Representing with model organisms: A refined DEKI account

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Abstract

In this article, we mobilize and refine the DEKI account of scientific representation to show that model organisms are not models but model 'carriers,' only abstracted and selected 'parts' of which are included in biological models. These parts correspond to phenomena of interest that are interpreted as mechanisms or other kinds of causal processes within certain theoretical domains. The models can then be used to represent similar target phenomena in other organisms. Our proposal paves the way to reconcile opposing positions apropos the representational status of model organisms and build a more robust epistemology of model organism-based research.

Keywords

Model organism; scientific representation; models; model carrier; DEKI account

1 Introduction

Widespread empirical practices in the biological sciences, in disciplines as varied as developmental genetics, microbiology, and neuroscience, rely upon the use of so-called 'model organisms' (e.g., the bacterium *Escherichia coli*, the baker's yeast *Saccharomyces cerevisiae*, or the roundworm *Caenorhabditis elegans*). These have been brought to and reared in standardized laboratory settings in attempts to gain projectible, general insights about biological processes and human-targeted biomedical applications (for recent overviews, see Ankeny & Leonelli, 2020; Green, 2024).

There is a *prima facie* general sense in which model organisms can be thought of as scientific *models*: they act as surrogates or stand-ins for varied target systems. But how could an organism, even if shaped through and embedded in standardized conditions, represent another, distantly related organism just as, say, a set of equations is taken to represent the dynamics of a target system? Along these lines, a debated issue in the philosophical literature has been to clarify the representational status (or lack thereof) of model organisms *qua* models, with seemingly entrenched 'representationalist' and 'non-representationalist' positions pitted against each other.

On the non-representationalist side, Arnon Levy and Adrian Currie (2015; Currie & Levy, 2019) contend that model organisms are not theoretical models but representative *specimens* of broader classes of target organisms. Unlike models, which exploit explicit and known analogies between model and target, model organisms allow for inferences about other organisms based on phylogenetic hypotheses of shared ancestry. In a similar vein, Veli-Pekka Parkkinen (2017) argues that model organisms are *surrogates* used for extrapolating results to target organisms, while theoretical models embody the assumed or already known structure of the targets and thus can be used to draw explicit inferences. In a different register, Marcel Weber (2014, p. 758) asserts that model organisms are not models because there is no mapping function that connects each aspect of the model with a specific element of the target. Instead, model organisms are primarily *tools* for the development of exportable techniques and knowledge (Weber, 2004, Chapter 6).

Scholars on the representationalist side of the debate are interested in clarifying the representational roles of model organisms without denying that these also fulfil other roles

in experimental research.[1] For instance, Jessica A. Bolker (2009) contends that model organisms are *exemplary models* that represent larger taxonomic groups to which they belong, or *surrogate models* for biomedical research. For their part, Rachel A. Ankeny and Sabina Leonelli (2011) argue that model organisms function as representations that are characterized by broad *representational scope* (i.e., they represent a wide range of organisms) and *representational target* (i.e., manifold phenomena can be investigated with them). In addition, Michael Weisberg (2013) has asserted that model organisms can be regarded as theoretical models despite the fact that they are not artificially constructed but rather discovered 'in the wild.'

Both sides of the representationalism/non-representationalism debate have uncovered and underscored important aspects of the epistemology of model organism-based research, although some of them might seem contradictory or hard to integrate. The account that we will lay down in the next sections seeks to overcome this tension. Specifically, we side with the non-representationalists in that model organisms are *not* models,[2] but we also concur with the representationalists in that scientists *do* routinely construct models of specific target phenomena using model organisms. In our view, both parties in the debate miss the mark by trying to settle their disagreement on the issue of whether organisms *are* models or representations because doing so overlooks the distinction between models proper and material model *carriers*—e.g., between the double-helix model of DNA structure and the six-feet-tall metal structure made by James Watson and Francis Crick in 1953 for readily visualizing molecular geometry. Taking this distinction seriously helps to unravel the representational role of model organisms without the need for endorsing the idea that they are *eo ipso* models or representations.

Among the diverse extant positions on scientific representation and models (e.g., conventionalism, similarity theory, inferentialism, structuralism, fictionalism, and artifactualism), the 'DEKI account' proposed by Roman Frigg and James Nguyen (Frigg & Nguyen, 2016, 2018, 2020, Chapter 8; Nguyen & Frigg, 2022, Chapter 4) is particularly relevant in this context because it explicitly deals with the distinction between models and

[1] Similarly, we recognize the zetetic importance of non-representational uses of model organisms, but these fall outside the purview of this article.

[2] Although we contend that strictly speaking model organisms are not models, we nevertheless stick to the common practice of using the term "model organism." We are not interested in fighting the term when it is simply a *façon de parler*. Quibbles emerge, we think, when the notion is literally interpreted as the organism being a model not unlike any other theoretical model in the sciences.

carriers, especially in the case of 'material models,' namely those in which the carrier is a material object.[3] Thus, unlike the traditional understanding of model organisms as literally being models (*M*; figure 1A), DEKI suggests that model organisms are, strictly speaking, carriers (*X*; figure 1B).

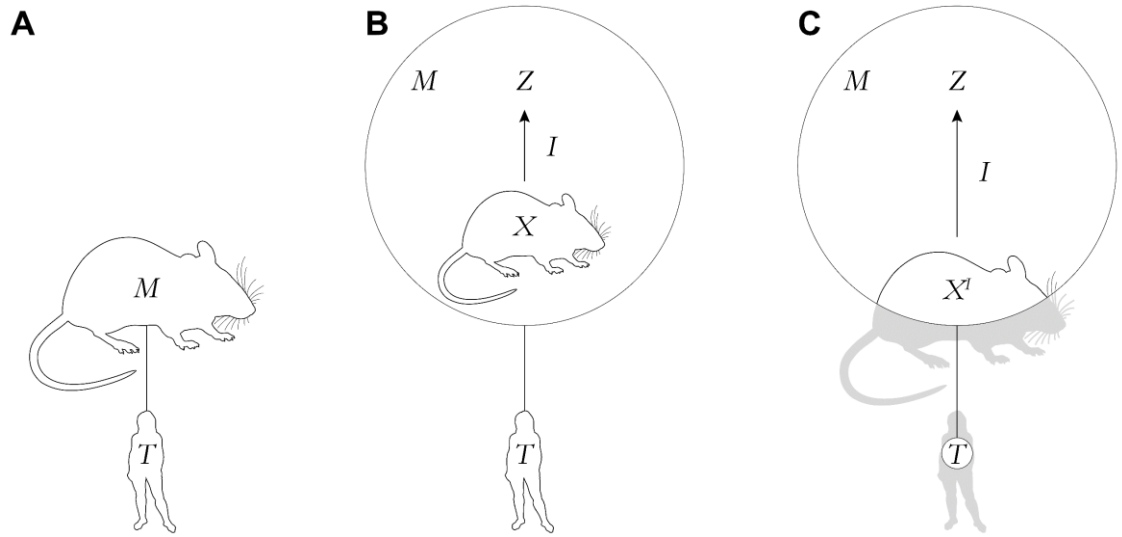

Figure 1. The place of model organisms in models. A. Traditional representationalist view of a model organism as a model *M* that represents a target organism *T*. **B.** DEKI account of model organisms as model carriers whereby a model consists of a carrier *X* together with an interpretation *I* of some of its features in terms of a domain *Z*. **C.** Our view of model organisms as carriers whereby only a part X^I of the carrier is included in the model and the target is a phenomenon in another organism rather than a whole organism.

Thus far, DEKI has been applied by two sets of authors to model organism-based research, namely by Ankeny and Leonelli (2020) and Lorenzo Sartori (2023). Curiously, though, partly because of these authors' interpretations of DEKI and partly due to some ambiguities in the DEKI account itself, these proposals reinforce the view that a model organism *as a whole* represents its target, which is usually also taken to be a *whole* organism. Consequently, the distinction between model and carrier is not taken in its full potential and

[3] Despite its advantages and conceptual sophistication, we are not committed to the DEKI account being the final word on scientific representation or the best theoretical framework to approach the conundrum of model organisms. We are open to refine our ideas with other approaches if these prove to offer more epistemic resources than the DEKI account.

the role of model organisms as carriers remains largely indistinguishable from their traditionally adjudicated role as models.

Here, our main point is that model organisms are indeed carriers in the sense outlined by DEKI, but only selected *parts* of them are included in models (X^1; figure 1C). These parts correspond to phenomena of interest that are usually interpreted as mechanisms—or causal processes more generally—within certain theoretical domains. The parts of model organisms interpreted in terms of certain domains constitute the models, which can then be used to represent similar target phenomena in other organisms.

This article is structured as follows. We start by summarizing the DEKI account of representation as described by its proponents (section 2). Then, we clarify the notions of *domain* and *target* in DEKI (section 3). Next, we discuss the nature of *model organisms* and propose a working definition of a *carrier* (section 4). We then argue that a *model* includes only the interpreted *part* of a carrier—rather than the whole carrier (section 5). We take stock of these conceptual clarifications to explain how representation with model organisms works (section 6). Finally, we show how our view mediates between representationalism and non-representationalism, and we explore some potential extensions (section 7).

2 The DEKI account of representation and model organisms

In the DEKI account, a model M consists of a carrier X interpreted by an interpretation function I that relates some features of the carrier (X-features) to features in a certain domain Z (Z-features). The carrier X can be any object—material or otherwise—and need not belong itself in the domain Z: all that is required for it to partake in a model is that (at least some of) its X-features are interpreted in terms of Z. Frigg and Nguyen often illustrate DEKI with the Phillips-Newlyn model, a 1950s hydraulic analogue computer based on the circulation of water through a circuit of pipes and reservoirs that represent money flow in a macroeconomy. Thus, in the case of this model, the carrier (X) is the Phillips-Newlyn machine (i.e., the material object made of pipes, reservoirs, valves, water, and a pump) and the domain (Z) is an 'open-IS-LM[4] economy'—hereafter, simply 'an economy.'

Evidently, in this case, the carrier does not belong to the domain, for it is a hydraulic machine that *prima facie* has little to do with the macro-economic domain. However, in the

[4] Here, "open" indicates the inclusion of international trade, "IS" means "investment-savings," and "LM" refers to "liquidity preference-money supply" (Frigg & Nguyen, 2020, p. 163). These details need not concern us here.

model, the machine is turned into an economy-representation (*Z*-representation) by means of an interpretation (*I*) of some of its machine-features (*X*-features) in terms of an economy-features (*Z*-features). Thus, the water circulating in the machine is interpreted as money, each reservoir is interpreted as a sector of the economy, the pipes are interpreted as connections of money transaction between the sectors, and so on (figure 2A).

Two important remarks are due at this point. First, not every feature of the carrier needs to be interpreted within the model. For instance, the Phillips-Newlyn model excludes a myriad of machine-features such as the material of which the reservoirs and pipes are made of, the exact chemical composition and temperature of the circulating liquid, or the pump that keeps it running. Consequently, according to DEKI, the model is *not* the carrier—e.g., the Phillips-Newlyn machine—but the carrier *together with* the interpretation of some of its features in terms of a certain conceptual or theoretical domain—e.g., an economy. Formally, the model is defined as a pair $M = (X, I)$ whereby X is the carrier and I the interpretation.[5] Second, Frigg and Nguyen impose no restriction to what counts as 'features' (often referred to as 'properties') in DEKI and point out that the sets to which they belong—e.g., the set of *X*-features, but also the sets of *Z*- or *Y*-features to be introduced in a moment—"can be highly structured, for instance with some features expressing relationships between other features" (Frigg & Nguyen, 2020, p. 178).

Thus defined, a model is a *Z-representation*[6] that does not need to have an actual target. For instance, the Phillips-Newlyn model "would be an economy-representation even if it had never been used as a representation of an actual economy (UK, USA, Guatemalan, or otherwise)" (Frigg & Nguyen, 2020, p. 169). For the model to be a *representation-of* a target system *T* (i.e., for the model *M* to represent an actual target *T* as *Z*), four conditions are jointly required that give the DEKI account its characteristic name.

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[5] According to Frigg and Nguyen, carrier and model are distinct *notions* that nonetheless refer to the same *object*. They make clear that "an object *X* [a carrier] is never a [model] just on its own accord: no interpretation, no [model]!" (Frigg & Nguyen, 2020, p. 168). According to DEKI, the object that functions as a carrier is *turned into* a model by an act of interpreting a subset of its features. For instance, in the Phillips-Newlyn model "we turn [a] system of pipes and reservoirs into an economy-representation by *interpreting* certain selected *X*-features as *Z*-features" (Frigg & Nguyen, 2020, p. 167; emphasis in the original). We find the distinction between carrier and model a main advantage of the DEKI account. In fact, we will go further and argue that carrier and model are not just different notions but also different objects (section 5.2).

[6] Frigg and Nguyen take the distinction between '*Z*-representation' and 'representation-of' from the work of Nelson Goodman (1976) and Catherine Z. Elgin (1983). For discussion, see Frigg and Nguyen (2017b).

First, the model *M* must *denote* (D) *T*, as when the Phillips-Newlyn model is used to denote, say, the UK economy. Second, *M* must *exemplify* (E) *Z*-features Z_1, …, Z_m, which means that it must *instantiate* them. The Phillips-Newlyn model instantiates economy-features because the carrier instantiates machine-features that are linked to economy-features via *I*. However, according to Frigg and Nguyen, not all the instantiated features are exemplified in every case. For exemplification to occur, it is further required that the model *highlights* certain instantiated features Z_1, …, Z_m, which means that they are selected as relevant and made epistemically accessible in a particular research context. For example, it could be the case that some of the water reservoirs in the Phillips-Newlyn machine are ignored when using the model for representing a particular economy, even though they are still part of the model *qua* (generalized) economy-representation, since they are still interpreted—albeit non-exemplified—parts of the carrier (i.e., they are instantiated by the model). Third, the set of features Z_1, …, Z_m exemplified by the model must be translated into a second set of features Y_1, …, Y_l via a *key* (*K*), which is a mapping function that transforms the features of the model into candidate features of the target. For instance, in the Phillips-Newlyn machine, a key is needed to convert the circulation period measured on the machine to a value that can meaningfully be imputed to the UK economy (see Frigg & Nguyen, 2020, p. 174). Fourth, the latter set is *imputed* (I) to *T* (figure 2A).

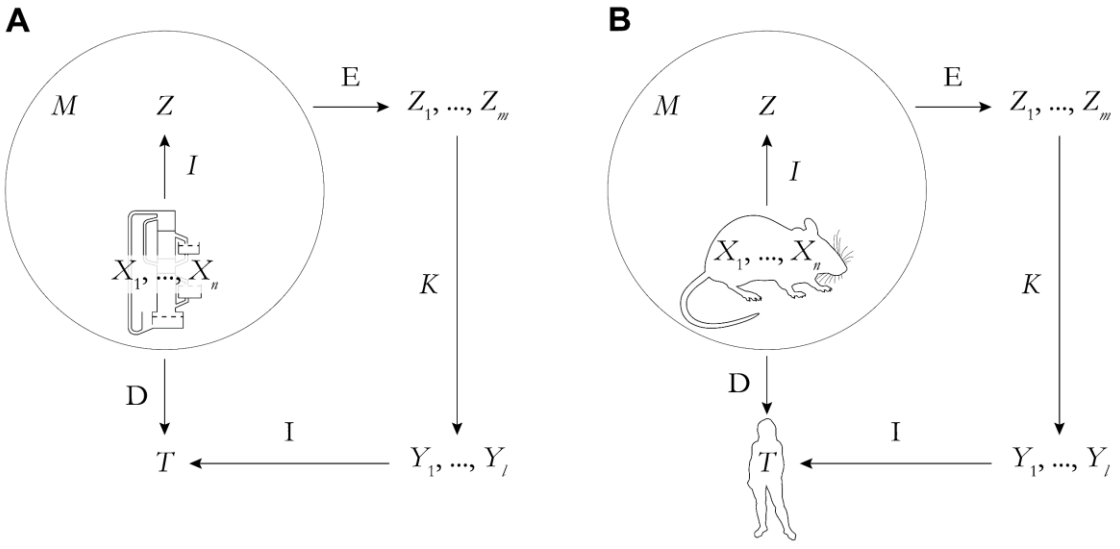

Figure 2. The DEKI account of representation. A. Schematic depiction of DEKI based on Nguyen and Frigg (2022, Figure 6) with the Phillips-Newlyn machine as the carrier. **B.** Same as in (A) but with a model organism as the carrier and another organism as the target. See description in the text. Abbreviations: D, denotation; E, exemplification; I, imputation; *I*, interpretation; *K*, key; *M*,

model; T, target; X_1, …, X_n, carrier features; Y_1, …, Y_l, keyed-up features; Z, domain; Z_1, …, Z_m, exemplified features.

Although the DEKI account might in principle accommodate both material and non-material carriers (for discussion, see Frigg & Nguyen, 2020, Chapter 9; Salis et al., 2020), it is especially suitable for dealing with 'material models.' Now, since model organisms are material objects, they seem to be obvious candidates for occupying the role of model carriers under DEKI (figure 2B). In fact, DEKI has been applied twice to the case of model organism-based research, namely by Ankeny and Leonelli (2020, pp. 25–30) and by Sartori (2023). Ankeny and Leonelli seek in DEKI a way of formalizing the idea that model organisms represent. However, their brief assessment lacks sufficient articulation and examples to show how representational practices with model organisms can be squared into DEKI. Sartori (2023) improves upon Ankeny and Leonelli's approach by focusing on exemplification and imputation, spelling out the keys involved, and explaining how these elements cohere in the justification of inferences drawn from model organisms.

Both Ankeny and Leonelli's and Sartori's approaches to model organisms under DEKI reveal three problem clusters, namely, (1) issues related to the *domain* and *target* of the representation; (2) issues regarding the nature of model organisms and the *carrier*; and (3) issues regarding the inclusion of the carrier within the *model*. We shall tackle each of these issues sequentially in sections 3–5.

But before moving forward, it is important to notice that, in their exposition of the DEKI account, Frigg and Nguyen deliberately leave the specification of each of DEKI's elements open. They explain that "[i]n every case of a carrier representing a target one has to specify what X is, how it is interpreted, what sort of Z-representation it is and what features it exemplifies, how denotation is established, what key is used, and how the imputation is taking place" (Frigg & Nguyen, 2020, p. 179)—and, we should add, what T is. Therefore, for the most part, the problems we identify arise from the specifications of DEKI's elements in the context of model organism-based research rather than from DEKI itself.

However, the notions of domain, target, scope, and carrier are not defined in the original DEKI account, which favors their misidentification. Moreover, the carrier is taken to be fully included within the model—recall that a model is defined as the ordered pair (X, I), whereby X is the whole carrier. For instance, the *whole* Phillips-Newlyn machine and the *whole* organism (or laboratory population of organisms) are said to be included within the

corresponding models and thus represent their targets (if any) as a whole. Since we want to fill in these definitional gaps and put into question the idea that carriers are fully included within models, our analysis should be read not only as a reassessment of modeling practices with model organisms in the light of DEKI but also as a reappraisal and friendly amendment of the DEKI account of scientific representation.

3 Models of what?

The first cluster of issues that need to be clarified can be summarized as follows: (i) it is not clear what counts as the *domain* of a representation, since it is not defined in the original DEKI account and, in the context of model organism-based research, is conflated with the target (in Ankeny & Leonelli, 2020) or is insufficiently specified (in Sartori, 2023); and (ii) there is ambiguity surrounding the *target*, which is not defined in DEKI and is variously referred to as a whole organism or population of organisms, or even as a specific phenomenon in organisms in model organism-based research (in Ankeny & Leonelli, 2020; Sartori, 2023). Let us tackle these problems separately.

3.1 Domain

The domain *Z* is not defined in the original account of DEKI and is misidentified in the context of model organism-based research. In particular, Ankeny and Leonelli (2020) do not distinguish it from the target but rather identify both as the "whole [organism] and other organism(s)" (27; see also their Figure 1). However, it should be kept in mind that, according to DEKI, the domain *Z* is relevant for the model *qua Z*-representation even in the absence of a target. Thus, domain and target should be clearly distinguished.

For his part, Sartori (2023) does distinguish between domain and target, but treats the domain rather vaguely. To see why, consider his case study on chromosomal crossover in *Drosophila melanogaster*: "The *mechanisms of chromosomal crossover*—the exchange of genetic material during sexual reproduction between two homologous chromosomes' non-sister chromatids—found and studied in populations of *Drosophila* […] have been crucial to understand the *same mechanisms* in more complex organisms" (7–8; emphasis added). Sartori submits that the "[t]he fact that *Drosophila* exemplifies chromosomal crossover crucially depends on the interpretation [*I*] of a *Drosophila* population [*X*] as a genome-representation [*Z*-representation]" (8). Therefore, according to Sartori, *Z* = genome, *X* = a *Drosophila*

population, and then $M = (X, I)$ = a *Drosophila* population interpreted *as a genome*.[7] We find this reconstruction unplausible partly because Z is too generic and unspecific.

That the domain is both difficult to distinguish from the target of the representation and in general hard to delineate is due to fact that it is a rather vague notion. Indeed, "Z can be a concept, a notion, an idea, or a phantasy—anything that can belong to a certain domain of discourse […] There are no limits to the choice of Z; anything that makes sense in a certain context is in principle acceptable" (Frigg & Nguyen, 2020, p. 171). However, it is helpful to regard Z as "a placeholder for the motif of a representation" (Frigg & Nguyen, 2017a, p. 44), this is, the domain Z is the element that stands for the *aboutness* of the model. Put differently, the domain is the answer to the question 'What is the model about?' In the case of model organism-based research, the aboutness of the models is usually clear from the descriptions offered by the researchers in the form "model of Z," "model for Z," or "model to study Z." For instance, the fungus *Neurospora crassa* is used "to study metabolism, gene regulation, chromosome behavior, DNA repair, DNA methylation and epigenetic phenomena, genome defense, photobiology, circadian rhythms, differentiation, development, and other biological phenomena of relevance to higher eukaryotes," the baker's yeast *Saccharomyces cerevisiae* is "an excellent model system for cell morphogenesis, chromosome stability, and even aging," and the nematode *Caenorhabditis elegans* has been used to elucidate the "mechanisms involved in programmed cell death, insulin signaling and aging, and neurobiology" (Müller & Grossniklaus, 2010, pp. 2056–2058; references removed).

With these examples in mind, notice the following three points. First, the processes and mechanisms listed in these examples are *not* targets but domains. This can be concluded from the fact that they point out what the models are about and refer to generalized descriptions of processes that need not have real targets. For instance, a mechanism of programmed cell death hypothesized from the study of *C. elegans* tells what the model is about (i.e., the model

[7] Leaving aside for a moment the issue whether the carrier in this case is a token organism or a population of *Drosophila* (see subsection 4.1), the awkward phrasing 'the model consists in *Drosophila* interpreted as a genome' could be fixed by stating either that (i) 'the model consists in *Drosophila* interpreted *as having* a genome' or, adjusting Z, that (ii) 'the model consists in *Drosophila* interpreted as *an organism (or population) endowed with* a genome.' However, these gambits distort the role of the interpretation function by reducing it to the mere ascription of properties such as "having a genome" to the carrier. The interpretation function maps *selected features of* the carrier onto *selected features of* the domain rather than the whole carrier onto the domain and, therefore, the ascription of properties to the carrier is a corollary of the interpretation rather than the interpretation itself.

is a mechanism-of-programmed-cell-death-representation) independently of whether the model is a representation-of a real mechanism in a different species or whether it is targetless. Second, at least in the context of model organism-based research, the domain is usually not a *thing* (e.g., "genome" in Sartori's example or "bulldog" in the example of pictorial representation in footnote 8) but a *process* or *mechanism* (e.g., "DNA methylation" or "cell morphogenesis"). Third, the examples show that the domain is usually indicated with varying degree of specificity—e.g., sometimes it is as broad as "aging" or "chromosome behavior."[8] However, it can be assumed that these simple descriptions are shortcuts for more specific hypothesized mechanisms that account for the phenomena under study (e.g., not "aging" *tout court* but something like "mechanism of cell aging").

From these considerations, we propose the following characterization:

> *Domain*: A domain *Z* is a generalized conceptualization or theoretical description of a phenomenon or type of phenomena, usually in the form of a hypothesized process or mechanism.[9]

We can now replace Sartori's *Z* = genome for a more specific mechanism that accounts for the phenomenon of interest in the *Drosophila* example: we submit that a set of molecular and cellular processes in *Drosophila* (*X*) constitutes the phenomenon of interest (X^I) that is interpreted (*I*) within the model (*M*) as a 'mechanism of chromosomal crossover' (*Z*). Thus, the model is a 'mechanism-of-chromosomal-crossover-representation' (rather than a 'genome-representation' in Sartori's interpretation).

[8] This also occurs in simpler cases. As an example, consider the oft-cited example of a caricature representing Winston Churchill *as* a bulldog. In this case, the picture is a bulldog-representation, but it could also be said to be a dog-representation, a mammal-representation, an animal-representation, a carnivore-representation, a pet-representation, and so on.

[9] Throughout the paper, we use the terms 'phenomenon' and 'mechanism' to mark a distinction between a more-or-less-directly accessible, empirical occurrence and its conceptual or theoretical description, respectively. By using the term 'mechanism' we do not imply that models are necessarily mechanismic, although in model organism-based research they frequently are (see, e.g., Parkkinen & Williamson, 2020). Likewise, we are not strongly committed to any particular philosophical position on how to construe the ontology and epistemology of mechanisms.

3.2 Target

The target is another crucial element about which the original DEKI account says little. In the context of model organism-based research, it is sometimes taken to be a whole organism, like when Ankeny and Leonelli (2020) describe it as "other species and the organism taken as a whole" (26) or when Sartori (2023) indicates that "MOs [model organisms] represent other organisms in the sense of the DEKI account" (10). Other times, it is identified as a circumscribed phenomenon, as when Ankeny and Leonelli claim that it is a "rather specific cluster of properties attributed to a wide range of organisms and to organisms taken as wholes" (28) or when Sartori points out that "a taxon [can be] used to represent numerous mechanisms [i.e., targets] in several species" (11).

We favor the second interpretation because it makes little sense to us to talk about a whole organism being a model's target, as if biologists were interested in modeling *whole* organisms—assuming that was epistemically possible—rather than selected features and phenomena *in* organisms. In the *Drosophila* example, taking the target to be a whole organism would amount to claim that the model (*M*) represents an organism (*T*) as a mechanism of chromosomal crossover (*Z*), which is obviously not the case.[10] Instead, we think that only circumscribed phenomena in organisms, rather than whole organisms, can be meaningfully represented by models as *Z* if we consider the fact that, as explained above, *Z* stands for 'mechanisms' that describe circumscribed phenomena in carriers.

To be clear, and postponing for a moment the notion of model, we define:

[10] Similarly to the case of the domain discussed above (footnote 7), a potential way of circumventing the problem would be to claim that (i) 'the model represents an organism as *having* a mechanism of chromosomal crossover' (more generally, '*M* represents *T* as *having Z*' rather than '*M* represents *T* as *Z*') or, by modifying *Z*, that (ii) 'the model represents an organism as *an organism that has* a mechanism of chromosomal crossover.' Our reply to this is alike to our response for the case of the domain: these maneuvers solve the problem only at the cost of reducing the role of the representation to the mere ascription of properties to the target, which is a corollary rather than the core of the representation. For instance, if the aim of a *Drosophila* model was merely to represent, say, *Homo sapiens* as having a mechanism of chromosomal crossover, the model would lack the epistemic leverage that it is expected to perform.

Target: A target *T* is a phenomenon of interest in a certain research context, consisting of a structured set of features of at least one system *S* (e.g., an organism) of a certain type (e.g., a species).[11]

Notice that the same target (or targets of the same type) can occur in more than one concrete system or types of concrete systems. For instance, money flow occurs in economies other than the UK's and the molecular and cellular processes described as 'endocytosis' or 'chromosomal cross-over' occur in many species of organisms.

Also notice that this definition respects the fact that in DEKI similarity between the model and target is not required for the model to represent the target. However, in the case of model organism-based research, similarity *does* play an important role—usually in the sense of *functional* similarity as the result of common ancestry—in establishing the connection between model and target. The target *T* is a phenomenon in an organism *S* that is presumed to be in some way similar (e.g., due to evolutionary conservation) to the phenomenon X^I in the model organism *X* interpreted within the model *M* as a *Z*. Appeal to this similarity between *T* and X^I—the idea that they are phenomena of the same kind—is what grounds the presumption that *T* is in principle amenable to also be represented by *M* as a *Z*.

A final point to consider is that, under DEKI, the representation typically exploits the fact that *T* is somewhat similar to X^I, but it does *not* require *S* to be similar in any way to *X*. Thus, the Phillips-Newlyn model relies on a certain similarity between the flow of water through pipes and reservoirs and the flow of money across the different sectors of an economy but does not require the Phillips-Newlyn machine to be similar to the UK economy *in toto*. Likewise, in pharmacological research, extrapolation from model organisms to humans "works by establishing causation in the model organism and establishing similarity of the model organism to humans. […] The similarity that needs to be established is *similarity of the mechanisms* of action in the model organism to those in humans" rather than between the whole model organism and the whole human (Parkkinen & Williamson, 2020, p. 74; emphasis added).

[11] The target should be understood as a phenomenon that is abstracted from the context in which it occurs. More on abstraction in subsection 5.1.

4 What is the carrier of the representation?

The second set of problematic issues in DEKI and its application to the case of model organism-based research can be summarized in the following points: (i) there is ambiguity about the nature of model organisms, which are variously referred to as individual organisms, laboratory populations, species, etc.; and (ii) it is not clear what counts as the *carrier* in DEKI—since it is not defined in the original account—and what counts as the carrier in the case of model organism-based research. We now assess these issues successively.

4.1 Model organism

In the extant literature, the label 'model organism' is ambiguously taken to refer to species, strains, standardized laboratory populations, or token organisms. For instance, Ankeny (2010) defines a model organism as "a particular *species* and *strain*" (94; emphasis added), whereas Ankeny and Leonelli (2020) posit that "*individual organisms* [are] the main unit of analysis" in model organism-based research (17) or that "model organisms are best understood as indicating a *family of material objects* with very similar characteristics and a common phylogeny" (22; emphasis added). In turn, Sartori (2023) argues that "the carrier is usually identified with a *laboratory population*, because it is that population that has undergone procedures of selection that allows it to exemplify certain relevant properties […] in a statistical way, thus not reducible to observations of individual organisms" (11–12; emphasis added). In fact, Sartori goes as far as to suggest that "[i]nsofar as [the] ideal of shared standards is approximated by different research groups, the carrier becomes the *entire set of the MO's laboratory populations* complying to those standards" (11; emphasis added).

This plurality of notions of what constitutes a model organism is important because when we inquire about the representational status of model organisms, we cannot expect that all *designata* (e.g., species, populations, or individuals), with different ontological characteristics and epistemic accessibility, will yield the same results. In particular, the materiality of model organisms *qua material* carriers in DEKI—and the materiality of X^I, T, and S—becomes questionable if they are regarded as species, families, sets, etc.

Nevertheless, a strong reason to sustain that model organisms are types of organisms (collections, statistical populations, sets, classes, or kinds) rather than token organisms is the fact that 'typological thinking' (*sensu* Love 2009) is as pervasive in model organism-based research as it is in biology at large. This means that researchers who work with model organisms are largely interested in *type* rather than *token* phenomena that occur in *type* rather

than *token* organisms. Accordingly, X^{I} and T should stand for types of phenomena, and X and S for types of organisms (e.g., species).

However, we do not think that the application of typological thinking—i.e., "representing and categorizing natural phenomena, including both grouping and distinguishing these phenomena according to different characteristics, as well as ignoring particular kinds of variation" (Love, 2009, p. 53)—means that the phenomena under study or the entities in which they occur are types. In fact, model organism-based research is mostly about organismal and sub-organismal phenomena that can only occur in individual organisms. For instance, the phenomenon in *D. melanogaster* interpreted as chromosomal crossover can only occur at the level of individual organisms, not at the level of the population, species, etc. It is for these reasons—i.e., preservation of the materiality of the carrier and the phenomena that biologists *de facto* study—that we think model organisms should be regarded as token organisms.

4.2 Carrier

As anticipated above, model organisms seem to be straightforward candidates for occupying the role of the carrier in the DEKI account and we think they generally play this role.[12] Since the notion of carrier is not defined in the original DEKI account, we propose the following:

> *Carrier*: A carrier X is a system (e.g., a model organism) of a certain type (e.g., a species) that is chosen or constructed in a certain modeling context.

We leave the characterization of the carrier quite broad because we think the problem of providing identity conditions for carriers (see Frigg & Nguyen, 2020, p. 17) is external to an account of representation and thus its solution should be sought elsewhere. Indeed, in the DEKI account, the representation is insensitive to the delineation of the carrier at large. To see why, consider the Phillips-Newlyn model again. Intuitively, the carrier in this model is

[12] It should be noticed, nonetheless, that this situation is not necessarily the case. For instance, it might occur that the carrier in a given experimental setting is not only the model organism but a model organism and certain items in its environment (e.g., a mouse and a labyrinth) or a population of interacting organisms. This might seem to contradict our conclusion in section 4.1 that model organisms are not populations but token organisms. However, notice that what we are saying here is not that model organisms can be populations, but that *carriers* can be, in certain instances, populations of model organisms.

the Phillips-Newlyn machine and it might be useful to consider it so. However, one could ask, what counts as the machine and therefore as the carrier? Are the adhesive tape that holds the cables on its back side, the pens that record the changes in the magnitudes measured, the labels on each compartment, the electricity that feeds it, and the operatives in charge of pushing buttons and switching valves part of it?

It is clear that the inclusion or exclusion of these features does not have any bearing on the representation unless these features are included in the phenomenon X^I of interest in the carrier that is described as a Z.[13] Thus, the only feature of the carrier that matters for the representation is that it possesses (or participates in) the phenomenon X^I. As explained earlier (subsection 3.2), the representation exploits a presumed similarity between a phenomenon X^I in the carrier and a target phenomenon T (rather than between systems X and S, or X and T) that the model connects as instances of a same Z. Thus, the representation only imposes a clear constraint on what the relevant *part* (i.e., a phenomenon X^I) of the carrier is via the *interpretation* (I). An immediate consequence of this is a change in the role of the carrier respective of its role in the original DEKI account. In our view, the representation-of a target is instantiated between a "part" of the carrier and the target, both of which are comparable phenomena in certain systems. Let us explain this proposal in detail in the next section.

5 What does the representing?

Both in the original DEKI account and in its previous applications to model organism-based research (see above), the carrier is taken to be fully included within the *model*. In this section we want to challenge this view by proposing that only the interpreted part of the carrier is included in the model.

[13] To be clear, we do not claim that objects such as machines and organisms have no ontological boundaries or that there are no meaningful ways to epistemically draw boundaries around such objects *qua* objects. Rather, we claim that the precise delineation of their boundaries *qua carriers* is ultimately irrelevant for the representation. The question would be, then, why not just dropping the notion of a carrier or why not using it to refer to the phenomenon X^I. The answer is that it is convenient to stick to the notion of a carrier because it is useful, especially when mobilized to denote relatively well-defined objects such as machines and organisms. We do not object the notion of a carrier; we only argue that it has no formal place in the representation as accounted for by the DEKI account.

5.1 Carrier part

As explained in subsection 4.2, the role of the carrier in a representation is restricted to it containing a phenomenon of interest that is interpreted by the model in terms of a certain domain. We refer to this phenomenon of interest in a carrier as a carrier *part*. In this context, a part should not be understood as an ontologically pre-existent or *a priori*-defined object, but rather as the result of a process of *abstraction* that consists in "focusing on, and selecting, certain [features of the carrier] while omitting most others" (Winther, 2011, p. 401; emphasis modified) according to "the epistemic function expected of the model thus obtained" (Leonelli, 2008, p. 521). As a consequence, a part need not be a spatiotemporally bounded "portion" of the carrier: it can contain any combination of features of the carrier (e.g., a phenotypic character and its underlying gene network), including whole-carrier features such as a certain behavior. Specifically, we define:

> *Carrier part*: A carrier part X^I is a phenomenon consisting of a structured set of features of a carrier X picked out in a given modeling context through a process of abstraction.

It is the part of a carrier the element that plays a direct role in a representation through its interpretation within a model, which means that only the carrier part—rather than the whole carrier—is included in the model (figure 3). For instance, in a balls-and-sticks model of molecular structure, only the part consisting of the relative position of the balls and their connectedness is *de facto* included in the model, whereas the material of which the carrier is made, its color, overall size, etc., are left out of the model. Similarly, in the Phillips-Newlyn model, only the part of the machine consisting of the features that are directly related to the flow of water are considered within the model while the rest of the machine and its context of operation are excluded from the model (figure 3A).

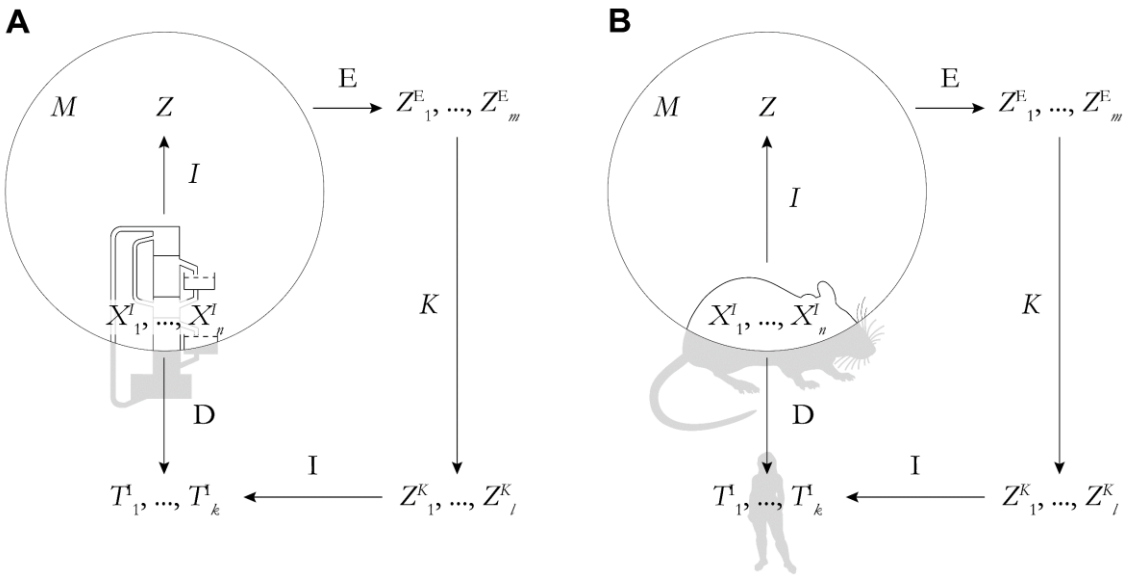

Figure 3. Modified DEKI schema. A. Schematic depiction of DEKI with the Phillips-Newlyn machine as the carrier only the interpreted part of which is included in the model (compare to figure 2A). **B.** Same as in (A) but with a model organism as the carrier and a part of another organism as the target (compare to figure 2B). In both panels, the partial overlap between the carrier's silhouette and the circle representing the model is intended to convey the idea of partial inclusion of the carrier in the model, whereby the area of overlap corresponds to the interpreted features X^I of the carrier and the gray area lying outside the model corresponds to the non-interpreted features of the carrier. Take heed of the fact that we use subscripts to highlight that only specific subsets of features of *T*, *X*, and *Z* participate in each mapping step. Abbreviations: D, denotation; E, exemplification; I, imputation; *I*, interpretation; *K*, key; *M*, model; $T^1_1, \ldots, T^1_k$, imputed features; $X^I_1, \ldots, X^I_n$, interpreted features; *Z*, domain; $Z^E_1, \ldots, Z^E_m$, exemplified features; $Z^K_1, \ldots, Z^K_l$, keyed-up features.

It goes without saying that most of the features of a carrier are physically inseparable and many of them are crucial to the functioning of the relevant carrier part. For instance, the rigidity of the carrier in a balls-and-sticks model is necessary for the model to consistently represent the relative position of the atoms in a molecule, even though this rigidity is not included in the model (i.e., it is not interpreted as a feature of the molecule). Likewise, the Phillips-Newlyn machine would not work without the pump that circulates the water, despite it being excluded from the model.

The same holds for model organisms (figure 3B), although in this case the inseparability of organismal features and the integrative character of model organism-based research have been invoked in defense of the idea that model organisms *qua* carriers are *wholly included* in the model. Sartori (2023) explains that "the properties that a MO exemplifies are usually

inseparable, at least in a practical sense, from the rest of the MO's properties [so] we cannot 'extract' [them] without keeping into consideration the relation of these properties with the others possessed […] by the MO under study." Therefore, he continues, "the representation is […] the entire model system that, *as a whole*, exemplifies only certain properties among the ones it instantiates" (11–12; emphasis added). For their part, Ankeny and Leonelli (2020, p. 28) argue that each particular instance of representation using a given model organism is to a large extent interwoven with background knowledge on the same model organism that has accumulated inside a larger "modeling ecosystem" in which the representation is embedded. Thus, partial or "specialized models" cannot be isolated from other models constructed on the same model organism, which means that it somehow represents *in toto*.

It is certainly the case that, as Sartori argues, organisms are integrated entities whose parts, features, and properties are ontologically inseparable—in fact, we tie in with the idea that whole organisms play the role of carriers. We also concede that the abstracted parts of a carrier are to some extent inseparable from the accumulated background knowledge on the same type of organism that characterizes the integrative nature of model organism-based research, as Ankeny and Leonelli rightly contend. However, neither of these are convincing reasons for claiming that the whole carrier organism is part of the model—and that *as a whole* represents the target—in model organism-based research.

To begin with, taking the whole model organism to be included in a model is, we think, a misrepresentation of actual scientific practice. As explained above, modeling always involves a process of abstraction of the object of study—i.e., foregrounding and backgrounding of different aspects of the object to meet specific epistemic aims. This is especially the case in model organism-based research, which is typically a quite reductionistic enterprise (e.g., focused on molecular-genetic mechanisms) even when the accumulation of knowledge and resources on a model organism has relatively high integrative potential compared to other types of research with non-model organisms. As Ankeny and Leonelli (2020) acknowledge, "[m]ost model organism research does in fact focus on […] specialized models, as researchers focus on one selected subgroup of questions (*and part of the organism*) at a time" (28; emphasis added).

To give an example, take a classic model derived from model organism-based research. The ABC model of flower development (Coen & Meyerowitz, 1991) was originally advanced to understand the mechanisms behind floral organ identity and specification in angiosperms. Building from genetic work in *Arabidopsis thaliana* and *Antirrhinum majus*, this model

postulated three distinct gene activities (A, B, and C), each of which is present in two adjacent whorls of developing flowers, acting alone or in combination to specify the four types of verticil: A on its own yields sepals, A+B generates petals, B+C produces stamens, and C on its own makes carpels. Crucially, the model only included three families of transcription factors and their (partially overlapping) spatial domains of expression in the flower meristem. It could hardly be said that the original ABC model included—or indeed needed—the whole organism to be a mechanism of flower development-representation or a representation-of the mechanism of flower development in other species. Instead, it is more precise to say that this model was built with some entities and processes of *A. thaliana*—genes and their expression in certain domains within the small outgrowths of cells on the flanks of the shoot apical meristem—picked out from the extremely vast set of features that *A. thaliana* possesses in particular moments of its ontogeny. This is so because the model is not a model of a whole organism but of the (molecular-genetic) mechanisms of flower development, and as such it includes only those entities and processes that are "just enough" for modeling the phenomenon of interest (i.e., flower development).

We can generalize this point by bringing in the notion of *proportionality* from the literature on causal explanation. According to Woodward (2010), in the context of scientific explanation, "the investigator's purposes or interests influence […] the choice of *explanandum* […], and once this is fixed, empirical considerations play a large role in influencing the 'level' at which an explanation for this *explanandum* is most appropriately sought." The choice of the correct level of detail of the *explanans* for a given *explanandum*, Woodward continues, is based on the idea that "causes should 'fit with' or be 'proportional' to their effects—proportional in the sense that they should be just 'enough' for their effects, neither omitting too much relevant detail nor containing too much irrelevant detail" (297). For instance, both the explanations that appeal to causes that are too detailed or specific, as well as those that appeal to causes that are too general or wide-ranging, fail to be proportional.

Importing this idea from causal explanation to modeling, we suggest the following principle:

> *Modeling proportionality*: Let $M = (X^I, I)$ be a model whereby X^I is the relevant part of a carrier X and I its interpretation in terms of a domain Z; Z^I the theoretical description of X^I; and T the target of the model. In a given modeling context, the following equivalences are satisfied: (a) $X^I \sim Z^I$; (b) $X^I \sim T$; and, by transitivity, (c) $Z^I \sim T$.

We argue that the part of the carrier is proportional to its conceptual or theoretical description by the model (a), which implies that it neither omits too many relevant features of the carrier nor contains too many irrelevant features of the carrier. For instance, the Phillips-Newlyn model includes only those features of the carrier (the Phillips-Newlyn machine) that are relevant for modeling the process of money flow in an economy (e.g., water, reservoirs, and pipes), while putting aside many other machine-features that are irrelevant for the task at hand (e.g., supporting frame, pump). Similarly, the ABC model only includes those features of *A. thaliana* that are relevant for modeling the genetic mechanism of flower development (i.e., certain genes and their expression in the apical meristem of the shoot) while abstracting away countless other features of *A. thaliana* that are deemed irrelevant in this context (e.g., those related to its overall morphology, phenology, biochemistry, physiology, development, ecology, and evolution).

When the model has a target, the part of the carrier included in the model and the target are proportional (b).[14] This point was already foreshadowed when we explained that representation is grounded on the assumption that T is somewhat "similar" to X^I (whereas S does not need to be similar to X; subsection 3.2). Finally, by transitivity, the model is proportional to the target (c). For example, the ABC model is a representation-of the phenomenon of flower development in other plant species by virtue of including the part of *A. thaliana* (e.g., certain genes and their expression patterns in meristems) that is proportional to the other plants' parts that the model intends to represent as a mechanism of flower development.

To sum up, attention to scientific practice as grounded on the process of abstraction and the requirement of modeling proportionality provides support for the idea that only the relevant part of the carrier in each context is *de facto* included in the model.[15]

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[14] In model organism-based research, the proportionality between carrier part and target—the fact that they are comparable in an epistemically meaningful way—is grounded on the fact that both phenomena are abstracted according to a commitment to certain kinds of entities and relations and ways to delineate them, which "allows us to state which objects and processes are similar to which other ones in which respects" (Winther, 2011, p. 401).

[15] It could be retorted that there is no harm in keeping the whole carrier in the model even if many of its features are ultimately not interpreted. Our reply is twofold. First, we think that the burden of the proof is on those who argue that the whole carrier is unproblematically included in the model. Specifically, they should provide (1) reasons for the inclusion of non-interpreted carrier-features in the model, as well as (2) criteria for delineating

5.2 Model

As explained in section 2, a model M is defined in the original DEKI account as the ordered pair (X, I), where X is a carrier and I is an interpretation of (selected features of) the carrier in terms of a given domain Z. However, as argued in subsection 5.1, *only the interpreted part of* the carrier is *de facto* included in the model. This part is the set of interpreted X-features or X^I that collectively constitute a phenomenon of interest for scientists in a given context. Therefore, we propose the following modified version of Frigg and Nguyen's (2020, p. 169) definition of a model:

> *Model*: A model M is a Z-representation, $M = (X^I, I)$, whereby X^I is a phenomenon of interest—the interpreted part of a carrier X—and I is an interpretation of X^I as an instance of a Z (i.e., as Z^I).

Having thoroughly clarified what counts as the domain, target, carrier, carrier part, and model in DEKI and in its application to model organism-based research, let us now show how these pieces fit together.

6 How does representation with model organisms work?

In this section, we take stock of the conceptual clarifications of sections 3–5 to offer a generalized and schematic description of how representation works according to DEKI. In

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the carrier—for without such criteria, *everything* (i.e., the whole universe) would in principle be included in the model. Second, we do think that the inclusion of non-interpreted features is potentially harmful in modeling contexts. The inclusion of irrelevant features could potentially mislead researchers into thinking that these features are equally relevant or necessary for the model and thus mask the core processes that account for the phenomenon under study. Also, the inclusion of too many *sui generis* features of the carrier would run against the pretension that models are to some extent unspecific and projectable beyond the particular model organisms from which they are built. More importantly, the objection misses the point that the process of abstraction is not only about selecting features of interest in the carrier and leaving the rest untouched but also *actively excluding* those features that "are likely to be untranslatable or just plain wrong" for the model. In abstracting the interpreted part of a carrier, researchers "willingly suspend disbelief [regarding the non-interpreted parts] in order to focus on the demonstrative power of those parts which do represent" (Morgan & Boumans, 2004, p. 387).

the paragraphs that follow, we refer the reader to figure 4. Although we focus on representational practices in model organism-based research, we consider that our account is valid, *mutatis mutandis*, for material carriers in general.

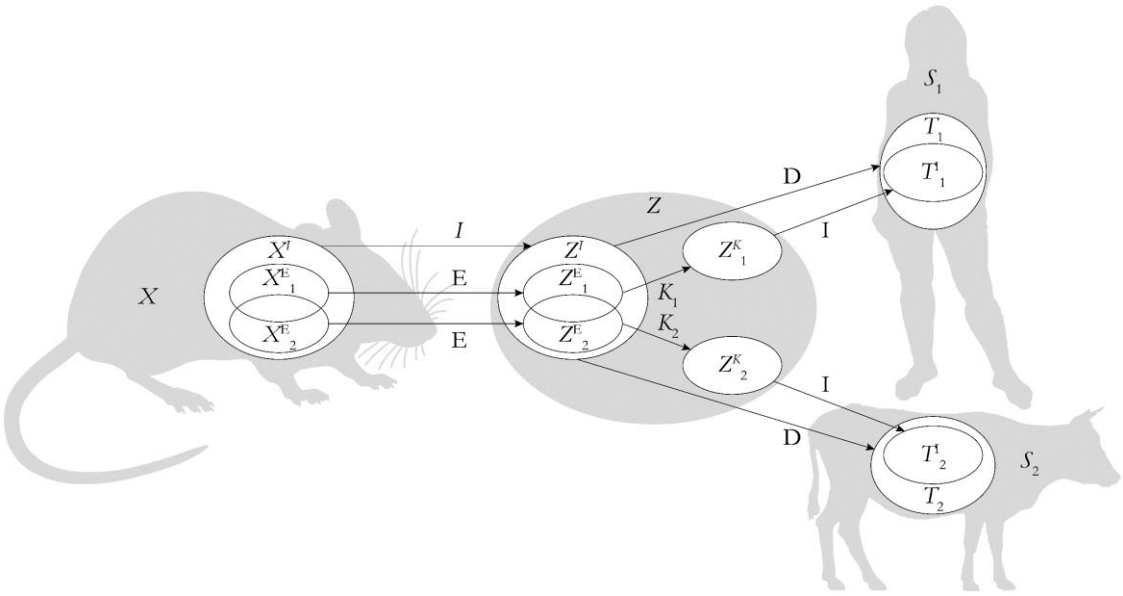

Figure 4. Mapping functions in DEKI. The figure shows an alternative diagrammatic representation of DEKI applied to model organism research showing all the sets of features involved in the representation. See description in the text. Abbreviations: D, denotation; E, exemplification; I, imputation; *I*, interpretation; *K*, key; *S*, concrete system; *T*, target; T^{I}, set of imputed features; *X*, carrier; X^{E}, set of exemplifying features; X^{I}, set of interpreted features; *Z*, domain; Z^{E}, set of exemplified features; Z^{I}, set of model features; Z^{K}, set of keyed-up features.

Representation with model organisms starts in one of two ways. Researchers may be interested on a certain phenomenon X^{I} discovered or studied in a model organism *X* (e.g., cellular and molecular processes related to chromosomal crossover in *D. melanogaster*) that may be known or thought to occur—with some variations—in other organisms S_n of a different kind. Alternatively, researchers may be interested on a target phenomenon *T* in certain organisms S_n (e.g., a disease in *Homo sapiens*) that is known to some extent. In either case, a phenomenon X^{I} is investigated in a model organism *X* with the hope that it would eventually allow for generalizations to other organisms (in the former case) or under the assumption that X^{I} is somewhat similar to *T*, and thus that inferences about *T* can be drawn from research on X^{I} (in the latter case). For instance (see figure 4), let's suppose a group of scientists is interested in certain molecular and cellular processes associated to cancer

proliferation either in the mouse *Mus musculus* (X^I in X) or in other organisms (T_1 in S_1 and T_2 in S_2). In both cases, *M. musculus* is chosen as a model organism for conducting research on X^I.

A model is devised to account for the phenomenon X^I by interpreting the set of carrier-features that compose X^I via an interpretation I in terms of a certain theoretical domain Z. As a result, X^I is theoretically described by the model as Z^I. In the hypothetical example, *M. musculus* is chosen as the carrier of the model and each of its molecular and cellular features that account for the phenomenon of interest is interpreted as processes and components in a mechanism of cancer proliferation. This theoretical description of the phenomenon X^I as a mechanism Z^I constitutes a model of cancer proliferation in *M. musculus*. As explained in section 5, the model includes the set of molecular and cellular features—i.e., a part—of *M. musculus* interpreted as a mechanism of cancer proliferation rather than the whole *M. musculus*. We do not claim that the non-interpreted parts of the carrier, although technically lying outside the model, are irrelevant to it. On the contrary, they play a crucial role in *situating* the model in its organismal context, and in many cases the accumulated knowledge on these non-interpreted parts might provide necessary background information for the model's construction, its potential extensions, and its integration with other models built with the same carrier organism.

Thus, the model is not the model organism but the phenomenon X^I in the model organism described as Z^I. This can then be used to represent a target phenomenon T similar to X^I in another organism S by taking Z^I to denote it (D). In the example, the mechanism of cancer proliferation in *M. musculus* is taken to denote certain phenomena related to cancer proliferation (T_1 and T_2), thought to be similar to the one investigated in *M. musculus*, in other organisms (S_1 and S_2). As pointed out in section 3, this means that the representation relationship is enacted between an interpreted *part* of the model organism and a similar *part* in other organisms rather than between whole organisms.

According to DEKI, representation not only involves denotation but also requires exemplification. This occurs in three logical steps. First, a subset X^E is picked out from the set of interpreted carrier-features X^I to exemplify (E) a subset Z^E of model-features Z^I. Second, these exemplified features Z^E are transformed into another set of features Z^K via a key (K). Bear in mind that these keyed-up features Z^K are not part of the mechanism Z^I that accounts for the phenomenon in the carrier due to their transformation by a key, but they nonetheless belong to the domain Z. Third, the keyed-up features Z^K are imputed (I) to the

target T, which means that it is hypothesized that T contains a set of features T^{I} that match the theoretical description Z^{K}. In the toy example, some features such as the tumor suppressor and proto-oncogenes in *M. musculus* ($X^{\mathrm{E}}{}_1$ and $X^{\mathrm{E}}{}_2$) exemplify aspects of the model of cancer proliferation ($Z^{\mathrm{E}}{}_1$ and $Z^{\mathrm{E}}{}_2$), which are translated into their—likely diverging—functional equivalents in *H. sapiens* ($Z^{K}{}_1$) and other organisms ($Z^{K}{}_2$). These, in turn, are imputed to the target phenomena (T_1 and T_2) in *H. sapiens* (S_1) and other organisms (S_2), meaning that the target phenomena are hypothesized to contain certain features ($T^{\mathrm{I}}{}_1$ and $T^{\mathrm{I}}{}_2$) that are describable by the model as components of a mechanism of cancer proliferation in the respective organisms.

When denotation, exemplification, keying-up, and imputation occur as described, the model $M = (X^{I}, I)$ is said to be a representation-of T as Z. In the example, a set of molecular and cellular processes in the mouse (X^{I}), interpreted (I) as a mechanism of cancer proliferation (Z), represents certain molecular and cellular processes in humans and other organisms (T_1 and T_2) as a mechanism of cancer proliferation (Z).

Summing up, we maintain that representation with model organisms connects a part of (or phenomenon in) a model organism (the carrier) with a somewhat similar target phenomenon in other organism(s).[16] The link is established through a theoretical model, which, in this case, is a description of the carrier part as a mechanism within a given theoretical domain and can be used as a representation of the target system. To give another example, the ABC model of flower development links a selected and abstracted part of the

[16] The idea that representation is enacted between circumscribed phenomena in organisms rather than between whole organisms is related to Daniel P. Steel's (2008), Monika Piotrowska's (2013), and Parkkinen and Williamson's (2020) accounts. Steel submits that the inferential problem at stake when representing with model organisms amounts to inferring "the mechanism and/or phenomenon *in the target*" from partial knowledge about it as well as knowledge about "the mechanism and the phenomenon *in the model*" (2008, pp. 87–88; emphasis in the original). Likewise, Piotrowska conceptualizes both the model and the target as mechanisms and contends that "similarity relations between mechanisms can justify our inferences from model to target" (2013, p. 452). Along the same line, Parkkinen and Williamson explain that extrapolation from model organisms to humans in pharmacological research exploits the similarity between the mechanisms of action in model organisms and in humans (see subsection 3.2). Our point of disagreement with these proposals is that we distinguish model from carrier and regard both the carrier part and the target as *phenomena* (material occurrences) rather than *mechanisms* (conceptual objects). In our view, the model does not relate similar mechanisms in the carrier and target but rather *provides the mechanism* that connects similar *phenomena* in the carrier and target as instantiations of a same mechanism.

model organism *A. thaliana* that constitutes the phenomenon of interest (i.e., genes and their expression domains in the shoot apical meristems) to a similar part in other plant species. The model is a theoretical description of the mechanism of flower development in *A. thaliana* that includes the interpretation of each of the features that constitutes the model organism's selected part in terms of their functions and activities within the hypothesized mechanism. When used as a representation of a target system, the model represents a phenomenon similar to the one investigated in *A. thaliana* in another plant species as a mechanism of flower development.

7 Toward an integrative view of representation with model organisms

The account presented in these pages clarifies and refines some aspects of the DEKI account of scientific representation and its application to model organism-based research. Far from merely being an exercise in conceptual clarification and explication, we believe our proposal paves the way for a deeper understanding of modeling practices in biology and scientific representation in general.

In particular, we have advanced a framework that is able to release tension in the representationalism/non-representationalism debate by showing that the issue at stake cannot be resolved by appealing to the status of model organisms as models. We have shown that non-representationalists are right in that model organisms are not, strictly speaking, models. However, it does not follow from this that model organisms as material carriers do not afford the construction of *bona fide* models for various targets with cross-species projectability and thus that they do not have crucial representational roles. It seems that many scholars who side with the representationalist side erroneously conceive model organisms as 'maps' and their target organisms as the 'territories' they are representing. Under this view, it makes sense to believe that a map as a whole, namely an organism as a whole, represents. But, in reality, any model organism is a territory in itself, and only certain parts of it *are mapped*. The resulting maps—i.e., models—are then used to navigate other territories, namely, other organisms. Thus, it is not the case that "experimental organisms are models that mediate between theory and the world" (Ankeny & Leonelli, 2020, p. 16): rather, models constructed *from* (abstracted parts of) model organisms mediate between phenomena in model organisms and related phenomena in other organisms.

Several topics are left open for further investigation. For instance, we are mindful that representation is a more dynamic and complicated matter than what our generalized schema suggests. In particular, it could be argued that we have presented a too-static view of representational practices with model organisms, whereby a fixed set of features in the carrier is interpreted in a given way and a fixed subset of features is exemplified, and so on. However, we think that our conceptualization provides the necessary ground for a dynamic view, for it straightforwardly accommodates the fact that models are progressively built, expanded, contracted, or, in general, modified. These modifications could be thought of as, for instance, the result of changes in the selection of exemplifying features, changes in the selection of interpreted features, or invention of new keys that allow for an expansion of the model's *representational scope* (*sensu* Ankeny and Leonelli 2011). Thus far, we have been assuming that the model remains more or less the same because the interpreted part of the carrier and the domain remain largely unchanged. However, it follows naturally from our account that *different models* can be constructed on a given model organism, which determines its *representational target* (*sensu* Ankeny and Leonelli 2011). We leave this important issue for a future contribution.

Moving to a different topic, we have not discussed how inferences from model organisms are justified. On this issue, Sartori (2023) discusses a useful distinction between 'derivational correctness' and 'factual correctness.' The former is predicated of the sequence of inferential steps according to the internal rules of the representation, whereas the latter is predicated of the factual claims about targets that are derived from the representation. Sartori argues that, in the case of model organisms, derivational correctness depends on the interpretation, exemplification, and, especially, the keys. In particular, he introduces the notion of 'functional identity key,' which is a mapping function between a set of elements in the mechanism described by the model and a functionally equivalent set of mechanistic elements in the target system. Instead, the justification of factual correctness, Sartori argues, largely depends on what Ankeny and Leonelli (2020) call the 'repertoire,' which includes elements as broad and disparate as background knowledge, experimental tractability, and research infrastructures. Although we in principle side with Sartori on this issue, we think that this is a topic that deserves further exploration. It seems to us that, on one hand, the keys are indeed important for derivational correctness in that they establish a fine-tuned relation between model-features and target-features, but they come into play only after the model is in place and denotation has been established. Therefore, they are uninformative

about other aspects of the justification of derivational correctness, such as the choice of the model organism or the enactment of the denotation between the model and the target system. For the selection of model organisms to tackle specific problems, considerations based on phylogenetic relatedness and evolutionary conservation are crucial, as Levy and Currie (2015) have argued. On the other hand, the different components of the repertoire seem to play specific roles in the justification of each aspect of the representation and thus the notion of repertoire might fill in the justificatory gaps left by the keys. However, the scientific repertoire is an extremely disparate collection that needs some unpacking before it can be mobilized in more productive ways. By untangling the different elements in DEKI and clearing up their roles, our account could aid in this task.

Our framework also provides a clear path to assessing the similarities and differences between model organisms and non-organismal carriers in biological and biomedical research, such as cell cultures and organoids, which are routinely used to construct models that are equivalent, complementary to, or even in competition with, those constructed with model organisms (see Liberali & Schier, 2024). In our view, both organismal and non-organismal "models" play the same representational role: they are material carriers that support the construction of models that establish a theoretical link between abstracted phenomena in the carriers and in other systems. Moreover, what distinguishes model organism-based research from modeling practices with these non-organismal carriers is not the inclusion of the whole organism in models, since in both cases only a part of the carrier is selected and modeled. Rather, the difference lies in the fact that, unlike non-organismal carriers, model organisms provide (non-interpreted) organismal context to the selected part, which comes with epistemic benefits but also limitations (see, e.g., Kim et al., 2020).

8 Conclusions

In this article, we tackled the problem of how scientific representations can be arrived at by using model organisms through the lens of the DEKI account. Through painstaking clarifications and refinements to the DEKI account, we offered a framework for understanding how representations work in the context of model organism-based research. We started by clarifying the notions of *domain* and *target* in DEKI (section 3). Specifically, we submitted that domains are generalized causal processes (e.g., mechanisms) that encapsulate the 'aboutness' of models, whereas targets are circumscribed phenomena in organisms—

rather than whole organisms. We also discussed the nature of *model organisms* and proposed a working definition of a *carrier* (section 4). We suggested that model organisms refer to token organisms—rather than species, strains, or laboratory populations—and that a carrier is a system whose role in a model rests upon the theoretical interpretation of a part of it. We then argued that a *model* includes only the interpreted *part* of a carrier—rather than the whole carrier (section 5). Finally, we profited from these conceptual clarifications to explain how representation with model organisms works in scientific practice and we presented several examples (section 6).

We think that our account constitutes a step forward in the debate over the representational role of model organisms, especially in the application of the DEKI framework. For one thing, it is internally consistent—for instance, unlike Ankeny and Leonelli's (2020), it clearly distinguishes 'domain' from 'target' or 'model' from 'carrier' and explains each of these elements' roles in DEKI. Furthermore, our account provides satisfactory reconstructions of case studies of modeling practices with model organisms. For example, unlike Sartori's (2023), it does not lead to untenable conclusions such as that a population of *D. melanogaster* is interpreted as a genome and represents other organisms as genomes. More generally, our exploration highlights that some central elements of a representation, such as the domain, target, and carrier, should be more thoroughly theorized in the philosophical literature on scientific representation. In particular, the case of model organisms as model carriers could be illuminating of how model carriers function in particular scientific disciplines and what role they play in constraining or enabling certain types of modeling practices.

By and large, our proposal lays the groundwork to reconcile opposing positions regarding the representational status of model organisms and build a more robust epistemology of model organism-based research in the life sciences.

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