Community response to enrichment is highly sensitive to model structure

Gregor F. Fussmann1,† and Bernd Blasius2

1Institut für Biochemie und Biologie, Universität Potsdam, Max-Planck-Allee 2, 14469 Potsdam, Germany
2Institut für Physik, Universität Potsdam, Am Neuen Palais, 14469 Potsdam, Germany
†Present address: Biology Department, McGill University, 1205 Avenue Docteur Penfield, Montreal, Quebec, H3A 1B1, Canada.

Biologists use mathematical functions to model, understand and predict nature. For most biological processes, however, the exact analytical form is not known. This is also true for one of the most basic life processes: the uptake of food or resources. We show that the use of several nearly indistinguishable functions, which can serve as phenomenological descriptors of resource uptake, may lead to alarmingly different dynamical behaviour in a simple community model. More specifically, we demonstrate that the degree of resource enrichment needed to destabilize the community dynamics depends critically on the mathematical nature of the uptake function.

Keywords: super-sensitivity; model structure; community dynamics; paradox of enrichment

1. INTRODUCTION

Simple community models predict that increasing the availability of resources will destabilize community dynamics from equilibria to oscillatory dynamics, a phenomenon termed the ‘paradox of enrichment’ (Rosenzweig 1971; Gilpin 1972; May 1972; Persson et al. 1996). Attempts to establish this effect in experiments or in the wild have met with only partial success (McCauley & Murdoch 1987, 1990; Persson et al. 2001), indicating that real communities respond to enrichment in a more complicated way than simple models suggest. Environmental conditions and properties of the community (web-like structure, shift to inedible prey, inducible defences) have been offered as explanations for why communities might fail to destabilize as a consequence of enrichment (Persson et al. 2001; Vos et al. 2004). Here, we offer a different explanation that is related to the properties of the mathematical model which was first used to put forth the ‘paradox’.

The classical Rosenzweig–MacArthur (R–M) model (Rosenzweig & MacArthur 1963) is probably the simplest formulation of a trophic community able to produce realistic dynamic behaviour (Turchin 2003). The model describes the changes over time of two populations coupled by predation:

\[ \frac{dx}{dt} = g(x) - f(x)y, \]
\[ \frac{dy}{dt} = f(x)y - my. \]

The prey population, \( x \), grows logistically at the rate \( g(x) = rx(1-x/K) \), where \( r \) is the growth rate of the prey and \( K \) is the carrying capacity. The predator, \( y \), consumes the prey and grows according to the nonlinear uptake function (functional response), \( f(x) \), and has mortality, \( m \). As is common practice (Rosenzweig 1971; Murdoch et al. 1998), enrichment is simulated in this model by increasing \( K \), i.e. by allowing the prey to grow to higher densities in the absence of predators.

We investigated whether the specific mathematical formulation of the functional response affects the community dynamics that the R–M model predicts. The surprising result is that the degree of destabilization caused by enrichment is extremely sensitive to the mathematical nature of the uptake function, that is, even functional response curves that are indistinguishable for all practical purposes may produce qualitatively and quantitatively different dynamics.

2. METHODS

Minimum requirements for realistic uptake functions, \( f(x) \), are that the function be zero at zero resource concentration, be monotonically increasing with resource density, and be saturating when resource density goes to infinity (Myerscough et al. 1996). To maximize similarity among different functional response curves we restrict ourselves to functions with negative curvature over the whole prey range (table 1; figure 1a). Ivlev’s function (Ivlev 1961) and Holling’s type II function (Holling 1959) are the most widely used functions that fulfil these requirements, but others, e.g. trigonometric functions, have been proposed (Jasby & Platt 1976). Given the error with which resource uptake by real organisms is measured, it is usually unjustified to identify a best-fitting model, and structurally different analytical forms may be used interchangeably. For our theoretical investigation, we chose a generic parameterization of Ivlev’s functional response \( (a_0=1, b_0=2) \) and used nonlinear least squares to maximize the phenomenological similarity with Holling’s type II response and a response curve based on a trigonometric function (table 1; figure 1a)

Graphical analysis revolves around plotting the curves (isoclines) in the prey–predator phase plane that denote zero growth of the model predator and prey populations. For Ivlev’s and Holling’s functional responses, the R–M model produces vertical predator isoclines (clines) in the prey–predator phase plane that denote zero growth of the model predator and prey populations. For Ivlev’s and Holling’s functional responses, the R–M model produces vertical predator isoclines (clines) in the prey–predator phase plane that denote zero growth of the model predator and prey populations. For Ivlev’s and Holling’s functional responses, the R–M model produces vertical predator isoclines (clines) in the prey–predator phase plane that denote zero growth of the model predator and prey populations. For Ivlev’s and Holling’s functional responses, the R–M model produces vertical predator isoclines (clines) in the prey–predator phase plane that denote zero growth of the model predator and prey populations.

3. RESULTS

It becomes immediately apparent that almost identical resource uptake curves (figure 1a) give rise to very
differently shaped prey isoclines (figure 1b,c), which have drastic consequences for the dynamic stability of the system. First, we study the case where the carrying capacity is set to unity, $K=1$ (figure 1b). In this case, only Holling's function has the potential to destabilize the population dynamics because only its prey isocline has an increasing portion for positive prey densities. With the two other functional responses, the prey isocline is decreasing and predator–prey dynamics settle on stable equilibria in both cases. This is also obvious from the simulated time-series of predator and prey densities starting from initial values close to the equilibrium (Electronic Appendix A). Using Holling's functional response, the equilibrium is stable and the trajectories settle into a stable limit cycle with large amplitudes. By contrast, the trigonometric function leads to a stable steady state. Ivlev's function produces a dynamical contrast, the trigonometric function leads to a stable limit cycle with large amplitudes. By the equilibrium is unstable and the trajectories settle from initial values close to the equilibrium (Electronic Appendix A). Using Holling's functional response, the prey isocline is decreasing and predator–prey dynamics settle on stable equilibria in both cases. This is also obvious from the simulated time-series of predator and prey densities starting from initial values close to the equilibrium (Electronic Appendix A). Using Holling's functional response, the equilibrium is stable and the trajectories settle into a stable limit cycle with large amplitudes. By contrast, the trigonometric function leads to a stable steady state. Ivlev's function produces a dynamical contrast, the trigonometric function leads to a stable limit cycle with large amplitudes. By the equilibrium is unstable and the trajectories settle from initial values close to the equilibrium (Electronic Appendix A). Using Holling's functional response, the prey isocline is decreasing and predator–prey dynamics settle on stable equilibria in both cases. This is also obvious from the simulated time-series of predator and prey densities starting from initial values close to the equilibrium (Electronic Appendix A). Using Holling's functional response, the equilibrium is stable and the trajectories settle into a stable limit cycle with large amplitudes. By contrast, the trigonometric function leads to a stable steady state. Ivlev's function produces a dynamical contrast, the trigonometric function leads to a stable limit cycle with large amplitudes. By the equilibrium is unstable and the trajectories settle from initial values close to the equilibrium (Electronic Appendix A).

Table 1. Critical enrichment values ($K_e$, carrying capacity) for dynamical stability in the R–M model formulated with three similar functional responses (figure 1a).

<table>
<thead>
<tr>
<th>level of enrichment</th>
<th>Holling $f_h(x) = a_1x^2/(1 + b_1x)$</th>
<th>Ivlev $f_i(x) = a_i(1 - \exp(-b_ix))$</th>
<th>trigonometric $f_t(x) = a_t\tanh(b_ix)$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$K&lt;0.45$</td>
<td>stable</td>
<td>stable</td>
<td>stable</td>
</tr>
<tr>
<td>$0.45&lt; K &lt;1.08$</td>
<td>unstable</td>
<td>stable</td>
<td>stable</td>
</tr>
<tr>
<td>$1.08&lt; K &lt;2.65$</td>
<td>unstable</td>
<td>unstable</td>
<td>stable</td>
</tr>
<tr>
<td>$2.65&lt; K &lt;10.12$</td>
<td>unstable</td>
<td>unstable</td>
<td>multi-stablea</td>
</tr>
<tr>
<td>$K &gt;10.12$</td>
<td>unstable</td>
<td>unstable</td>
<td>unstable</td>
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* Initial conditions determine whether dynamics are oscillatory or settle on equilibria.

To conclude, even though the resource uptake curves are nearly identical, the resulting time-course of predator and prey densities is very different in the three cases. This also has consequences for the extinction risk. Using the trigonometric response curve, both predator and prey abundance are always far from zero and therefore the populations have a high expectation of persistence. By contrast, with Holling's function the oscillating densities pass through very small values, putting them at a high risk of extinction. Again, the Ivlev response curve leads to intermediate behaviour. Initially, while the time solutions are still oscillatory there is a moderate extinction risk. However, with increasing time, the amplitude of the oscillations, and therefore the extinction risk, are more and more reduced.

With enrichment (by raising the carrying capacity), all three functions become potentially destabilizing, but not to the same degree (table 1; figure 2). Enrichment, by a fourfold increase of the carrying capacity ($K=4$) and leaving all other parameters unchanged, leads to limit cycles if Holling's or Ivlev's responses are used (figure 1c). However, with the same amount of enrichment the equilibrium remains locally stable in a system that is based on the trigonometric function. Nevertheless, for an appropriate choice of initial values, limit cycle oscillations can also be observed in this system, because in this range of intermediate enrichment, the trigonometric function results in multi-stability with coexistence of stable equilibrium and oscillatory dynamics (table 1). The system needs to be enriched even more ($K>10.12$) before destabilization occurs globally (table 1). Thus, the enrichment level at which the equilibrium is destabilized varies by a factor of more than 20 (table 1; figure 2). Although enrichment eventually leads to destabilization in all models, the vastly differing conditions at which it occurs will be disconcerting to anyone using mathematical models as a predictive tool.

The three functional responses can be ranked according to their potential to destabilize the dynamics of the R–M model (Holling $II >$ Ivlev $>$ trigonometric function). We found this pattern to be very general and extremely robust over wide ranges of the parameters $a_i$ and $b_i$, which determine the steepness and saturation level of the uptake function. The ranking remained largely constant even when we constrained our fits either to have the same slope at the origin or the same saturation level as Ivlev's function (Electronic Appendix A).

4. DISCUSSION

The dynamic stability of the R–M model and other models has been shown to depend on the type of functional response used (Oaten & Murdoch 1975; Armstrong 1976; Williams & Martinez 2004). It is important to understand that our result is of a very different nature. We did not study the effect on system stability of different functional response curves that represent mechanistically motivated alterations of a basic function, e.g. Holling's type I, II and III responses (Holling 1959). On the contrary, our goal was to investigate the effect of response functions that are as similar as possible phenomenologically, but are derived from entirely different mathematical foundations. What we found is that three functions, which are identical for any one using mathematical models as a predictive tool.

Sensitivity to model structure has been described for the R–M (Myerscough et al. 1996) and other ecological models (Wood & Thomas 1999; Gross et al. 2004), but we offer a simple explanation for this striking phenomenon based on the structural similarity...
of the mathematical functions that occur in the R–M model. Here, logistic prey growth, $g(x)$, and resource uptake, $f(x)$, are structurally very similar at small prey numbers, $x$. This has consequences for the prey isocline, $\gamma(x) = g(x)/f(x)$. (Recall that the stability of the equilibrium depends on the slope of $\gamma(x)$ at equilibrium.) In the extreme case that the two functions are exactly identical, the isocline is a constant $\gamma(x) = 1$, and has a slope of zero everywhere. Thus, linear stability is not well defined and the system is structurally unstable. But assume that in some range close to the equilibrium point the two functions differ slightly, except for a constant: $g(x) = g(x) + \varepsilon(x)$, where $\varepsilon(x)$ is a small function. Now the isocline can be approximated as $\gamma(x) \approx \alpha(1 - \varepsilon(x))/g(x)$ and in this range the sign of the slope of $\gamma(x)$ entirely depends on the difference, $\varepsilon(x)$. Therefore arbitrary small deviations of resource uptake, $f(x)$, from the prey growth rate, $g(x)$, determine the stability of the equilibrium.

We emphasize that the whole argument relies on the fact that, in the relevant interval, prey growth, $g(x)$, and resource uptake, $f(x)$, are structurally very similar functions. In the R–M model this is always the case for small prey numbers because both $g(x)$ and $f(x)$ start from zero as negatively curved functions (this becomes apparent from a Taylor expansion of $f(x)$ up to second order). Thus, whenever the equilibrium is at small prey levels, e.g. for small mortality, $m$ (as in figure 1), the R–M model is sensitive to minor variations in the form of the functional response curve. By contrast, if the equilibrium is at large values of $x$, where prey growth and resource uptake are significantly different functions, e.g. at large or intermediate levels of mortality, $m$, the effect of sensitivity to the model structure is not observed.

The same mechanism lies at the heart of one of the major drawbacks of the original Lotka–Volterra model, which is a special case of the R–M model where prey growth and resource uptake are linear functions, i.e. $g(x) = ax$ and $f(x) = bx$. In this model the expression $g(x)/f(x)$ is constant per definition, which leads to structural instability in the whole parameter range. With the introduction of nonlinear logistic prey growth and saturating functional response, Rosenzweig and MacArthur tried to circumvent these problems. Indeed this works out for most parameter ranges. However, as shown above, the same difficulties of sensitivity to infinitesimal variations in the model structure are still inherent in the R–M model and are able to enter through the back door in, for example, cases of small mortality.

Sensitivity to model structure may be responsible for the failure to observe destabilization as a result of enrichment in real communities. This is not to say that mechanistic explanations should generally be ruled out. McCauley et al. (1999), for example,
showed convincingly that competition between inedible and edible prey can reduce the effective carrying capacity of the prey and thereby stabilize the community dynamics. We caution, however, that such conclusions should not be drawn prematurely, based on a mismatch between a particular theoretical model and empirical results. Instead, we advise an evaluation of the robustness of model predictions for alternative mathematical formulations whenever the exact mechanistic nature of the resource uptake is not known. Currently, ecological modellers use Holling’s type II function as a standard in consumer–resource models although the true uptake mechanism may vary across and within communities (Jeschke et al. 2002; Mols et al. 2004). Our analysis has demonstrated that a much higher degree of enrichment may be required for destabilization than such standard models predict. We conclude that, unless the exact mechanistic nature of the relationship between consumer and food is known, caution should be used when predicting predator–prey dynamics and the effect of enrichment without considering the effects of sensitivity to model structure.

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