

Available online at www.sciencedirect.com**ScienceDirect**

Physics of Life Reviews ••• (••••) •••–•••

**PHYSICS of LIFE
reviews**www.elsevier.com/locate/plrev

Comment

The role of Dynamic Energy Budget theory in predictive modeling of stressor impacts on ecological systems

Comment on: “Physics of metabolic organization” by Marko Jusup et al.

Nika Galic*, Valery E. Forbes

Department of Ecology, Evolution and Behavior, University of Minnesota, USA

Received 10 January 2017; accepted 11 January 2017

Communicated by J. Fontanari

Human activities have been modifying ecosystems for centuries, from pressures on wild populations we harvest to modifying habitats through urbanization and agricultural activities. Changes in global climate patterns are adding another layer of, often unpredictable, perturbations to ecosystems on which we rely for life support [1,2]. To ensure the sustainability of ecosystem services, especially at this point in time when the human population is estimated to grow by another 2 billion by 2050 [3], we need to predict possible consequences of our actions and suggest relevant solutions [4,5]. We face several challenges when estimating adverse impacts of our actions on ecosystems. We describe these in the context of ecological risk assessment of chemicals. Firstly, when attempting to assess risk from exposure to chemicals, we base our decisions on a very limited number of species that are easily cultured and kept in the lab. We assume that preventing risk to these species will also protect all of the untested species present in natural ecosystems [6]. Secondly, although we know that chemicals interact with other stressors in the field, the number of stressors that we can test is limited due to logistical and ethical reasons. Similarly, empirical approaches are limited in both spatial and temporal scale due to logistical, financial and ethical reasons [7,8]. To bypass these challenges, we can develop ecological models that integrate relevant life history and other information and make testable predictions across relevant spatial and temporal scales [8–10].

To ensure better predictive capacity, the models we develop need to be based on consistent and coherent principles representing core biological and ecological processes. The Dynamic Energy Budget (DEB) Theory describes the specifics of metabolic organization and life history of all life forms, and is based on thermodynamic principles [11,12]. Applying a standardized theory such as DEB, which has been tested in many systems and contexts [11], minimizes the risk of erroneous assumptions about model structure. This is especially relevant when we aim to explicitly model species physiology because there is more than one way to represent processes of resource acquisition and allocation to meet metabolic requirements [13]. Researchers may choose different ways to represent organismal physiology, often depending on their preference and background, and indeed some established approaches may seem to be more

DOI of original article: <http://dx.doi.org/10.1016/j.plrev.2016.09.001>.

* Corresponding author at: 140 Gortner Laboratory, 1479 Gortner Avenue, St. Paul, MN 55108, USA.

E-mail address: ngalic@umn.edu (N. Galic).

<http://dx.doi.org/10.1016/j.plrev.2017.01.008>

1571-0645/© 2017 Published by Elsevier B.V.

straightforward (i.e. no abstract state variables such as reserve) and contain fewer parameters [13]. However, basing species physiology and life history on first principles creates a model which we can apply to conditions that are different from those for which the model was originally designed. Ultimately, we need to apply our models to conditions for which we lack empirical data for model testing. For instance, as ecological systems are exposed to a potentially large number of stressors in different combinations, appropriate and tailored management efforts are required to ensure sustainability of ecosystem processes and services. Some chemical groups, e.g. pesticides, are well researched and we have a good understanding of how they affect suborganismal processes and organismal responses. We understand much less about how these chemicals impact populations and ecosystem services [9,14]. In addition, we know to a certain extent how global warming may impact ecological systems [15]. What we do not know is how the combination of chemical stressors and global warming may impact different levels of biological organization. However, we need to make predictions based on best available knowledge and principles [16]. Such predictions are likely to be more robust if they are based on first principles which have been tested in different systems and under novel conditions [17,18].

Furthermore, DEB theory provides a logical and mechanistic link between molecular and ecosystem processes [14] through common state variables, such as mass and energy, which reflect important features of each level of biological organization. More importantly, relevant feedbacks between levels of organization are explicitly included. Both intra- and inter-specific interactions, for instance, constrain organismal properties, either through predation or competition for a common resource. Changes in organismal properties then further change properties of populations, communities and ecosystem processes. These changes and dynamics emerge from several core principles of metabolic organization [17]. For example, feeding inhibition may yield organismal responses that go from almost no impact to substantial impacts on body sizes. This may result in initially no visible impacts on population properties – due to feedbacks and compensation processes – to a sudden extinction of populations [16]. Allowing for these important feedbacks to emerge mainly from first principles is at the core of next-generation models that promise better predictive capacity [17].

Finally, we address the question and challenge of basing our estimations of adverse impacts of chemicals and other stressors on several species we can culture in labs, while we are mainly concerned with avoiding risks to species in the field. Many such species are protected, which makes it nearly impossible to directly test impacts of chemicals [7]. Ecological models can extrapolate both stressor impacts and life histories across species. They do, however, need parameterization and validation data, and for many species we severely lack even basic life history and ecological information. The US regulation for pesticide registration, for instance, requires that assessments of potential risks be conducted for ~ 1600 endangered and threatened species [4,7]. Approaches for extrapolating effects of chemicals across species using taxonomically related species [19] and interspecies correlation models [20], are continually being developed, but also questioned [21]. Extrapolating life history and ecological information across species brings us to allometry, briefly discussed in Jusup et al. [11], as a method that is often used to assign life-history parameter values based on maximum species sizes [22]. However useful such empirical approaches may be for model parameterization when we lack specific life-history data, the lack of explicit mechanisms could limit model application (to novel conditions, for example) and confine the model's predictive capacity in relevant scenarios.

DEB theory holds the promise to do a better job at interspecies extrapolation because of structural similarity of metabolic organization across organisms [11,23]. Differences between species lie in parameter values, some of which are extensive (i.e. depend on maximum body size), and some are intensive (i.e. independent of body size and species specific) [11]. Future studies should increasingly focus on synthesizing DEB parameters and creating relationships which could be used to address parameter scarcity for species of interest [24–26].

We do, however, have to keep in mind that the DEB theory focuses exclusively on details of metabolic organization and physiology and largely ignores other important aspects of species biology and ecology. Adaptive behaviors such as reproductive strategies, dispersal or habitat selection are beyond the scope of DEB theory, but are required for representing ecology of individuals, populations, communities and ecosystems [27,28]. We therefore see DEB theory as a starting point, but not the ultimate solution, for developing models that predict the response of ecological systems from the response of its individuals and their interactions [7–9,29].

Ecological systems, on which we rely to provide services for our needs, are expected to receive more pressure as the human population continues to grow. We thus need to develop more predictive and robust tools and relevant approaches that can reliably assess the magnitude of our activities and inform the selection of appropriate management efforts that ensure ecosystem service provision [9,14,16]. DEB theory can play a central role in such approaches.

Acknowledgements

We thank Volker Grimm for providing helpful suggestions about this comment.

References

- [1] Millenium Ecosystem Assessment, *Ecosystems and Human Well-being: Biodiversity Synthesis*, 2005, World Resources Institute, Washington, D.C.
- [2] Seifert L, et al. Warming-induced changes in predation, extinction and invasion in an ectotherm food web. *Oecologia* 2015;178(2):485–96.
- [3] Lutz W, Sanderson W, Scherbov S. The end of world population growth. *Nature* 2001;412(6846):543–5.
- [4] Council NR. Science and decisions: advancing risk assessment, 2009.
- [5] Mouquet N, et al. REVIEW: predictive ecology in a changing world. *J Appl Ecol* 2015;52(5):1293–310.
- [6] Sappington LC, et al. Contaminant sensitivity of threatened and endangered fishes compared to standard surrogate species. *Environ Toxicol Chem* 2001;20(12):2869–76.
- [7] Forbes VE, et al. Assessing the risks of pesticides to threatened and endangered species using population modeling: a critical review and recommendations for future work. *Environ Toxicol Chem* 2016;35(8):1904–13.
- [8] Galic N, et al. Potential application of population models in the European ecological risk assessment of chemicals II: review of models and their potential to address environmental protection aims. *Integr Environ Assess Manag* 2010;6(3):338–60.
- [9] Forbes VE, Galic N. Next-generation ecological risk assessment: predicting risk from molecular initiation to ecosystem service delivery. *Environ Int* 2016;91:215–9.
- [10] Galic N, et al. The role of ecological models in linking ecological risk assessment to ecosystem services in agroecosystems. *Sci Total Environ* 2012;415(0):93–100.
- [11] Jusup M, et al. Physics of metabolic organization. *Phys Life Rev* 2017. <http://dx.doi.org/10.1016/j.plrev.2016.09.001> [in this issue].
- [12] Kooijman S. *Dynamic Energy Budget Theory for Metabolic Organisation*. Cambridge, UK: Cambridge University Press; 2010.
- [13] Sibly RM, et al. Representing the acquisition and use of energy by individuals in agent-based models of animal populations. *Methods Ecol. Evol.* 2012.
- [14] Forbes VE, et al. A framework for predicting impacts on ecosystem services from (sub)organismal responses to chemicals. *Environ Toxicol Chem* 2017 [accepted] .
- [15] Daufresne M, Lengfellner K, Sommer U. Global warming benefits the small in aquatic ecosystems. *Proc Natl Acad Sci* 2009;106(31):12788–93.
- [16] Galic N, Forbes V, Grimm V. Impaired ecosystem process despite little effects on populations: modeling combined effects of warming and toxicants. *Glob Change Biol* 2017. <http://dx.doi.org/10.1111/gcb.13581> [in press].
- [17] Grimm V, Berger U. Structural realism, emergence, and predictions in next-generation ecological modelling: synthesis from a special issue. *Ecol Model* 2016;326:177–87.
- [18] Evans MR, et al. Predictive systems ecology. *Proc R Soc Lond B, Biol Sci* 2013;280(1771).
- [19] Banks JE, Ackleh AS, Stark JD. The use of surrogate species in risk assessment: using life history data to safeguard against false negatives. *Risk Anal* 2010;30(2):175–82.
- [20] Raimondo S, Mineau P, Barron MG. Estimation of chemical toxicity to wildlife species using interspecies correlation models. *Environ Sci Technol* 2007;41(16):5888–94.
- [21] Banks JE, et al. Parasitoids and ecological risk assessment: can toxicity data developed for one species be used to protect an entire guild? *Biol. Control* 2011;59(3):336–9.
- [22] Hendriks AJ. Allometric scaling of rate, age and density parameters in ecological models . *Oikos* 1999;86(2):293–310.
- [23] Sousa T, et al. Dynamic energy budget theory restores coherence in biology. *Philos Trans R Soc Lond B, Biol Sci* 2010;365(1557):3413–28.
- [24] Cardoso JFMF, van der Veer HW, Kooijman SALM. Body-size scaling relationships in bivalve species: a comparison of field data with predictions by the Dynamic Energy Budget (DEB) theory. *J. Sea Res.* 2006;56(2):125–39.
- [25] Kooijman SALM. Waste to hurry: dynamic energy budgets explain the need of wasting to fully exploit blooming resources. *Oikos* 2013.
- [26] Maino JL, Kearney MR. Ontogenetic and interspecific metabolic scaling in insects. *Am Nat* 2014;184(6):695–701.
- [27] Railsback SF, Harvey BC. Trait-mediated trophic interactions: is foraging theory keeping up? *Trends Ecol Evol* 2013;28(2):119–25.
- [28] Grimm V, Martin BT. Mechanistic effect modeling for ecological risk assessment: where to go from here? *Integr Environ Assess Manag* 2013;9(3):e58–63.
- [29] Grimm V, Ayllón D, Railsback SF. Next-generation individual-based models integrate biodiversity and ecosystems: yes we can, and yes we must. *Ecosystems* 2016:1–8.