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Metabolic organization across scales of space and time

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Cover Letter

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Dear Editor,

Please find attached a manuscript entitled “**Metabolic organization across scales of space and time**”, by myself, Nina Marn, Tiago Domingos, Ramon Filgueira, Konstadia Lika, Kim Rakel, and Tin Klanjšček, which we are submitting for publication in Ecological Modelling as an editorial piece introducing the virtual special issue DEB2023.

I look forward to hearing back from you soon.

On behalf of the co-authors,
Romain Lavaud

Metabolic organization across scales of space and time

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Introduction

The need for predictive models is increasing as we face changes that impact species and ecosystems at local, regional and global scales. Numerical modelling is a critical asset that scientists, policy makers, and societies use to anticipate the effects of these changes. However, the complexity of biological systems represents a severe challenge since models are simplified representations of reality, which depend on our comprehension of natural processes and on the quality of data used to build them. In this context, unifying theories, providing a general framework for describing and explaining biological mechanisms, appear necessary to predict the effects of the changes to come.

Dynamic Energy Budget (DEB) theory allows building families of related models that are based on a mechanistic description of individual metabolic processes (Kooijman, 2010). DEB models link functional traits to environmental conditions through variables rooted in energy and mass conservation laws. These links enable strong predictions of state variable dynamics under changing conditions. Predicting the effects of global change on individuals and populations, quantifying the effects of environmental stressors on physiological functions, better understanding geographical patterns of species, optimizing bio-production, managing exploited resources, and invasive species control are all examples of applications for which a quantitative characterization of metabolism is key and for which DEB theory provides a tested framework.

Since its inception in 1979, DEB theory has been used in about 1,200 publications (DEB library[1]), while DEB parameters have been estimated for more than 5,000 animal species (AmP, 2024). The theory has time and again proven to be a common ground where experts across disciplines can work together to provide quantitative solutions to applied problems. This special issue gathers the latest advances in and applications of DEB theory, following the 8th edition of the International School and Symposium on DEB theory for Metabolic Organization, DEB2023.

DEB2023 showcased contributions around the theme "**Metabolic organization across scales of space and time**", which provided a common ground for a wide range of studies integrating multiple biological levels of organization. Dealing with specific scales of space and time is inherently part of DEB theory as it builds upon the individual level to scale up and down levels of biological organization (Kooijman, 2001). Some biological processes such as ion transport or enzymatic activities are important at small space-time scales and determine many traits at the individual level. Other processes such as behavior emerge at the individual scale, but their importance to population dynamics may be diluted by the number of members of that population. The birth and death rates in populations of organisms can shape species abundance and ecosystem structure but are not as immediately important when looking at cellular processes or individual organisms' lives. While the theory has continuously evolved, the applicability of DEB theory across different scales of time, space, and maybe more generally across levels of organization remains a fundamental feature of the theory (Kooijman et al., 2024).

Contributions to this special issue demonstrate the broad applicability of DEB, utilizing the theory in studies ranging from the implementation of cellular processes (Stechele and Lavaud, 2024) to understanding populations and community dynamics (Kooijman, 2024a; van der Meer et al., 2024); from a specific part of the life cycle of a species (Romoli et al., 2024; Raapoto et al., 2024; Schwemmer et al., 2024) to its entire life cycle (Lanjouw et al., 2024); from a single species' life history traits (Davis et al.,

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[1] https://www.zotero.org/groups/500643/deb_library/library

2024; Richard et al., 2024) to comparisons between individuals or breeds (Oliveira et al., 2024) to species (Klagkou et al., 2024; Stavrakidis-Zachou et al., 2024; Le Moan et al., 2024; Kooijman, 2024b); from the use of historical data to explain life histories (Stavrakidis-Zachou et al., 2024; Nepal et al., 2024) to the use of projected future conditions to predict impacts on energy budgets (Lavaud et al., 2024). We provide here a synthesis of these contributions.

Predicting life histories

DEB theory describes metabolic organization at the individual level, as mass and energy balances are relatively easy to quantify at this level compared to the sub- or supra-individual levels. Individuals are also the primary unit of selection, as individual traits define survival, and individual behavior is key to food intake and reproduction. The life cycle of organisms can be complex and include several metabolic switches. The initiation of development, feeding, or reproduction are examples of metabolic switches that define the life histories of organisms. DEB theory uses the concept of maturity to track the occurrence of metabolic switches through time. Many DEB applications deal with the entire life cycle, while others deal with the adult stage only or focus just on early development. The environmental conditions experienced during early stages can carry over to effects throughout the life of an organism. This is exemplified by the influence of environmental variables on the metabolic acceleration experienced by many organisms during their development (Kooijman, 2014). As such, DEB models focusing on early stages of development can be key to understanding a species' biology.

In coastal and estuarine ecosystems, hypoxia may affect the growth and hatching time of many fish species. Schwemmer et al. (2024, this issue) investigated which DEB parameters could be linked to observed physiological responses of Atlantic silverside (*Menidia menidia*) larvae, an ecologically important forage fish and model species, exposed to hypoxia. Using the DEBkiss model –a simplified

DEB model without a reserve compartment (Jager et al., 2013)– they determined that a reduced conversion efficiency of assimilates into structure and an increase in two mortality rate parameters were the most likely means of action by which hypoxia impacts the growth, development, and survival of this species. Through different scenarios, they further identified that single effects on conversion efficiency only explained some of the observed changes due to exposure to hypoxia, while effects applied to maintenance rate yielded poor fits to the data. To explain their findings the authors hypothesized that damage from anaerobic byproducts and less efficient ATP production under anaerobic respiration could impair the conversion of assimilates to structure. Unrepaired damage from anaerobic byproducts along with reserve shortages may also be related to failure to reach a viable level of complexity before depletion of the yolk sack, leading to increased mortality. This study demonstrates the value of identifying means of action of environmental stressors to explain whole-organism effects.

The larval stage of bivalves is a critical aspect of their development, particularly due to the fact that larvae are subject to transport by currents, which determines their success in settlement and further development. Raapoto et al. (2024, this issue) coupled a DEB model for the pearl oyster (*Pinctada margaritifera*) to a hydrodynamic model to characterize and quantify the connectivity between geographically isolated Pacific atolls. The model showed that food availability and meso-scale turbulence in these atolls jointly constrained larval dispersal, reducing potential connectivity with other archipelagos. The authors also revealed seasonal and interannual variability in the connectivity related to food and temperature conditions. These results provide important information for a major industry in the region, by adequately capturing dispersal and connectivity patterns and identifying appropriate management units at such a large scale.

The metamorphosis of anurans (frogs and toads) is a phenotypically plastic process that can be affected by natural and anthropogenic stressors. Filling a gap in currently existing models lacking explicit inclusion of this crucial life event, Romoli et al. (2024, this issue) developed a DEB model for Anuran metamorphosis following a list of stylized facts (in the spirit of Sousa et al., 2008). The model is an expansion of the typical ‘abj’ model (Marques et al., 2018) with two sub-modules designed to accurately capture the transformation from aquatic tadpoles to terrestrial frogs: first, the re-purposing of tadpole structural energy (from gills and tails) to ensure the emergence of viable individuals with not completely depleted reserves after peak metamorphosis as no feeding occurs during this phase and, second, a thermal control on the fraction of energy allocated to soma as a mechanism to produce smaller froglets at higher temperatures. The extended model is successfully tested on four anuran species and paves the way for improved predictions of the impact of environmental conditions on the fitness of amphibians, a taxon facing severe extinction risks (Luedtke et al., 2023).

From one to several species

Developed based on core principles of thermodynamics and sound biological and chemistry concepts shared by all living beings, DEB theory is by essence generalist. Species are defined by a common set of DEB parameters that constitute a solid base for comparisons. Because the parameters represent well defined physiological processes and are driven by observed data, such comparisons may translate into better understanding of species advantages or vulnerabilities rooted in physiological capacities.

A few studies in this special issue present new parameter sets that contribute to the growth of the AmP collection (AmP, 2024). Lanjouw et al. (2024, this issue) estimated the DEB parameters for the grooved carpet shell, *Ruditapes decussatus*, a clam species with increasing potential for aquaculture in western and southern Europe. Comparing this species to other cultivated bivalves in the region, they showed that the grooved carpet shell possesses highly favorable traits for aquaculture including a high growth coefficient, low maintenance requirements, and high trophic efficiency.

Nepal et al. (2024, this issue) developed a DEB model for blue catfish, *Ictalurus furcatus*, in the Eastern United States. Their results indicate that blue catfish have low maintenance costs and a relatively high reserve capacity, two traits that help understand the success of this invasive species and help managers design effective control strategies.

Other works can be specifically aimed at species comparisons. Stavrakidis-Zachou et al. (2024, this issue) studied the DEB parameters and life history of another invasive fish, the marbled spinefoot, *Siganus rivulatus*, in comparison with those of the native salema porgy, *Sarpa salpa*, in the Eastern Mediterranean Sea. They identified mechanistic physiological characteristics based on DEB parameters to explain the invasive capacity of the marbled spinefoot. We discuss further these two studies in the next section on time scales.

In another comparison of species, Klagkou et al. (2024, this issue) developed DEB models for two species of stink bugs, *Euschistus heros* and *Nezara viridula*, which are responsible for damages to soybean cultures globally. While the former is expanding in neotropical regions, particularly in South America, the latter has declined in the last decades. Testing different typified models and assumptions, the authors determined that isomorphic nymphal growth (‘sbp’ model) provided the best fit to the data for each species, while a lack of available observations prevented any decision regarding the energy allocation scheme in the adult stage. They further investigated the impact of environmental conditions on the energy budget of these pests, showing that temperature had a higher impact on the duration of life stages and survival, while food availability affected more egg production. This study provides essential work to further explore what implications differences in individual growth and life cycles can have for population dynamics and the development of pest management strategies, especially in the context of climate change.

Elevating the comparison of species to new heights, Le Moan et al. (2024, this issue) used the AmP multi-species estimation procedure to compare five species of scallops in their capacity to depurate toxins from harmful microalgae. They investigated inter-specific differences in energetic traits potentially linked to the rate of toxin depuration to identify relevant physiological processes and take a step towards ecotoxicological models. Observing variations in assimilation rates, somatic maintenance rates, and reserve mobilization rates between species, the authors determined that the latter (i.e., the energy conductance parameter) consistently increased along the ‘slow-to-fast’ depuration capacity gradient. This study may help with decision making in aquaculture and fisheries practices. The approach also constitutes a valuable example of the multi-species estimation tool for the DEB community.

A recent series of studies have started to explore patterns in parameters to explain differential life histories, including fish (Augustine et al., 2022; Kooijman and Lika; 2014; Lika et al., 2022), petrels and penguins (Kooijman, 2020), cephalopods (Kooijman and Augustine, 2022a), turtles and crocodiles (Marn and Kooijman, 2022), and carnivores and pangolins (Kooijman and Augustine, 2022b). The contribution by Kooijman (2024b, this issue) continues this systematic analysis of wider taxa through the exploration of patterns from 103 species of branchiopods (which include the water fleas, which had a major role in the initial development of DEB theory). The study discusses key energetics and life history traits, including the particularly short life cycle of most branchiopods. This characteristic makes them great examples of the waste-to-hurry hypothesis by Kooijman (2013), according to which increased somatic maintenance and assimilation lead to increased growth and reproduction. The study confirms previously observed relationships in other taxa, such as the near equivalence between lifetime cumulative neonate mass production and maximum weight. Such systematic reviews of well represented groups within the AmP collection allow the identification of outliers, which may require further checking, and a better understanding of the ecophysiology of each taxon.

From past to future predictions

As a mechanistic framework, a strength of DEB theory compared to more empirical or implicit approaches is that it relies on explicit processes for predictions. Implicit or statistical models can generate predictor functions relating survey conditions to detectability but are phenomenological; they do not incorporate biological constraints, therefore using them to predict into unsampled time and space is risky (Saleeba et al., 2020). DEB models allow the connection of functional traits to predictive variables using equations that depict physiological processes of organisms. For these reasons the deductive power of DEB models is superior, even when empirical models yield better numerical predictions.

Climate changes affect species distribution and interactions. In their study of a native and invasive fish species in the Mediterranean Sea (described previously), Stavrakidis-Zachou et al. (2024, this issue) explored the effects of historical changes in temperature between a colder past and a warmer recent period on the performance of the native salema porgy compared to the invasive marbled spinefoot. The study shows a progressive benefit in growth for the invasive spinefoot compared to the native salema, translating into a competitive advantage for the former, which may contribute to understanding its rapid northward expansion in the Eastern Mediterranean Sea. The authors also suggest that food competition and differences in reproductive traits may be responsible for recruitment failures in the native species. These trends are expected to be reinforced with climate change in the region.

Nepal et al. (2024, this issue) studied another invasive species, the blue catfish, and showed how their life history traits contribute to the invasive capacity of this species (also described in the previous section). The authors tested hypotheses linked to competition for food and its quality to explain observed variations in population dynamics during different stages of invasion between the 1990s and the 2010s. This study showed that both ontogenetic shifts in diet and changes in population densities affected the observed patterns in growth and reproduction. The implications of these findings for the management of this invasive species brought the authors to caution against actions limited to increased harvesting, instead calling for diverse techniques to curb the spread of the species that consider the plasticity of blue catfish physiology.

Exploring potential future impacts of climate change, Lavaud et al. (2024, this issue) quantified the potential outcomes for eastern oyster restoration and aquaculture development in the Gulf of Mexico. They built performance indices based on DEB model outputs linked to survival, time to reach market size, and reproductive metrics along the coasts of Texas and Louisiana, United States. Comparisons between current (2014–2020) and future (2041–2050) conditions indicated that oyster aquaculture and restoration potential in presently occupied areas might decrease in the future. However, the authors highlighted the lack of projected environmental data in coastal areas, particularly for salinity, which restricts the scope of the conclusions. They also linked contrasted growth and reproductive patterns between the two states to differences in the variability of temperature and salinity, providing important tools for a better management of the fishery and more successful restoration initiatives.

Climate change, together with nutrient loading leading to eutrophication, might also result in more recurrent, more extreme and longer lasting hypoxic conditions in coastal waters. The capacity of certain species (or their most sensitive life-stages) to cope with low dissolved oxygen (DO) concentrations becomes increasingly critical to the survival of many species. Davis et al. (2024, this issue) and Schwemmer et al. (2024, this issue) both tackled the issue of hypoxia for eastern oysters and Atlantic silverside, respectively. Davis et al. (2024, this issue) tested the implementation of a DO correction factor that constrained assimilation, mobilization, and ingestion rates. Applied to major growing sites in the Chesapeake Bay, United States, the model indicated that hypoxia caused reduced growth for oysters both in shell length and tissue mass, as well as reductions in oyster fecundity and alterations to spawning frequency during the summer, which collectively has the potential to negatively affect oyster performance. Schwemmer et al. (2024, this issue), following a similar approach, revealed that reductions in conversion efficiency of assimilates into structure in Atlantic silverside exposed to hypoxia affected the growth, hatch timing, and survival to hypoxia-induced damages in this fish species. They also suggested exploring sub-organismal processes co-occurring with the observed whole-organism responses to hypoxia to narrow down the DEB processes involved in this response.

Population dynamics

DEB models are, by default, oriented towards individuals, as they focus on the energy budget of an individual in a (dynamic) environment. The integration of DEB models into agent-based population models (ABMs) is a natural extension of the modelling framework. One of the first steps in that direction, published already more than a decade ago, was a DEB-IBM link and tutorial-of-sorts, complete with integration into the free population modelling software NetLogo (Martin et al., 2012; http://ccl.northwestern.edu/netlogo). Individual-population interfaces can also be built with other approaches, such as Semi-Structured Models, Escalator Boxcar Trains, and Cohort Projection Models (see e.g. https://www.bio.vu.nl/thb/deb/deblab/add_my_pet/popDyn/popDyn.html). All these approaches have in common that (i) they follow states of a population instead of (or in addition to) states of single individuals, and (ii) they are compatible with DEB models, as the (basic) code for their implementation into AmP routines has already been developed (see link above). All these approaches also share a similar problem: a realistic model of an individual, when integrated into a population model, can give rise to unrealistic population dynamics (van der Meer, 2016).

The paradox of realistic individual models giving rise to unrealistic population models, for example via juvenile-driven cycles where many small individuals out-compete few larger adults, can be solved within DEB theory using an approach of ‘thinning’ (Kooijman et al., 2020): the hazard rate is such that the feeding rate of a cohort of neonates remains constant if food density is constant. Even though this approach does solve the paradox, and does so by not over-complicating the model, other approaches and solutions might be possible. Kooijman (2024a, this issue) explored six approaches, in addition to thinning, for *Daphnia magna*. Out of these approaches, thinning, pulsed food, and scatter in certain parameter values (e.g. in maturity level at puberty) seem to be the most satisfying options, as they can reduce or even eliminate the juvenile-driven cycles. Socialization could reduce the cycles to some extent, while immigration hardly had an effect, sleep enhanced the cycles, and two food types (with a food switch between the juvenile and adult stage) resulted in highly complex effects.

Models for a (stable) population enable further scientific exploration. van der Meer et al. (2024, this issue) developed and compared two such models: a von Bertalanffy growth equation extended for reproduction, and a DEB-based population model which includes thinning. Combining (i) primary and compound parameters at the individual and population level, (ii) taxonomic and habitat metadata from the AmP collection, and (iii) the derived characteristics for a stationary population of constant size, they explore trophic efficiency in an ecosystem. In more concrete terms, they theoretically analyze the extent to which differences in trophic efficiency (i.e., assimilation efficiency and production efficiency) of a population can be linked to basic physiological processes (i.e., belonging to a certain group of species). Their results suggest that the differences in trophic efficiency, defined as the production-assimilation ratio and then predicted by DEB theory, appear to be strongly correlated with the von Bertalanffy growth coefficient, and the ultimate reproduction rate. Birds, and to a lesser extent mammals, have a much lower ratio than other taxa. Benthic marine invertebrate grazers (mainly molluscs) showed a higher ratio than pelagic grazers (mostly arthropods), which may have consequences for overall ecological efficiency when marine coastal systems get more dominated by the benthic compartment. The paper provides a solid working example of theoretical evolutionary exploration using model parameters and taxonomic, ontogeny, and habitat metadata curated in the AmP collection.

Module extensions and general advancements

As models are simplified representations of the real world, they are generally built with the minimal complexity required to address the posed research question (Kooijman et al., 2024). DEB model extensions can easily be included in a basic model due to its modularity and simple setup for tracking processes and state variables. Almost a dozen typified models have been derived as extensions of the standard (std) model (Marques et al., 2018; Kooijman, 2010). Such extensions are regularly developed and published, and this special issue is no exception. A good example is the previously mentioned study of Romoli et al. (2024, this issue) where the typified 'abj' model is adjusted to include (i) an additional process of tissue repurposing during peak metamorphosis, and (ii) a temperature dependence of allocation between growth and development, modulated via the parameter kappa. By introducing the temperature-dependency of kappa, the observed pattern of tadpoles finalizing their metamorphosis at a smaller size at higher temperature (and same food availability) is predicted. Smaller sizes at hatching have been correlated to higher temperatures for fish and turtles (Devauchelle et al., 1987; Glen et al., 2003), which constitutes a basis for the temperature-dependency of kappa proposed by Romoli et al. (2024, this issue). Although this relationship is phenomenological and does not constitute a mechanistic explanation, further exploration may provide a deeper understanding.

The effect of temperature on the (final) size of individuals was explored also in the study by Richard et al. (2024, this issue). Unraveling the mechanisms behind the temperature-size rule (TSR), i.e., the general observation that many organisms reach smaller sizes at high temperatures, has been the topic of intense research for decades. Richard et al. (2024, this issue) take a step further from the general observation that all physiological rates must scale equally with temperature and observe the physiological rates as 'external' or 'internal'. A crucial step is in recognizing that rates of food searching and handling can be considered as 'external', and therefore have a different dependence on temperature in relation to 'internal' rates. In their paper, they use an extensive dataset of Daphnia life history response to temperature to show that introducing temperature-dependence in the functional response is sufficient for DEB models to predict the TSR and identify the most likely mechanism explaining it.

Studying an individual's response to variations in food and temperature is relatively straightforward within the DEB framework. Other environmental variables, however, are becoming increasingly relevant to predict species traits, and ocean acidification is one of them. Stechele and Lavaud

(2024, this issue) implemented the mechanics of bio-calcification within the DEB framework to tackle the potential effect of ocean acidification, as the saturation state of calcium carbonates (affected by ocean acidity) will impact the process of biogenic calcification. Expanding on the work by Pecquerie et al. (2012) on fish otoliths, they described the relevant physiological and energetic mechanisms of biogenic calcification, presenting them as stylized facts. Although the focus was on bivalves, for which more data are available, the approach is applicable to any organisms forming calcified structures, including fish otoliths, coral exoskeletons, or, to an extent, crustacean carapaces. One aspect not included in the space-time scale described in earlier sections but integral to DEB theory lies in the application of the theory to both very applied work and more theoretical investigations. While the majority of DEB models are parameterized for specific applications and a single species, the continuous development of analytical methods and the exploration of properties and patterns is a marker of the theory’s potential to unify various disciplines under a general mechanistic framework. In this way, DEB models can provide valuable insight into the impacts of ocean acidification on marine species through process-based prediction, despite a lack (yet a growing amount) of data. Such theoretical developments and investigations anchor DEB theory into a wider perspective by evidencing unique patterns and emerging properties directly derived from the theory’s assumptions.

A good example of this is the contribution by Lika and Kooijman (2024a, this issue). Previously, the ultimate size, a critical aspect in growth, has been explored as a function of metabolic parameters (Lika et al., 2019). In this issue, Lika and Kooijman emphasized the metabolic interpretation of the well-known von Bertalanffy growth rate (vBGR) in the context of DEB. DEB theory allows for a more detailed interpretation of the vBGR and provides insights into how this rate is affected by metabolism, temperature, and food availability, by combining insight obtained from patterns in DEB parameters for >4500 species in the AmP collection with metabolic and physiological interpretations of growth models and data. The widely known geometrical interpretation of the vBGR (i.e., the vBGR being equal to the slope of the tangent line at zero length divided by the ultimate length) is also discussed in the manuscript.

However, the often-overlooked metabolic interpretation is the main topic of this manuscript. Exploring the metabolic interpretation in the DEB context, Lika and Kooijman link the vBGR to several compound and five primary parameters, where compound parameters are generally easier to estimate from data, but each primary parameter is linked to a single underlying physiological process. An example of a compound parameter is ultimate (structural) length, for which they explore both intra- and inter-specific relationships with the vBGR. Finally, by investigating the link between the vBGR and the two DEB primary parameters (the maintenance rate of structure $[\dot{p}_M]$ and the mobilization rate of reserve $\dot{v}$) that affect its value, Lika and Kooijman highlight the issues in estimating these two parameters from growth data only (at a single food level) and the importance of using multiple data types simultaneously for DEB parameter estimation.

Estimation and determination (i.e., confidence intervals) of model parameters is explored further in an accompanying paper (Lika and Kooijman, 2024b, this issue). In this piece, Lika and Kooijman tackle a common issue in DEB parameter estimation related to the fact that observed data provide some information about particular parameters, but do not determine them accurately. Indeed, deterministic models, such as DEB models, differ from stochastic models in that the source of error and mismatch between model predictions and data is not known or fully defined. This contribution extends a long line of previous works devising methods for parameter estimation processes within biological context (Lika et al., 2011a,b; Marques et al., 2019; Lika et al., 2020; Filgueira et al., 2020) and studies dealing with ill-posedness, i.e., parameters that relate to information not present in the data and that, therefore, cannot be estimated (van der Meer, 2006; Kooijman et al., 2008; Lika et al., 2014). Similar to Augustine et al. (2020) who explored interval estimates of parameters of survival data, Lika and Kooijman target interval estimates for simple stochastic and deterministic model parameters in general, and for $[\dot{p}_M]$ and $\dot{v}$ specifically, using two methods for parameter estimation: the maximum likelihood (ML) and the symmetric bound (SB) loss functions. The applicability of the SB loss function (developed specifically with DEB parameter estimation in mind) seems to surpass that of ML, but emphasis is again given to ‘estimation-in-context’ (Kooijman et al., 2024), and to keeping mechanistic and biological principles in mind, ideally working with more sets of data which can then constrain possible combinations and values of specific parameters more efficiently.

A novel approach to the ‘estimation-in-context’ principle is presented by Oliveira et al. (2024, this issue), where individual-specific parameter values can be obtained through an iterative multi-tier estimation process. Using a breed of cattle as a case study, the information (and parameter set(s)) obtained at a higher tier (breed, and later trial) are used with individual-specific data to obtain information at a lower tier (e.g., trial, and ultimately individual), finally arriving at individual-specific values for a selected list of parameters that are reasonably well defined by individual-level data. The multi-tier parameter estimation shares the same loss function and minimization procedure to find parameter estimates as does the conventional DEB parameter estimation, it makes use of pseudo-data to anchor parameters in a biologically realistic parameter space, and it follows the ‘estimation-in-context’ principle. It therefore offers a fully compatible way (with classical DEB techniques) of obtaining a realistic range of values for a certain parameter within a species, breed, or a population, and has the potential for characterizing parameters of interest in commercial (e.g., selective breeding), conservation (e.g., reintroduction or targeted conservation), and theoretical applications.

Conclusions

DEB theory, akin to the real biological world it aims to model, is a dynamic environment. Each new element added, be it an application of a well-tested typified DEB model or a cutting-edge development of the theory, further validates the theory and contributes to a better understanding of the physiology of species, the interactions between them, or their place in ecosystems. Ultimately, this enables us to explore the potential effects of historical and future environments and better anticipate changes to come.

The dynamic community contributing to the diverse and ever-growing scope of DEB theory is essential to its continued development. We are excited about the potential new applications that will showcase, once more, the importance of the theory. This includes deeper explorations of the links between DEB parameters and evolutionary biology, its increased use as a standard method in ecotoxicology and risk assessment, further explorations of comparative bioenergetics between taxa, integration into wider modelling frameworks, and applications with regard to species management and restoration.

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CRediT author statement

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.