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What Is behind the Term "Model" Organisms?

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Abstract

Model organisms play a central role in biological research, yet the conceptual questions they raise continue to provoke debate among philosophers. This article examines one such question: What are the distinctive features that qualify model organisms as scientific models? Building on and extending previous work, we propose a refined conceptual framework for understanding model organisms in the context of contemporary scientific practice. Our framework highlights six key features that, collectively, uniquely characterize model organisms. We argue that model organisms should not be viewed merely as components within experimental systems but rather as autonomous experimental systems in their own right.

1. Introduction

Model organisms have long served as indispensable instruments in biological research. Standardized through genetic manipulation, inbreeding, and other techniques, these organisms not only facilitate the investigation of fundamental life processes but also act as testbeds for therapeutic innovations. Despite their empirical centrality, the conceptual questions they raise continue to provoke debate among philosophers. In this article, we explore one such question: What are the distinctive features of model organisms as scientific models?

Building on and extending previous work, this article offers a refined conceptual framework for understanding model organisms in light of contemporary scientific practice. We elucidate six distinctive features of these models that, when considered collectively, are unique to model organisms. To our knowledge, some of these features, including the self-modifying capacity (detailed in the following text), have not been addressed in the literature. In addition, our conceptual framework differs from the existing literature in at least three ways. First, contrary to the views held by Weber (2001, 2004), we argue that establishing the generalizability of findings from a particular organism to other populations or species cannot be achieved by relying solely on phylogenetic arguments in conjunction with a distinction between high-level and low-level phenomena. Second, in contrast to Weber's (2004, 2018) conception of experimental systems as integrated assemblages of research materials, procedures, and instruments—where model organisms are only one part of this

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system—we argue that model organisms function as experimental systems in their own right. This reconceptualization emphasizes their capacity to embody and instantiate phenomena, thereby endowing them with direct epistemic significance. Similarly, whereas Rheinberger characterizes model organisms as "organic instruments" primarily designed to facilitate experimental inquiry, we contend that they are "epistemic things" in their own right (Rheinberger 2011).

The article unfolds in two main sections. First, we offer a succinct overview of key concepts from the philosophy of science literature on models, focusing on those that elucidate why an organism qualifies as a "model." In this section, we focus on one of the central epistemic functions of model organisms: the representation of biological phenomena. Second, we identify six characteristics of model organisms that, when taken together, reveal their unique epistemic qualities as scientific models. This comprehensive set of characteristics not only demarcates the unique epistemic profile of model organisms but also establishes sufficient criteria for their identification as distinct models. In doing so, our work aims to stimulate further philosophical inquiry into how experimental practices in the life sciences shape knowledge production, and to provide a more nuanced understanding of what it means for an organism to serve as a model.

2. Key epistemic functions of model organisms

2.1 A mosaic of idealized "models of" and "models for"

Although the idea that many scientific models are constructed representations is well established (Teller 2001), applying this conception to model organisms demands a closer examination. Classical accounts hold that models represent their targets through analogy—so that a model's validity depends on the relevant similarities it shares with its target (Godfrey-Smith 2006; Teller 2001). In scientific practice, models are employed to capture specific aspects of the world for particular investigative purposes (Giere 2004; Parker 2020). This point is especially crucial for model organisms, which gain epistemic legitimacy not by virtue of universal validity but in relation to specific research questions or hypotheses.

In biological research, model organisms are employed to capture specific aspects of biological phenomena while enabling experimental intervention. Researchers deliberately *idealize* these organisms—simplifying certain variables or interactions—to render complex systems more comprehensible or to isolate key causal mechanisms. As a result, the representation of biological phenomena by model organisms is not merely a passive mirroring of reality but also instead fulfills a dynamic, dual function: Model organisms both represent a target phenomenon and serve as experimental setups for manipulation or intervention (Morrison and Morgan 1999). In other words, they function dually as *models of* the target phenomena—providing a constructed representation—and as *models for* experimental inquiry—serving as tools for manipulation and measurement (Fox Keller 2000; Ratti 2020). More specifically, a model organism sets the conditions under which a phenomenon is realized, delineating the variables that can be manipulated and measured (Baetu 2014). In this context, the choice of a model organism is guided by the scientific objective, with judgments of relevance concurrently shaping both the representation of the phenomenon and the experimental protocols that yield pertinent data (Peschard and Fraassen 2014).

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Importantly, biologists rarely rely on a single model organism. In many scientific investigations, multiple model organisms, each based on different assumptions, are used to capture distinct facets of the target system (Weisberg 2007). Knowledge is advanced through cross-model comparisons, a strategy Baetu (2014) refers to as *mosaicism*. This mosaic approach reinforces the epistemic foundation of model organisms research by revealing which aspects of a phenomenon are robust across different models.

Altogether, these aspects—the use of idealization, the integration of intervention with representation, and the practice of mosaicism—are fundamental for understanding the unique epistemic status of model organisms as scientific models.

Despite general agreement that model organisms frequently serve a representational role, debates persist in philosophy of science over whether representation is always involved (Germain 2014; Levy and Currie 2015; Sartori 2023; Weber 2014). For instance, organisms can be studied for what has been called "preparative experimentation" (Weber 2004). Through the studies on model organisms, practical knowledge, protocols, and tools are produced. This expertise on rearing conditions or genetic engineering, for example, shapes how experiments are conducted and interpreted. In some research teams, developing and validating such tools is the sole purpose of model organism-based research, rather than modeling an external target.

Thus, model organisms can also serve as practical instruments for tool development, even though they most often act as representations of a target. In this regard, the notion of representation has been refined in two distinct ways in the context of model organisms by the philosophers Leonelli and Ankeny: the *representational target* and the *representational scope*.

2.2. Representational target and scope

Within the context of model organisms, the "representational target" refers to the phenomena that can be investigated through the use of an organism (Ankeny and Leonelli 2011, 2020). Model organisms serve to represent a diverse array of targets, ranging from specific biological processes to diseases or even entire human patients (Green 2024). Some scholars differentiate between models of human diseases—often labeled "surrogates"—and models of general phenomena, known as "exemplars" (Baetu 2014; Bolker 2009). The distinction is based on the fact that in models of general phenomena, the phenomenon is both instantiated in and represented by the organism, whereas in disease models, the organism does not fully manifest the target but represents only certain of its features.

Defining the representational target of model organisms raises a subsequent question regarding the generalizability of findings. This idea is captured by the notion of "representational scope," often termed external validity, which refers to the degree to which a result can be applied to broader contexts or populations. In model organism research, external validity is frequently underpinned by evolutionary considerations (Schaffner 2001; Weber 2004). While known phylogenetic relationships provide a rationale for extrapolating findings, they do not guarantee that a biological process will generalize without limitation: Species-specific differences can and do constrain the applicability of results. Importantly, the evolutionary argument does

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not negate these differences but rather explains why generalization may be plausible in the first place.

Depending on the research objectives, the scope of a given model organism may be narrow, applicable only to individuals within the same species, or broader. When the scope is confined to one species, two scenarios emerge. In one case, the target phenomenon is unique to that species, so the findings pertain solely to its members. In the other case, while the target exhibits species-specific characteristics, the study nevertheless yields insights that contribute to a more general understanding. For instance, to understand the principles underlying information coding in the central nervous system, studies are conducted using various species. For each model organism, the representational scope is inherently limited by species-specific peculiarities. Neurotransmitter actions may vary significantly: In arthropods, glutamate functions as an inhibitory agent, whereas in mammals it serves an excitatory role. Nonetheless, by comparing and integrating findings from multiple models, each with its own constrained scope, researchers are able to build a broader theoretical framework for neural information coding that applies across species (Laurent 2020). In other words, although the unique characteristics of any single species may constrain the scope, the transfer of results across different models enables the construction of a broader conceptual understanding. This target is not represented by any single model organism in isolation but is constructed from the collective knowledge generated by multiple models, each with its own limited scope. Such an integrative approach ultimately influences the interpretation of experimental results obtained within the restricted scope of each model organism.

Among both scientists and philosophers, it is frequently assumed that the representational scope of a model organism can be partly determined by a priori considerations. Such considerations typically take into account, on one hand, the phylogenetic distance between the model and the target species, and on the other hand, the nature of the phenomenon or mechanism under investigation. Among philosophers, these arguments have been notably developed by Weber (2004). According to this perspective, it is plausible to hypothesize that exocytosis—a cellular process in which vesicles fuse with the plasma membrane to release their contents—constitutes a low-level, highly conserved mechanism with broad generalizability. In contrast, complex phenomena such as elaborate behavioral patterns (e.g., food intake-related obesity), or emotional states, might be expected to exhibit a narrower scope, thereby confining their study to mammalian models.

However, we contend that neither a phylogenetic proximity nor a low-/high-level distinction is sufficient to determine representational scope. To illustrate, while exocytosis mechanisms show remarkable similarities between unicellular eukaryotes and human neuronal synapses (Emes and Grant 2011), comparative studies reveal that mouse and human synapses differ in the composition of key proteins (Bayés et al. 2012). This indicates that even for low-level processes presumed to be broadly conserved, important variations can constrain generalization. Conversely, high-level complex phenomena can, in fact, be studied using organisms that are often considered "simpler." For instance, genes associated with obesity in humans have also been identified in *C. elegans*, and manipulating these genes in worms exposed to a high-fructose diet results in weight gain (Ke et al. 2021). Another example is provided by studies that have investigated the patterns of neuronal activity underlying

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emotional states in *zebrafish* larvae and *drosophila* (Athéa et al. 2024). Consequently, classifying phenomena as low-level (and likely to be conserved) or high-level (and unlikely to be conserved) does not provide a sufficiently reliable method for determining the generalizability of results.

Another version of this argument might maintain that we should instead rely on gene conservation as the basis for extrapolating findings. We contend that this approach can also be misleading. For instance, consider a gene from *Salpingoeca rosetta*, a unicellular organism that is closely related to animals, which encodes what is typically known as a synaptic protein. In multicellular organisms, synaptic proteins are integral components of nerve cells; they are localized at synapses (the specialized junctions where neurons communicate) and are crucial for transmitting signals. However, in *S. rosetta*, although the gene retains protein domains usually associated with synaptic function, it is expressed in the nucleus where it performs functions unrelated to neural communication (Burkhardt et al. 2014). This example illustrates that even when gene sequences appear conserved, the actual cellular context and the resultant functions may differ markedly. Consequently, a more reliable assessment of representational scope requires analyzing the conservation of multiple genes together with a detailed understanding of the corresponding protein-level mechanisms.

These considerations lead us to propose that the representational scope of model organisms is more effectively assessed a posteriori and through systematic comparisons across different models. In practice, extrapolation is evaluated by comparing and ranking results obtained from a spectrum of models—from *C. elegans* and other invertebrates to primates, and even to reduced models such as cell lines—under varying experimental conditions. This holistic strategy of multiple comparisons ensures that the external validity of findings is continuously interrogated and reevaluated (Baetu 2016). Ultimately, the external validity of results from any single model organism depends on the extent to which these results can be coherently integrated with those from other models, thereby constructing a robust and comprehensive understanding of the target phenomenon.

3. Specific features of model organisms

Having established in the first section the sense in which model organisms can be regarded as scientific models, we now turn our attention to the specific features that uniquely characterize them. In this section, we will explore how model organisms differ from other types of models by examining their dual nature as both tangible specimens and human-engineered artifacts, as plastic entities capable of adaptive change, and as dynamic experimental systems. This deeper analysis will elucidate the distinctive epistemic qualities of model organisms.

3.1 Between specimens and artifacts

A first distinguishing characteristic of model organisms is that they are actual, living specimens—tangible exemplars of the biological world. To our knowledge, the literature does not explain in what sense their status as specimens has epistemic relevance. We argue that it does: The very fact that a model organism is a living specimen fundamentally affects the validity of the knowledge it generates. Unlike computational or physical models, which may omit unknown yet crucial parameters,

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a living specimen inherently embodies all its biological attributes, both those that are known and those that remain undiscovered. This inherent completeness ensures the minimal validity of model organisms.

It is evident that this inherent completeness is necessary, yet insufficient. Even if all variables are present within a model organism, overlooking certain factors can undermine their interpretative contribution, regardless of their causal significance. Nonetheless, because model organisms serve as natural exemplars rather than as reduced models, successive empirical studies can incrementally reveal these hidden variables. In this way, model organisms function as idealized models that retain the authenticity of a complete exemplar.

Beyond their status as natural specimens, model organisms are also artifacts, defined as objects intentionally created or modified by human intervention to fulfill specific research objectives. For example, standard laboratory mouse strains are produced through inbreeding to achieve a level of genetic uniformity that does not occur in wild populations. Another example is provided by animal models of genetic diseases. In these models, the mutation known to cause the disease in humans is introduced, typically into mice, to replicate the condition, thereby enabling the study of its underlying mechanisms. The artifactual nature of model organisms underscores their dual character: They are simultaneously natural exemplars, embodying the full complexity of the organism, and products of experimental design, subject to the practical constraints of biological manipulation (Ankeny and Leonelli 2011; Bolker 2017; Rader 2004).

3.2 Plastic entities

Model organisms are, in part, artifacts precisely because they can be genetically modified in ways that do not occur naturally. These modifications are employed either to *construct* the model—as in the case of mouse models of genetic diseases, where the introduced mutation serves as the etiological cause of the pathology—or to *use* the model, for instance by altering a specific gene to study its function. In both cases, however, the intervention can never be "ideal" in Woodward's sense (2010) because of the inherent plasticity of living organisms.

For instance, in genetically modified organisms, a phenomenon sometimes referred to as genetic compensation may occur. Here, the observed phenotype results not solely from the intentional genetic alteration but also from compensatory changes in the expression of other genes (Jakutis and Stainier 2021). This dynamic response indicates that a model organism is not merely an artifact of an "ideal intervention"; it is a self-modifying entity whose internal state can shift in unforeseen ways. Such plasticity complicates our idea that model organisms are inherently valid because they are natural exemplars: If we cannot ascertain which variables are modified through compensatory processes, then generalizing findings becomes problematic. Yet, there are instances where similar systemic effects occur in both the model organism and the target. Consider genetically modified organisms designed to model specific genetic diseases. For instance, a mutation in the FMR1 gene leads to its silencing, thereby causing Fragile X syndrome, a condition associated with intellectual disability and features of autism spectrum disorder. Genetically modified mice have been developed to represent this disease by mimicking the loss of FMR1

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gene expression (Santos et al. 2014). In these models, one might expect compensatory mechanisms to obscure the disease phenotype; however, the genetic compensation occurs in both the mouse models and in human patients. In both cases, this compensation is better named "systemic effects" because it does not prevent the pathology. This similarity suggests that such compensatory responses are not unique to the model organism but are shared features of the pathology, thereby reinforcing rather than detracting from the model's validity. Thus, the self-modification capacities do not necessarily compromise the model organism's epistemic reliability.

Equally important is phenotypic plasticity, defined as the ability of a single genotype to give rise to different phenotypes under varying environmental conditions (Pigllucci 1996; Nicoglou 2024). For example, a rodent maintained under standardized laboratory conditions is markedly different from one living in the wild. Empirical studies have shown that enriched housing environments can alter brain structure and connectivity (Bennett et al. 1964). These findings underscore that the conditions under which model organisms are maintained critically shape their biological responses, thereby reinforcing that model organisms function as both natural exemplars and as artifacts of experimental design.

3.3 An experimental system

Moreover, model organisms must be understood in the context of the experimental conditions in which they are studied, as these conditions shape the phenomena that the organisms bring forth. In many experiments, variables are controlled to a significant extent, which in turn restricts the range of phenomena that emerge and are ultimately represented by the model organism. In other words, contrary to Weber's suggestion, we argue that the representation provided by a model organism is inseparable from the experimental settings and the parameters measured.

Consider, for example, investigations into how the sensory cortex processes environmental information. In one series of studies, the neural activity of a rat's somatosensory cortex was recorded while its whiskers were mechanically stimulated. Initial experiments conducted on anesthetized rats yielded one pattern of activity; subsequent recordings in head-fixed awake animals produced different results; and further studies correlating cortical responses with whisker touch in freely moving rats revealed yet another pattern (Erchova et al. 2002; Nicolelis and Fanselow 2002). These variations indicate that the biological process being represented is deeply influenced by the experimental conditions, such that the phenomenon is not an invariant property of the organism but is coconstituted by the methodological framework. This perspective aligns with the view in the philosophy of experiment that phenomena are, in many cases, brought into being through experimental practices rather than simply being discovered (Hacking 1983, 1992).

Even when the phenomenon is considered in its full complexity, researchers focus on selected elements by controlling or omitting certain variables. This process of idealizing the target results in a model that is not solely the organism but a composite of the organism, the specific experimental settings, and the chosen measured parameters. The way in which a phenomenon is understood depends on this intricate interplay between the organism and its experimental context, as well as on the

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variables selected for observation. In the end, the study of the organism provides an idealized explanation of the biological process that is being targeted.

In summary, organisms can only function as models when they are embedded within an experimental protocol and a broader body of background knowledge that justify experimental choices (Hacking 1983; Shelley 2010). While the living organism constitutes the central component, it is part of an entire experimental system. Thus, the construction and validation of a model depend on background assumptions (such as fundamental concepts of cell biology), methodological constraints, and the experimental conditions imposed. In other words, the relationship between the model and the instruments or protocols used to manipulate it is *constitutive* (Rheinberger 1997). Regarding Rheinberger's terminology, we find ourselves largely in agreement with his characterization of "experimental systems" as the smallest integral working units of research—that is, as complete experimental arrangements designed to produce knowledge, and characterized by technical, epistemic, social, and institutional aspects. However, we diverge from his perspective on model organisms. Indeed, he does not regard model organisms as epistemic things and reduces them to mere "organic instruments." In contrast, based on the arguments developed in the preceding text, we regard model organisms as full-fledged experimental systems that oscillate between being epistemic entities and technical objects. As Rheinberger states, "[A]n epistemic object is first and foremost a question-generating machine" (1997, 32), which we maintain is precisely the fundamental role that model organisms fulfill.

As a result, a model organism is a dynamic entity on three levels: the biological organism, the experimental procedures (including procedural adjustments), and the conceptual framework used to justify experimental choices (defining the target, selecting concepts to interpret results, etc.). These components may be modified during the course of a research project to address new questions or to enhance the reliability (internal validity) or generalizability (external validity) of the results. In every case, the model's selection and construction are guided by the choice of the components to be represented, a choice that depends on the scientific question.

3.4 A way to do science

Finally, the use of model organisms embodies a distinctive mode of scientific practice. The standardization of model organisms; through controlled breeding, uniform housing conditions, and harmonized experimental protocols; is a collective enterprise shaped by the scientific community. This standardization facilitates the sharing of critical resources, such as reference genomes and neural connectomes, through centralized platforms like WormBase or FlyWire (Devineni 2024; The C. elegans Sequencing Consortium* 1998). Thus, the utility of a model organism is not solely a function of its biological properties but also of the infrastructural, methodological, and communal support that underpins its use in research (Ankeny and Leonelli 2011, 2020).

3.5 Summary: The six characteristics of model organisms

In summary, our analysis distinguishes six interrelated features that elucidate the unique epistemic status of model organisms and set them apart from other types of scientific models:

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1. *Diversity of representational targets*. Model organisms are employed to investigate a wide spectrum of phenomena, from basic biological processes to clinical conditions. Each target is typically explored through a range of models.
2. *A representational scope grounded in evolutionary justification*. The generalizability of findings from a model organism is supported by evolutionary arguments, rendering it a priori plausible to extrapolate results across species. However, as we have demonstrated, this alone is not sufficient to justify such extrapolations.
3. *A distinctive mode of representation.* Unlike other scientific models, model organisms function as both natural exemplars, embodying the full complexity of biological systems, and as products of artifactual, idealized experimental design.
4. *A self-modifying capacity*. Model organisms are not static entities, but actively interact with, and adapt to, their experimental environments.
5. *A dynamic experimental system*. Living organisms are deeply embedded within evolving experimental and theoretical frameworks. All these components (the biological organism, as mentioned in point 4, the experimental procedures, and the conceptual framework) can evolve during the course of a research project.
6. *Unique practical dimensions*. The use of model organisms brings with it distinct practical methodologies and research practices. These include standardized breeding, controlled housing conditions, and collaborative infrastructures, all which contribute to the epistemic strength of the models.

Collectively, these six characteristics not only delineate the distinct nature of model organisms but also provide a framework for understanding their role as scientific models.

4. Conclusion

In this article, we have advanced a refined framework for understanding model organisms that departs from traditional accounts in several key respects. First, model organisms should not be seen merely as components within larger experimental systems, but rather as experimental systems in their own right. This broader perspective emphasizes that model organisms integrate research materials, procedures, instruments, and data analyses into a cohesive epistemic whole. Second, our characterization implies that model organisms are not merely modified research tools; rather, they are epistemic things—entities that, by instantiating the phenomena under investigation, possess intrinsic epistemic value. Third, our analysis reveals two overlooked, interrelated features of model organisms. We have highlighted their plasticity, that is, their capacity to adapt and self-modify under experimental conditions. This characteristic adds complexity to their epistemic status and necessitates a careful examination of the interplay between biological variability and experimental control. Moreover, by emphasizing that model organisms are actual biological specimens, we clarify their distinctive mode of representation. This mode, grounded in the inherent completeness of the organism, crucially supports the model's validity by ensuring that both known and yet-to-be-discovered parameters are, in principle, accessible for investigation. Fourth, we have highlighted the issues inherent in establishing the generalizability of findings from a particular model

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organism solely on the basis of phylogenetic arguments or a distinction between high-level and low-level phenomena.

Our discussion has also led us to take a stand within the subtle disagreement concerning the representational target of model organisms. Rather than equating the target solely with patient populations (Guala 2003) or narrowly with specific biological processes (Weber 2004), we advocate for an understanding of the target as the phenomena to be explored. Drawing on the work of Ankeny and Leonelli, as well as the conceptual frameworks of Bogen and Woodward, we maintain that phenomena, conceived as constructs that label and define the objects of scientific inquiry, constitute the appropriate targets for experimental investigation.

Collectively, these propositions invite a reappraisal of the epistemic status of model organisms. By reconceptualizing them as dynamic, plastic experimental systems that enable the generation of new research questions, we offer a perspective that illuminates the intricate processes underlying scientific knowledge production in the life sciences. We hope that this framework, grounded in contemporary scientific practice, will foster a deeper understanding of model organisms that closely mirrors their actual uses in research.

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