Where do functional traits come from? The role of theory and models

Michael R. Kearney[1], Marko Jusup[2], Melodie A. McGeoch[3], Sebastiaan A. L. Kooijman[4], and Steven L. Chown[5]

[1]School of BioSciences, Faculty of Science, The University of Melbourne, Victoria 3010, Australia

[2]Tokyo Tech World Hub Research Initiative, Institute of Innovative Research, Tokyo Institute of Technology, Tokyo 152-8550, Japan

[3]Department of Ecology, Environment and Evolution, School of Life Sciences, La Trobe University, Melbourne, Victoria 3086

[4]VU University, 1081 HV Amsterdam, the Netherlands

[5]Securing Antarctica's Environmental Future, School of Biological Sciences, Monash University, Victoria 3800, Australia

Acknowledgments

We thank Nicole Kearney and Nat Briscoe for discussion. M.R.K. & S.L.C. were funded by Australian Research Council Discovery Project (ARCDP) DP140101240, M.R.K and M.J. were funded under ARCDP DP200101279, MM by ARCDP DP200101680 and MJ from Japan Society for the Promotion of Science (JSPS) KAKENHI Grant No. JP21K04545.

Authors' Contributions

M.R.K., S.L.C. & M.A.M conceived the initial ideas, M.R.K. led the writing, M.J. designed the final figures, all authors contributed conceptually and to writing the text and gave final approval of the manuscript.

Abstract

1. The use of traits is growing in ecology and biodiversity informatics, with initiatives to collate trait data and integrate it into biodiversity databases. A need to develop better predictive capacity for how species respond to environmental change has in part motivated this focus. Functional traits are of most interest—those with a defined link to individual survival, development, growth, and reproduction.

2. Non-trivial challenges arise immediately in deciding which functional traits to prioritise and how to characterise them. Here we discuss the advantages of a theoretical perspective for defining functional traits in the context of dynamical systems models of energy and mass exchange that link organisms to their environments. We argue that the theoretical frameworks upon which such models are built (biophysical ecology, metabolic theory) provide clear criteria to decide upon functional trait definitions, measurement requirements, and associated metadata, via their mathematical connection to model parameters and state variables, and thus to system performance (survival, development, growth, and reproduction).

3. We distinguish 'descriptive' traits from 'functional' traits by dividing the latter into four classes—parameter, model, threshold, estimation—according to whether they are model parameters, define model structure, are threshold state variables, or can be used to estimate model parameters.

4. We develop a decision tree for this classification and illustrate it in the context of mammalian heat exchange but emphasise the scheme's generality to any kind of organism.

5. We show how a theoretical perspective may change how we prioritise traits for collection and databasing in ways that are not necessarily more difficult to achieve, especially with new technologies, and provide clear guidance for requisite metadata. The use of theoretically driven criteria for prioritising the collection of functional trait data will maximise the generality, quality and consistency of trait databases for comparative analyses. Such databases will simultaneously facilitate the development of integrated predictive modelling frameworks across multiple organisational scales from individuals to ecosystems.

Keywords

biophysics, life history, metabolic ecology, physiological ecology, mechanistic niche models

Introduction

The trait concept is now commonplace in ecology and biodiversity informatics (Garnier et al., 2015; Gibert et al., 2015), but it has a long history of analysis and application in biology (Calow, 1987; Nock et al., 2016; Warming, 1909). Functional traits have been defined as those that affect organismal performance, i.e. survival, development (increase in complexity/differentiation), growth (increase in size/mass) and reproduction (Violle et al., 2007). Such traits have always been central to comparative and ecological physiology (Lambers et al., 2008; Prosser, 1991). Traits are also deeply embedded in evolutionary theory, with the meaning of 'functional' being very close to that of 'adaptive' (Calow, 1987). In community ecology, interest is growing in the use of representative species traits to characterise community and biodiversity function (Laughlin et al., 2020; McGill et al., 2006; Violle et al., 2007). The fields of macrophysiology (Chown & Gaston, 2008), metabolic scaling (Sibly et al., 2012) and functional biogeography (Violle et al., 2014) are wholly concerned with how functional traits vary across body size and environment at different spatial and temporal scales, and what the eco-evolutionary implications are of such variation. Now, with the problem of predicting how species will respond to environmental change growing ever more significant, there is great interest in using functional traits as the basis for forecasting shifts in distribution and abundance (Buckley, 2010; Kearney et al., 2010; Pollock et al., 2012; Regos et al., 2019).

Concurrent with the accelerated conceptual interest in traits has been the emergence of online trait datasets. Pioneering efforts have been focused on plant traits (e.g. Kattge et al., 2011), but databases for animals have followed closely behind (Bennett et al., 2018; Grimm et al., 2014; Madin et al., 2016; Marques et al., 2018; Myhrvold et al., 2015; Oliveira et al., 2017; Parr et al., 2016). Much discussion and planning for better coordination, integration, and accessibility of such data has followed (Gallagher et al., 2020). Five different Essential Biodiversity Variables for observing and monitoring trait variation within populations have been proposed (phenology, morphology, reproduction, physiology, and movement), with the purpose of promoting standardization, harmonisation, and estimation of trait data (Jetz et al., 2019; Kissling et al., 2018).

Thorny questions arise in the development of such databases: At what level do we attribute traits—to individuals, populations, species (Shipley et al., 2016; Siefert et al., 2015; Start & Gilbert, 2019)? Should habitat associations be considered as traits (Grimm et al., 2014; Madin et al., 2016; Oliveira et al., 2017)? How do we standardise measurement and what metadata are necessary for context (Moretti et al., 2017; Pérez-Harguindeguy et al., 2013)? Which traits should we prioritise for measurement and databasing?

How do we know what we are missing? How should the data be stored and connected (Parr et al., 2016)? Much progress is already being made on these topics (Gallagher et al., 2020). As always, choices here take varying precedence depending on the question being asked with the data, and often the principle motivation is simply to collate as much existing data as possible for general use.

Rarely mentioned in discussions of trait data collation is the role of theory. Yet a strong theoretical perspective can aid interpretation and prioritisation of trait data, especially when it involves the collation of observations made under different environmental conditions. Theory also leads to new observations previously unimagined, such as Schrodinger's proposal of an aperiodic crystal to encode genetic information (Schrodinger, 1944). Our aim is to emphasise how an explicitly theoretical perspective can facilitate and add value to endeavours to collate and deliver functional trait data. We particularly discuss the advantages of a strong theoretical underpinning to the definition of functional traits using the context of dynamical systems models (DSMs, see Box 1 for a glossary of terms) of energy and mass exchange between organisms and their environments as an example.

We first explain the nature of such DSMs, their theoretical basis and current capacity, and why they are the most useful starting point for defining functional traits and associated metadata. We then place the trait concept within the context of the parameters and state variables of DSMs. We do so first by defining sub-classes of functional traits according to how they are tied to a given model. Then we provide a decision tree with which to apply the classification. We illustrate the concepts by considering a range of commonly measured observations associated with thermal tolerance, using a mammalian case study. We show which observations would classify as functional traits from this perspective, and more generally how such a scheme can facilitate trait data collation, interpretation, and application.

Thermodynamic systems models of organisms

The thermodynamic view of the world involves the abstraction of drawing a boundary around some entity and following the flows of energy between this 'system' and everything outside, i.e. the 'environment'. Open thermodynamic systems involve the exchange of mass and energy across the system boundary. Organisms can be considered open thermodynamic systems (von Bertalanffy, 1950) that involve structured chemical transformations which act to maintain them in a highly ordered and stable state relative to their surroundings (Lotka, 1925), i.e. to maintain some degree of homeostasis (Cannon, 1926). The state of the organism when conceived in this way is completely described in terms of physical and chemical quantities such as volume, energy, mass, pressure, temperature, entropy, and information—

these are ‘state variables’. A model of an organism as a thermodynamic system involves equations for the computation of state variables as a function of parameters and environmental variables from which one can infer performance (Fig. 1). If we can successfully model organisms as thermodynamic systems across their ontogeny, we can obtain a fundamental perspective on their ability to function, i.e. to survive, develop, grow, and reproduce, given different environmental sequences.

There are of course many other aspects to organisms besides these thermodynamic ones, such as the reproductive mode, sexual behaviours, modes of communication and perception, predator avoidance mechanisms, which can also be tackled with DSMs and may have complex environmental feedbacks (e.g. Clark & Mangel, 2000; Soyer, 2012). But the thermodynamic constraints are the most fundamental and general functional connections between organism and environment. They are thus a judicious starting point for defining and modelling the effects of functional traits.

An important distinction to make in this context is between theories and mathematical models. A scientific theory is a set of clearly stated assumptions that aims to offer the most parsimonious explanation of observations. Models complement the theory as direct or derived mathematical and algorithmic formulations of the theoretical assumptions. For thermodynamic processes, these models take the form of a DSM. Models that are not derived from a theory are often termed ‘empirical’, ‘correlative’ or ‘statistical’ and cannot offer mechanistic understanding precisely because the link to the theoretical assumptions—and thus to the underlying mechanisms and processes—is implicit. From this viewpoint, theoretical models act as bridges between qualitative statements implied by the theory and quantitative observations gathered via experiments or fieldwork.

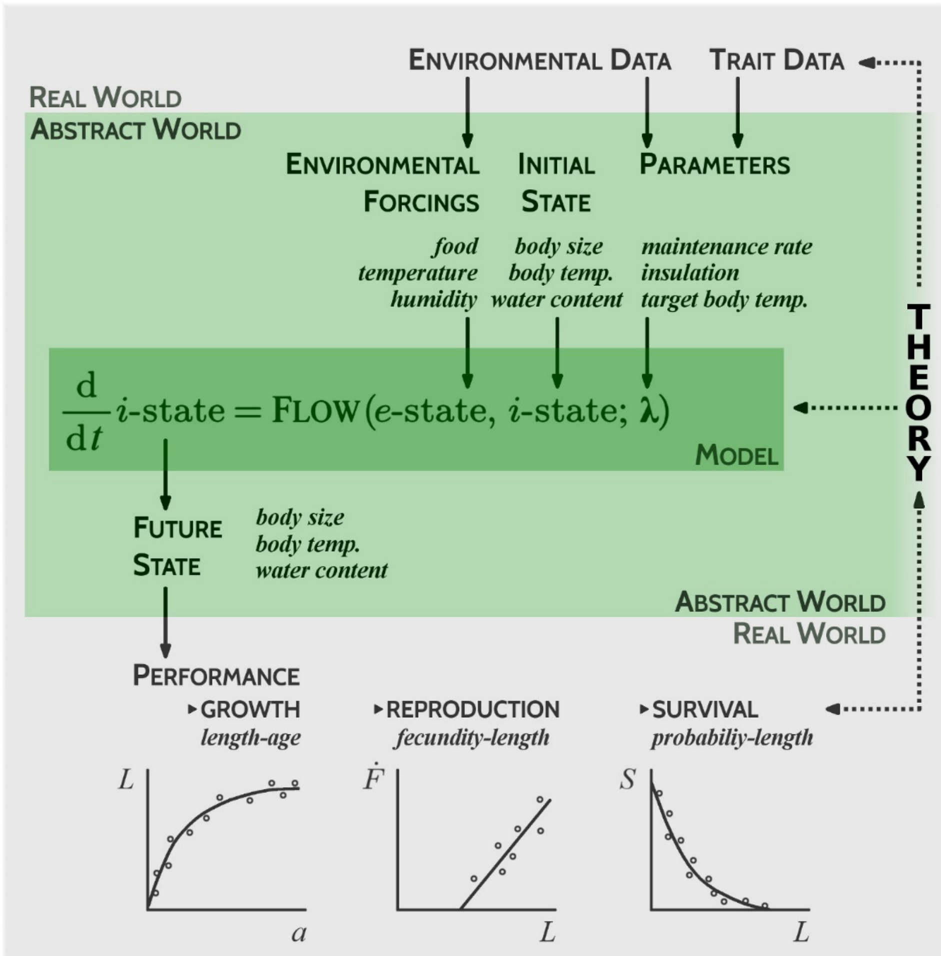

Figure 1. Relationships between parameters, state variables of the individual (*i*-state), environmental variables (*e*-state), and traits in a dynamical systems model of organismal performance. The theory is used to define the equations of a model, which then defines the required variables and parameters. The model defines the state of the system which quantifies performance in terms of survival, development, growth, and reproduction. Trait data are used to define parameters, model structure, or critical threshold states.

The two theoretical branches of ecology that aim to achieve a thermodynamically-based, 'dynamical systems' depiction of living things are biophysical ecology (Gates, 1980; Porter & Gates, 1969) and metabolic theory (Brown et al., 2004; Kearney, 2020; Nisbet et al., 2000). Both branches explicitly apply the general laws and theoretical assumptions of physics and chemistry to develop DSMs that capture the way organisms exchange and transform energy and matter. They additionally include biology-specific assumptions, for example that heat generation is uniform within the body (biophysical ecology) or that the organism can be considered as a set of pools of fixed chemical composition (metabolic theory).

Biophysical ecology is concerned mainly with the flow of heat, water, and respiratory gases while metabolic theory is concerned with the uptake of resources and their internal chemical transformations. Heat, chemical energy, and mass flows, including water, are tightly coupled in a series of interacting equations involving the summation of energy and mass budgets (Fig. 2); the first law of thermodynamics governs their solution.

The full thermodynamic scheme of energy and mass flows between an organism and its environment is depicted in Figure 2, comprising coupled dynamical systems models, each with inherent biological, chemical, and physical assumptions. The heat budget, for example, comprises a set of terms representing a flow of heat energy, each term including one or more environmental variables (e.g. direct and diffuse solar radiation) and one or more parameters (e.g. solar reflectivity of the organism's outer surface and the area of that surface). The theory guides the choice of state variables, the structural form of the equations, the nature of the parameters and the required environmental (or 'forcing') variables. The equations may be solved for given environmental trajectories and parameters through numerical integration of a set of ordinary differential equations (ODEs).

The formulation and solution of such equations and their application to organisms in natural environments have a long history (e.g. Dunham et al., 1989; Porter & Gates, 1969; Porter & Tracy, 1983), but have more recently been called 'mechanistic niche modelling' (Kearney & Porter, 2009). The application of mechanistic niche modelling methods continues to rise, both in sophistication and taxonomic scope (Levy et al., 2017; Pincebourde & Woods, 2012; Riddell et al., 2019; Riddell & Sears, 2017), and general modelling packages are being developed (Kearney & Porter, 2019). A well-recognized limitation of mechanistic niche modelling, however, is the high data requirements (Dormann et al., 2012), and the emergence of generic tools for mechanistic niche modelling creates an imperative to develop trait databases to drive such models.

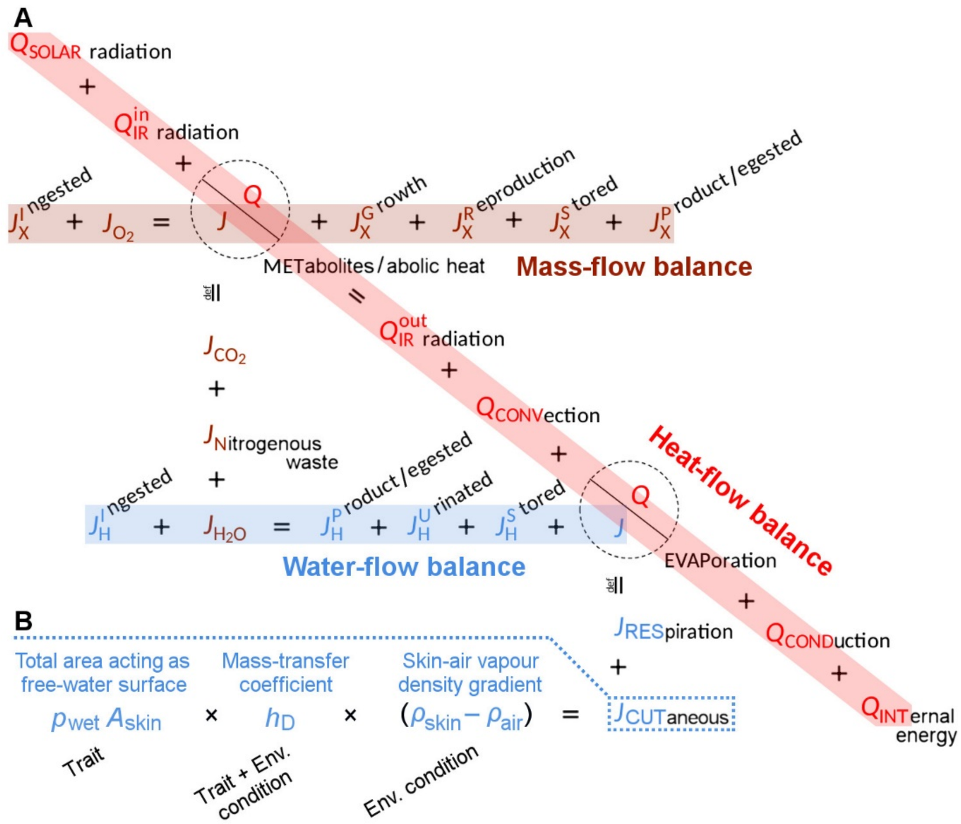

Figure 2. Theory highlights mechanisms and processes that are, in turn, functions of environmental conditions and organismal traits. A, Thermodynamic analysis starts by drawing a boundary between the system (i.e., the organism) and the environment, and then following the exchange of heat (*Q*) and matter (*J*, including water) across such a boundary. Organisms absorb solar and infrared radiation, while also producing metabolic heat by breaking down complex, organic molecules from food. Heat is released via infrared radiation, convection, evaporation, and conduction. Outside of a thermal steady-state, heat surpluses (or deficits) increase (or decrease) internal energy as reflected in body-temperature changes. As with the described heat-flow balance, the mass-flow balance accounts for food ingestion, utilisation, and egestion, all of which is coupled to oxygen consumption (in heterotrophic aerobes) and metabolite excretion (carbon dioxide, nitrogenous wastes, and water). The water-flow balance is fundamental to the organism's ability to tolerate certain environments. The three balances interact at the scale of individuals; food metabolism generates metabolic heat and metabolites, while evaporative heat loss can have a substantial effect on the water-flow balance. The coupling of the heat and mass balances reduces the degrees of freedom of the system and thus reduces overall model complexity. B, Zooming in on one process, for example cutaneous water loss, reveals the dependence on environmental conditions and organismal traits. In the case of cutaneous water loss,

the existence of a boundary layer creates a skin-air water vapour density (ρ) gradient whose maintenance is more costly, in terms of lost water, when the air is drier. A key trait here is the skin surface area (A_{skin}), but also the proportion of that area acting as a free-water surface (p_{wet}), which can be almost 100% for amphibians, but less than 0.1% for reptiles. The other parameter determining the actual cutaneous water loss is the mass-transfer coefficient (h_d) that characterises the rate of mass transport of water through the boundary layer. This rate is dependent on both environmental conditions (e.g. air speed and temperature) and traits (shape and diameter).

Defining functional traits from theoretical models

How do the input requirements of energy and mass balance models, based on thermodynamic systems theory, relate to the way the concept of a functional trait is used in ecology? As discussed above, such models involve equations with parameters and variables that define the evolution of the state of the organism through time as a function of environment. The state of the organism in turn defines performance of the system with respect to the processes of survival, development, growth, and reproduction. In this context, are functional traits simply the parameters for energy and mass balance models? Or are they the data we need to estimate those parameters? What is the role of the state variables in functional traits? And is a functional trait a property of an individual at an instant in time, an individual over its ontogeny, or representative of a population or a species?

In the absence of a clear definition of a trait these questions do not have clear answers. Existing collections of functional trait data reflect a combination of what is practical to measure and what aspects are considered functionally important for the processes of survival, development, growth, and reproduction. To a greater or lesser degree, there is always some kind of theory or model associated with the concept of a trait. For example the TRY plant database was developed in part from the inputs required for vegetation models, and some of the traits included can been seen as state variables, parameters, or data relating to parameters for first-principles models of plant photosynthesis and growth dynamics models (Kattge et al., 2011). But often the model in the background represents a loosely connected, implicit set of ideas rather than an explicit, quantitatively resolved framework; therefore, there is often no clear concept of parameters or state variables.

Here, we define functional traits as properties of individual organisms (more particularly, wherever the system boundary is drawn) that have a connection to organismal performance in terms of survival, development, growth, and reproduction, as defined by a dynamical systems model. If no such connection can be made, then the trait should be described as a 'descriptive' rather than 'functional'. This is similar to the notion of 'soft' versus 'hard' traits in the plant literature (Lavorel & Garnier, 2002).

Moreover, we see four distinct ways that functional traits can be classified when defined by their role in a dynamical systems model:

1. *'Parameter' functional trait*: acts directly as a model parameter;
2. *'Threshold' functional trait*: acts directly as a threshold state variable affecting performance by terminating or altering the behaviour of the system;
3. *'Model' functional trait*: acts directly by determining model structure;
4. *'Estimation' functional trait*: acts indirectly as an observation used to estimate a model parameter, with the model defining the required metadata for the estimation process.

Violle et al. (2007) argued that a functional trait should be definable without reference to environmental conditions—i.e. to the 'forcing data' or variables of equations of state. But there is almost always some degree of environmental contingency on the measurement and interpretation of a functional trait, especially those in the 'estimation' category.

We have developed a decision tree as an aid to classifying measurable aspects of an organism according to this scheme (Fig. 3). The first branch of this tree distinguishes between environmental (external to the system) or organismal (internal to the system) properties. External aspects are then classified as 'environmental variables' if they are explicit in the model as a term or a rate, or as a 'descriptive condition or resource' if not. Of those aspects relating to the organism itself, they are first classified according to whether they are explicitly quantified in a model. This may be as an ontogenetically constant term in the model, in which case it is classified as a functional trait of the 'parameter' category; here we would also include traits that may vary through phenotypic plasticity in response to environmental information. Alternatively, if it is expressed as a rate or a time it must be a functional process in the model relating to model performance; otherwise, it is a state variable. If it is a threshold state variable that alters or terminates the organism as a system, it is a functional trait of the 'threshold' category. If it is an aspect of an organism that is not an explicit term or rate in the model, then it is a determinant of the structural setup of the model and is a functional trait of the 'model' category. Otherwise, if it can be used in the estimation of a model parameter, it is a functional trait of the 'estimation' kind, but this functionality will be contingent on whether the required contextual data, i.e. the metadata, are also available. If this is not possible due to a lack of data or because it cannot be tied to a theoretical model, it is regarded as a 'descriptive trait'. For example, in Fig. 3, colour is a descriptive trait; it is indicative of the process of solar heat gain, but a full spectrum measure of solar reflectance would be required to quantify this for a heat budget model.

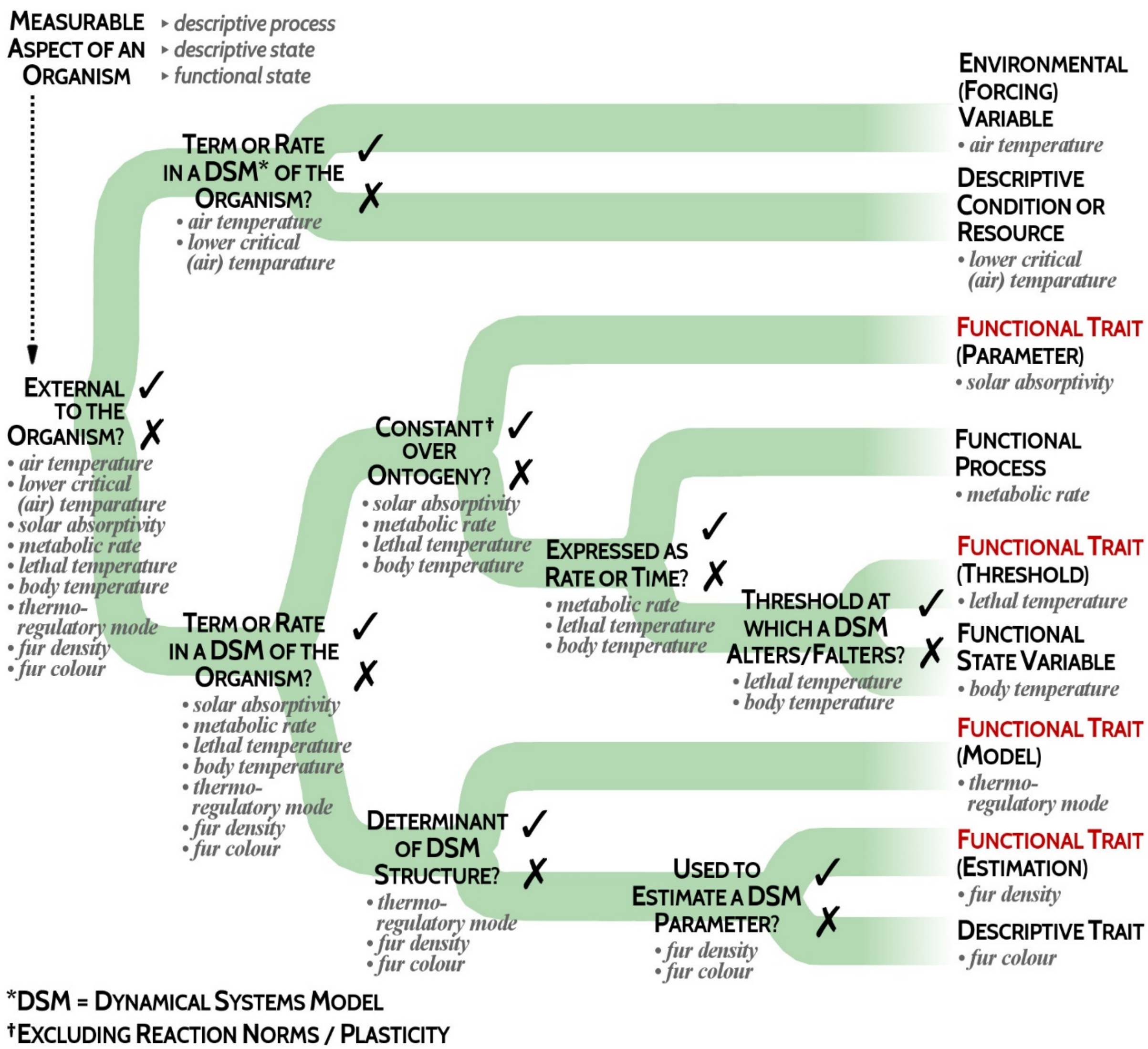

Figure 3. A decision tree for determining if a measurable aspect of an organism classifies as a functional trait, with four subclasses of functional trait being possible. Nine observations relating to thermal tolerance are used as examples. See main text for further details and figures S1 and S2 in the Supporting Information for other examples of its application.

A worked example: Thermal tolerance

The functional trait definitions and decision tree we have just presented can be applied to any aspect of the processes depicted in Fig. 2, for any type of organism. To illustrate the concepts, we apply them to the issue of thermal tolerance—an example of a functional trait that is a threshold value of a state variable, i.e. body temperature. Tolerance of high or low body temperature is clearly relevant to the performance measure of survival and, in any dynamical systems model, acts either to (i) terminate the simulation entirely through death of the individual, (ii) determine limits to activity (especially in ectothermic animals), (iii) induce the loss of a body part (plants), or (iv) alter physiological state (endotherms). Various collations of thermal tolerance observations have been made (Araújo et al., 2013; Bennett et al., 2018; Khaliq et al., 2015; Sunday et al., 2011). These include a wide range of experimental measures relating to thermal tolerance such as body temperatures causing death, coma, locomotor failure, and other defined endpoints for ectotherms, as well as the upper and lower boundaries of the thermoneutral zone for endotherms. Are these threshold observations functional traits in the 'threshold functional trait' sense? We consider this question first from a biophysical perspective, and second from a physiological perspective.

Biophysical perspective of heat tolerance

Viewing the situation for a mammal through the underlying equations of the heat budget of Fig. 2, the first issue to note is that, in the case of a homeothermic endotherm, one does not solve for body temperature but instead solves for the metabolic rate required to achieve a target core temperature. As shown in the inset of Figure 4, measurement of a mammal's metabolic rate in a metabolic chamber across a sufficiently broad range of air temperatures will reveal the thermoneutral zone of air temperatures, outside of which metabolic rate will begin to rise from its minimum possible value. Below the lower critical temperature, metabolic heat production must increase if body temperature is to remain at the target. Above the upper critical temperature, heat must be lost by evaporation if body temperature is to be prevented from rising, which often involves muscular work (e.g. panting) and hence elevated metabolic rate. However, these experimentally measured upper and lower critical temperatures are of limited value in characterising thermal tolerance of an endotherm, especially under natural conditions (see also discussion in Mitchell et al., 2018). If we apply the decision tree of Figure 3, upper and lower critical temperatures are classified as descriptive environmental conditions and not as functional traits. These air temperature reference points are only relevant to the radiative environment, humidity, and wind speed to which the animal was exposed during the experiment.

So, what does the theory guide us to measure as functional traits of endotherm heat tolerance? The equations to compute the heat budget (Porter et al., 1994), and thus the thermoneutral zone, require information on the shape (including posture), size, surface areas, insulation, solar reflectance and water loss of the organism, in addition to target core temperature and minimum allowable metabolic rate. The effective fur thermal conductivity itself depends on the depth of the fur, hair diameter and density. The evaporative heat loss depends on the cutaneous water loss (as explained in Figure 2) and hence on the area of the skin acting as a free-water surface. Evaporative heat loss also depends on the respiratory water loss, which can be calculated if oxygen extraction efficiency is known. Figure 4 summarises functional trait data that are required to characterise aspects of an endotherm's thermal tolerance from a theoretical heat budget perspective. As indicated in Figure 3, these include functional traits of the 'model' category (endothermy, determining what the model solves for), 'estimation' category (fur depth, to estimate fur thermal conductivity), 'threshold' category (basal metabolic rate), and 'parameter' category (fur solar reflectance). Many of these traits can be modified by behaviour or autonomic responses, and thus must be specified as a range of possibilities that can be adjusted incrementally as a thermoregulatory response (e.g. piloerection, changes in posture).

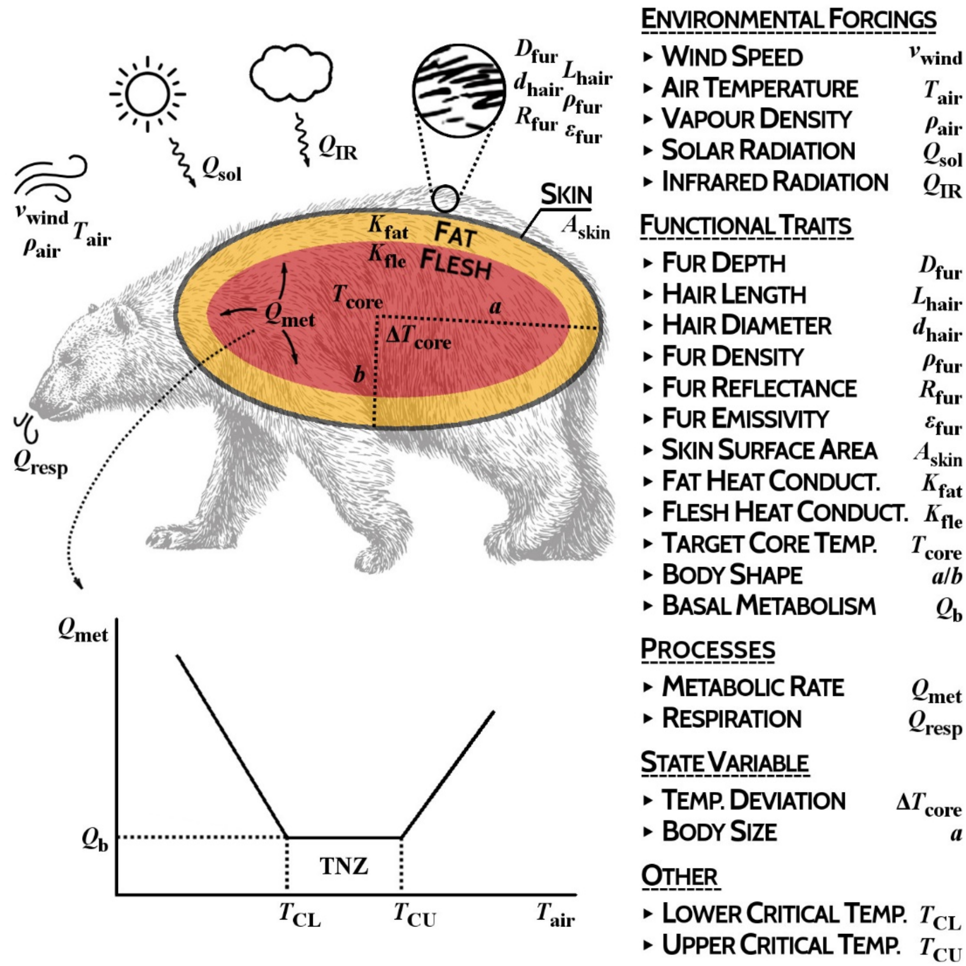

Figure 4. Observations relevant to the heat tolerance (represented by the thermal neutral zone, TNZ) of an endothermic organism. Those observations that are external to the organism, but are model terms, classify as environmental (forcing) variables. Observations that characterise the organism itself are functional traits if they inform model development, serve as model constants, or represent (possibly time-dependent) thresholds of a model's validity. Other time-dependent observations are processes, if their dimension is time or time^{-1}, or state variables otherwise. Lower and upper critical air temperatures are external to the organism and specific to a particular radiative environment, humidity, and wind speed, and as such cannot be model terms; these temperatures classify as a descriptive condition.

The theoretical approach does not mean that the experimental data on upper and lower critical temperatures have no utility, but rather that they require more cautious interpretation (see McKechnie et al., 2017; Mitchell et al., 2018). At the least, such experiments provide one of the critical functional traits, the basal metabolic rate, as well as data to test the model if the environmental conditions (e.g. humidity, wind speed) and other aspects of the organism's behaviour are included as metadata. In this case, the theoretical perspective emphasises the importance of observing the posture of endotherms during such experiments for interpreting the results—something rarely done (Porter et al., 1994). The theoretical perspective also points to a set of morphometric traits relating to body shape and fur properties that should be prioritised for measurement and databasing. These are not necessarily harder traits to measure; for example, shape can be determined from appropriate photographs and fur data can be collected from museum specimens. Surface areas emerge as generally important in biophysical models and are challenging to measure, but new technologies such as computer-aided tomography (Westneat et al., 2008) are breaking down technical barriers.

Physiological perspective of heat tolerance

For ectotherms and endotherms, when the physiological and behavioural regulatory processes are unable to counter environmental or internal heat loads, the target body temperature range will not be maintained, and physiological malfunction and damage may ensue. A theoretical basis to this physiological aspect of heat stress is less developed than the biophysical, but progress is being made, especially with respect to high temperature stress in ectotherms.

Thermal tolerance which affects individual death is typically determined by mortality assays, which has long been known to require knowledge of the temperature experienced by individuals but also the duration of that experience (Brett, 1956; Cossins & Bowler, 1987). Recently, the log-linear slope of the time-temperature survival relationship (noted as z) and the predicted body temperature giving rise to 50% mortality of a sample after exposure of 1 minute (T_{max}) have been proposed as important traits to characterise thermal tolerance (Rezende et al., 2020; see also Jørgensen et al., 2019). This provides a way to unify the time-temperature relationship for thermal tolerance that deserves further exploration, especially given the value of comparing data that may have been generated using different experimental designs.

Thermal tolerance affecting heat stupor in ectotherms is typically assayed by determining the temperature at which coordinated movement is interrupted while temperature is raised experimentally at a given rate (Cooper et al., 2008; Terblanche et al., 2011). Time-temperature interactions occur for such critical thermal maximum (CT_{max}) values too, in part as a consequence of the rate variable, and the proposal has been made that these values lie in the unified time-temperature space described above (Rezende et al., 2020). Whether this is the case is not yet fully clarified (e.g. Kovacevic et al., 2019). Nonetheless, CT_{max} is widely compared as a descriptive trait for understanding thermal responses of ectothermic organisms to the environment, and what risks populations and species might face in the future. The CT_{max} could be considered as a threshold functional trait in our scheme if it is used as an extreme value to constrain activity or microhabitat selection. But it is not so clearly equated with survival of high body temperatures (Chown & Nicholson, 2004). For endotherms, heat stress may involve similar biochemical and physiological issues to those of ectotherms, but with additional complications due to dehydration and pressures on the cardiovascular system (Li et al., 2013; Maloney & Forbes, 2010; McKechnie & Wolf, 2010; Ratnayake et al., 2019).

Given the importance of both temperature and duration of exposure, and some other aspects of the experimental design such as prior thermal experience, the use of high temperature tolerance traits as threshold functional traits in a dynamical systems model requires explicit accompanying metadata on the experimental design. Providing such information would render large databases such as those being advocated through Open Traits Networks (Gallagher et al., 2020) most useful for comparative dynamical systems models and for both understanding and forecasting the abundances and distributions of species.

Developing databases from theoretically defined traits

What would a trait database developed from a theoretical framework look like? One example in biology is the 'Add My Pet' (AmP) database for Dynamic Energy Budget (DEB) theory (Marques et al., 2018) which is primarily a collection of data and parameter estimates for various related models of animal metabolism derived from DEB theory (see also Table S1, Supporting Information, for a preliminary list of biophysical and metabolic functional traits). The observations needed for the inverse fitting of DEB parameters involve a required minimal set (Lika et al., 2014), but over 200 different types of observations have been used to fit the >2800 species in the collection. All these trait observations can be quantified via the DEB models, i.e. equations can be written to calculate each of these observations given a set of parameters and environmental conditions. Thus, DEB theory has defined an explicit set of functional traits of the 'estimation' category, as well as explicitly defining the environmental context, i.e. metadata, required for their use and interpretation. By our criteria, many commonly measured traits could classify as 'estimation' functional traits if the requisite metadata are reported.

Concluding remarks: Let the concept of trait be theoretical!

Energy and mass budget models of organism are emerging for both animals and plants (Higgins et al., 2012; Kearney & Porter, 2020; Levy et al., 2016; Schouten, 2020). We argue that they can provide a fundamental basis for making the link (via parameter, threshold, model or estimation functional traits) between traits and performance. However, our scheme for defining functional traits is not restricted to individual energy and mass budgets; it is relevant to any situation where a dynamical systems model can be specified that links traits and environment to individual performance via clearly defined state variables and parameters. The scheme can also incorporate plastic responses whereby model parameters change according to environmental conditions. In such cases, it may be that the state variable is information, relating for example to photoperiod cues or perceived predation risk, and dynamical systems models of such behavioural responses can be developed (Clark & Mangel, 2000) similarly to the thermodynamic models emphasised here.

Our focus on the use of dynamical systems models to define functional traits has emphasised traits as individual-level phenomena, since the system being modelled is most often an individual organism. But individuals are always part of populations, species, and communities, and at these levels other important dynamics emerge which can be connected to functional traits (de Roos et al., 2013; Durinx et al., 2008; Leibold & Chase, 2017; Metz & Diekmann, 1986). There are clear linkages between the individual processes of growth, development, reproduction, and survival, as defined by dynamical systems models of individuals and their functional traits, to the dynamics at the population level and hence to evolutionary processes. Building on Figure 1, there is a growth function $\dot{G} = \dot{G}$(*e*-state, *i*-state; λ) that specifies the rate of change in body size over time, where *e*-state variables (e.g., food abundance, temperature, stressors, etc.) determine the state of the environment, *i*-state variables (e.g., size, condition, maturity, etc.) determine the state of the individual, and λ is a vector of mechanistic parameters whose values are estimable via available traits. Similar functions exist for fecundity $\dot{F} = \dot{F}$(*e*-state, *i*-state; λ), and survival, $\dot{S} = \dot{S}$ (*e*-state, *i*-state; λ). The functions $\dot{G}$ and $\dot{F}$ are fully constrained by balances in Figure 2, and all functions can be additionally influenced by interspecies interactions (e.g., parasitism or predation). Such an approach constrains the functional form of the fecundity and survival functions, makes their dependence on the environment explicit, and via the growth function relates size and other individual state variables to age. Thus, no new assumptions, and therefore parameters and traits, are needed when transitioning from the individual to the population level. Evolutionary processes can then be incorporated if the genetic basis to parameter values is known.

Violle et al.'s (2007) influential paper 'Let the concept of trait be functional!' argued strongly for the importance of defining traits that affect 'performance'. Here we have added to this notion by arguing for an additional criterion that a theoretical link to performance must be made quantitatively via a dynamical systems model of the organism's performance. Doing so should facilitate the development of robust functional trait databases which, in turn, will accelerate progress across fields from evolutionary ecology to predicting the responses of biodiversity to environmental change.

References

Araújo, M. B., Ferri-Yáñez, F., Bozinovic, F., Marquet, P. A., Valladares, F., & Chown, S. L. (2013). Heat freezes niche evolution. *Ecology Letters*, *16*(9), 1206–1219. https://doi.org/10.1111/ele.12155

Bennett, J. M., Calosi, P., Clusella-Trullas, S., Martínez, B., Sunday, J., Algar, A. C., Araújo, M. B., Hawkins, B. A., Keith, S., Kühn, I., Rahbek, C., Rodríguez, L., Singer, A., Villalobos, F., Ángel Olalla-Tárraga, M., & Morales-Castilla, I. (2018). GlobTherm, a global database on thermal tolerances for aquatic and terrestrial organisms. *Scientific Data*, *5*, 180022. https://doi.org/10.1038/sdata.2018.22

Brett, J. R. (1956). Some principles in the thermal requirements of fishes. *The Quarterly Review of Biology*, *31*(2), 75–87. https://doi.org/10.1086/401257

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, *85*(7), 1771–1789.

Buckley, L. B. (2010). The range implications of lizard traits in changing environments. *Global Ecology and Biogeography*, *19*(4), 452–464.

Calow, P. (1987). Towards a definition of functional ecology. *Functional Ecology*, *1*(1), 57. https://doi.org/10.2307/2389358

Cannon, W. B. (1926). Physiological regulation of normal states: Some tentative postulates concerning biological homeostatics. In A. Pettit (Ed.), *Jubilee Volume for Charles Richet*. Éditions Médicales.

Chown, S. L., & Gaston, K. J. (2008). Macrophysiology for a changing world. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1642), 1469–1478.

Chown, S. L., & Nicholson, S. (2004). *Insect Physiological Ecology: Mechanisms and Patterns*. Oxford University Press.

Clark, C. W., & Mangel, M. (2000). *Dynamic State Variable Models in Ecology: Methods and Applications*. Oxford University Press, Incorporated. http://ebookcentral.proquest.com/lib/unimelb/detail.action?docID=430517

Cooper, B. S., Williams, B. H., & Angilletta, M. J. (2008). Unifying indices of heat tolerance in ectotherms. *Journal of Thermal Biology*, *33*(6), 320–323. https://doi.org/10.1016/j.jtherbio.2008.04.001

Cossins, A. R., & Bowler, K. (1987). *Temperature Biology of Animals*. Chapman and Hall.

de Roos, A. M., Persson, L., & de Roos, A. M. (2013). *Population and Community Ecology of Ontogenetic Development*. Princeton University Press. http://ebookcentral.proquest.com/lib/unimelb/detail.action?docID=1042917

Dormann, C. F., Schymanski, S. J., Cabral, J., Chuine, I., Graham, C., Hartig, F., Kearney, M. R., Morin, X., Romermann, C., Schroder, B., & Singer, A. (2012). Correlation and process in species distribution models: Bridging a dichotomy. *Journal of Biogeography*, *39*(12), 2119–2131. https://doi.org/10.1111/j.1365-2699.2011.02659.x

Dunham, A. E., Grant, B. W., & Overall, K. L. (1989). Interfaces between biophysical and physiological ecology and the population ecology of terrestrial vertebrate ectotherms. *Physiological Zoology*, *62*(2), 335–355.

Durinx, M., (Hans) Metz, J. A. J., & Meszéna, G. (2008). Adaptive dynamics for physiologically structured population models. *Journal of Mathematical Biology*, *56*(5), 673–742. https://doi.org/10.1007/s00285-007-0134-2

Gallagher, R. V., Falster, D. S., Maitner, B. S., Salguero-Gómez, R., Vandvik, V., Pearse, W. D., Schneider, F. D., Kattge, J., Poelen, J. H., Madin, J. S., Ankenbrand, M. J., Penone, C., Feng, X., Adams, V. M., Alroy, J., Andrew, S. C., Balk, M. A., Bland, L. M., Boyle, B. L., … Enquist, B. J. (2020). Open Science principles for accelerating trait-based science across the Tree of Life. *Nature Ecology & Evolution*, 1–10. https://doi.org/10.1038/s41559-020-1109-6

Garnier, E., Navas, M.-L., & Grigulis, K. (2015). *Plant Functional Diversity: Organism traits, community structure, and ecosystem properties*. Oxford University Press. https://oxford.universitypressscholarship.com/view/10.1093/acprof:oso/9780198757368.001.0001/acprof-9780198757368

Gates, D. M. (1980). *Biophysical Ecology*. Springer Verlag.

Gibert, J. P., Dell, A. I., DeLong, J. P., & Pawar, S. (2015). Scaling-up trait variation from individuals to ecosystems. In *Advances in Ecological Research* (Vol. 52, pp. 1–17). Elsevier. https://doi.org/10.1016/bs.aecr.2015.03.001

Grimm, A., Ramírez, A. M. P., Moulherat, S., Reynaud, J., & Henle, K. (2014). Life-history trait database of European reptile species. *Nature Conservation*, *9*, 45–67. https://doi.org/10.3897/natureconservation.9.8908

Guralnick, R., Walls, R., & Jetz, W. (2018). Humboldt Core – toward a standardized capture of biological inventories for biodiversity monitoring, modeling and assessment. *Ecography*, *41*(5), 713–725. https://doi.org/10.1111/ecog.02942

Higgins, S. I., O'Hara, R. B., Bykova, O., Cramer, M. D., Chuine, I., Gerstner, E.-M., Hickler, T., Morin, X., Kearney, M. R., Midgley, G. F., & Scheiter, S. (2012). A physiological analogy of the niche for projecting the potential distribution of plants. *Journal of Biogeography*, *39*(12), 2132–2145. https://doi.org/10.1111/j.1365-2699.2012.02752.x

Jetz, W., McGeoch, M. A., Guralnick, R., Ferrier, S., Beck, J., Costello, M. J., Fernandez, M., Geller, G. N., Keil, P., Merow, C., Meyer, C., Muller-Karger, F. E., Pereira, H. M., Regan, E. C., Schmeller, D. S., & Turak, E. (2019). Essential biodiversity variables for mapping and monitoring species populations. *Nature Ecology & Evolution*, *3*(4), 539–551. https://doi.org/10.1038/s41559-019-0826-1

Jørgensen, L. B., Malte, H., & Overgaard, J. (2019). How to assess Drosophila heat tolerance: Unifying static and dynamic tolerance assays to predict heat distribution limits. *Functional Ecology*, *33*(4), 629–642. https://doi.org/10.1111/1365-2435.13279

Kattge, J., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Bönisch, G., Garnier, E., Westoby, M., Reich, P. B., Wright, I. J., Cornelissen, J. H. C., Violle, C., Harrison, S. P., Bodegom, P. M. V., Reichstein, M., Enquist, B. J., Soudzilovskaia, N. A., Ackerly, D. D., Anand, M., … Wirth, C. (2011). TRY – a global database of plant traits. *Global Change Biology*, *17*(9), 2905–2935. https://doi.org/10.1111/j.1365-2486.2011.02451.x

Kearney, M. R. (2020). What is the status of metabolic theory one century after Pütter invented the von Bertalanffy growth curve? *Biological Reviews*. https://doi.org/10.1111/brv.12668

Kearney, M. R., & Porter, W. P. (2009). Mechanistic niche modelling: Combining physiological and spatial data to predict species' ranges. *Ecology Letters*, *12*, 334–350.

Kearney, M. R., & Porter, W. P. (2019). NicheMapR - an R package for biophysical modelling: The ectotherm and Dynamic Energy Budget models. *Ecography*, *42*, 1–12. https://doi.org/10.1111/ecog.04680

Kearney, M. R., & Porter, W. P. (2020). NicheMapR – an R package for biophysical modelling: The ectotherm and Dynamic Energy Budget models. *Ecography*, *43*(1), 85–96. https://doi.org/10.1111/ecog.04680

Kearney, M. R., Simpson, S. J., Raubenheimer, D., & Helmuth, B. (2010). Modelling the ecological niche from functional traits. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1557), 3469–3483. https://doi.org/10.1098/rstb.2010.0034

Khaliq, I., Fritz, S. A., Prinzinger, R., Pfenninger, M., Böhning-Gaese, K., & Hof, C. (2015). Global variation in thermal physiology of birds and mammals: Evidence for phylogenetic niche conservatism only in the tropics. *Journal of Biogeography*, *42*(11), 2187–2196. https://doi.org/10.1111/jbi.12573

Kissling, W. D., Walls, R., Bowser, A., Jones, M. O., Kattge, J., Agosti, D., Amengual, J., Basset, A., Bodegom, P. M. van, Cornelissen, J. H. C., Denny, E. G., Deudero, S., Egloff, W., Elmendorf, S. C., García, E. A., Jones, K. D., Jones, O. R., Lavorel, S., Lear, D., … Guralnick, R. P. (2018). Towards global data products of Essential Biodiversity Variables on species traits. *Nature Ecology & Evolution*, *2*(10), 1531–1540. https://doi.org/10.1038/s41559-018-0667-3

Kovacevic, A., Latombe, G., & Chown, S. L. (2019). Rate dynamics of ectotherm responses to thermal stress. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1902), 20190174. https://doi.org/10.1098/rspb.2019.0174

Lambers, H., Chapin, S. F., III, & Pons, T. L. (2008). *Plant Physiological Ecology*. Springer.

Laughlin, D. C., Gremer, J. R., Adler, P. B., Mitchell, R. M., & Moore, M. M. (2020). The net effect of functional traits on fitness. *Trends in Ecology & Evolution*, S0169534720301907. https://doi.org/10.1016/j.tree.2020.07.010

Lavorel, S., & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. *Functional Ecology*, *16*(5), 545–556. https://doi.org/10.1046/j.1365-2435.2002.00664.x

Leibold, M. A., & Chase, J. M. (Eds.). (2017). *Metacommunity Ecology, Volume 59*. https://press.princeton.edu/books/hardcover/9780691049168/metacommunity-ecology-volume-59

Levy, O., Borchert, J. D., Rusch, T. W., Buckley, L. B., & Angilletta, M. J. (2017). Diminishing returns limit energetic costs of climate change. *Ecology*, *98*(5), 1217–1228. https://doi.org/10.1002/ecy.1803

Levy, O., Buckley, L. B., Keitt, T. H., & Angilletta, M. J. (2016). Ontogeny constrains phenology: Opportunities for activity and reproduction interact to dictate potential phenologies in a changing climate. *Ecology Letters*.

Li, T., Horton, R. M., & Kinney, P. L. (2013). Projections of seasonal patterns in temperature- related deaths for Manhattan, New York. *Nature Climate Change*, *3*(8), 717–721. https://doi.org/10.1038/nclimate1902

Lika, K., Augustine, S., Pecquerie, L., & Kooijman, S. A. L. M. (2014). The bijection from data to parameter space with the standard DEB model quantifies the supply–demand spectrum. *Journal of Theoretical Biology*, *354*, 35–47. https://doi.org/10.1016/j.jtbi.2014.03.025

Lotka, A. J. (1925). *Elements of Physical Biology*. Williams and Wilkins.

Madin, J. S., Anderson, K. D., Andreasen, M. H., Bridge, T. C. L., Cairns, S. D., Connolly, S. R., Darling, E. S., Diaz, M., Falster, D. S., Franklin, E. C., Gates, R. D., Harmer, A. M. T., Hoogenboom, M. O., Huang, D., Keith, S. A., Kosnik, M. A., Kuo, C.-Y., Lough, J. M., Lovelock, C. E., … Baird, A. H. (2016). The Coral Trait Database, a curated database of trait information for coral species from the global oceans. *Scientific Data*, *3*(1), 160017. https://doi.org/10.1038/sdata.2016.17

Maloney, S. K., & Forbes, C. F. (2010). What effect will a few degrees of climate change have on human heat balance? Implications for human activity. *International Journal of Biometeorology*, *55*(2), 147–160. https://doi.org/10.1007/s00484-010-0320-6

Marques, G. M., Augustine, S., Lika, K., Pecquerie, L., Domingos, T., & Kooijman, S. A. L. M. (2018). The AmP project: Comparing species on the basis of dynamic energy budget parameters. *PLOS Computational Biology*, *14*(5), e1006100. https://doi.org/10.1371/journal.pcbi.1006100

McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, *21*(4), 178–185.

McKechnie, A. E., Coe, B. H., Gerson, A. R., & Wolf, B. O. (2017). Data quality problems undermine analyses of endotherm upper critical temperatures. *Journal of Biogeography*, *44*(10), 2424–2426. https://doi.org/10.1111/jbi.12941

McKechnie, A. E., & Wolf, B. O. (2010). Climate change increases the likelihood of catastrophic avian mortality events during extreme heat waves. *Biology Letters*, *6*(2), 253–256. https://doi.org/10.1098/rsbl.2009.0702

Metz, J. A. J., & Diekmann, O. (Eds.). (1986). *The dynamics of physiologically structured populations*. Springer.

Mitchell, D., Snelling, E. P., Hetem, R. S., Maloney, S. K., Strauss, W. M., & Fuller, A. (2018). Revisiting concepts of thermal physiology: Predicting responses of mammals to climate change. *Journal of Animal Ecology*, *87*(4), 956–973. https://doi.org/10.1111/1365-2656.12818

Moretti, M., Dias, A. T. C., Bello, F. de, Altermatt, F., Chown, S. L., Azcárate, F. M., Bell, J. R., Fournier, B., Hedde, M., Hortal, J., Ibanez, S., Öckinger, E., Sousa, J. P., Ellers, J., & Berg, M. P. (2017). Handbook of protocols for standardized measurement of terrestrial invertebrate functional traits. *Functional Ecology*, *31*(3), 558–567. https://doi.org/10.1111/1365-2435.12776

Myhrvold, N. P., Baldridge, E., Chan, B., Sivam, D., Freeman, D. L., & Ernest, S. K. M. (2015). An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles. *Ecology*, *96*(11), 3109–3109. https://doi.org/10.1890/15-0846R.1

Nisbet, R. M., Muller, E. B., Lika, K., & Kooijman, S. A. L. M. (2000). From molecules to ecosystems through dynamic energy budget models. *Journal of Animal Ecology*, *69*, 913–926.

Nock, C. A., Vogt, R. J., & Beisner, B. E. (2016). Functional Traits. In John Wiley & Sons Ltd (Ed.), *ELS* (pp. 1–8). John Wiley & Sons, Ltd. https://doi.org/10.1002/9780470015902.a0026282

Oliveira, B. F., São-Pedro, V. A., Santos-Barrera, G., Penone, C., & Costa, G. C. (2017). AmphiBIO, a global database for amphibian ecological traits. *Scientific Data*, *4*(1), 170123. https://doi.org/10.1038/sdata.2017.123

Parr, C. S., Schulz, K. S., Hammock, J., Wilson, N., Leary, P., Rice, J., & Corrigan, R. J. (2016). TraitBank: Practical semantics for organism attribute data. *Semantic Web*, *7*(6), 577–588. https://doi.org/10.3233/SW-150190

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M. S., Cornwell, W. K., Craine, J. M., Gurvich, D. E., Urcelay, C., Veneklaas, E. J., Reich, P. B., Poorter, L., Wright, I. J., Ray, P., Enrico, L., Pausas, J. G., Vos, A. C. de, … Cornelissen, J. H. C. (2013). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, *61*(3), 167–234. https://doi.org/10.1071/BT12225

Pincebourde, S., & Woods, H. A. (2012). Climate uncertainty on leaf surfaces: The biophysics of leaf microclimates and their consequences for leaf-dwelling organisms. *Functional Ecology*, *26*(4), 844–853. https://doi.org/10.1111/j.1365-2435.2012.02013.x

Pollock, L. J., Morris, W. K., & Vesk, P. A. (2012). The role of functional traits in species distributions revealed through a hierarchical model. *Ecography*, *35*(8), 716–725. https://doi.org/10.1111/j.1600-0587.2011.07085.x

Porter, W. P., & Gates, D. M. (1969). Thermodynamic equilibria of animals with environment. *Ecological Monographs*, *39*(3), 227–244. https://doi.org/10.2307/1948545

Porter, W. P., Munger, J. C., Stewart, W. E., Budaraju, S., & Jaeger, J. (1994). Endotherm energetics: From a scalable individual-based model to ecological applications. *Australian Journal of Zoology*, *42*, 125–162.

Porter, W. P., & Tracy, C. R. (1983). Biophysical analyses of energetics, time-space utilization, and distributional limits. In R. B. Huey, E. R. Pianka, & T. W. Schoener (Eds.), *Lizard ecology: Studies of a model organism* (918; pp. 55–83). Harvard University Press.

Prosser, C. L. (Ed.). (1991). *Environmental and Metabolic Animal Physiology*. Wiley-Liss.

Ratnayake, H. U., Kearney, M. R., Govekar, P., Karoly, D. J., & Welbergen, J. A. (2019). Forecasting wildlife die-offs from extreme heat events. *Animal Conservation*. https://doi.org/dx.doi.org/10.1111/ACV.12476

Regos, A., Gagne, L., Alcaraz-Segura, D., Honrado, J. P., & Domínguez, J. (2019). Effects of species traits and environmental predictors on performance and transferability of ecological niche models. *Scientific Reports*, *9*(1), 4221. https://doi.org/10.1038/s41598-019-40766-5

Rezende, E. L., Bozinovic, F., Szilágyi, A., & Santos, M. (2020). Predicting temperature mortality and selection in natural Drosophila populations. *Science*, *369*(6508), 1242–1245. https://doi.org/10.1126/science.aba9287

Riddell, E. A., Iknayan, K. J., Wolf, B. O., Sinervo, B., & Beissinger, S. R. (2019). Cooling requirements fueled the collapse of a desert bird community from climate change. *Proceedings of the National Academy of Sciences*, *116*(43), 21609–21615. https://doi.org/10.1073/pnas.1908791116

Riddell, E. A., & Sears, M. W. (2017). Physical calculations of resistance to water loss improve species range models: Reply. *Ecology*, *98*(11), 2965–2968. https://doi.org/10.1002/ecy.2022

Schouten, R. (2020). Integrating dynamic plant growth models and microclimates for species distribution modelling. *Ecological Modelling*, 14.

Schrodinger, E. (1944). *What is Life?* Cambridge University Press.

Shipley, B., De Bello, F., Cornelissen, J. H. C., Laliberté, E., Laughlin, D. C., & Reich, P. B. (2016). Reinforcing loose foundation stones in trait-based plant ecology. *Oecologia*, *180*(4), 923–931. https://doi.org/10.1007/s00442-016-3549-x

Sibly, R. M., Brown, J. H., & Kodric-Brown, A. (2012). *Metabolic Ecology: A Scaling Approach*. Wiley-Blackwell.

Siefert, A., Violle, C., Chalmandrier, L., Albert, C. H., Taudiere, A., Fajardo, A., Aarssen, L. W., Baraloto, C., Carlucci, M. B., Cianciaruso, M. V., Dantas, V. de L., Bello, F. de, Duarte, L. D. S., Fonseca, C. R., Freschet, G. T., Gaucherand, S., Gross, N., Hikosaka, K., Jackson, B., … Wardle, D. A. (2015). A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters*, *18*(12), 1406–1419. https://doi.org/10.1111/ele.12508

Soyer, O. S. (Ed.). (2012). *Evolutionary Systems Biology* (Vol. 751). Springer New York. https://doi.org/10.1007/978-1-4614-3567-9

Start, D., & Gilbert, B. (2019). Trait variation across biological scales shapes community structure and ecosystem function. *Ecology*, *100*(9), e02769. https://doi.org/10.1002/ecy.2769

Sunday, J. M., Bates, A. E., & Dulvy, N. K. (2011). Global analysis of thermal tolerance and latitude in ectotherms. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1713), 1823–1830.

Terblanche, J. S., Hoffmann, A. A., Mitchell, K. A., Rako, L., Roux, P. C. le, & Chown, S. L. (2011). Ecologically relevant measures of tolerance to potentially lethal temperatures. *Journal of Experimental Biology*, *214*(22), 3713–3725. https://doi.org/10.1242/jeb.061283

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional! *Oikos*, *116*(5), 882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x

Violle, C., Reich, P. B., Pacala, S. W., Enquist, B. J., & Kattge, J. (2014). The emergence and promise of functional biogeography. *Proceedings of the National Academy of Sciences*, *111*(38), 13690–13696. https://doi.org/10.1073/pnas.1415442111

von Bertalanffy, L. (1950). The Theory of Open Systems in Physics and Biology. *Science*, *111*(2872), 23–29. https://doi.org/10.1126/science.111.2872.23

Warming, Eugenius. (1909). *Oecology of plants: An introduction to the study of plant-communities*. Oxford :Clarendon Press,. https://www.biodiversitylibrary.org/item/64041

Westneat, M. W., Socha, J. J., & Lee, W. K. (2008). Advances in biological structure, function, and physiology using synchrotron X-ray imaging. *Annual Review of Physiology*, *70*, 119–142. https://doi.org/10.1146/annurev.physiol.70.113006.100434

Wieczorek, J., Bloom, D., Guralnick, R., Blum, S., Döring, M., Giovanni, R., Robertson, T., & Vieglais, D. (2012). Darwin Core: An Evolving Community-Developed Biodiversity Data Standard. *PLOS ONE*, *7*(1), e29715. https://doi.org/10.1371/journal.pone.0029715

Box 1. Glossary

Term	Definition
biophysical ecology	Theory governing the application of thermodynamic systems principles to quantify heat, water, and gas exchange between organisms and their environments.
dynamical system	A time-evolving system defined completely by a set of state variables, their changes being describable with one or more differential equations.
environmental (forcing) variable	An aspect of the environment of a dynamical system that has an impact on its state variables.
functional trait	A property of a biological thermodynamic system (usually an individual) that functions in the quantification of the performance of that system in terms of survival, development, growth, and reproduction. This function may be direct as a parameter, a threshold state variable value at which the system breaks down or changes behaviour, or in determining overall model structure. It may also be indirect, as a requirement in the estimation of a parameter.
metabolic theory	Theory governing the application of thermodynamic systems principles to quantify the uptake and use of substrates by organisms for development, growth, and reproduction, and the rate of ageing.
organism	An open thermodynamic system using energy to maintain and increase its ordered state, and matter to grow and reproduce, under the instruction of internally referenced information (RNA/DNA).
parameter	A (usually constant) term in an equation that determines the sensitivity of a dynamical system's state to environmental (forcing) variables.
state variable	A quantity such as volume, mass, pressure, energy content, or temperature that defines the state of a dynamical system.
system boundary	A conceptual surface separating a thermodynamic system of interest from its environment.
thermodynamic system	A region of the universe, defined by a system boundary, across which the exchange and transformation of energy (closed system) or energy and matter (open system) is quantified.

Figure S1. A decision tree for determining if a measurable aspect of an organism classifies as a functional trait, with four subclasses of functional trait being possible. Nine observations relating to water balance are used as examples. See main text for further details.

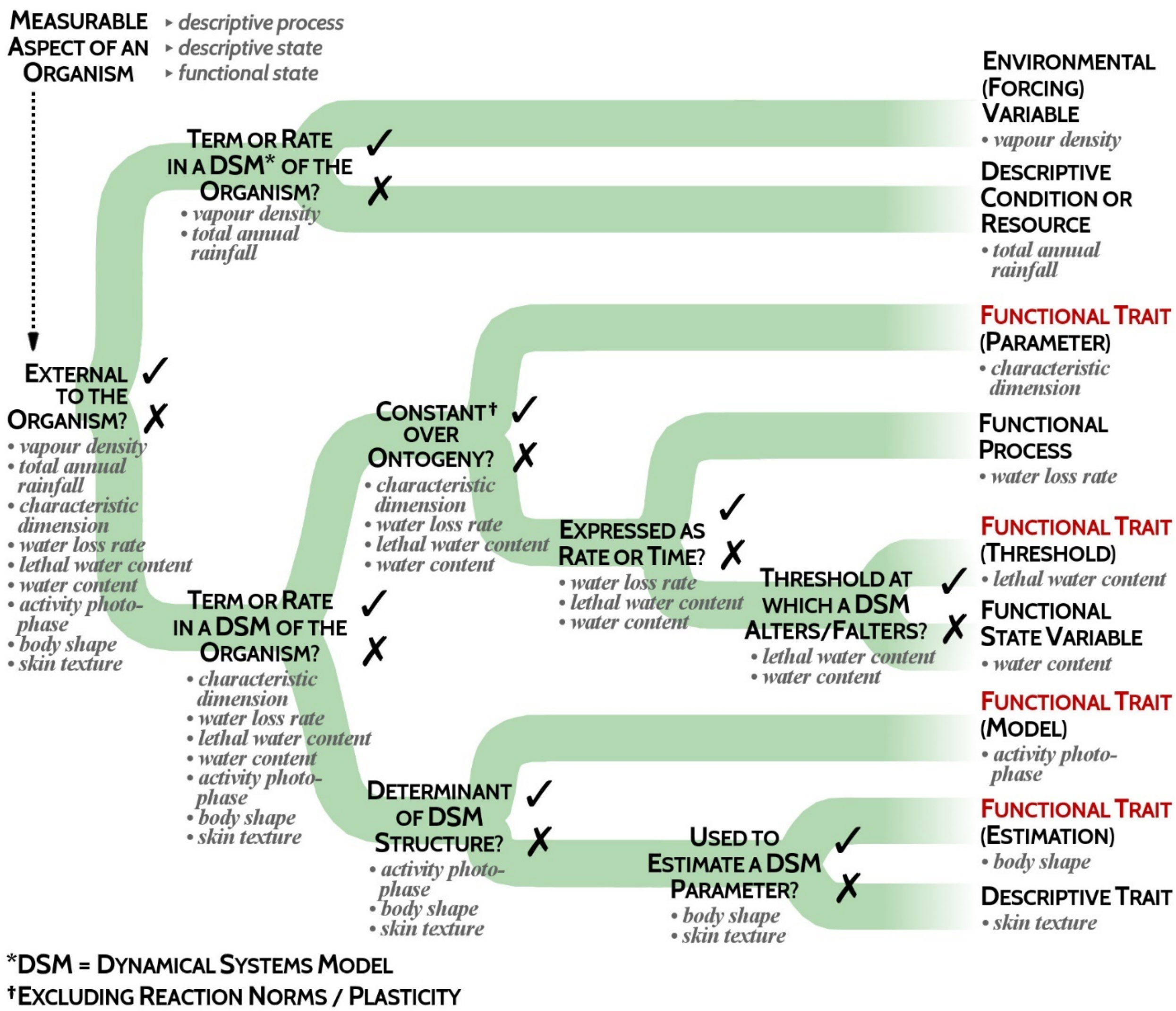

Figure S2. A decision tree for determining if a measurable aspect of an organism classifies as a functional trait, with four subclasses of functional trait being possible. Nine observations relating to feeding are used as examples. See main text for further details.

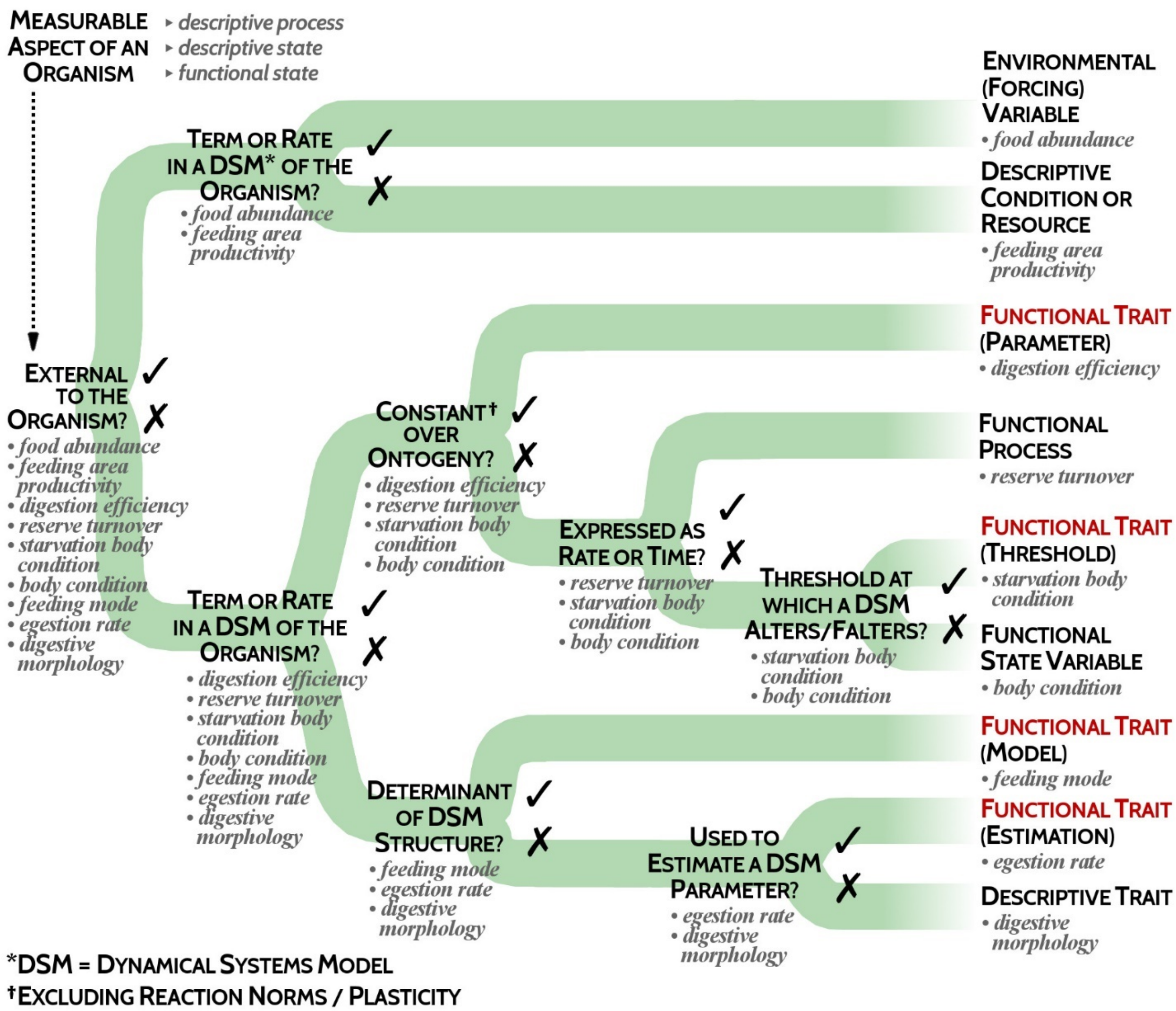

Table S1. A preliminary list of mechanistically defined traits that include Dynamic Energy Budget theory traits as well as the biophysical traits required for solving heat and water budgets of ectotherms and endotherms. Other theoretical models linking organismal performance to environment should similarly generate their own list of traits. There is no current database of biophysical traits. The DEB trait observations associated with the AmP project https://www.bio.vu.nl/thb/deb/deblab/add_my_pet/ (Marques et al., 2018) are embedded in parameter estimation scripts. But they could easily be ingested into a trait database and formally connected to other trait frameworks using Darwin Core data standards. The 'Trait Category' column indicates which of the four functional trait categories defined in the main manuscript the decision tree (see Figs. S1 & S2 above) assigns them. The 'estimation' traits are all connected in some way to the equations of models generated by the associated theory. These trait categories and types, and the associated metadata, could be usefully aligned and incorporated into biodiversity informatics standards to further facilitate the sharing of information on biological diversity (Guralnick et al., 2018; Wieczorek et al., 2012)**(Guralnck et al. 2018, Wiekzorek et al. 2012). In particular, clear criteria could be developed for determining whether a 'descriptive trait' can graduate to an 'estimation functional trait' according to the associated metadata.**

Descriptive Category	Trait Category	Data Type	Data Labels	Dimension	Metadata Requirements	Description
Metabolic	estimation	Scalar	ah	time	body temperature, food availability	age at h=hat
Metabolic	estimation	Scalar	ab	time	body temperature, food availability	age at birth
Metabolic	estimation	Scalar	tg	time	body temperature, food availability	gestation tim
Metabolic	estimation	Scalar	ax	time	body temperature, food availability	age at x=fled
Metabolic	estimation	Scalar	as	time	body temperature, food availability	age at s=star
Metabolic	estimation	Scalar	aj	time	body temperature, food availability	age at j=end
Metabolic	estimation	Scalar	ap	time	body temperature, food availability	age (or time
Metabolic	estimation	Scalar	aR	time	body temperature, food availability	age at R=first
Metabolic	estimation	Scalar	ae	time	body temperature, food availability	age at e=eme
Metabolic	estimation	Scalar	am	time	body temperature, food availability	age at death

Metabolic	estimation	Scalar	Lh	length	maternal food availability (or initial egg energy)	length at h
Metabolic	estimation	Scalar	Lb	length	maternal food availability (or initial egg energy)	length at b
Metabolic	estimation	Scalar	Lx	length	food availability	length at x
Metabolic	estimation	Scalar	Ls	length	food availability	length at s
Metabolic	estimation	Scalar	Lj	length	food availability	length at j
Metabolic	estimation	Scalar	Lp	length	food availability	length at p
Metabolic	estimation	Scalar	LR	length	food availability	length at R
Metabolic	estimation	Scalar	Li	length	food availability	length at i=ul
Metabolic	estimation	Scalar	Ab	area	food availability	total physica
Metabolic	estimation	Scalar	Ap	area	food availability	total physica
Metabolic	estimation	Scalar	Ai	area	food availability	total physica
Metabolic	estimation	Scalar	Vb	volume	food availability	volume at b
Metabolic	estimation	Scalar	Vp	volume	food availability	volume at p
Metabolic	estimation	Scalar	Vi	volume	food availability	volume at i
Metabolic	estimation	Scalar	Ww0	mass	maternal food availability (or initial egg energy)	wet weight a
Metabolic	estimation	Scalar	Wwh	mass	maternal food availability (or initial egg energy)	wet weight a
Metabolic	estimation	Scalar	Wwb	mass	maternal food availability (or initial egg energy)	wet weight a
Metabolic	estimation	Scalar	Wwx	mass	food availability	wet weight a
Metabolic	estimation	Scalar	Wws	mass	food availability	wet weight a
Metabolic	estimation	Scalar	Wwj	mass	food availability	wet weight a
Metabolic	estimation	Scalar	WwR	mass	food availability	wet weight a
Metabolic	estimation	Scalar	Wwp	mass	food availability	wet weight a
Metabolic	estimation	Scalar	Wwe	mass	food availability	wet weight a
Metabolic	estimation	Scalar	Wwi	mass	food availability	wet weight a
Metabolic	estimation	Scalar	Wd0	mass	maternal food availability (or initial egg energy)	dry weight at
Metabolic	estimation	Scalar	Wdh	mass	maternal food availability (or initial egg energy)	dry weight at
Metabolic	estimation	Scalar	Wdb	mass	maternal food availability (or initial egg energy)	dry weight at
Metabolic	estimation	Scalar	Wdx	mass	food availability	dry weight at
Metabolic	estimation	Scalar	Wds	mass	food availability	dry weight at
Metabolic	estimation	Scalar	Wdj	mass	food availability	dry weight at
Metabolic	estimation	Scalar	Wdp	mass	food availability	dry weight at
Metabolic	estimation	Scalar	Wde	mass	food availability	dry weight at
Metabolic	estimation	Scalar	Wdi	mass	food availability	dry weight at

Metabolic	estimation	Scalar	WdR_Wd	mass	food availability	gonad dry we
Metabolic	estimation	Scalar	WC0	mass	maternal food availability (or initial egg energy)	carbon weigh
Metabolic	estimation	Scalar	WN0	mass	maternal food availability (or initial egg energy)	nitrogen wei
Metabolic	estimation	Scalar	E0	energy	food availability	reserve ener
Metabolic	estimation	Scalar	Eh	energy	food availability	reserve ener
Metabolic	estimation	Scalar	Eb	energy	food availability	reserve ener
Metabolic	estimation	Scalar	Ej	energy	food availability	reserve ener
Metabolic	estimation	Scalar	EbE0	ratio	food availability	ratio of reser
Metabolic	estimation	Scalar	EXx	energy	food availability	cumulated fo
Metabolic	estimation	Scalar	r	1 / time	body temperature, food availability	specific grow
Metabolic	estimation	Scalar	rB	1 / time	body temperature, food availability	von Bertalan
Metabolic	estimation	Scalar	Ri	number / time	body temperature, food availability	reproduction
Metabolic	estimation	Scalar	R_L	number / time	body temperature, food availability	reproduction
Metabolic	estimation	Scalar	R_W	number / time	body temperature, food availability	reproduction
Metabolic	estimation	Scalar	GSI	ratio	food availability	gonado-soma
Metabolic	estimation	Scalar	Ni	number	food availability	(total) numbe
Metabolic	estimation	Scalar	Fm	volume / time	body temperature	maximum cle
Metabolic	parameter	Scalar	K	~ / volume		half saturatio
Metabolic	estimation	Scalar	pXi	energy / time	body temperature	maximum in
Metabolic	estimation	Scalar	pAi	energy / time	body temperature	maximum as
Metabolic	estimation	Scalar	pL	energy / time	body temperature, food availability, body size	lactation flux
Metabolic	parameter	Scalar	kapX	fraction	diet	digestion effi
Metabolic	estimation	Scalar	RQ	ratio		respiration q
Metabolic	estimation	Scalar	JXi	number / time	body temperature	food consum
Metabolic	estimation	Scalar	JLi	number / time	body temperature, food availability	milk product
Metabolic	estimation	Scalar	JOb	number / time	body temperature, food availability	O2 consump
Metabolic	estimation	Scalar	JOi	number / time	body temperature, food availability	O2 consump
Metabolic	estimation	Scalar	JCi	number / time	body temperature, food availability	CO2 producti
Metabolic	threshold	Scalar	ss	dimensionless		supply stress
Metabolic	estimation	Scalar	xi_WE	energy / volume	food availability	energy densi the reproduc
Metabolic	estimation	Matrix	t-Le	time, length	body temperature, food availability	time, embryo
Metabolic	estimation	Matrix	t-L	time, length	body temperature, food availability	time, length

Metabolic	estimation	Matrix	t-LR	time, length	body temperature, food availability	time, length
Metabolic	estimation	Matrix	t-Ae	time, area	body temperature, maternal food availability (or initial egg energy)	time, surface
Metabolic	estimation	Matrix	t-A	time, area	body temperature, food availability	time, surface
Metabolic	estimation	Matrix	t-V	time, volume	body temperature, food availability	time, volume
Metabolic	estimation	Matrix	t-VYe	time, volume	body temperature, maternal food availability (or initial egg energy)	time, embryo
Metabolic	estimation	Matrix	t-Wwe	time, weight	body temperature, maternal food availability (or initial egg energy)	time, embryo
Metabolic	estimation	Matrix	t-WwYe	time, weight	body temperature, maternal food availability (or initial egg energy)	time, embryo
Metabolic	estimation	Matrix	t-WwVe	time, weight	body temperature, maternal food availability (or initial egg energy)	time, embryo
Metabolic	estimation	Matrix	t-Ww	time, weight	body temperature, food availability	time, wet we
Metabolic	estimation	Matrix	t-WwR	time, weight	body temperature, food availability	time, gonad
Metabolic	estimation	Matrix	t-Wde	time, weight	body temperature, maternal food availability (or initial egg energy)	time, embryo
Metabolic	estimation	Matrix	t-WdYe	time, weight	body temperature, maternal food availability (or initial egg energy)	time, embryo
Metabolic	estimation	Matrix	t-WdVe	time, weight	body temperature, maternal food availability (or initial egg energy)	time, embryo
Metabolic	estimation	Matrix	t-Wd	time, weight	body temperature, food availability	time, dry wei
Metabolic	estimation	Matrix	t-WdR	time, weight	body temperature, food availability	time, gonad
Metabolic	estimation	Matrix	t-WC	time, weight	body temperature, food availability	time, carbon
Metabolic	estimation	Matrix	t-M_PLC	time, mass	body temperature, food availability	time, mass of carbohydrate

Metabolic	estimation	Matrix	t-M_N	time, mass	body temperature, food availability	time, mass o
Metabolic	estimation	Matrix	t-M_DNA	time, mass	body temperature, food availability	time, mass o
Metabolic	estimation	Matrix	t-M_RNA	time, mass	body temperature, food availability	time, mass o
Metabolic	estimation	Matrix	t-E	time, energy	body temperature, food availability	time, energy
Metabolic	estimation	Matrix	t-pX	time, energy/time	body temperature, food availability, body size	time, food en
Metabolic	estimation	Matrix	t-p+	time, energy/time	body temperature, food availability	time, heat pr
Metabolic	estimation	Matrix	t-R	time, #/time	body temperature, food availability	time, reprod
Metabolic	estimation	Matrix	t-N	time, #	body temperature, food availability	time, numbe
Metabolic	estimation	Matrix	t-F_f	time, #/time	body temperature	time, filtering
Metabolic	estimation	Matrix	t-JX	time, energy/time	body temperature, food availability	time, ingesti
Metabolic	estimation	Matrix	t-JOe	time, mass/time	body temperature, maternal food availability (or initial egg energy)	time, embryo
Metabolic	estimation	Matrix	t-JCe	time, mass/time	body temperature, maternal food availability (or initial egg energy)	time, embryo
Metabolic	estimation	Matrix	t-JNe	time, mass/time	body temperature, maternal food availability (or initial egg energy)	time, embryo
Metabolic	estimation	Matrix	t-JO	time, mass/time	body temperature, food availability	time, O_2 co
Metabolic	state variable	Matrix	t-T	time, temperature		time, body te
Metabolic	estimation	Matrix	t-S	time, fraction	body temperature, food availability	time, survivi
Metabolic	estimation	Matrix	t-dC	time, ration	body temperature, food availability	time, conditi
Metabolic	estimation	Matrix	ax-Wwx	time, weight	body temperature, food availability	age at fledgi
Metabolic	estimation	Matrix	X-aj	mass/time	body temperature	food density,
Metabolic	estimation	Matrix	X-ap	mass/time	body temperature	food density,
Metabolic	estimation	Matrix	X-am	mass/time	body temperature	food density,
Metabolic	estimation	Matrix	X-Ri	mass/time	body temperature	food density,
Metabolic	estimation	Matrix	X-JX	mass/time	body temperature, body size	food density,
Metabolic	estimation	Matrix	X-JP	mass/time	body temperature, body size	food density,
Metabolic	estimation	Matrix	X-JC	mass/time	body temperature, body size	food density,

Metabolic	estimation	Matrix	L-V	length, volume		length, volun
Metabolic	estimation	Matrix	L-Wwe	length, weight	maternal food availability (or initial egg energy)	length, embr
Metabolic	estimation	Matrix	L-Ww	length, weight	food availability	length, wet v
Metabolic	estimation	Matrix	L-Wde	length, weight	maternal food availability (or initial egg energy)	length, embr
Metabolic	estimation	Matrix	L-Wd	length, weight	food availability	length, dry w
Metabolic	estimation	Matrix	L-WwR	length, weight	food availability	length, gonac
Metabolic	estimation	Matrix	L-WC	length, weight	food availability	length, carbo
Metabolic	estimation	Matrix	L-WN	length, weight	food availability	length, nitrog
Metabolic	estimation	Matrix	L-E	length, energy	food availability	length, total
Metabolic	estimation	Matrix	L-N	length, #	body temperature, food availability	length, numb
Metabolic	estimation	Matrix	L-R	length, #/time	body temperature, food availability	length, repro
Metabolic	estimation	Matrix	L-GSI	length, ratio	food availability	length, gonac
Metabolic	estimation	Matrix	L-F	length, #/time	body temperature, food availability	length, filteri
Metabolic	estimation	Matrix	L-JX	length, mass/time	body temperature, food availability	length, food
Metabolic	estimation	Matrix	L-X	length, mass	food availability	length, cumu
Metabolic	estimation	Matrix	L-JO	length, mass/time	body temperature, food availability	length, O_2 c
Metabolic	estimation	Matrix	L-JC	length, mass/time	body temperature, food availability	length, CO_2
Metabolic	estimation	Matrix	Ww-N	weight, #	body temperature, food availability	wet weight, r
Metabolic	estimation	Matrix	Ww-R	weight, #/time	body temperature, food availability	wet weight, r
Metabolic	estimation	Matrix	Ww-JX	weight, mass/time	body temperature, food availability	wet weight, i
Metabolic	estimation	Matrix	Ww-X	weight, energy	food availability	wet weight, c
Metabolic	estimation	Matrix	Ww-JO	weight, mass	body temperature, food availability	wet weight, C
Metabolic	estimation	Matrix	Ww-JN	weight, mass	body temperature, food availability	wet weight, N
Metabolic	estimation	Matrix	Ww-p+	weight, energy/time	body temperature, food availability	wet weight, h
Metabolic	estimation	Matrix	Ww-pX	weight, energy/time	body temperature, food availability	wet weight, f
Metabolic	estimation	Matrix	Wd-JO	weight, mass/time	body temperature, food availability	dry weight, C
Metabolic	estimation	Matrix	Wd-JC	weight, mass/time	body temperature, food availability	wet weight, C
Metabolic	estimation	Matrix	Wd-JN	weight, mass/time	body temperature, food availability	dry weight, N
Metabolic	estimation	Matrix	WC-JX	weight, mass/time	body temperature, food availability	carbon weigh

Metabolic	estimation	Matrix	JX-ap	mass/time	body temperature, food availability	ingestion rat
Metabolic	estimation	Matrix	JX-am	mass/time	body temperature, food availability	ingestion rat
Metabolic	estimation	Matrix	JX-Vp	mass/time	body temperature, food availability	ingestion rat
Metabolic	estimation	Matrix	JX-Vi	mass/time	body temperature, food availability	ingestion rat
Metabolic	estimation	Matrix	JX-Ri	mass/time	body temperature, food availability	ingestion rat
Metabolic	estimation	Matrix	T-ah	temperature, time	food availability	temperature
Metabolic	estimation	Matrix	T-ab	temperature, time	food availability	temperature
Metabolic	estimation	Matrix	T-aj	temperature, time	food availability	temperature
Metabolic	estimation	Matrix	T-ap	temperature, time	food availability	temperature
Metabolic	estimation	Matrix	T-am	temperature, time	food availability	temperature
Metabolic	estimation	Matrix	T-t	temperature, time	food availability	temperature
Metabolic	estimation	Matrix	T-R	temperature, #/time	food availability, body size	temperature
Metabolic	estimation	Matrix	T-N	temperature, #	food availability, body size	temperature
Metabolic	estimation	Matrix	T-JX	temperature, mass/time	food availability, body size	temperature
Metabolic	estimation	Matrix	T-JO	temperature, mass/time	food availability, body size	temperature
Metabolic	estimation	Matrix	T-JC	temperature, mass/time	food availability, body size	temperature
Metabolic	estimation	Matrix	T-JN	temperature, mass/time	food availability, body size	temperature
Behavioural	threshold	Scalar	T_F_min	temperature		Minimum for (also affects l
Behavioural	threshold	Scalar	T_F_max	temperature		Maximum fo
Behavioural	threshold	Scalar	T_B_min	temperature		Minimum ba
Behavioural	threshold	Scalar	T_RB_min	temperature		Minimum ter will move fro °C
Behavioural	threshold	Scalar	T_pref	temperature		Preferred bo
Physiological	threshold	Scalar	CT_max	temperature		Critical therm burrow dept used to impo
Physiological	threshold	Scalar	CT_min	temperature		Critical therm burrow dept used to impo
Behavioural	model	Scalar	nocturn	none		Diurnal activ
Behavioural	model	Scalar	diurn	none		Nocturnal ac
Behavioural	model	Scalar	crepus	none		Crepuscular a

Behavioural	model	Scalar	burrow	none	Shelter in bu
Behavioural	model	Scalar	climb	none	Climbing to s 0=no
Behavioural	model	Scalar	fossorial	none	Fossorial act
Physiological	parameter	Scalar	pct_wet	percentage	% of surface exchanger, fo water loss
Morphological	parameter	Scalar	pct_eyes	percentage	% of surface eyes, for com (only when a
Morphological	parameter	Scalar	pct_mouth	percentage	% of surface mouth, for co loss
Morphological	parameter	Scalar	alpha_max	proportion	maximum so
Morphological	parameter	Scalar	alpha_min	proportion	minimum sol
Morphological	estimation	Matrix	A_Ww	area	total surface
Morphological	estimation	Matrix	Asil_Ww	area	silhouette su
Morphological	estimation	Scalar	Ab	area	outer surface
Morphological	estimation	Scalar	Ap	area	outer surface
Morphological	estimation	Scalar	Ai	area	outer surface
Behavioural	parameter	Scalar	pantmax	none	maximum mu for respirato
Physiological	parameter	Scalar	F_O2	percentage	% oxygen ext respiratory w
Physiological	parameter	Scalar	delta_air	temperature	temperature expired and i respiratory w
Morphological	parameter	Scalar	fatosk	proportion	configuration calculations (
Morphological	parameter	Scalar	fatosb	proportion	configuration infrared calcu
Morphological	parameter	Scalar	rinsul	length	insulative fat
Morphological	parameter	Scalar	pct_cond	percentage	percentage c substrate (%)
Morphological	parameter	Scalar	c_body	energy / (mass temperature)	specific heat
Morphological	parameter	Scalar	k_flesh	energy / (time length temperature)	thermal cond
Morphological	parameter	Scalar	rho_body	mass / volume	density of fle
Morphological	parameter	Scalar	epsilon	fraction	emissivity of
Morphological	parameter	Scalar	fur_depth	length	depth of pela
Morphological	parameter	Scalar	hair_diam	length	diameter of h
Morphological	parameter	Scalar	hair_length	length	length of hai
Morphological	parameter	Scalar	hair_rho	density	density of ha
Physiological	parameter	Scalar	pct_H_P	percentage	water in faec
Physiological	parameter	Scalar	pct_H_N	percentage	water in excr (%)
Physiological	parameter	Scalar	pct_H_X	percentage	water conter
Physiological	threshold	Scalar	pct_H_R	percentage	minimum tol wet mass) - p than this

Physiological	threshold	Scalar	pct_H_death	percentage	maximum to wet mass) - c this
Physiological	parameter	Scalar	T_A	temperature	Arhhenius te
Physiological	parameter	Scalar	T_AL	temperature	Arrhenius ter below lower range T_L (K)
Physiological	parameter	Scalar	T_AH	temperature	Arrhenius ter above upper range T_H (K
Physiological	parameter	Scalar	T_L	temperature	lower bound tolerance ran response
Physiological	parameter	Scalar	T_H	temperature	upper bound tolerance ran response
Stoichiometric	parameter	Scalar	d_V	fraction	dry mass frac
Stoichiometric	parameter	Scalar	d_E	fraction	dry mass frac
Stoichiometric	parameter	Scalar	d_Egg	fraction	dry mass frac
Stoichiometric	parameter	Scalar	mu_X	energy / number	molar Gibbs of food (J/mo
Stoichiometric	parameter	Scalar	mu_E	energy / number	molar Gibbs of reserve (J/
Stoichiometric	parameter	Scalar	mu_V	energy / number	molar Gibbs of structure (
Stoichiometric	parameter	Scalar	mu_P	energy / number	molar Gibbs of faeces (J/r
Metabolic	parameter	Scalar	kap_X_P	fraction	faecation eff
Stoichiometric	parameter	Matrix	n_X	fraction	chem. indice
Stoichiometric	parameter	Matrix	n_E	fraction	chem. indice
Stoichiometric	parameter	Matrix	n_V	fraction	chem. indice structure
Stoichiometric	parameter	Matrix	n_P	fraction	chem. indice
Stoichiometric	parameter	Matrix	n_M_nitro	fraction	chem. indice nitrogenous
Reproductive	model	Scalar	viviparous	none	viviparous re
Phenological	threshold	Scalar	photostart	time	photoperiod decreasing, +
Phenological	threshold	Scalar	photofinish	time	photoperiod decreasing, +