

Scaling up: how do exogenous fluctuations in individual-based resource competition models re-emerge in aggregated stochastic population models?

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Abstract In applied population dynamics the choice of stochastic per capita growth function has implications for population viability analyses, management recommendations, and pest control. This model choice is often based on statistical criteria, mathematical tractability or personal preferences, and general ecological guidelines are either too vague or entirely missing. To identify such guidelines, it is important to understand how exogenous and endogenous factors interact at the individual level and re-emerge at the aggregated population level. We therefore study different types of resource competition (contest vs. scramble competition) and different types of exogenous fluctuations (food and weather fluctuations) at the individual level in a simple individual-based simulation model. We statistically fit the resulting time series to find out (1) which functional form of the growth function ('hyperbolic' or 'exponential') better describes contest and scramble competition and (2) whether the pattern of population fluctuations resulting from the simulations can be assigned

to vertical, lateral or nonlinear perturbations in the stochastic growth function (a classification scheme suggested by Royama 1992, Analytical Population Dynamics, Chapman and Hall, London). We found that the same type of competition can result in 'hyperbolic' or 'exponential' functional forms, depending on the type of exogenous fluctuations. So it is the interplay between exogenous variability and endogenous resource competition that affects model performance. In contrast to the widespread assumption of vertical (additive) perturbations, our findings highlight the importance of (non-additive) lateral and nonlinear perturbations and their combinations with vertical perturbations. The choice of the stochastic growth function should therefore consider not only statistical criteria but also ecological guidelines. We derive such ecological guidelines from our analysis.

Keywords Environmental noise · Model aggregation · Population dynamics · Stochastic growth rate · Time series analysis

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Introduction

One of the more challenging tasks in applied population dynamic theory, including time series analyses, is to determine how natural populations will respond to changing environmental conditions such as climate change. It requires an understanding of how endogenous and exogenous factors affect density dependent population growth and dynamics and is closely related to issues of model choice and aggregation (Pascual and Levin 1999). Exogenous factors such as weather conditions or food supply generate fluctuations in the reproduction or survival of individuals and thus generally impose stochasticity on

population growth (e.g., Lande 1993; Johst and Wissel 1997; Ripa and Heino 1999; Bjørnstad and Grenfell 2001; Ellner et al. 2002; Brännström and Sumpter 2006). Endogenous factors such as intra-specific competition for resources impose density dependence on population growth and result in a density-dependent per capita growth rate $R(N)$ (called R -function e.g., Royama 1992; Abrams 2009). The ways in which endogenous and exogenous factors may interact are manifold and have implications for the resulting stochastic population dynamics and for the sensitivity of a particular species to environmental change (e.g., Lundberg et al. 2002; Johst and Drechsler 2003; Coulson et al. 2004; Greenman and Benton 2005; Owen-Smith 2011). Therefore, an understanding of these interactions and how they re-emerge in aggregated stochastic growth models is pivotal to forecasting the consequences of climate change to biodiversity (e.g., Saether et al. 2000; Stenseth et al. 2002).

Royama (1992) classified and generalized stochasticity in the R -functions by introducing three categories of exogenous perturbations: vertical, lateral and nonlinear perturbations. Vertical perturbations affect the maximum growth rate such that the relative position of the $R(N)$ -curve shifts up and down along the R -axis (i.e., ‘vertically’) if environmental conditions change. Lateral perturbations affect equilibrium population size (carrying capacity) without altering maximum growth rate such that the $R(N)$ -curve is scaled along the N -axis (i.e., ‘laterally’). Nonlinear perturbations affect the intensity of competition via the curvature of the stochastic R -function (see “[Lateral, vertical and nonlinear perturbations](#)” for details). Despite the widespread assumption of vertical perturbations in time series analyses, it is largely unknown to which extent lateral and nonlinear perturbations impact dynamics as well and improve statistically inferred growth functions. Moreover, the type of competition (scramble or contest) may impact the functional form of the growth function (e.g., Royama 1992; Brännström and Sumpter 2005). There are arguments that ‘exponential’ forms (sensu Royama 1992) such as the Ricker equation (see “[Functional form](#)”) better describe scramble competition and ‘hyperbolic’ forms (sensu Royama 1992) such as the Maynard Smith and Slatkin (MSS) equation (see “[Functional form](#)”) better describe contest competition (Royama 1992); but there are also arguments that one functional relationship can describe the whole range from scramble to contest competition (e.g., Hassell 1975; Anazawa 2010).

Which functional form (‘hyperbolic’ or ‘exponential’ functions) should be chosen in combination with which perturbation (lateral, vertical or nonlinear) for which situation is therefore often equivocal (for Soay sheep e.g., this debate is summarized in Coulson et al. 2008). Modellers frequently choose models according to individual

preferences, based on statistical criteria, or to obtain mathematical tractability. However, model choice has implications for population viability analyses, management recommendations, and pest control. Given that all parameters are the same, ‘exponential’ functions give rise to more violent fluctuations than ‘hyperbolic’ functions in the presence of exogenous fluctuations. Moreover, the choice of perturbation (lateral, vertical or nonlinear) in the stochastic R -function may be critical in determining the effect of exogenous influences (e.g., Lindström et al. 2005; Berryman and Lima 2006; Lima et al. 2008a, b; see also Brännström and Sumpter 2006). Thus, on the one hand, model choice is often problematic but has, on the other hand, essential consequences for model predictions (see e.g., Higgins et al. 1997; Ripa and Heino 1999; Sibly et al. 2007). As one way out of this dilemma it has been proposed to exploit the joint statistical properties inherent to many time series and to investigate how well statistical measures (e.g., noise colour) of a single, very general stochastic population growth model comprise the various details of different population dynamics (e.g., different competition types). This approach works well for forecasting quasi-extinction risk (Holmes et al. 2007). Another way is to use more specific but still sufficiently general, aggregated stochastic growth functions based not only on statistical criteria but also on ecological guidelines.

However, as described above, firm ecological guidelines for the choice of the stochastic growth function are still lacking and it is even unclear whether such guidelines can be derived at all. We therefore investigate whether and to what extent different types of resource competition (scramble vs. contest competition) interact differently with the same type of exogenous fluctuations and how these interactions subsequently re-emerge in the aggregated stochastic R -function. In the style of time series analyses, we perform a statistical analysis of the density dependent stochastic population growth resulting from an individual-based simulation model (IBM, for a general overview of individual-based modelling see e.g., Grimm and Railsback 2005). Figure 1 illustrates our approach.

We consider four types of resource competition in the IBM (pure scramble and contest competition as well as competition that falls between these two extremes) in combination with two typical exogenous factors influencing individual performance: (1) variation in a limiting resource affecting the reproductive output and survival of adults competing for it (referred to as food fluctuations) and (2) variation in a non-limiting factor affecting directly the survival of young (referred to as weather fluctuations). We study which aggregated (statistically inferred) stochastic R -function results from which type of competition and environmental variation assumed in the IBM (e.g., when does an MSS function with lateral perturbations

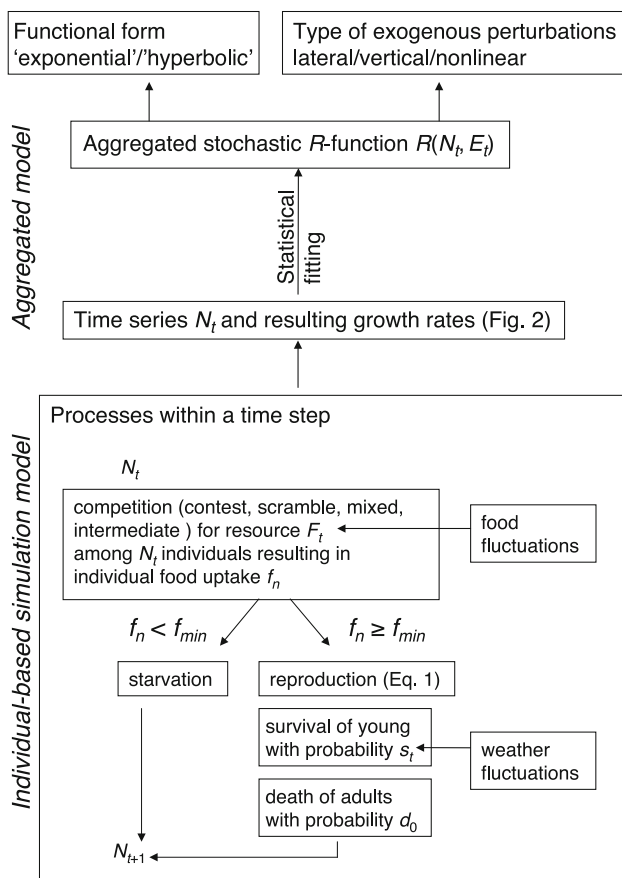


Fig. 1 Scheme of our approach including the relations between individual-based simulation model (IBM) and aggregated (statistically inferred) stochastic R -function

result from the IBM simulations or when does a Ricker function with vertical perturbations result, and so on).

This allows us to investigate whether it is possible to detect the type of competition and/or the type of exogenous fluctuations via the form of the (statistically inferred) aggregated stochastic R -function. We hypothesize that scramble competition in the IBM should result in ‘exponential’ Ricker functions and contest competition in ‘hyperbolic’ MSS functions (Royama 1992). With respect to the type of exogenous fluctuations, we hypothesize that food fluctuations should arise as lateral perturbations influencing the carrying capacity of population dynamics, and weather fluctuations should arise as vertical perturbations affecting the maximum growth rate at low population densities.

We will answer two basic questions: (1) Is it possible to differentiate competition types (scramble vs. contest competition) in stochastic environments by the functional form (MSS vs. Ricker) of the statistically inferred aggregated stochastic R -function? (2) Is it possible to assign exogenous influences (food and/or weather fluctuations) to specific perturbations in this R -function (vertical, lateral or

nonlinear) or does this assignment also depend on competition type?

To examine and understand how exogenous and endogenous factors interact at the individual level and re-emerge at the aggregated population level we keep our individual-based approach as simple as possible. Based on this understanding it is possible to formulate general ecological guidelines for model selection, which can be used in addition to statistical criteria to support time series analyses and applied population dynamics.

Methods

Individual-based model (IBM)

Birth and death of individuals according to food supply

We assume a resource F (we are mainly thinking about food) consisting of F_t units (items or packets) available in time step t to be distributed among N_t individuals, with N_t being the size of the population (non-negative integer values) in time step t . Resource dynamics are not explicitly considered, however, units F_t may fluctuate over time (see below). During the resource partitioning individuals get resources in single units and those that have received sufficient resources to satisfy their demand (f_{Max}) are removed from the process of resource partitioning. When all individuals have obtained f_{Max} units or F_t is exhausted then resource distribution in time step t ceases. At the end of this process, the n -th individual in the population will have received $0 \leq f_n \leq f_{\text{Max}}$ units of the resource. Those individuals receiving $f_n \geq f_{\text{Min}}$, the quantity needed to keep an individual alive (f_{Min} – maintenance cost), give birth in proportion to the fraction of the maximum demand that is met

$$b_n = B_{\text{Max}} \frac{f_n - f_{\text{Min}}}{f_{\text{Max}} - f_{\text{Min}}}; \quad f_n \geq f_{\text{Min}} \quad (1)$$

where b_n is the number of offspring born to the n -th individual rounded down to the nearest whole number and B_{Max} is the maximum possible per capita birth rate. The total number of offspring Y in time step t is the sum of all b_n of N_t individuals. Survival of these offspring occurs with probability s . To include demographic stochasticity the number of actually surviving offspring is drawn from a binomial distribution with mean sY . After reproducing, parents die with probability d_0 . Those individuals receiving $f_n < f_{\text{Min}}$ die of starvation without reproducing. Thus, both reproduction and survival of adults are density dependent. Surviving offspring and adults become the population entering the next time step (a flow chart of the simulation model is given in Fig. 1). The individual-based model and

resulting population dynamics in constant or just slightly variable environments have been analysed in Johst et al. (2008).

Resource competition among individuals

In the IBM we simulate four basic resource partitioning schemes exemplifying pure contest and scramble competition and two strategies in between these extremes. Note that a variety of possibilities exist for defining these “in-between” strategies. To check the impact of different choices on the results we chose two different strategies.

Scramble competition (S-model) is characterized by random resource partitioning and represents competition between socially equivalent individuals. The single units of the available resource are given to individuals drawn at random from the population.

Contest competition (C-model) is characterized by social dominance. Some successful (dominant) animals (at maximum F/f_{Max} rounded down) get all the resources they require for survival and reproduction (f_{Max}) and the unsuccessful animals get nothing. For example, at the parameter set p2 (given in the caption of Table 1) 25 individuals get f_{Max} ($F/f_{\text{Max}} = 1000/40 = 25$).

Mixed competition (CS-model) is a mix of the two pure strategies of the C- and S-model. To generate this mix a constant number of dominant individuals (we assumed 5 individuals) gets all the resource needed (C part), the rest of the resource is then distributed randomly among the

other individuals (S part). Note that selecting a different number of dominant individuals (i.e., more or less than 5) would vary the proportion of contest versus scramble competition within mixed competition. Selecting 25 dominant individuals ($25 = F/f_{\text{Max}}$) the CS-model equals the C-model (pure contest competition) and, selecting zero dominant individuals, the CS-model equals the S-model (pure scramble competition). Thus, choosing less (more) dominant individuals does not change the conclusions but makes the results just more similar to those of pure scramble (contest) competition.

Intermediate competition (I-model) is another way to describe competition in between the pure strategies (C- and S-model). Again food is given to individuals drawn at random from the population but contrary to the S-model, individuals have the ability to monopolise resources and can consume more than one food item at once. The number of items per individual is drawn from a Poisson distribution with mean $= f_{\text{Max}}^{0.5}$. Similar to the CS-model, the I-model includes the limits of pure scramble (mean $= f_{\text{Max}}^0$) and pure contest (mean $= f_{\text{Max}}^1$) by adapting the exponent.

Types of exogenous fluctuations influencing individual performance

We distinguish two types of exogenous fluctuations; (1) fluctuations in resource availability (referred to as food fluctuations), which influence the reproduction (according to Eq. (1)) and survival of adults via intra-specific

Table 1 Summary of the general results of model selection

Fluctuations Model	Set	Food fluctuations	Weather fluctuations	Food and weather fluctuations
C-model	p1	MSS L + NL	MSS V + L	MSS L + NL + V
	p2	MSS L + NL	MSS V + L	MSS L + NL + V
	p3	MSS L + NL	MSS V + L	MSS L + NL + V
S-model	p1	Ricker L + NL	MSS V + L	Ricker L + NL* + V
	p2	Ricker L + NL	Ricker V + NL	Ricker L + NL + V
	p3	Ricker L + NL	MSS V + L	Ricker L + NL* + V
CS-model	p1	Ricker L + NL	MSS V + L	Ricker L + NL* + V
	p2	MSS L + NL	Ricker V + L	Ricker L + NL + V
	p3	MSS L + NL	Ricker V + NL	Ricker L + NL + V
I-model	p1	MSS L + NL	Ricker V + L	MSS L + NL* + V
	p2	MSS L + NL	Ricker L + NL	Ricker L + NL + V Ricker L + NL* + V
	p3	MSS L + NL	MSS V + L	

The influence of the type of exogenous fluctuations (columns) and the type of competition (rows) in the IBM on the functional form and perturbation type of the (statistically inferred) stochastic R -function for three different parameter sets (reference parameter set p2: $B_{\text{Max}} = 8$, $f_{\text{Min}} = 10$, $f_{\text{Max}} = 40$, $d_0 = 0.3$, $\bar{F} = 1000$, $\bar{s} = 0.5$; parameter set p1: p2 but $f_{\text{Min}} = 5$; parameter set p3: p2 but $f_{\text{Max}} = 100$). Perturbation type: V stands for vertical, L for lateral and NL for nonlinear perturbations in the R -function (see “Lateral, vertical and nonlinear perturbations”). The types of competition (C-, S-, CS-, or I-model) are explained in Methods Sect. “Resource competition among individuals”. MSS stands for a ‘hyperbolic’ and Ricker for an ‘exponential’ functional form of the R -function (see “Functional form”). The asterisk indicates which covariate (weather or food*) was used for the nonlinear perturbations

competition for a limiting resource F , and (2) fluctuations in the subsequent survival of young (referred to as weather fluctuations). These two types were chosen as they represent basically different exogenous influences: one influence acts via competitive interactions of individuals for a limiting resource and the other one acts independently of it. Separately and in combination they result in the following three types of exogenous fluctuations.

(a) *Exogenous fluctuations in the limiting resource (food fluctuations)* were simulated by letting the food F_t vary randomly over time. For simplicity, we assumed a uniform distribution of F_t between $\bar{F} \pm \sigma_F \bar{F}$, where \bar{F} is the mean food supply and σ its variation range. As differences in ‘hyperbolic’ versus ‘exponential’ model performance could not be detected in constant or slightly variable environments (Johst et al. 2008) we used a rather high level of variability ($\sigma_F = 0.5$). Our conclusions do not depend on the specific value of this variability.

(b) *Exogenous fluctuations in the survival of young (weather fluctuations)* were simulated by randomly varying the survival probability of offspring Y in each time step t (i.e., s becomes s_t ; e.g., through varying yearly weather conditions) such that the mean number of surviving offspring at time t is then $s_t Y$. For simplicity, we assume a uniform distribution of s_t between $s_t = \bar{s} \pm \sigma_s \bar{s}$, where $\bar{s} = 0.5$ is the mean survival and σ_s the variation range (for demonstration purposes we use maximum variability of s_t between zero and one i.e., $\sigma_s = 1$). Note that we also tested Gaussian distributions, which did not alter our general conclusions.

(c) *Combined exogenous fluctuations (food and weather fluctuations)* were simulated by including fluctuations in both the limiting resource [as described in (a)] and survival of offspring [as described in (b)].

R-functions

Time-discrete per capita R -functions are defined as:

$$R(N_{t-1}) = \ln(N_t/N_{t-1}) = R_{\text{Max}} + \tilde{f}((N_{t-1}/K)^a) \\ = R_{\text{Max}} + f(a \times (\ln N_{t-1} - \ln K)) \quad (2)$$

R_{Max} is the maximum per capita change over a discrete time step, N_t refers to individual numbers at time t , and K is the equilibrium density or carrying capacity of the environment. The parameter a alters the curvature of the R -functions, with small values giving rise to greater convexity ($d^2R/dN^2 > 0$) and large values greater concavity ($d^2R/dN^2 < 0$). Note that this parameter is multiplicative at logarithmic scale $\ln(N_t)$. The variety of functional relationships suggested for Eq. (2) can be classified into two basic functional forms (Royama 1992).

Functional form

For comparison with the IBM simulations, we first use a ‘hyperbolic’ (sensu Royama 1992) functional form: $\frac{N_t}{N_{t-1}} = \frac{e^{R_{\text{Max}}}}{1 + (e^{R_{\text{Max}}} - 1)(N_{t-1}/K)^a}$ called MSS equation as it has been introduced by Maynard Smith and Slatkin (1973). Logarithmic transformation according to Eq. (2) results in:

$$R(N_{t-1}) = R_{\text{Max}} - \ln[1 + (e^{R_{\text{Max}}} - 1)(\exp(a \times (\ln N_{t-1} - \ln K)))] \quad (3)$$

Second, we use an ‘exponential’ (sensu Royama 1992) functional form known as generalized Ricker equation: $\frac{N_t}{N_{t-1}} = \exp(R_{\text{Max}} \times (1 - (N_{t-1}/K)^a))$. Logarithmic transformation according to Eq. (2) results in:

$$R(N_{t-1}) = R_{\text{Max}} - R_{\text{Max}} \exp(a \times (\ln N_{t-1} - \ln K)) \quad (4)$$

Lateral, vertical and nonlinear perturbations

Following Royama (1992), environmental stochasticity E_t influencing these R -functions can be classified as vertical, lateral or nonlinear exogenous perturbations (see also Lima et al. 2008a, b).

(a) *Vertical perturbations* describe situations in which environmental influences affect the density-independent term R_{Max} and there is no interaction between E_t and population density. Thus, Eq. (2) results in

$$R(N_t, E_t) = R_{\text{Max}}(E_t) + f(a \times (\ln N_t - \ln K)) \quad (5)$$

i.e., environmental influences are additive at a log-scale.

(b) *Lateral perturbations* describe situations in which the environmental factor affects the carrying capacity K . Then, environmental influences are non-additive and Eq.(2) can be generally written as

$$R(N_t, E_t) = R_{\text{Max}} + f(a \times (\ln N_t - \ln K(E_t))) \quad (6)$$

(c) *Nonlinear perturbations* describe situations in which the environmental factor influences the nonlinear curvature a of the R -function. Environmental influences are again non-additive and Eq. (2) can be written as

$$R(N_t, E_t) = R_{\text{Max}} + f(a(E_t) \times (\ln N_t - \ln K)) \quad (7)$$

Note that a population may be subject to all these types simultaneously.

Statistical fitting of the stochastic R-functions resulting from the IBM simulations

We evaluated the effectiveness of the functional forms (Eqs. (3), (4)) in describing the observed relationships between growth rate and density by fitting them to the simulated data points of the stochastic R -function

generated by 50 simulation runs. The perturbation type (lateral, vertical, nonlinear) was included by shifting Eqs. (3), (4) along the y -axis (i.e., vertically according to Eq. (5)) or x -axis (i.e., laterally according to Eq. (6)), or by varying the nonlinear curvature a of these equations (according to Eq. (7)). Equations (3) and (4) were then fit by nonlinear regression using the *nls* library in the program R and computing the $AIC = -2 \times \log(\text{likelihood}) + 2 \times (\text{number of parameters})$ (Bates and Watts 1988). The stochastic R -function was selected according to lower AIC values indicating a more parsimonious model. The use of the AIC is justified because the number of parameters is different among the competing models: instead of comparing only lateral, vertical or nonlinear perturbation effects on each type of competition model (Eqs. (3), (4)), we were also interested in testing if one type of exogenous fluctuations (food or weather) can influence more than one parameter simultaneously (e.g., combined lateral and vertical perturbations).

Results

Figure 2 shows the ‘true’ stochastic R -functions resulting from the IBM simulations. These R -functions differ with respect to the type of competition (see “[Resource competition among individuals](#)”) and the type of exogenous fluctuations (see “[Types of exogenous fluctuations influencing individual performance](#)”). Comparably low fluctuations arise from demographic stochasticity inherent to the IBM simulations (dark grey points). One of the characteristics of all R -functions is the constant plateau at low population densities. This exhibits the range of density independent population growth: all individuals obtain sufficient resources to satisfy their maximum demand f_{Max} , and therefore population growth at maximum rate R_{Max} is possible. This is also outlined in the analytical considerations ESM 1 of the Electronic Supplementary Material (ESM) for pure scramble and contest competition. As the analytical formulas derived in ESM 1 are simplified representations of the dynamics of the IBM and are valid only in the corresponding density ranges, predictions of the impact of exogenous fluctuations (food or weather fluctuations) on the combination of perturbations in the statistically inferred R -function as a whole (i.e., $R(N)$ covering the whole density range) are not possible. The same is true for predictions on the functional form of the R -function directly from Fig. 2. In the style of time series analyses, we therefore perform a statistical analysis of the density dependent stochastic population growth resulting from the IBM simulations. We study which combination of perturbations in the aggregated stochastic R -function results from which type of competition (scramble, contest and types in-

between) in which environment (food and/or weather fluctuations). ESM 2/Table S1 shows detailed results of the statistical analysis, including the sensitivity analysis. Table 1 summarizes these results and gives an overview of which model performed best (that is showed the lowest AIC) in which situation.

‘Exponential’ or ‘hyperbolic’ functions

‘Hyperbolic’ MSS functions (Eq. (3)) and ‘exponential’ Ricker functions (Eq. (4)) performed differentially in describing the simulated data. Table 1 shows that for pure contest competition (C-model) all types of exogenous fluctuations and parameter sets were better described by MSS functions. For pure scramble competition (S-model) 7 out of 9 scenarios were better described by Ricker functions. For competition in between pure contest and scramble competition (CS- and I-model), MSS functions better described food fluctuations and Ricker functions generally better described weather and combined food and weather fluctuations.

Lateral, vertical or nonlinear perturbations

Food fluctuations generally emerged as combined lateral and nonlinear perturbations, irrespective of the type of resource competition (Table 1). These perturbations were implemented into MSS functions, except for pure scramble competition, for which a generalized Ricker function performed better.

Weather fluctuations emerged as combinations of vertical and lateral perturbations (9 out of 12 scenarios). The remaining 3 scenarios resulted in combined vertical and nonlinear perturbations (Table 1). For pure contest competition (C-model), weather fluctuations emerged as a combination of vertical and lateral perturbations implemented into an MSS function. For the other types of competition, MSS and Ricker functions did similarly well to describe weather fluctuations depending on the parameter set (Table 1).

The combination of food and weather fluctuations re-emerged in all cases as a combination of lateral, vertical and nonlinear perturbations (Table 1). This result did not depend on which covariate (weather or food) was used for the nonlinear perturbations (ESM 2/Table S1). For all types of resource competition, Ricker functions fitted best with exception of the C-model for which MSS functions fitted best.

Discussion

Using a simple individual-based simulation model (IBM) in combination with a statistical fit of the resulting time

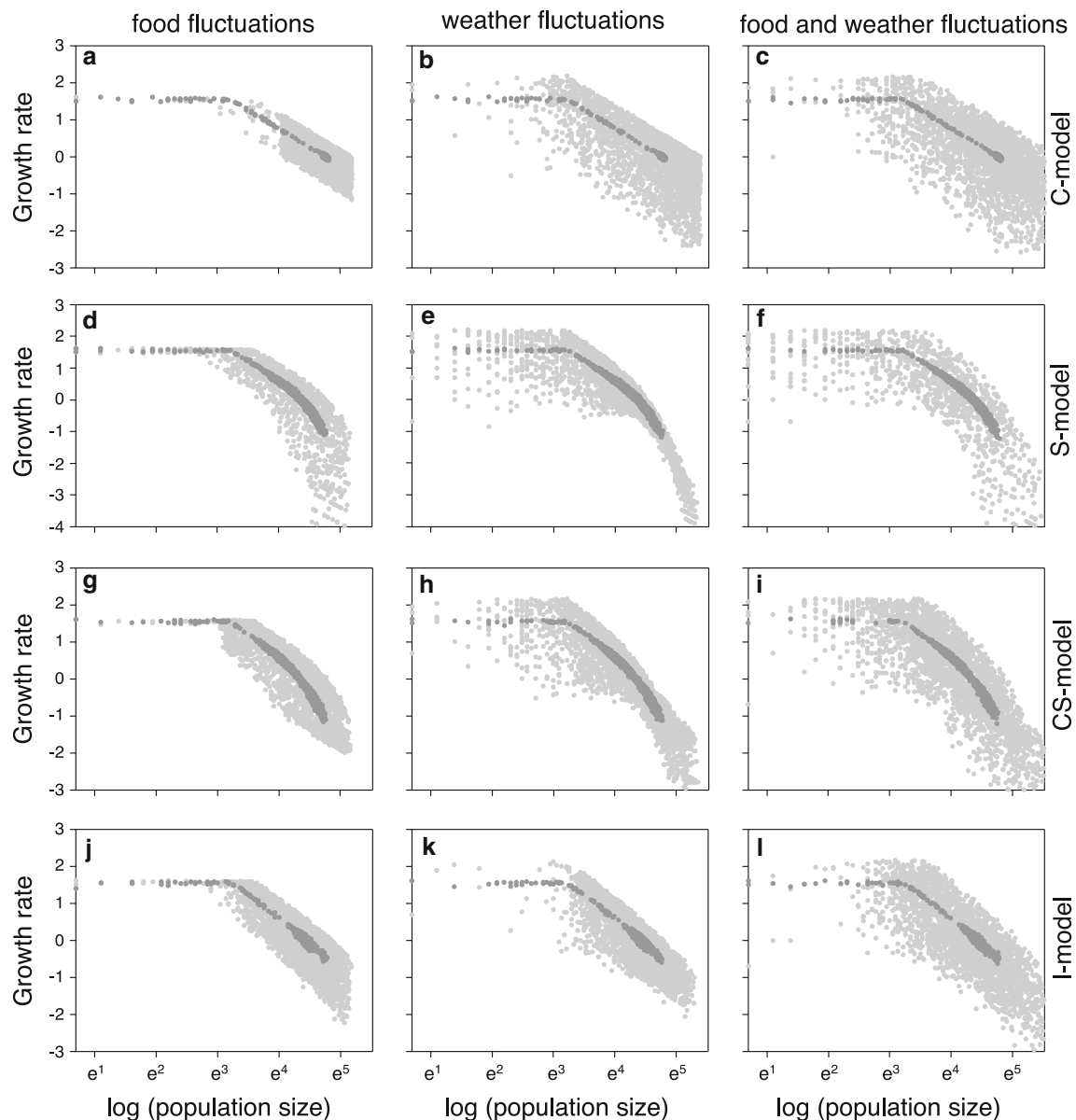


Fig. 2 Stochastic per capita population growth rates $R(N_{t-1}) = \ln(N_t/N_{t-1})$ resulting from the IBM simulations versus the natural logarithm of population size. Different scenarios of environmental fluctuations (columns) and resource competition (rows) are shown (for details see “Resource competition among individuals”, “Types of exogenous fluctuations influencing individual performance”; for

parameters see caption of Table 1). Light gray points show growth rates including demographic and environmental stochasticity. Dark gray points refer to a constant environment with demographic stochasticity inherent to the IBM. The scales of the vertical axes differ among the panels

series, we studied the impact of different exogenous factors (food and/or weather fluctuations) at the individual level in interaction with different types of individual competition (contest, scramble and competition in between these two extremes) on the resulting aggregated (statistically inferred) stochastic R -function. We focus on functional form (i.e., ‘hyperbolic’ MSS or ‘exponential’ Ricker functions, Eqs. (3), (4)) and on perturbation type (i.e., lateral, vertical and nonlinear perturbations, Eqs. (5)–(7)). Exogenous influences are simulated through stochastic fluctuations of

particular parameters in the IBM and resource competition types through different partitioning schemes among the individuals (see “Resource competition among individuals”). We keep our IBM as simple as possible to understand how exogenous and endogenous factors interact and re-emerge in an aggregated population model.

Our results clearly show that in variable environments the performance of an aggregated growth function to describe the resulting dynamics depends on the synergistic effects of the type of individual competition for resources

(C-, S-, CS- or I-model), the resource requirements (f_{Min} and f_{Max}) and the nature of exogenous fluctuations (food and/or weather fluctuations). This is now discussed in more detail.

Function choice ('hyperbolic' or 'exponential' functions)

Although in constant or only weakly variable environments 'hyperbolic' MSS and 'exponential' Ricker functions performed equally well in describing different types of competition (Johst et al. 2008), we found that in more variable environments the function choice generally depends on the type of competition and the nature of exogenous fluctuations. The strength of environmental variability at which the different performance of the two functional forms becomes apparent may vary with the type of competition, the resource requirements and the type of exogenous influences. Therefore, no clear thresholds can be given.

Nevertheless, it can be argued that in variable environments the MSS function was generally more appropriate for describing pure contest competition (C-model) whereas the Ricker function was generally more appropriate for describing pure scramble competition (S-model) in accordance with arguments based on the competition type alone (Royama 1992). This result is independent of the type of exogenous fluctuations (food and/or weather fluctuations).

If competition cannot be adequately described as pure contest or scramble competition but is in between these two extremes, both MSS and Ricker functions were appropriate depending on the type of exogenous fluctuations (Table 1). Both the CS- and the I-model behave similar to a 'hyperbolic' contest model for food fluctuations (Table 1, compare also Fig. 2g, j with Fig. 2a), but like an 'exponential' scramble model for combined weather and food fluctuations (Table 1, compare also Fig. 2i, l with Fig. 2f). In the case of pure weather fluctuations, both MSS and Ricker functions were appropriate depending on the resource requirements (see different parameter sets in Table 1). These results demonstrate that arguments for using a certain functional form to describe competition in between pure contest and pure scramble competition depend not only on the competition type but also on the interplay between endogenous and exogenous (respectively deterministic and stochastic) factors.

There is growing evidence, also from other analyses, that deterministic skeleton and environmental variation can interact (e.g., Coulson et al. 2004; Benton et al. 2006; Boyce et al. 2006). However, mechanistic explanations for this interaction are still needed. Based on our IBM, we can give an ecological mechanistic explanation for this interaction and how it shapes our results. Food fluctuations operate only when food supply is limiting, i.e., at high

densities and low food supply, respectively. Then the CS-model behaves similarly to the pure contest model: a small part of the population gets all the resource needed ($f_n = f_{\text{Max}}$), the rest (which is in the CS-model scrambling for the resources) gets nothing ($f_n = 0$). Therefore when food fluctuates, the CS-model (and similarly the I-model) behaves like a 'contest' model (compare Fig. 2g, j with Fig. 2a). Weather fluctuations operate via external mortality effects and not via competitive interactions between the individuals. Thus, they operate across all densities but their relative impact changes: At low to intermediate densities, a few individuals get all they need and even the rest of the population scrambling for resources gets sufficient food for reproduction. Subsequently, a large number of offspring is produced by scramble competition and weather fluctuations affect their survival. At larger densities, weather fluctuations have less impact as the number of offspring is low (similar to pure scramble competition, compare Fig. 2h with Fig. 2e). Thus, with weather fluctuations the scramble part dominates the dynamics and the CS-model behaves more similar to an S-model.

Perturbation choice (lateral, vertical or nonlinear perturbations)

In contrast to function choice which was determined by the synergistic effects of both endogenous and exogenous (respectively deterministic and stochastic) factors, perturbation choice was mainly determined by the exogenous factors alone.

Lateral perturbations performed well in all cases that consider food fluctuations at the individual level (generally imbedded in an MSS function, except for pure scramble competition where it is a Ricker function). Recent analyses of ecological time series have revealed the importance of considering lateral perturbations whenever a limiting resource such as food is influenced by climate (Berryman and Lima 2006; Lima and Berryman 2006; Lima et al. 2006, 2008a, b; Andreo et al. 2009; Estay et al. 2009; Previtali et al. 2009). Our results confirm this and our hypothesis that lateral perturbations represent food fluctuations much better than other perturbation types. However, the best representation was a combination of lateral and nonlinear perturbations (Table 1) suggesting that besides the effect on the equilibrium density (carrying capacity) an extra effect on the curvature of the aggregated R -function is generated.

This extra effect can be understood by considering the constant plateau at low population densities (Fig. 2, see also Johst et al. 2008). As explained above, this plateau is characteristic to all types of resource competition and exhibits the range of density independent population growth at which all individuals get what they need (f_{Max}).

Density dependent population growth sets in at population sizes larger than $N_{dd} = F/f_{\text{Max}}$. Thus, fluctuations in F (food) affect not only equilibrium density (carrying capacity K) but also this onset value N_{dd} of density dependence (see also Analytical considerations in ESM 1). As a consequence, there is an extra effect of food fluctuations on the nonlinear curvature of the aggregated R -function. Nevertheless it is important to state that in ecological time series there are often few or no data points at very low population densities. In case of food fluctuations (i.e., fluctuations in a limiting resource) simple models including only a lateral perturbation can then be the best option.

Contrary to our expectations, weather fluctuations in the IBM did not re-emerge as pure vertical perturbations but as combined vertical and lateral perturbations or combined vertical and nonlinear perturbations (Table 1). Although weather fluctuations operate via an external mortality of young and therefore independent of population density, their relative impact can be stronger (weaker) at lower (higher) densities. As the aggregated R -function has to cover the whole range of densities, weather fluctuations at the individual level can re-emerge as complex fluctuations at the population level such that population growth and equilibrium density are affected not only by (additive) vertical perturbations but also by (non-additive) lateral or nonlinear perturbations in the per capita growth rate. This suggests that unequivocal conclusions from a single perturbation type (e.g., lateral perturbations) in a statistically inferred R -function resulting from time series analyses to the actual exogenous factor at the individual level (e.g., food or weather fluctuations) are not possible.

Based on these results, some general ecological guidelines for model selection can be formulated. These guidelines can be used to save time and reduce the number of trials required to find the right, ecologically reasonable model structure.

Ecological guidelines for model choice of the stochastic growth function

Fluctuations of limiting exogenous factors (e.g., food fluctuations) should be described by a combination of lateral and nonlinear perturbations imbedded into ‘hyperbolic’ functions (except for pure scramble competition which requires ‘exponential’ functions). Fluctuations of non-limiting exogenous factors (e.g., weather fluctuations) should be described by a combination of vertical and lateral/nonlinear perturbations imbedded into ‘exponential functions’ (except for pure contest competition which requires ‘hyperbolic’ functions). If both non-limiting and limiting exogenous factors fluctuate (e.g., food and weather fluctuations), combinations of vertical, lateral and nonlinear perturbations should be considered imbedded into

‘exponential’ functions (except for pure contest competition which requires ‘hyperbolic’ functions).

Conclusions

Model choice for the stochastic per capita growth function in population dynamics and time series analysis should carefully consider two different aspects: function choice (i.e., the question of the deterministic functional form) and perturbation choice (i.e., the question of the stochastic ‘lateral, vertical or nonlinear’ perturbation type).

In general, our results suggest that for competition in between pure contest and scramble which is common in nature the question concerning the functional form cannot be answered without considering the type of environmental variability (i.e., whether non-limiting or limiting exogenous factors fluctuate). Our results highlight that even ‘simple’ exogenous fluctuations at the individual level (food and weather fluctuations) can re-emerge as complex fluctuations of the per capita growth rate at the population level with combinations of lateral, vertical and nonlinear perturbations. This has strong implications for time series analyses of empirical data. In contrast to the widespread assumption of vertical perturbations in time series analyses, our findings highlight the importance of lateral and nonlinear perturbations and suggest that these (non-additive) perturbations should be considered on an equal footing with vertical (additive) perturbations.

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