	2577.6	<0.0001
\hat{a}_{43}	0.209	0.0040	19.2	38.3	<0.0001
\hat{a}_{34}	0	0.0058	0.027	0.053	0.82
\hat{a}_{14}	0	0.190	0	0	1

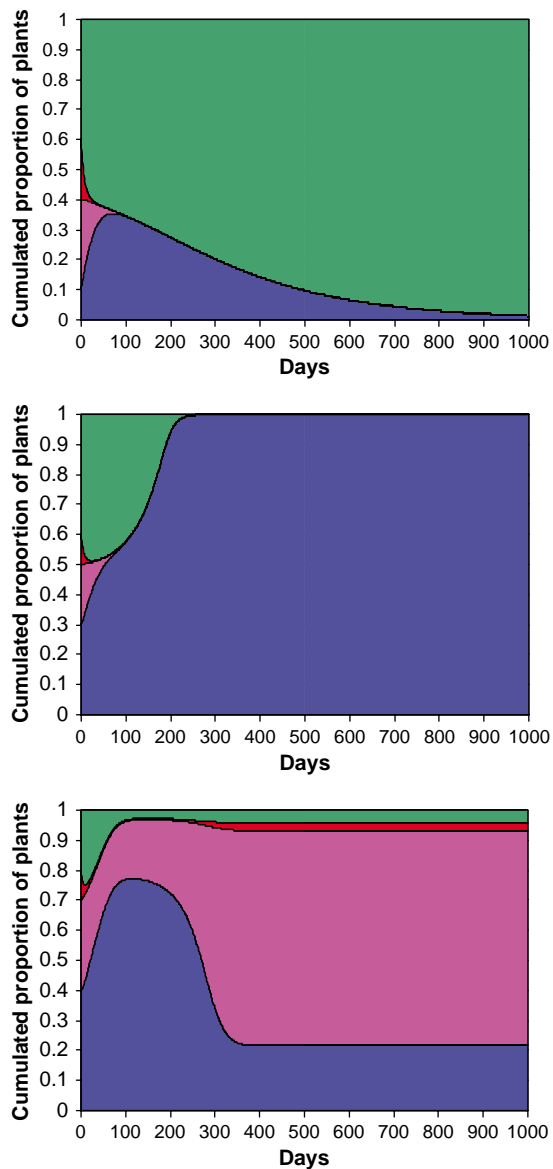


Figure 4. Predictions for Scenario 1 based on the matrix model (eq. 1) and with parameter values given in Table 3 for three different initial state distributions. Upper panel: 40% in State 1, 10% in State 2, 30% in State 3, and 20% in State 4. Middle panel: 40% in State 1, 30% in State 2, 20% in State 3, and 10% in State 4. Lower panel: 20% in State 1, 40% in State 2, 30% in State 3, and 10% in State 4. Colours as in Fig. 2.

and back to the underlying population dynamics can be established via the footprints.

In this study we used plants as the units of measurement. However, the footprints obtained from Scenarios 2 and 3 (Fig. 2) indicate that this spatial unit may not be optimal because State 3 dominates at the expense of especially State 1 and 4. Thus, using a smaller spatial scale (e.g. a leaf as in Nachman 1999) will increase the proportion of the empty patches and patches occupied by only a single species. Applying a smaller scale would also make sampling easier and increase the creditability of absences (Soberón 2010). On the other hand, if sampling units become very small, occupied patches will become too rare. It is therefore important to choose an appropriate spatial unit for measuring and interpreting spatial dynamics (Wiens 1989, Rahbek 2005).

The transition matrices were found to be non-stationary, confirming our expectation that at least some of the transition probabilities vary with time. As Gurney and Nisbet (1978), we assumed that the temporal variations in transition probabilities are due to feed-backs between state variables and transition probabilities, although the relationships linking them are not necessarily linear (as assumed by Gurney and Nisbet 1978). By fitting a generic model to the transition probabilities obtained from Scenario 1 we were able to describe this non-stationarity: the results demonstrate a strong positive feed-back between the chance that an empty plant becomes colonized by prey and the proportion of plants already occupied by prey. Likewise, plants without predators will quickly become occupied by predators when this species already inhabits the majority of plants.

Extinction probabilities, on the other hand, were not always state-dependent. In the cases where extinction probabilities were found to be state-dependent, the functional relationships show that extinction probability increases as the number of extant populations declines. This creates positive feedbacks which tend to accelerate existing trends and make the system sensitive to perturbations that eventually lead to extinction. The stability analysis revealed that the projection model based on Scenario 1 is non-ergodic, i.e. its asymptotic state distribution depends on its initial state (Caswell 2001). Six different equilibria were identified: a) all plants are clean, b) all plants are inhabited by prey, c) all plants are occupied by both prey and predators, d) 99.95% plants are occupied by prey while the remaining are clean, and e) 4.46% of the plants are clean, 21.67% infested with prey alone, 71.26% with both prey

and predators and 2.61% with predators alone. Case a is trivial, while case b and c represent unstable equilibria because infinitely small deviations from equilibrium will change case b to case d and case c to case e. From a biological point of view case b and c represent artifacts, which can be attributed, at least partly, to the fact that the model does not explicitly incorporate plant condition, which means that plants can host high densities of prey without suffering permanent damage.

The advantages of using model-generated data to parameterize a discrete state model are: 1) it is a quick and easy way of obtaining lots of detailed data, 2) we know exactly the processes that have produced these data, and 3) we do not need to worry about sampling error (cf. Gaston and McArdle 1994). Consequently, we can be quite confident that the estimated parameters are representative for the studied system. However, the drawback of using artificial data is that they can never be more correct than the model that has generated them. Complex simulation models, irrespective of how realistic they are, or believed to be, will always represent unrealistic simplifications that can bias the results. Thus, by using simulated data to parameterize a Markov chain model, we risk to exaggerate errors already present in the simulated data. It is therefore important to validate model predictions against real data originating from field studies before the model is used for practical purposes.

It is possible to parameterize discrete state transition models directly from field data (Woolhouse and Harmsen 1989). However, field data are likely to be too coarse-grained unless sampling takes place with very short (e.g. daily) intervals, and to be influenced by factors that cannot be controlled by the experimenter such as the weather. In contrast, a simulation model can be developed by means of data obtained from specific experiments conducted under controlled conditions.

Clements and Harmsen (1991) used a mechanistic simulation model to complement an empirical transition matrix model of an acarine predator-prey system and concluded that the transition matrix produced accurate predictions, but could not provide information on what will happen if the system under study was subject to manipulation. In contrast, the mechanistic (or reductionist) simulation approach provided information on how complex biological interactions affect population dynamics, but could not be used as a predictive tool.

The projection matrix employed in this paper simulates the system deterministically, by regarding the transition probabilities as the expected rates of state transitions. However, if the system consists of a finite number of patches (plants) and especially if this number is small, stochastic phenomena may play an important role (Nisbet and Gurney 1982). Even if the environment is constant, endogenous stochastic processes like extinctions and colonizations will perturb the system and, depending on its current state, be able to push it from one stability domain to another. Such sudden shifts in predator-prey dynamics have been observed in experimental studies of spider mites and predatory mites (van de Klashorst et al. 1992, Janssen et al. 1997, McCauley et al. 2000) and do also occur when the system is modeled by means of a stochastic simulation model (Nachman 1987b).

The deterministic projection model can be made stochastic by using Monte Carlo methods to generate the actual number of transitions in a system consisting of N plants based on the multinomial distribution (Supplementary material eq. S1). In a following paper we plan to pursue this approach in order to develop a stochastic version of a discrete state transition model that can be used as a tactical tool to forecast short and long-term changes in the system. The reliability of the predictions will be evaluated on basis of the amount information available at day 0 (depends on sample size) and the length of the forecasted period. Finally, it should be noted that although the matrix model only needs input data on a classification scale (i.e. presence/absence) and yields predictions on the same scale, proportions of sampling units with prey and/or predators can easily be converted to densities using regression models based on e.g. the negative binomial distribution (Wilson and Gerrard 1971) or the Weibull distribution (Nachman 1984).

References

- Anderson, T. W. and Goodman, L. A. 1957. Statistical inference about Markov chains. – *Ann. Math. Stat.* 28: 89–110.
- Burkey, T. V. 1989. Extinction in nature reserves: the effect of fragmentation and the importance of migration between reserve fragments. – *Oikos* 55: 75–81.
- Caswell, H. 2001. *Matrix population models*. – Sinauer.
- Clements, D. R. and Harmsen, R. 1991. A mechanistic simulation to complement an empirical transition matrix model of acarine population dynamics. – *Ecol. Model.* 59: 257–277.
- Dharmadhikari, S. W. 1963. Functions of finite Markov chains. – *Ann. Math. Stat.* 34: 1022–1032.
- Gaston, K. J. and McArdle, B. H. 1994. The temporal variability of animal abundance: measures, methods and patterns. – *Phil. Trans. R. Soc. B* 345: 335–358.
- Gurney, W. S. C. and Nisbet, R. M. 1978. Predator-prey fluctuations in patchy environments. – *J. Anim. Ecol.* 47: 85–102.
- Gurney, W. S. C. et al. 1998. Circles and spirals: population persistence in a spatially explicit predator-prey model. – *Ecology* 79: 2516–2539.
- Hanski, I. 1999. *Metapopulation ecology*. – Oxford Univ. Press.
- Helle, W. and Sabelis, M. W. 1985. *Spider mites. Their biology, natural enemies and control*. – Elsevier.
- Hilborn, R. and Mangel, M. 1997. *The ecological detective*. – Princeton Univ. Press.
- Holling, C. S. 1959. Some characteristics of simple types of predation and parasitism. – *Can. Entomol.* 91: 385–398.
- Huffaker, C. B. 1958. Experimental studies of predation: dispersal factors and predator-prey oscillations. – *Hilgardia* 27: 343–383.
- Huffaker, C. B. and Messenger, P. S. 1964. The concept and significance of natural control. – In: DeBach, P. (ed.), *Biological control of insect pests & weeds*. Chapman and Hall, pp. 74–117.
- Huffaker, C. B. et al. 1963. Experimental studies on predation: complex dispersion and levels of food in acarine predator-prey interaction. – *Hilgardia* 34: 305–330.
- Janssen, A. et al. 1997. Metapopulation dynamics of a persisting predator-prey system in the laboratory: time-series analysis. – *Exp. Appl. Acarol.* 21: 415–430.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. – *Bull. Entomol. Soc. Am.* 15: 237–240.

- Lotka, A. J. 1925. Elements of physical biology. – Williams and Wilkins. Reprinted in 1956. Elements of mathematical biology. Dover Publ.
- Lusseau, D. 2003. Effects of tour boats on the behaviour of bottlenose dolphins: using Markov Chains to model anthropogenic impacts. – *Conserv. Biol.* 17: 1785–1793.
- Maynard Smith, J. 1974. Models in ecology. – Cambridge Univ. Press.
- McCauley, E. et al. 2000. Inferring colonization processes from population dynamics of spatially structured predator–prey systems. – *Ecology* 81: 3350–3361.
- Nachman, G. 1981. Temporal and spatial dynamics of an acarine predator–prey system. – *J. Anim. Ecol.* 50: 435–451.
- Nachman, G. 1984. Estimates of mean population density and spatial distribution of *Tetranychus urticae* (Acarina: Tetranychidae) and *Phytoseiulus persimilis* (Acarina: Phytoseiidae) based upon the proportion of empty sampling units. – *J. Appl. Ecol.* 21: 903–912.
- Nachman, G. 1987a. Systems analysis of acarine predator–prey interactions. I. A stochastic simulation model of spatial processes. – *J. Anim. Ecol.* 56: 247–265.
- Nachman, G. 1987b. Systems analysis of acarine predator–prey interactions. II. The role of spatial processes in system stability. – *J. Anim. Ecol.* 56: 267–281.
- Nachman, G. 1999. The effect of dispersal on the dynamics and persistence of an acarine predator–prey system in a patchy environment. – In: Needham, G. R. et al. (eds), Proc. IXth Int. Congress of Acarology, pp. 175–184.
- Nachman, G. 2001. Predator–prey interactions in a nonequilibrium context: the metapopulation approach to modelling “hide-and-see” dynamics in a spatially explicit tri-trophic system. – *Oikos* 94: 72–88.
- Nachman, G. 2006a. The effects of prey patchiness, predator aggregation, and mutual interference on the functional response of *Phytoseiulus persimilis* feeding on *Tetranychus urticae* (Acari: Phytoseiidae, Tetranychidae). – *Exp. Appl. Acarol.* 38: 87–111.
- Nachman, G. 2006b. A functional response model of a predator population foraging in a patchy environment. – *J. Anim. Ecol.* 75: 948–958.
- Nisbet, R. M. and Gurney, W. S. C. 1982. Modelling fluctuating populations. – Wiley.
- Rahbek, C. 2005. The role of spatial scale and the perception of large-scale species-richness patterns. – *Ecol. Lett.* 8: 224–239.
- Soberón, J. 2010. Niche and distributional range: a population ecology perspective. – *Ecography* 33: 159–167.
- Sokal, R. R. and Rohlf, F. J. 1995. Biometry, 3rd ed. – W. H. Freeman.
- Solomon, M. E. 1949. The natural control of animal populations. – *J. Anim. Ecol.* 18: 1–32.
- van de Klashorst, G. et al. 1992. A demonstration of asynchronous local cycles in an acarine predator–prey system. – *Exp. Appl. Acarol.* 14: 185–199.
- Wiens, J. A. 1989. Spatial scaling in ecology. – *Funct. Ecol.* 3: 385–397.
- Wilson, L. F. and Gerrard, D. J. 1971. A new procedure for rapidly estimating European pine sawfly (Hymenoptera: Diprionidae) population levels in young pine plantations. – *Can. Entomol.* 103: 1315–1322.
- Woolhouse, M. E. J. and Harmsen, R. 1987a. Prey–predator cycles and lags in space: descriptive models from a laboratory experiment. – *Theor. Popul. Biol.* 32: 366–382.
- Woolhouse, M. E. J. and Harmsen, R. 1987b. A transition matrix model of seasonal changes in mite populations. – *Ecol. Model.* 37: 167–189.
- Woolhouse, M. E. J. and Harmsen, R. 1989. A transition matrix model of European red mites (*Panonychus ulmi*) population dynamics in a managed apple orchard. – *Ecol. Model.* 46: 269–282.
- Woolhouse, M. E. J. and Harmsen, R. 1991. Population dynamics of *Aphis pomi*: a transition matrix approach. – *Ecol. Model.* 55: 103–111.
- Yemshanov, D. and Perera, A. H. 2002. A spatially explicit stochastic model to simulate boreal cover transitions: general structure and properties. – *Ecol. Model.* 150: 189–209.

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