Applying DEB-theory in Globif

George A.K. van Voorn

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1 Introduction

The study of theoretical population ecology goes back a long way; already in 1926 the famous Lotka-Volterra (LV) model was developed. Several 'upgraded' models have been proposed since then (Monod, Holling, Marr-Pirt, Droop), none of which are truly undisputed. DEB, as developed by Kooijman [5], provides a new framework and shows that all the before-mentioned models are special cases of a more generalized model (although still disputed).

In this essay I will discuss the possibilities that DEB-theory offers for my project, Globif. Globif is a project in which bifurcation analysis is used as a primary tool to do research on the interactions between species in communities and to investigate which bifurcations could be of significant influence on population dynamics. First, I'll evaluate some problems that exist with (ecological) modeling in general. Next, I'll discuss which of those problems are (partly) solved in DEB, followed by an assessment of the results DEB has led to so far. Finally, a discussion section follows on what DEB could contribute to Globif during the project. For that, I distinguish between two aspects in Globif: a mathematical part (what can we do?) and an ecological part (what would we like to do?).

2 Ecological modeling in general and in DEB

Much of the work done today is still based on the 'older' models present in theoretical ecology. However, several problems are known to exist regarding these models.

One apparent (and general) problem with modeling is that models, with regard to concepts used by more experimentally focused researchers, are relatively simple. Experimentalists emphasize the apparent complexity of Nature, while many ecological models discard all forms of variation in species traits and spatial heterogeneity (unstructured population models). For instance, the predicted increasing instability of larger food webs (May, 1973 [6]) seems to collide with the 'intuitive' ideas of experimental ecologists. On the other hand, 'simple' models have already been shown to be able to demonstrate 'complex' behaviour, such as the 'paradox of enrichment' (POE).

A second problem is that many models suffer from inconsistencies and dubious assumptions. For example, LV models the prey-population as 'self-maintaining'. As a result, LV often violates the law of mass preservation this way. Consequently, any conclusions drawn from a LV-based model should be checked for realism and range in which these results are valid (this is, by the way, part of the problem I have with the POE, ironically the reason I got interested in theoretical biology in the first place: it was found using a LV-based model, so when are the hidden assumptions true?)

Younger, more advanced models still demonstrate the problem with implicit assumptions. There is still the issue of 'homogenized' populations and environments, partly simply because the appropriate mathematical tools are not developed yet. And many times also the basic principles of preservation of mass or explicit description of energy flow are still neglected.

One of the major improvements in ecological modeling is the explicit description of nutrients (the zero-trophic level) and energy flow. This allows for a complete mass balance. The drawback here is one has more equations to solve, while the major asset is that it avoids primary inconsistencies.

The primary contribution of DEB to modeling (in general) is the division of individual biomass into reserves and structure. DEB differs from other population models in that it is 'individual-oriënted' instead of population oriënted. This division into reserves and structure however does complicate calculations. Additionally, assumptions need to be made to go from 'individual-oriënted' to populations.

Another contribution of DEB is the concept of 'synthesizing units' (SU's). The application of SU's can have significant consequences for the functional response (as for example demonstrated by Ferreira, 2003 [1]), which is important for the interactions between populations.

3 Results with the DEB-model

As mentioned in the previous section, one of the contributions of DEB to modeling is the distinction between structure and reserves. One of the results of applying DEB in population modeling (that is also demonstrated in Marr-Pirt) is that populations need a certain minimum value of prey/nutrient biomass to invade the system. Reserves and maintenance have been incorporated in previous models (Droop and Marr-Pirt, respectively), but never on the individual level.

An interesting thing to point out is the partition ability of reserves. In DEB-theory the reserves can be divided into separate flows for several elements. The nice thing with DEB is that you can focus on the limiting flow (mostly N or P) and add any level of detail you wish for. Light can be taken into account as a limiting resource as well, since DEB treats the mechanism for capturing photons basically the same as mechanisms for the uptake of nutrients or carbon-dioxide (again, through SU's).

One of the problems in ecological modeling is the necessity to 'keep it simple', therefore many models are unstructured. In DEB however it is possible, under certain circumstances, to simplify a structured populations of V1-morphs to an unstructured one ([5], p. 315). Under certain conditions the individual mass of V1-morphs is a simple function of volume, hence the population biomass is a linear function of individual mass. As a result, there's no distinction between structured and unstructured populations of V1-morphs. This is of course a major gain, since the math involved in structured population models is awfully complex.

In contrast with May's predictions DEB seems to stabilize food webs at a higher level, due to the implementation of maintenance and reserves. Compared to Monod (neither) and Marr-Pirt (only maintenance) the DEB model for bi- and tritrophic food chains appears to exhibit increased stability ([5], p. 314 and 3.49). Furthermore, it has been shown that in a bi-trophic DEB food chain another level-two species can invade next to the existing species, seemingly defying the under experimentalists generally accepted concept of 'competitive exclusion' ([5], p. 350).

4 Discussion

In the Globif project there's a focus on the use of bifurcation analysis, so it's interesting to discuss the change in bifurcation behaviour of models based on DEB compared to other models. Kooi et al. [3] have already pointed out some of the consequences that DEB has for the bifurcation analyses of such models, for instance that a multi-species community cannot exist for very small dilution rates combined with low concentrations of substrate in the reservoir (as compared with Monod). Rather, higher trophic levels can only exist when both of these factors are large enough. It also seems to combine features of both Marr-Pirt-based and Droop-based models (which coincides with combining maintenance and reserves). It seems that the general outline of transcritical and Hopf-bifurcations in DEB is comparable with that of

Marr-Pirt, while DEB and Droop have a Bautin point in common on the Hopf-3 line, as well as that the codimension point M1 is a codimension 2 point.

The second aspect of Globif is the study of interactions in food webs. One thing that seems to become clear in explicitly describing the nutrient flows is that trophic interactions are not so well-defined as they are commonly said to be. For example, species X and Y have some form of relationship in which X produces a substance that's beneficial for Y and Y makes a source available for X. When due to some reason X does not produce the substance under certain circumstances, rather than 'mutual beneficial', this relationship would now be named 'parasitic'. The explicit description of nutrient flows could shed more light under what sort of circumstances the relationship might change.

A suggestion that follows from DEB is regarding the principle of 'competitive exclusion'. From DEB-theory it follows that two populations of V1-morphs would only compete with each other when their specific population growth rates are identical. This only happens when the energetic properties of the two species are identical. This defies the general belief that since no two species can live on one substrate, this relationship is linear and no more than X species can live on X substrates. DEB suggests that species on the same trophic level can perfectly co-exist, since differences in preferences and partial overlap in food prevent competition ([5], p. 302). One problem, however, could be the question whether the same goes for isomorphs. Nevertheless, these results are stimulating: increasing diversity seems to go well with stability.

Part of the research in the very near future is supposed to address the issue of interactions between populations. One of those case studies regards the problem of how the POE can be eliminated in the unstructured (DEB-) models. The proposed mechanism will be the mutual interference between individuals [7] (or social interaction, as it is called in DEB, but I prefer the historical term by Hassell [2]), which could provide a clue about possible interactions in general between organisms. So far, the (sparse) results seem promising. On the other hand, many mechanisms have already been proposed to eliminate the POE, although it should be taken into account what models where used in those cases. Part of the contribution of this case study will be just to evaluate how DEB itself is doing.

Another aspect of Globif is about the (in)stability of ecosystems. Case studies using DEB-theory will be developed in future research to either verify or falsify the idea that increased diversity does not lead to instability. So far, studies seem to confirm stability in ecosystems through complexity. Kooi and Kooijman [4] found that invading competiting prey can stabilize a bi-trophic food web, and a study of a closed community consisting of prey that are infected by pathogens and preyed upon by predators revealed that predators, by having a preference for the weak, actually increase ecosystem stability [8].

Remains the very important issue whether the benefits from DEB are not outweighted by the mathematical complexity due to the increase in equations. Also, it remains to be seen under what kind of assumptions or conditions the DEB individuals are correctly scaled up to populations. The importance of reserves depends on what kind of organisms the model applies to (although I prefer general models). For instance, it is known that mice and other small mammals need to feed often or they die of starvation (DEB has an explanation for this as well). On a larger time scale, one could say it's not really interesting to specifically look at the reserves of such organisms, and therefore one shouldn't bother with such an increase in detail.

Concluding, Globif could benefit well from DEB through the explicit description of the nutrient level. The way that structured populations under certain conditions can simplify to unstructured populations can generalize results gained with the unstructured models that will be used. Regarding the ecological side of Globif, it seems that DEB could clarify many aspects of community dynamics as a result of closed mass balances and the explicit description of nutrient, such as ecosystem (in)stability through species interactions. On the other hand, the number and/or complexity of the equations increases significantly, and practically spoken DEB will need to be beneficial enough to validate its use.

References

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