

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

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## 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 and 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, mechanistic niche models, metabolic ecology, physiological ecology

## 1 | 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; Volaire et al., 2020). Functional traits have been defined as those that affect organismal performance, that is, 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 has followed for better coordination, integration and accessibility of such data (Gallagher et al., 2020; Guralnick et al., 2018; Wieczorek et al., 2012). 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 standardisation, 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.

The role of theory is rarely mentioned in discussions of trait data collation. 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 subclasses 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.

## 2 | 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, that is, the 'environment'. Open thermodynamic systems involve the exchange of mass and energy across the system boundary. Organisms can be considered as 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), that is, 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 (Figure 1). If we can successfully model organisms as thermodynamic systems across their ontogeny, we can obtain a fundamental perspective on their ability to function, that is, to survive, develop, grow and reproduce, given different environmental sequences.

**BOX 1 Glossary**

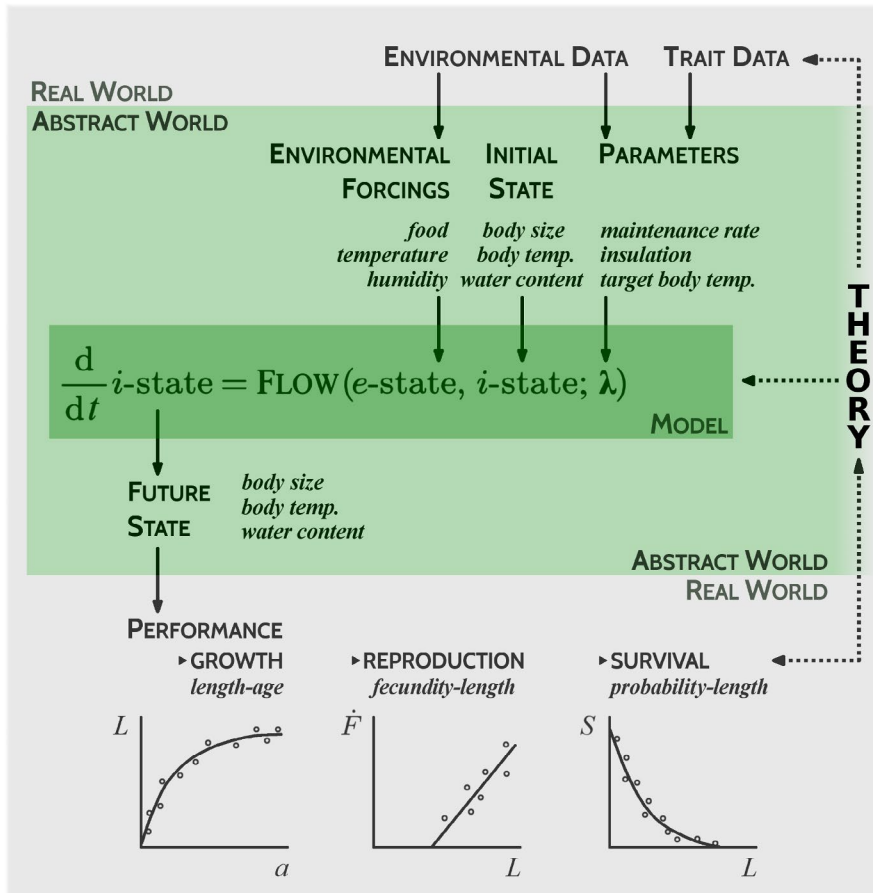
Term	Definition
biophysical ecology	Theory governing the application of thermodynamic systems principles to quantify heat, water and gas exchange between organisms and their environments
dynamical system	A time-evolving system defined completely by a set of state variables, their changes being describable 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

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 which 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.

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, 2021; 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 (Figure 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 DSMs, each with inherent biological, chemical and physical assumptions. The heat budget, for example, comprises a set of terms representing the 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).



**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

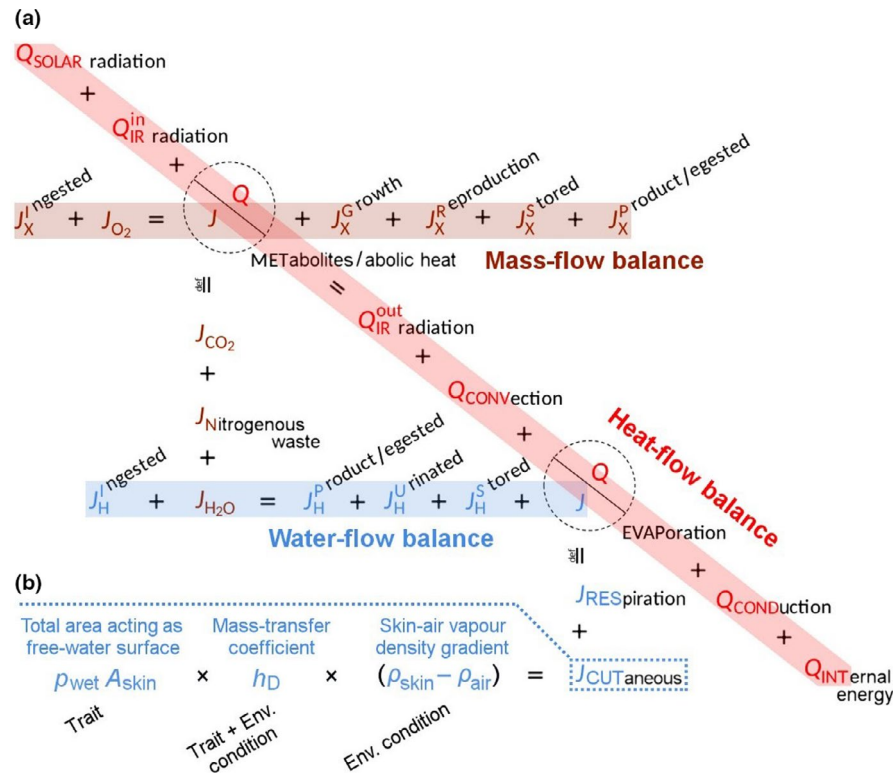
The formulation and solution of such equations to understand constraints on organisms in natural environments has a long history (e.g. Dunham et al., 1989; Porter & Gates, 1969; Porter & Tracy, 1983) and is now referred to as ‘mechanistic niche modelling’ (Kearney & Porter, 2009). The application of 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-recognised 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.

### 3 | 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 defining 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 be 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.



**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, a heat surplus (or deficit) increases (or decreases) internal energy as reflected in body temperature change. 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 ( $\rho$ ) 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 ( $A_{\text{skin}}$ ), but also the proportion of that area acting as a free-water surface ( $p_{\text{wet}}$ ), which can be almost 100% for amphibians, but <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)

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 DSM. 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 DSM:

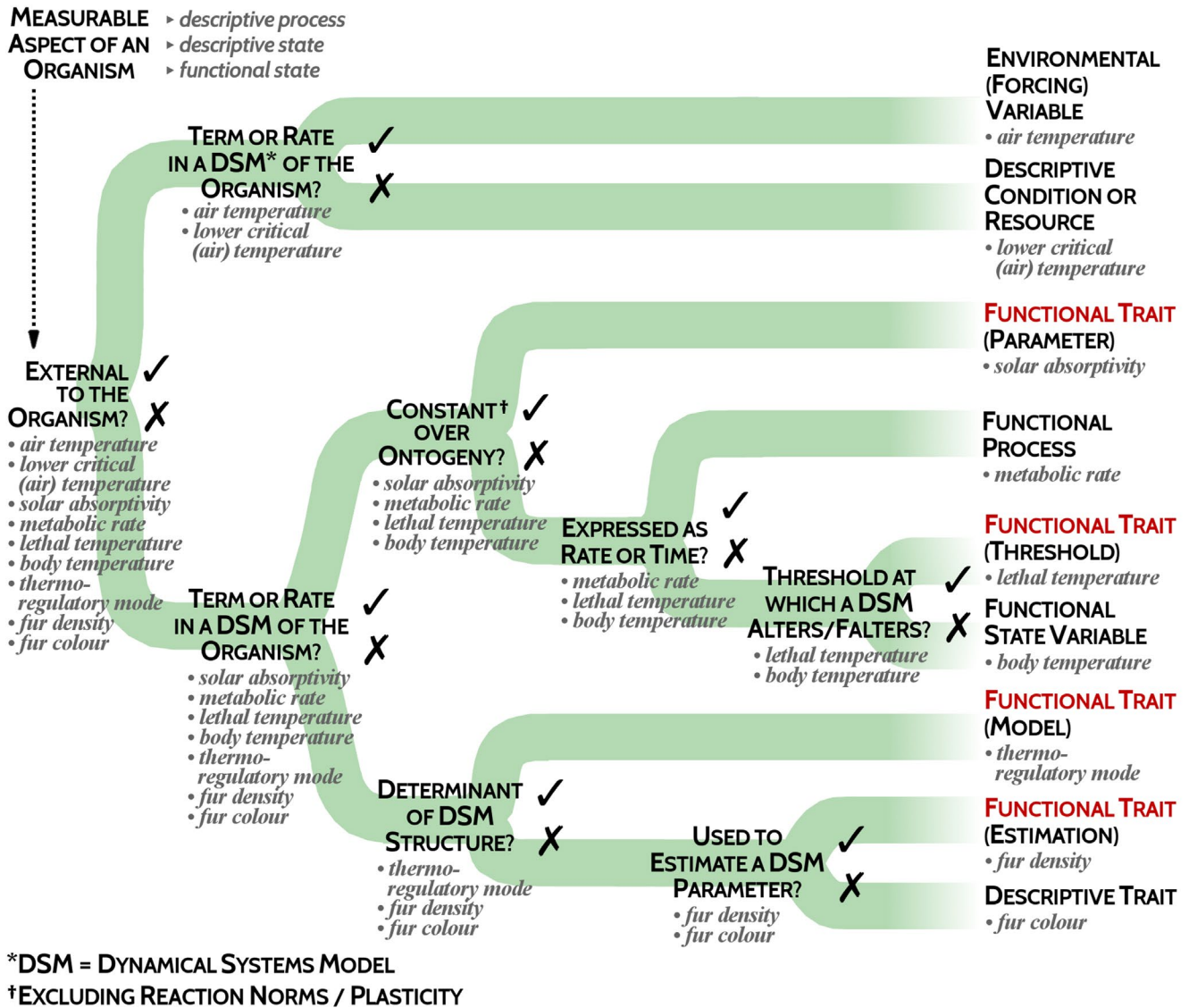
1. *'Parameter' functional trait*: acts directly as a model parameter;
2. *'Threshold' functional trait*: acts directly as a threshold state variable affecting performance by terminating or altering the behaviour of the system;

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—that is, 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 (Figure 3).





**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 for other examples of its application

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, namely, 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 Figure 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.

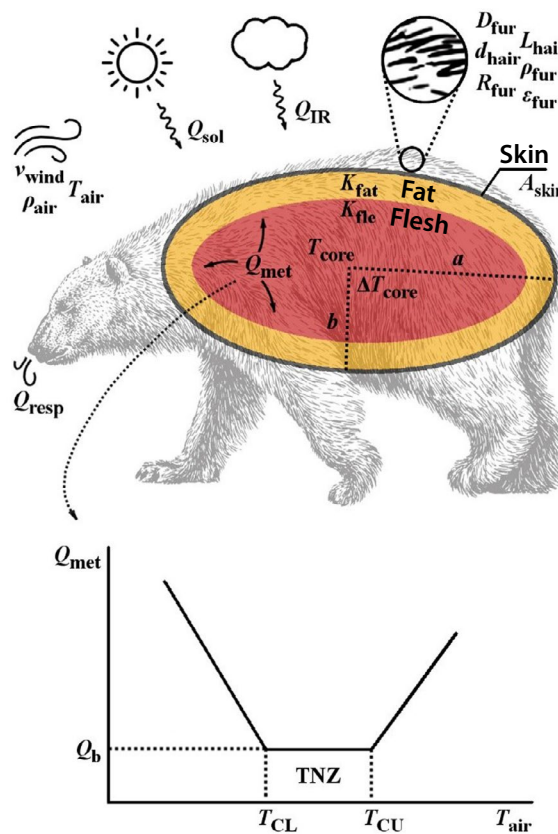
## 4 | A WORKED EXAMPLE: THERMAL TOLERANCE

The functional trait definitions and decision tree we have just presented can be applied to any aspect of the processes depicted in Figure 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, namely, body temperature. The tolerance of high or low body temperature is clearly relevant to the performance measure of survival and, in any DSM, acts either to (a) terminate the simulation entirely through death of the individual, (b) determine limits to activity (especially in ectothermic animals), (c) induce the loss of a body part (plants) or (d) 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. Should these threshold observations be classified as functional traits in the ‘threshold functional trait’ sense? We consider this question first from a biophysical perspective, and second from a physiological perspective.

### 4.1 | Biophysical perspective of heat tolerance

Viewing the situation for a mammal through the underlying equations of the heat budget of Figure 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.

**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  $\text{time}^{-1}$ , 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



#### Environmental forcings

- Wind speed  $v_{wind}$
- Air temperature  $T_{air}$
- Vapour density  $\rho_{air}$
- Solar radiation  $Q_{sol}$
- Infrared radiation  $Q_{IR}$

#### Functional traits

- Fur depth  $D_{fur}$
- Hair length  $L_{hair}$
- Hair diameter  $d_{hair}$
- Fur density  $\rho_{fur}$
- Fur reflectance  $R_{fur}$
- Fur emissivity  $\epsilon_{fur}$
- Skin surface area  $A_{skin}$
- Fat heat conduct.  $K_{fat}$
- Flesh heat conduct.  $K_{fle}$
- Target core temp.  $T_{core}$
- Body shape  $a/b$
- Basal metabolism  $Q_b$

#### Processes

- Metabolic rate  $Q_{met}$
- Respiration  $Q_{resp}$

#### State variable

- Temp. deviation  $\Delta T_{core}$
- Body size  $a$

#### Other

- Lower critical temp.  $T_{CL}$
- Upper critical temp.  $T_{CU}$

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 the 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).

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.

## 4.2 | 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 for 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 have 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 min ( $T_{max}$ ) 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 the 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 to the 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 DSM 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 DSMs and for both understanding and forecasting the abundances and distributions of species.

## 5 | 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, 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 >2,900 species in the collection. All these trait observations can be quantified via the DEB models, that is, 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, that is, 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.

## 6 | 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 DSM 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 DSMs of such behavioural responses can be developed (Clark & Mangel, 2000) similar to the thermodynamic models emphasised here.

Our focus on the use of DSMs 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 survival, development, growth and reproduction, as defined by DSMs 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  $\dot{G} = \dot{G}(e\text{-state}, i\text{-state}; \lambda)$  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  $\lambda$  is a vector of mechanistic parameters whose values are estimable via available traits. Similar functions exist for fecundity  $\dot{F} = \dot{F}(e\text{-state}, i\text{-state}; \lambda)$  and survival  $\dot{S} = \dot{S}(e\text{-state}, i\text{-state}; \lambda)$ . 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 no new parameters and traits, are needed when transitioning from the individual to the population level. Evolutionary processes can then be incorporated if the genetic basis for 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 DSM 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.

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## AUTHORS' CONTRIBUTIONS

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

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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