

Accepted Manuscript

Linking levels of life

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PII: S1571-0645(17)30024-6
DOI: <http://dx.doi.org/10.1016/j.plrev.2017.01.024>
Reference: PLREV 849

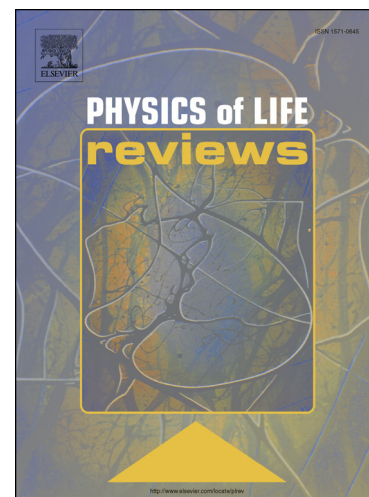
To appear in: *Physics of Life Reviews*

Received date: 20 January 2017

Accepted date: 26 January 2017

Please cite this article in press as: Klepac P. Linking levels of life. *Phys Life Rev* (2017), <http://dx.doi.org/10.1016/j.plrev.2017.01.024>

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

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Energy is a unifying currency of physics and biology. In physics it is one of the fundamental quantities, essential to the laws of thermodynamics. In biology, it is what all organisms need in order to grow, it is a link between different trophic levels in foodwebs, and can serve as a link between different levels of biological organization from individuals, to populations, communities and ecosystems. Dynamic Energy Budget (DEB) theory provides potentially unifying framework, yet so far there has been a disconnect between theoretical and empirical work. The level of model complexity and the lack of data means that the biggest strength of the theory – its many possible applications – has not been fully appreciated. In their thorough review, Jusup et al [1] set to unify the theoretical and empirical branches of DEB theory, simplify its derivation and illustrate its potential through diverse set of applications – from conservation of endangered species and bioaccumulation of pollutants, to extensions to population viability and effects of climate change.

Dynamic Energy Budget (DEB) theory [2] is a framework for modeling assimilation and utilization of energy from food for maintenance, growth, reproduction and development of organisms. The basic idea is simple – all heterotrophic organisms require energy in order to grow, develop and reproduce, and get that energy by the uptake of food from the environment. Food uptake is assumed to be proportional to body surface area and environmental food density and assimilated energy from food is added to reserves. In the standard, κ -rule model by Kooijman [3], the founder of the DEB theory, fraction κ of this energy is used for somatic maintenance and growth, and the remaining fraction $(1 - \kappa)$ is used for maturation, reproduction and maturation maintenance. The more energy is used for growth, the less is available for reproduction, so the environmental food availability introduces a trade-off. Most biological models model reproduction and growth separately, and hence ignore this trade-off since they do not consider organism’s energy budget. By building on the laws of conservation of mass and energy, dynamic energy budget models capture the changes of energy fluxes throughout the lifecycle of an organism.

While the basis for DEB model is simple and intuitive, the resulting model has been criticized for having a considerable number of parameters and equations – a summary of the standard model has eleven different parameters [1], but often there are many more (18 in [4]). In addition, none of the state variables can be directly measured. DEB theory expresses organisms’ structures and reserves in molar masses, so organic compounds are expressed in units of gram per mole of carbon ($\text{g C}\cdot\text{mol}^{-1}$). Even if measurements of organism’s dry mass were readily available it would still be challenging to disentangle which proportion of dry mass is due to organism’s structure and which due to organism’s reserve, the two main

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