# Model Organisms as Scientific Representations

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### Abstract

In this paper, I argue that model organisms (MOs) function as representations of other organisms, in the same way in which scientific models function as representations of their targets. This offers a response to the question of how we justify inferences from MOs to other biological systems. Building on Ankeny and Leonelli's (2020) account of MOs and drawing on the resources of the DEKI account of scientific representation (Frigg and Nguyen 2020), I argue that MO-based inferences are justified iff they exemplify properties that are translated into the ones imputed to the target system by an appropriate mapping function. Then, I defend this account against the charges of Levy and Currie (2015) and Weber (2004), who have proposed non-representational accounts of MOs.

**Keywords**: model organism, scientific representation, justification, DEKI, scientific models, philosophy of biology, specimen

## Contents

# 1 Introduction

Recent debate in philosophy of biology shows considerable disagreement over the role of so-called model organisms (MOs), a group of organisms intensively studied in biological and medical research. Characteristic examples of MOs are the fruit fly (*Drosophila melanogaster*), the nematode worm *Caenorhabditis elegans*, several strands of mice (for example, *Mus musculus*), the plant *Arabidopsis thaliana*, and the bacterium *Escherichia coli*. MOs constitute one of the main instruments for discoveries in biological research and still occupy centre stage in the investigation of several medical conditions in humans (cf. Ankeny and Leonelli 2020 and references therein). It is common to use MOs to draw inferences about properties of other, often very different, organisms. One important philosophical question, then, is how to justify such inferences.

Rather than addressing the question of justification directly, the discussion of MOs in the philosophical literature tended to focus on whether MOs are scientific models. This way of approaching the issue becomes understandable once the two questions are related by the observation that both models and MOs are surrogate systems used to draw inferences about other objects. In the case of models, we draw inferences about their target systems, and in the case of MOs, about other organisms. It is often emphasized that models are idealized versions of their targets, meaning that models end up being different than their targets. The same holds for MOs, which are used to draw inferences about very different organisms. The philosophical discussion about models has provided us with an understanding of the issue of justification concerning model inferences: inferences from models to targets are justified if the model is an accurate representation of the target.[1] Hence, if we take MOs to be models, this justificatory strategy carries over to MOs: a MO-based inference is justified insofar as the MO is an accurate representation of its designated target. This puts the spotlight on the questions whether MOs are representations and, if so, how exactly inferences from MOs to other organisms can be justified.

I identify three relevant positions in the current debate. Ankeny and Leonelli (2011, 2020), take MOs to be a type of model. They support this claim by assuming that MOs function as representations, where representation is understood along the lines of the DEKI account (Frigg and Nguyen 2020, pp. 159–213). Then, there are two non-representational accounts of MOs. First, Levy and Currie (2015, 2019) explicitly deny that MOs are representations like models are, and classifies them instead as specimens of a larger class of organisms. Second, Weber (2004) takes representation to be a non-primary feature of MOs and focuses instead on their use as tools to develop new experimental techniques. This leads him (2014) to conclude that there is a substantial difference between MOs and models.

The central claim of this paper is that a representational view of MOs is correct, and that inferences from MOs to other organisms are justified by appeal to MOs representational capacities. In section 2, I introduce and further develop Ankeny and Leonelli's (2011, 2020) analysis of MOs. I argue that this account is on the right track but lacks an articulation of many important points, specifically concerning justification. I fill these lacunae by deploying the resources offered by DEKI to the case of MOs. Particularly, the concepts of exempli-

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[1] I set aside accounts of models that side-line the role of representation, such as Knuuttila (2005) and Isaac (2013).

fication and keying-up; then, I turn to the two alternative views on MOs. In section 3, I discuss Levy and Currie's (2015, 2019) account and argue that they are mistaken in drawing a sharp distinction between MOs and models. Then, in section 4, I argue that Weber's (2004) account is compatible with the representation view defended in this paper once we drop his excessively demanding requirements on model-target relations.

## 2 The representation view of MOs, upgraded

### 2.1 MOs and DEKI

As the name suggests, the representation view takes MOs to function primarily as representations of other organisms. Ankeny and Leonelli (AL) start from the unproblematic assumption that MOs are a subclass of the vaster group of 'experimental organisms', namely, any organism that is studied in biology laboratories. According to AL, what distinguishes MOs from the rest of this broader class 'is the representational power attributed to them' (2020, p. 9). The representational power of a system has two conceptually distinct dimensions, namely the 'representational scope' and the 'representational target'. The representational scope describes 'how extensively the results of research conducted on a group of specimens [...] can be projected onto a wider group of organisms' (2020, p. 6). For example, the representational scope of a property observed in a population of mice may be the class of all mice, or it could include other species (like humans), the entire family of mammals, or even all animals. However, what really makes MOs a special class for AL is their broad representational target, by which AL mean the number and detail of mechanisms of other organisms that MOs can represent. Instead of representing only a specific mechanism — say, respiration, or flowering — MOs are taken to represent a very wide range of mechanisms, usually considered essential for a great number of species (*ibid.*, p. 8).

AL then try to find the roots of MOs' representational power in what they call the 'repertoire'. The repertoire is the entire corpus of background knowledge that informs and supports MO-based research, comprising various aspects of the research practice in biological and medical sciences. They mention 'principles (e.g., evolutionary conservation)', 'the fit with other models such as simulations, diagrams, and mathematical models of development'; 'pragmatic factors', like tractability and accessibility; and also methodological norms, institutions, and the collaboration between different laboratories (*ibid.*, p. 27).

The question whether MOs have more representational power than other experimental organisms can however be answered only once we specify what exactly 'representation' means. AL fill this gap by adopting the DEKI account of scientific representation, developed by Frigg and Nguyen (2020, pp. 159–213). According to DEKI, a model $M$ is an object $O$ (the material carrier of the representation) interpreted by an interpretation function $I$. $O$ can be any material object, from a system of plastic balls and sticks to a string of marks on a page. The function $I$ is what turns a mere object into a symbol: we interpret the balls as nuclei and the sticks as chemical bonds, or water and reservoirs as money and banks. The interpretive function makes $O$ become what Goodman (1976) calls a $Z$-representation, where $Z$ is the domain in terms of which the object is interpreted (in our examples, molecules and economies).

According to DEKI, a model system $M$ is a representation of a target system $T$ iff four conditions jointly apply:

(i) $M$ *denotes* $T$,
(ii) $M$ *exemplifies* properties $P_1$..., $P_n$,
(iii) $P_1$..., $P_n$ are associated with a second set of properties $Q_1$..., $Q_n$ via a *key*,
(iv) $Q_1$..., $Q_n$ are *imputed* to $T$.

The four elements give the account its name. Before moving on, let us characterize them more explicitly. Denotation is the relation connecting a symbol to what the symbol stands for. It ensures that $M$ is about its target system. Exemplification is to be understood in the technical sense of Goodman (1976) and Elgin (1983, 1996): a model $M$ exemplifies a property $A$ in a context $C$ iff $M$ instantiates $A$, and $M$ refers to $A$ in $C$. Exemplification implies that some properties of $M$ are highlighted, or made salient, with respect to others. This allows to $M$'s users to have epistemic access to these properties. Imputation is property ascription, which can be right or wrong. In this way, the account allows $M$ to misrepresent $T$ and still be a representation. Finally, the exemplified properties $P_1$..., $P_n$ need not to be imputed unaltered: they can be, and usually are, translated in another set of properties $Q_1$..., $Q_n$ by a key, namely, a mapping function between the properties of $M$ and the properties that are eventually imputed to $T$.

The key is a pivotal element of DEKI because it allows us to impute some properties to the target without $M$ instantiating them. A model of a bridge exemplifies spatial measures that are translated by the key into another set of spatial measures by a scale factor. Newton's model of the solar system exemplifies orbits that are not exactly the ones then imputed to the real planets. Scientists have thus the possibility to approximate their predictions by "correcting" the model's properties. Approximations, limit functions, scale factors, analogical relations and projections are all examples of keys in DEKI's terminology.[2]

While AL explicitly endorse DEKI, they do not give much detail of how exactly MOs fit in the account. Aim of the next two subsections is to fill this gap. This will also allow us to address the question of justification, which remains mostly unexplored in AL's analysis of MOs.

## 2.2 Justification: the key and the repertoire

AL pay little attention to exemplification and the keys. Concerning exemplification, AL only briefly mention it in the context of their illustration of DEKI (2020, p. 26), but they remain non-committal about which properties are exemplified in certain contexts. The same happens with the keys, as there is no clear example in AL's book of such a mapping function in the context of MO research.

In part this may be a consequence of the fact that AL define the key in a way that diverges considerably from the way in which it was initially conceptualized. AL identify the key with their repertoire, which, as we have seen, contains the entire theoretical, pragmatical and institutional background that inform our scientific practices on MOs. In contrast, Frigg and Nguyen (FN) identify the key with a mapping function between the properties of the model and the properties that are eventually imputed to the target. Certainly, keys can become extremely complex, involving many different steps. Sometimes they require multiple ways of property-mapping, depending on the specific property or the exact designated target system. A Galilean model of a ball rolling in a U-shaped cavity, for example, exemplifies the

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[2] Many details of the DEKI account are not essential here and can be found in Frigg and Nguyen (2020, pp. 159–213).

principle of inertia. The principle is only counterfactually true for most mechanic systems, but it becomes approximately so with interstellar objects, where the effect of friction becomes negligible, and not simply abstracted away (cf. Sartori 2023 pp. 9–10, 20). However, in FN's account, keys always remain mapping functions, and as such they are not equivalent to AL's repertoire.

To keep the two distinct, I refer to AL's keys as broad keys, and to FN's as local keys. I suggest that the two keys are useful for two different purposes, both concerning the justification of our inferences from MOs. Yet, I also argue that the broad key remains inert as regards justification if a clear specification of the local key is not provided.

To see how keys function in justifications, it is helpful to distinguish between two different justificatory tasks. The two tasks concern what FN (2022, p. 296) call the 'derivational correctness' and 'factual correctness' of inferences drawn from a representation about its designated target system:

> An inference drawn from a representation is derivationally correct [about the target] if the inferential steps that lead to the conclusion are correct with respect to the rules of the representation and only use premises that form part of the representation. The conclusion of an inference is factually correct if the conclusion is true of the representation's target.

Accordingly, the first type of justification concerns the question whether the inferences we draw in a representation are correct according to the representational framework set by the representation itself. For example, when I read a map, I have to interpret it as the legend says I should. FN hold that DEKI's key is the locus of justification for derivational correctness, as it specifies the rules to interpret the representation and to perform inferences about the target. These rules are associated with the representation itself, like a legend is associated with a map. In order to understand the map, I have to read it in the light of the legend associated with it. To this analysis, I add that also the interpretive function $I$ of the object as a $Z$-representation and exemplification play an important role in this context. The interpretation as a $Z$ gives a way to read the material properties of the model carrier as a symbol, and exemplification provides the necessary input for the key, which is just a set of formal instructions. The map, *qua* territory-representation, exemplifies certain properties — say, distances and topological relations — and exclude others — say, altitude. The legend specifies how the exemplified properties are to be translated into information about the actual territory. Of course, nothing rules out the possibility that the map be wrong: the 'X' indicating the treasure on the map could just point to an empty cavern.

The justification of factual correctness, instead, is an altogether different matter. Factual correctness concerns the truth-values of the claims about a designated target system that we obtain from the representation through the imputation of the $Q$-properties to $T$. In my previous example, we are asking whether the treasure is actually in the point marked by the 'X' on the map. FN insist that these truth-values 'are not something that the representation adjudicates, let alone justifies' (*ibid.*, 297). They argue that to justify the factual correctness of a representational inference, we need to look outside of the representation. This can be done in many, not mutually exclusive ways. If we can, we perform an observation/experiment directly on the target and see whether the claims bear out. We may also ask whether the results obtained from the representation are compatible with the rest of our empirical and theoretical knowledge. Also, the keys employed in a specific epistemic context may have proved to be particularly successful in that type of context. Using Goodman's (1983) terminology about predicates, we can say that our keys are taken to be projectible: they are well entrenched with the development of those specific scientific practices.

Now, let us recall that AL's main goal was not an account of justification of MO-based inferences. They wanted to spell out all the factors playing a relevant role in contemporary MO-based research, with an emphasis on institutional, organizational, and pragmatic factors. Yet, their concept of repertoire is clearly relevant for the problem of justification: in the absence of direct experimental tests, AL's broad key can furnish arguments for the factual correctness of our inferences. This is because the repertoire encompasses all potential elements and factors that may be relevant to the justificatory analysis of a representation's factual correctness: overarching theoretical principles, currently employed models in the field, and empirical data.

The importance of this type of justification is indisputable. However, and this is my main point here, in order to assess the factual correctness of a representational inference, one has to specify what counts as derivationally correct. Namely, we need to clarify what the MO exemplifies, and what key is involved.

Assume we have a MO, observe an interesting property in it, and want to export our results to other organisms of interest, like humans. Before drawing on the repertoire to justify the factual correctness of an inference, we must specify what we are actually inferring. To this end, we need to spell out what local key we employ and what properties the key representation is imputing to the target. We can ask whether the property attribution is correct only once we are clear what the property in fact is.

This is tantamount to saying that we have to specify the semantics of our representation (what does the representation mean?) before delving into the epistemology of it (is a representation's claim about the target true and justified?). This, in turn, is equivalent to saying that we have first to ascertain the derivational correctness of a representation, and only afterwards try to justify the claims thus generated on the basis of the repertoire.[3]

The impossibility of moving to the level of factual correctness without dealing with derivational correctness may become even clearer if we compare the case of MOs with the case of models employed in mechanics. Mathematical models in mechanics exhibit, among a vast array of keys, a considerable use of limit keys, a use that has been extensively spelled out (Nguyen and Frigg 2020, pp. 195–203). Limit keys have a precise way to associate limit values of quantities in the model to more realistic values in the target system. Thus, it is clear how to interpret our models in mechanics because, while models exemplify values at the limit, we have a key to take these values back to other values. Once the key is specified, and thus the derivational correctness of the results is established, one can proceed and offer a justification of their factual correctness. Here, we do not always need to perform direct experimental tests on our targets to know that our models are accurate — for example, when we have to send rockets to space. Contextual knowledge (AL's repertoire, but in the context of mechanics) is usually sufficient to justify our inferences from mathematical models used in mechanics because we have specified that limit keys come into play and how we are expected to deal with them. In contrast, we could not do this in the case of MOs because we lack a precise illustration of the derivational correctness of our inferences — which properties are exemplified and what key is employed. Without such a clarification, it is impossible to employ the resources of the repertoire in the first place.

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[3] The temporal adverbs here only express a logical priority for an analysis of the justification of these inferences. In practice, the broad and the local keys continuously interact with each other (see below).

In sum, before we can provide a justification of the factual correctness of our inferences from a representation by appealing to the repertoire, we need a clarification of what properties are exemplified, and what key is employed. In the next section I give examples of how this can be done.

## 2.3 Exemplification and local keys in MOs

To understand local keys, let us consider the case of *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* (and their implications for genomic selection) have been crucial to understand the same mechanisms in more complex organisms; among them 'moths, pigeons, cats, silkworms, rabbits, and several species of plants' (Levy and Currie 2015, p. 333).[4] The *Drosophila* then exemplifies the mechanism of chromosomal crossover. This is because it exhibits the crossover itself and in addition highlights the mechanism, due to giant chromosomes isolated from larval salivary glands of the *Drosophila*. Exemplification is essential because it allows scientists epistemic access to certain previously unknown aspects of the crossover.

Exemplification is not an intrinsic feature of a system: it depends on the context, and the interpretation we endow the system with. The fruit flies that get inside your kitchen, for example, do not exemplify anything. The fact that *Drosophila* exemplifies chromosomal crossover crucially depends on the interpretation of a *Drosophila* population as a genome-representation, as well as the modifications and controls applied to the laboratory populations on the part of the scientists. According to DEKI, the interpretation of an organism must be coupled with also denotation and property imputation via the key. Denotation and imputation are granted by the empirical fact that the scientific community used and still use *Drosophila*'s genetic mechanisms to generate hypotheses about other species.

Let us then turn to the (local) key. It is important to recall that keys simply provide a way to read our results when we try to export them to the target system. As part of the representation system, therefore, keys can be wrong. Some representations, like some modern maps, have their keys stipulated from the start. This is usually not the case with MOs. They are no exception though in the domain of scientific representation: it is often difficult to understand how to translate the properties of a model onto properties of a target. This is just a version of the general problem of external validity of our models and experimental results. A further complication for an analysis of keys in MO research is that current scientific works on MOs often are not clear on how exactly we learn from a MO about other organisms. Scientists often leave this implication implicit. For instance, in a recent study of the neurobehavioural impairment caused by anaesthetic drugs in *C. elegans* (Nambyiah and Brown 2021), the results are explicitly taken to be relevant for humans. Nevertheless, the article gives little detail on how exactly the behavioural features of the worms translate into behavioural features of humans.

This does not entail that keys are not in fact employed. For instance, the dosage of a certain substance (like a drug) for a specific effect (healing from a disease) will have to be adapted from the MO to the case of humans. One way to do this is to multiply quantities on the basis of, say, body weight and other basic differences between the MO and the target

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[4] On the role of *Drosophila* in genetics, cf. Weber (2004, Sect. 3.2, 6.1) and Oriel and Lasko (2018).

organism. In other cases, we have model values that tend to a limit and then have to be re-adapted by limit keys. For example, Seim (2019) discusses the case of an immortalized cell line of macrophages (called RAW 264.7), in which cells keep undergoing division for their entire life, making their population grow to infinity. This does not happen with normal cells and must be considered when the results are extrapolated to non-modified organisms.

However, most interesting discoveries in MOs require much more complex keys. This complexity is a challenge for both the scientist and the philosopher and calls for a deeper conceptual analysis.

In order to deal with a more complex example, I first need to introduce a new type of key, which I call functional identity key (FIK). A FIK is a function mapping a (set of) elements $E_1$ of a mechanism $M_1$ in the model system onto a (set of) element(s) $E_2$ of another mechanism $M_2$ in the target system, where $M_1$ and $M_2$ have the same overarching function, and the elements $E_1$ and $E_2$ associated by the FIK are identical with respect to their sub-function within their respective mechanisms.

This characterization is intentionally flexible in order to be adaptable to different conceptualizations of 'mechanism' and 'function' that may play a role in biology. Nevertheless, the reference to the concepts of function and mechanism is by no means arbitrary or vague, as it can count on a vast and deep philosophical investigation (cf. Huneman 2013, Nicholson 2012, Wouters 2003). Also, I do not make any specific ontological assumptions, limiting myself to understand mechanisms as theoretical descriptions (not necessarily linguistic ones) of possible causal structures. Given that DEKI already implies an interpretation of the carrier, it takes a model to always involve a model description. It is this description of the interpreted carrier that includes the exemplified mechanisms. These properties are then mapped via the key onto properties that constitute the final description of the target (the set of propositions describing the imputed properties). In this sense, the material genes, cells and tissues of the MO are connected to the corresponding elements of reality of the target, but this connection is mediated via mechanistic descriptions.

An example of a FIK can be found in the review of Moretti *et al.* (2020), which reconstructs the results obtained from the study of the three-dimensional organization of genome in *Drosophila*. How the genome bends and arranges itself spatially is crucial for processes like the 'regulation of gene expression during development, cell differentiation, and cell identity maintenance' in many metazoans (p. 92). Now, there are many relevant differences between *Drosophila* and humans in the way their genome organizes in three spatial dimensions. I focus on one difference specifically, which concerns the set of architectural proteins responsible for the shape of the chromosomal bending.

These proteins in *Drosophila* are different from the proteins in other organisms (in particular, humans). For example, 'dCTCF, the main driver of TAD [topologically-associated domain] formation in vertebrates [...] is only found [in *Drosophila*] at 28% of TAD borders, with no evidence for a specific motif orientation, contrary to what is observed in vertebrates' (p. 95). Moreover, '[i]n flies, other architectural proteins such as BEAF-32, CP190 and Chromator are probably more important than dCTCF in TAD boundary formation' (*ibid.*).

So, we can see that the set of architectural proteins responsible of the chromosomal topology in *Drosophila* are associated with different, yet functionally analogous proteins in the humans. This association is done via a FIK, which maps the *Drosophila*'s architectural proteins to corresponding proteins in humans. The two sets of proteins are different, as is also the overall mechanisms, and of course the resulting chromosomal topology. However, the general mechanisms have the same function — shaping the genome 3-dimensionally. Also, the two sets of proteins serve the same sub-function within their respective mechanism. The reference to mechanisms will also allow for different levels of detail, depending on different goals set by the relevant scientific enquiry.

Drug dosages, limit keys and functional identity keys provide a first illustration of what kind of local keys we can find in MOs. This list is of course not exhaustive. Different keys are at work when MOs are used to find correlations between genes and diseases, a common application of MOs. For example, some variants of *C. elegans* exhibit a gene homologous to the human gene BRCA1, which is now known to be associated with human breast cancer (Ankeny and Leonelli 2020, p. 8). A key then is required to translate the gene-cancer correlation in *C. elegans* into the gene-cancer correlation in humans. This will require a complex key that associates, on the one hand, homologous genes with each other via phylogenetic relations, and different types of cancerous cellular development on the basis of comparable cellular development mechanisms, on the other.

All these examples reveal a general pattern relating MOs to their targets. MOs denote other biological systems, which grounds their use as surrogates to draw inferences about their targets. MOs drive these inferences by exemplifying specific properties, and thus allowing epistemic access to them. The imputation of related properties to the target system is done via a key that correlates properties of the MO with the properties of a designated target system. So, we see that we have all four conditions of DEKI satisfied, and we have a general framework to investigate each specific case study. Hence, MOs represent other organisms in the sense of the DEKI account, which also provides an answer to the question of derivational correctness: our MO-based inferences are justified insofar as we impute properties to a target that are exemplified by MOs, by applying the proper key function.

The justification of the factual correctness of our results, if any, remains largely extrinsic to the specific representational system, and can be achieved only by looking at the repertoire, which constitutes AL's broad key. Once we have a local key at work, the repertoire will provide the contextual knowledge to justify the claims that it generates. In the case of a FIK, the repertoire provides the theoretical knowledge and empirical evidence to justify the functional equivalence of mechanisms and their elements. For example, in the case of the *Drosophila*'s 3D genome organization, the repertoire will give us the grounds to associate different sets of architectural proteins, even though those sets of proteins diverge at a considerable extent.

In practice, the relation between the broad key and the local key becomes a process of feedback between the specific characteristics of the specific representational system and a more general conceptual framework. Scientists develop keys on the basis of their background knowledge but at the same time also try to find reasons to ground their local inferences from their models in further confirmation from further, independent means of investigations (experiments, simulations, models). The two levels, the local key and the repertoire, are of course intertwined and may end up redefining each other, until they eventually reach a reflective equilibrium. However, it is still important to keep them conceptually distinct in order to achieve a better understanding of our inferences from representations and their justification.

Also, it does not seem to be the case, as AL hold, that MOs generally exhibit greater representational power than other experimental organisms. For representational power becomes a function of the set of exemplified properties and the local key. For example, taken as a 3D-genome-organization model, *Drosophila* has a very narrow representational target (in AL's sense). More generally, even if a taxon is used to represent numerous mechanisms in several species, DEKI pushes us to distinguish different studies performed on that taxon, depending on which specific properties are exemplified and which keys are employed.

Finally, what counts as MOs' actual representational carrier: the species, a particular strain (or a number of strains), a laboratory population, or an individual organism? From what I said so far, a natural answer is that what counts as the carrier depends on the specific context, the purpose of investigation, and the assumptions of the relevant epistemic community. In the case of MOs, the carrier is usually identified with a laboratory population, because it is that population that has undergone the procedures of selection that allows it to exemplify certain relevant properties. Yet, as AL (2020, p. 31-33) also argued at length, different laboratories adopt common standards to select and modify the same MOs in order to share their results — ending up creating what AL call 'worm community', '*Arabidopsis* community', and so on. Insofar as this 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.

At this point, one may ask why I keep calling 'representation' the MO as a whole, or the MO laboratory population, if what we need is just the set of exemplified properties and the key to translate them. For what concerns the MO as a whole, the reason is that the properties that a MO exemplifies are usually inseparable, at least in a practical sense, from the rest of the MO's properties. As other types of models, MOs are often non-modular: we cannot 'extract' the exemplified properties without keeping into consideration the relation of these properties with the others possessed (but not necessarily exemplified) by the MO under study. This is actually considered one of the epistemic advantages of complex, *in vivo* representations with respect to abstract models and computer simulations: they provide a much more holistic picture of how a certain mechanism relates to others. Similarly, when it comes to the key to use, one will have to consider the context in which a specific property is embedded. The same reasoning extends naturally to MO populations: they may exemplify relevant properties only in a statistical way, thus not reducible to observations of individual organisms. All this is captured by the DEKI account: the representation is not the final outcome of our investigation, but the entire model system that, as a whole, exemplifies only certain properties among the ones it instantiates.

## 3 Levy and Currie's account and its difficulties

Let us now turn to the main accounts of MOs that seem to conflict with the representation view that I have just presented. The first account I consider is due to Levy and Currie in their article "Model Organisms Are Not (Theoretical) Models" (2015).

From the beginning, Levy and Currie (LC) specify that their 'discussion doesn't touch on ontological or semantic questions, such as what models are or how they represent [... Our] aim is to account for the justificatory structure underlying the inferential move from models to targets' (*ibid.*, p. 329). So, their focus is on justification, but, in contrast to the view presented so far, they separate this issue from semantics and, more precisely, from the fact that MOs represent and how they do so. They go on to argue that 'inferences from work on [MOs] are empirical extrapolations, whereby biologists treat the organism as a representative specimen of a broader class' (*ibid.*, p. 332). They note that, while inferences made from MOs 'are broadly model-like, [...] they diverge in their epistemic roles from theoretical models. The type of stand-in at issue is different' (*ibid.*, p. 336).

Let us look at the terminology. LC take the expression 'theoretical model' to denote any scientific model, from material scale models of bridges to mathematical models like the Lotka-Volterra model (*ibid.*, pp. 329–21).[5] In their (2015), LC do not give a detailed illustration of their concepts of 'specimen' and 'representative', but they do so in a later paper (Currie and Levy 2019): they define a specimen as a typical instance, where being typical 'can be understood in terms of similarity — in the limit, sameness — of focal properties' with the other members of the relevant class of extrapolation (*ibid.*, p. 1072). In the same article (*ibid.*, p 1078), they also explicitly contrast being a specimen with being a model representation:

> a specimen is a *representative instance* of the target. But this sense of 'representation' is critically different from that applicable to models. Experimental systems [...] represent similarly to how statistical samples do — by being not-unusual subsets of the larger class [...] This is not representation in an intentional sense, and the difference is reflected in the epistemology: in a successful experiment the object is a specimen, and confirmation is possible because it has been procured via an unbiased procedure [...] In contrast, a model represents the world by being *about* it.

Because they talk about intentionality, LC here distinguish specimens and models on a semantic level, and this also affects the epistemological nature of MO-based inferences, in contrast with what they say in their 2015 paper. Therefore, LC's overall distinction between MOs and models leaves some room to interpretation, and there are two plausible readings of their claims. On the one hand, following their 2019 paper, one can read LC as arguing that there is an essential difference, both semantic and epistemological, between specimens and models. Alternatively, one can read LC as making the weaker claim that, while specimens are representations in a loose semantic sense, MOs and models still exhibit important epistemological differences concerning the justification of the inferences that we draw from them about their targets.

In Sect. 3.1, I show that the strong interpretation of LC's distinction does not stand up scrutiny, irrespective of the philosophical account of representation one adopts. The weak interpretation needs some unpacking, and in Sect. 3.2 I look at what LC (2015) offer to support it. My conclusion is that there is no principled distinction between justification of model inferences and justification of MO inferences, the difference being at most a matter of degree.

Therefore, for both interpretations of LC's point, I show that their arguments remain wanting and their views do not provide an accurate understanding of the use of MOs and models.

## 3.1 Specimen vs. representation

Let us now scrutinize the stronger reading of LC's thesis. On this reading, a MO is a specimen of a target class $\mathfrak{T}$ iff it instantiates focal properties similar to the properties instantiated by the members of $\mathfrak{T}$, where a focal property is a property regarded as relevant in our extrapolation. Finally, specimens are not intentional — they are not about their targets — while models are.

The first difficulty for this account is that, as I argued in section 2.3, not all MOs work with a simple identity key, so, not all MOs are literally specimens of $\mathfrak{T}$, or the relevant

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[5] For details on the model, see Weisberg and Reisman (2008).

biological kind. For we need a key to translate the exemplified properties into the imputed properties, and $\mathfrak{T}$ is defined by the latter. So, *contra* LC's claim, MOs often do not function as specimens.

The second difficulty is that, even when MOs do function as specimens, it is just wrong to say that they are not intentional: MOs are studied in order to formulate hypotheses concerning the other organisms in $\mathfrak{T}$, so the results of our investigations on a MO are in effect about those other organisms. And this is the case for all experimental specimens that are used to formulate hypotheses about other systems.[6]

Now, it is true that not all representations are specimens in LC's sense. A painting of a horse is not a member of the class of horses. However, it seems clear that the converse holds: all specimens, MOs included, are representations. And this is all we need to undermine the strong interpretation of LC's claim.

The fact that specimens are representational symbols is a cornerstone of DEKI, as well as the representation-as view (Goodman 1976, Elgin 1983, 1996): both hold that one of the main aspects of representation is exemplification, of which specimens are perfect instances. The turquoise patch in a draper's window represents the turquoise clothes in the shop by being a specimen of turquoise clothing, that is, by instantiating that colour and referring to it given the contextual interpretation of the relevant agents.[7] In fact, in these accounts, specimens are regarded as paradigmatic examples of representation.

Nevertheless, LC (2019, p. 1073) attempt to drive a wedge between their 'specimens' and exemplification:

> in contrast to Elgin, we place weight on *how* a specimen was obtained [...] a specimen is an object drawn (in an unbiased way) from the world. Assumptions about how it was obtained [...] matter for justifying conclusions drawn from the specimen regarding the object of study.

Here, two aspects would distinguish specimens from Elgin's exemplars (that is, exemplifying systems): specimens are (1) drawn from the wild via (2) an unbiased selection process. However, on a closer look, the purported difference dissolves. I postpone a discussion of the epistemological value of (1) to Sec. 3.2. For the purpose of of analysing the strong interpretation of LC's distinction between specimens and models, however, we can recall that nothing stops Elgin's exemplars from being drawn from the wild too. For what concerns (2), LC characterize specimens as obtained via an unbiased selection process. In general, as LC put it, 'statistics provides methods for making such selections', and we should 'understand an unbiased selection process as one that reduces the risk of selecting an unusual object, and which preserves typicality [...] relative to the aims of the experiment' (*ibid.*).

However, statistics won't help us much here, because a statistical analysis alone won't tell us whether, say, *Drosophila* is a specimen of a class $\mathfrak{T}$ that includes humans. For whether something is or isn't a specimen depends on what features we focus on and what reference class we consider. These are decisions we have to make prior to any statistical analysis. And it may well be that the same organism is a specimen with respect to feature $F_1$ and reference class $C_1$, but not with respect to feature $F_2$ and reference class $C_2$. Thus, once we have

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[6] Certainly, an experiment can be performed on a system because we are interested only in that specific system. And, we do the same with targetless models — cf. Weisberg's (2013, § 7) models of four-sex organism populations and Norton's dome (2008). However, it is not clear if such experimental system still functions as a specimen, for it has no extrapolation class.

[7] Cf. Goodman 1976, pp. 52–56 and Elgin 1983, pp. 71–95, 1996, pp. 171–86.

established that something is a specimen, then it is also an exemplar (in Elgin's sense) that eventually proved to be successful for a specific purpose.

Since I have so far focused on the representation-as accounts and DEKI, one might worry that I am assuming a concept of representation that already presupposes my conclusion that specimens are representations. This is not so. The same conclusion can be reached from all main accounts of representation. The accounts of representation based on similarity (see Weisberg 2013 or Giere 2004) generally hold that, for a model $M$ to be a representation of a target $T$, it must be the case that $M$ is similar to $T$ (namely, they share some properties) and that an agent uses this similarity for certain (epistemic) purposes. Now, by definition, LC's specimens instantiate the focal properties of the target class, and scientists definitely use these similarities to draw inferences about that target class. Therefore, in the framework of the similarity views, LC's specimens are representations.

The same holds for structuralist accounts (see Bueno *et al.* 2012, Da Costa and French 1990, French and Ladyman 1999), which define representation in terms of (partial) isomorphism (or homomorphism) between the mathematical structure of the model and the mathematical structure of the target. Given the broad way in which an object can instantiate such a structure, here too a specimen of a class represents that class insofar as it instantiates structural properties that are also possessed by the members of the class. Interestingly, if one is a realist about mathematical structures, we have the converse implication that all representations, by instantiating a certain mathematical structure, will also be specimens of the class of objects instantiating that structure.

Finally, the inferential accounts of representation — see Hughes (1997), Suárez (2004) and Contessa (2007) — normally require representations simply to allow inferences about their targets. In these accounts too, there is no principled reason to distinguish specimens from other types of representations, as the former also function as epistemic surrogative systems.

In sum, not all MOs are specimens in LC's sense, all specimens are intentional, and all philosophical accounts of scientific representation unanimously recognize specimens as instances of representation. Therefore, the strong interpretation of LC's distinction between MOs and models, as both semantic and epistemological, is untenable.

## 3.2 Are MOs different from models?

Let's now turn to the weaker interpretation of LC's characterization of MOs. LC's point would be that, even if we grant that both MOs and models are representations in a loose sense, there is still an important difference in their epistemology, namely, in the way we justify the inferences we draw from them. They offer arguments in support of this claim in their 2015.

First, they claim that while models are intrinsically 'idealized constructions', MOs, 'in contrast, are drawn from a wild population' (*ibid.*, p. 334), a point that we have already encountered in the previous subsection.

Second, they say that a model's 'properties are either wholly stipulated or specified so as to represent some target', which is the reason for 'the modeller's intimate knowledge of, and high degree of control over, the model's] makeup' (p. 331). This is contrasted with the lesser amount of knowledge biologists possess about MOs.

Third, LC hold that 'theoretical models are assessed for structural resemblance to real world targets' (p. 337), and the relation between models and their targets is a 'direct comparison' (*ibid.*, p. 339), 'grounded in an explicit procedure of feature-matching' (p. 336). Instead, in 'model organism work, the inference from model to target is mediated via indirect evidence [...] One kind of indirect evidence is what we have called circumstantial evidence, the other is shared phylogeny' (*ibid.*). While LC admit that phylogeny is not the only way in which MOs relate to their targets,[8] they repeatedly highlight that this form of inference 'sets apart [MO] work from other kinds of theoretical methods' (*ibid.*) and that standard use of MOs 'is best understood as an application of phylogenetic inference' (*ibid.*, p. 339).

We can then summarize LC's position in three main claims:

(a) MOs are drawn from the wild while models are idealized constructions.
(b) The full specification of models' properties allows for a more intimate examination of their properties than with MOs.
(c) Models are directly analogous to their targets, while MO-based inferences are typically mediated by phylogenetic assumptions.

On the basis of these three claims, LC insist that MOs are relevantly different from models. These claims do not affect my overall application of DEKI to MOs. However, as LC's differences would bear on the justification of MO-based inferences, I also need to show that these differences should not worry us. So, I argue that these differences are at best a matter of degree rather than principle.

Let us start with (a), which I will call the 'materiality of MOs' to facilitate the discussion. First, materiality is neither a sufficient nor necessary condition for the justification of a MO-based inference. That *Drosophila* is drawn from the wild is not sufficient to justify, say, inferences from how the *Drosophila*'s genome folding works to how it works in humans. Nor it is necessary: we have seen that the material elements of the mechanism involved are different in *Drosophila* and humans, and we need a key to associate them.

Therefore, the burden of cashing out how exactly the materiality of MOs justifies the inferences we draw from them falls back on LC's shoulders. The crucial issue, I suggest, is not really whether MOs are drawn from the wild, but rather how their material features are interpreted for our inferences, an act of interpretation that DEKI captures nicely. As we have seen, sometimes the material properties instantiated by the MO are not exemplified; and those that are exemplified are sometimes translated into different ones via the key. Therefore, the justificatory role of MOs' material features is a matter of degree, depending on the context. But then, materiality does not amount to a clear-cut epistemological distinction between MOs and the rest of material models.

Let us move on to point (b), namely that models' constructed nature facilitate a more intimate, detailed knowledge and examination. First, as LC acknowledge (2015, p. 333), MOs too are idealized and controlled, as they usually undergo a sophisticated process of selection and genetic engineering. In addition, the experimental settings of MO laboratories are highly idealized. Illustrations of these elements of artificiality abound in the literature[9]. All this being said, it is also not generally true that (i) models have their properties wholly specified, nor that (ii) even if that was the case, this necessarily facilitates a more intimate

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[8] As Bolker (1995) and Gilbert (2009) argue, some emblematic MOs are clearly taxonomic outliers, as their genetic sequences often relevantly diverge from the ones possessed by their targets (Ankeny and Leonelli 2011, p. 318). Phylogenetic relations are sometimes just irrelevant: we have seen in section 2.3 that the FIK associates sets of proteins on the basis of functional identity. Fagan (2016, p. 133) also criticizes LC's excessive emphasis on phylogeny.

[9] On *Drosophila*, see Kohler (1991, 1993); on *C. elegans*, cf. Ankeny (2000); on *Arabidopsis thaliana*, see Leonelli (2007).

examination.

Concerning (i), models' assumptions are seldom known from the start and have no fixed interpretation. The elements of the model have to be interpreted as standing-in for elements of reality, and which interpretation is the "right" one depends on the purpose of the representation (see also below, Sect. 4.2). In other words, we need to use an appropriate key in each specific context. Therefore, the difference between models and MOs is again a matter of degree, and along this dimension, not all models are better off with respect to all MOs.

Concerning (ii), models are dynamic instruments, from which we constantly obtain new information. This is because scientists are not logically omniscient. It took physicists 200 years to realize that Newtonian models can exhibit stochastic behaviour (cf. Parker 1998). The more complex models are, the less they allow for the sort of intimate, detailed examination LC take for granted. Except for toy models like the original Lotka-Volterra model, models can be considerably opaque in their inferential patterns. So, it is not always easy to recognize the relations between the different inferential steps, or what are the rules that govern the evolution of the model system. The concept of 'opacity' has indeed become central in the literature on formalized models and computer simulations:[10] for example, Beisbart (2021) illustrates different levels of opacity via a case study from the science of climate, namely the Hadley Centre Coupled Model 3 (HadCM3). In this and many other cases, how the model "works" internally is not entirely known from the beginning: it must be studied in itself. Again, how much a model's properties can be transparent varies in degree. In this respect, many models exhibit a level of complexity that makes them not very different to MOs.

Let us now turn to thesis (c), which I take to be LC's strongest argument for there being a difference between MOs and models. LC argue that the inferences linking MOs to their targets, being mediated by indirect evidence and phylogenetic assumptions, are crucially different from the 'analogical', resemblance-based, unmediated inferences that characterize models. I argue that, even when phylogenetic assumptions are in place, this does not constitute a clear rupture with other models. For virtually all model inferences are mediated by some assumptions and indirect evidence, exactly like MO-based inferences are mediated by phylogenetic assumptions and indirect evidence.

To begin with, it is worth recalling that analogy, in its technical meaning (see Bartha 2010), is just one among the many ways in which a model can relate to its target: approximation, projections, limit functions, and conventional rules are other distinct ways in which the properties of a model relate to the properties of the target.[11] These model-target relations are rarely based on 'direct' or evident similarities, as LC seem to assume. On the contrary, basically any feature-matching activity involved in modelling is usually 'mediated' by some assumptions, empirical or theoretical. For example, the system described by the Lotka-Volterra equations is not intrinsically similar to any real population's dynamics. The model system describes the two populations in a very idealized and distorted way. What provides the theoretical justification for considering this fictional system as analogous, and relevantly so, to real populations? LC pass over this aspect of models in silence, but this is crucial for the tenability of their argument. We need basic assumptions concerning ecologic regularities

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[10] See Beisbart (2021) and references within. In contrast with some authors (Humphreys 2009, Winsberg 2001), I do not acknowledge any philosophical novelty of computer simulations with respect to scientific models (cf. Frigg and Reiss 2009).

[11] For an overview on different types of model-target relations, see Frigg (2022, pp. 468–74).

and empirical observations on real populations in order to warrant an analogy between the model and the target populations.

Generally, the distortions in the model must be accounted for in some way. Either they are shown to be acceptable in a specific context — for instance, the absence of air resistance in kinematic models is deemed legitimate because it is negligible for some epistemic enquiry — or there is a key that translates the distortions in a meaningful property. For example, in the case of a Mercator map of the Earth, we have precise equations to convert the distorted distances between points on the bidimensional map into actual distances on the planet's curved surface (cf. Nguyen and Frigg 2022).

Of course, reference to phylogenetic relations in the case of MOs is not arbitrary: they derive from the theory of evolution, one of the cornerstones of modern biology. So, it is reasonable to find phylogenetic assumptions in play. But this does not distinguish MOs from the rest of models: all the relevant similarities between a representation and its target are in fact mediated by some assumptions, empirical data, rules and conventions (see Nguyen 2020 for a generalized argument).

In conclusion, all the differences that LC highlight between models and MOs are, at best, a matter of degree, and they do not undermine my general claim that MOs are representations like models are.

## 4 Weber's concerns about representation

Let's now look at Weber's concerns about MOs as representations. While Weber expressed his disagreement with a representational view of MOs during the online presentation of Ankeny and Leonelli's volume (2020),[12] he did not argue at length against it in print. However, in a footnote (2014, p. 758) he writes:

> my argument against [MOs] being theoretical models is that any theoretical model must be associated with a mapping function that specifies what part or aspect of the model is supposed to represent or stand for what (e.g., that the function symbol "F" in a mechanical model stands for the mechanical force). Such a function is not uniquely defined for a [MO] because such organisms may serve a variety of different purposes, only some of which are representational.

We can then individuate two main theses: (1) MOs have many purposes, only some of which are representational, and (2) because of it, MOs cannot be equipped with a uniquely defined function that univocally assigns to each element of the model an element in the target system, a requisite for a system to be a model.

I first deal with (1) and show that it is not problematic for the account presented in this paper. Then I move to (2) and show that Weber's requirement of a univocal function is too demanding because his view of the model-target relation is too simplistic: the interpretation of the model varies on the basis of the target and the specific purposes of our study.

### 4.1 The multiple function of MOs

Weber talks about a 'variety of different purposes' for MOs besides representation. What are then the functions of a MO that are non-representational, at least in DEKI's broad

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[12] The integral video can be found at this link.

sense? Weber (2004, Ch. 6) has put forward his own view of the main function of MOs in biological research, which he calls ‘preparative experimentation’. On this view, MOs are best understood as material and conceptual arenas: the space where new experimental procedures arise and scientists learn how to manipulate biological systems experimentally, achieving a know-how that may become useful for future applications or interventions. Weber’s preferred example is the work carried out on *Drosophila* in order to understand how the process of genetic cross-over occurs and its implications for genome selection. As he shows, the study of *Drosophila* has brought about the acquisition of new techniques to be employed in new contexts of investigation. He particularly insists on the development of the so-called ‘chromosomal walking’ (*ibid.*, pp. 160–62), a technique to clone DNA sequences about which only their chromosomal location is known.

I agree with Weber that preparative experimentation is not a representational use of MOs, at least in DEKI’s sense. One may interpret it as a prescriptive form of representation: a system exemplifies some techniques and prescribes how to apply them in other contexts. Yet, in its present form, DEKI cannot deal with prescriptive cases.[13] However, this does not seem to be a problem. In the literature on models, nobody argues that scientific models are only functioning as representations (cf. Frigg and Nguyen 2020, p. xii). Representation is indeed just one of the several functions that models can serve.

So, in order for Weber’s argument to be effective against the representation view presented here, either (a) Weber needs to identify a function of MOs that is incompatible with representation in DEKI’s sense; or (b) he must argue that MOs’ representational function is secondary or negligible to understand MOs’ use in biology, even when we interpret representation in DEKI’s sense. Neither of these options look promising. As regards (a), it should be clear that there is no logical incompatibility between Weber’s preparative experimentation and representation. Indeed, it is common to find examples of models used for preparative experimentation that are then also used as representations.[14]. This is just because models are useful tools not only to identify properties to map onto our targets, but also to test or develop theories, to integrate them with data or other theories, and to develop new formal or empirical methods of analysis. And, in the case of many models, MOs included, these functions are carried out with the same material objects. Namely the MO populations studied in the laboratory serve to represent other organisms, to develop explanations and predictions of certain phenomena, to enhance our understanding (both know-that and know-how). Therefore, the plurality of MOs’ functions in biology is not necessarily a problem, nor an exception with respect to the rest of scientific models.

Concerning (b), is representation a negligible use of MOs? This is an empirical question that has to be answered by investigating how MO-based inferences can be reconstructed and justified. In Sect. 2, I argued that this requires an account of representation, and that the best account to offer such a reconstruction is DEKI. Until we have an argument to the contrary, showing that representation is not needed after all, or that DEKI is the wrong account to fit the bill, the conclusion stands: understanding MO-based inferences is best done with an account of representation, and hence representation is not negligible.

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[13] On normative models and their relation with descriptive ones, see Beck and Jahn (2021) and Roussos (2022).

[14] For example, see Hartmann (1995, p. 9) for a use of models to develop new formal techniques in quantum chromodynamics.

## 4.2 Univocal functions and interpretation

As regards (2), I grant Weber's point that, in a very general sense, we need some form of interpretation of each part of the model, and then a function that relates parts of the model to parts of the target. In the account adopted in this paper, this is done via an interpretation of the object as a model and the subsequent adoption of a key. However, first, a key only applies to the properties exemplified in that specific context. Second, as I will show now, it allows a reasonable level of flexibility, which Weber's univocal function does not.

Weber seems to suggest that the basic terms of a model always must have a precise physical or biological interpretation, while the basic terms of MOs do not. In the case of the Lotka-Volterra model, for example, each of the two differential equations describing the model system are endowed with a clear physical-biological interpretation — for instance, a variable is univocally the number of the prey, another indicates the number of predators, and so forth.

There are a number of considerations that show that the alleged precision that Weber sees in the interpretation of models is too simplistic. For, in fact, mathematical or formalized models sometimes employ terms endowed with a precise definition that nevertheless do not seem to refer to anything real in the world. For example, the variable denoting the prey actually denotes a prey population that grows limitlessly if it weren't for the presence of the predator, and this physical-biological interpretation of $V$ does not map precisely to anything in the biological kingdom. The Lotka-Volterra model is no exception in this respect: the very term $F$ that Weber uses to make his point in the above quotation stands for a theoretical entity: nobody has ever observed Newtonian forces, only their effects. As Cartwright (1999, Ch. 3) pointed out, it is arduous to even specify what counts as a force in the first place.

All this means that the physical or biological interpretation of the theoretical terms employed in a model is far from being uniquely defined: it depends on the target system and the context of application. That's why we need a key in the first place. This becomes even more evident when we look at cases in which the "same" model is applied to represent different targets. This phenomenon, which, following Bradley and Thébault (2017), we may call 'model migration', is ubiquitous in science. Hydrodynamic models were used to represent electromagnetic phenomena, and mechanistic models of particles are used to represent stock markets. Even the chromosomal walk that Weber analyses in his book is a version of the so-called random walk, which was used to model the Brownian motion of particles.

Once we realize that Weber's demand of a unique interpretation of the terms and elements of our models is untenable, it is also clear that MOs are actually like other scientific models in this respect. So, for example, in *C. elegans*, the mechanisms of cellular programmed death (Ankeny and Leonelli 2020, p. 8) can easily be taken to be a simplified version of more complex mechanisms of cell self-destruction in other organisms. Here, the elements of the self-destruction mechanism in the worm's cell stands for the analogous mechanisms in the cell of the designated target organism. The same can be said about the genetic cross-over in the *Drosophila*, where its specific chromosomes, fragments of DNA and the process of chromosomal walking stand for chromosomes, DNA and chromosomal mechanisms in a large array of other biological systems.

Just like in the Lotka-Volterra model, some elements of the mechanisms that the MO exemplifies will not map onto elements of the same mechanisms of the target species. But this is just another way to say that we need a key to export our results to other biological systems, adapting the interpretation of the elements of the model to each specific context.

In the case of our architectural proteins, this becomes manifest: proteins are not mapped onto other proteins one by one, but they are grouped according to their function in the mechanism.

In conclusion, Weber's preparative experimentation is compatible with MOs being used as representations, and his requirement for a uniquely defined function is too strict, because the use of a system as a representation of another is highly context- and target-dependent.

## 5 Conclusion

By taking full advantage of the resources offered by the DEKI account of representation, I have shown how exemplification and the key play crucial roles in the inferences drawn from MOs about other organisms. I have also provided an account of the justification of MO-based inferences: an inference from a MO to a target system is justified insofar as the MO exemplifies a set of properties that are mapped onto the target via an adequate key.

I have then addressed two views of MOs that challenge the representation view. I have shown that Levy and Currie's (2015) arguments do not undermine my view of MOs as representations, and I have argued that Weber's (2004) preparative experimentation view is compatible with my view.

Finally, my analysis shows that representation does not imply unmediated analogy, nor uniquely defined functions for each single part of the model. In contrast, representation is always mediated by, and embedded in, theoretical assumptions and empirical knowledge. At the same time, representation always remains local, insofar as it is context- and target-dependent. Therefore, the justification of our inferences from a representation always consists of an interplay between the justification internal to the specific representational framework (the key), on the one hand, and, on the other, the justification provided by the rest of our knowledge (the repertoire), which remains largely extrinsic to the single representation.

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## Declarations

I confirm that I have no conflict of interest and that I adhere to all the requirements of the COPE guidance.

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