

# Species as Models

**Abstract:** This paper argues that biological species should be construed as abstract models, rather than biological or even tangible entities. Various (phenetic, cladistic, biological etc.) species concepts are defined as set-theoretic models of formal theories, and their logical connections are illustrated. In this view organisms relate to a species not as instantiations, members, or mereological parts, but rather as phenomena to be represented by the model/species. This sheds new light on the long-standing problems of species and suggests their connection to broader philosophical topics such as model selection, scientific representation, and scientific realism.

## 1 Introduction

Biological species has arguably been one of the most controversial topics in the philosophy of biology. Philosophers and biologists alike have long debated over “correct” concepts of species and their ontological status. The traditional account took species as a category, class, or type instantiated by individual organisms. After the advent of evolutionary theory, the typological concept came under fire by those who identify species with a part of biological lineage (Ghiselin 1974; Hull 1976). They forcefully

argued that a species is not an abstract type but a concrete historical entity of which individual organisms are mereological bits. Although this individualist thesis became a de-facto standard in the philosophy of biology in the last century, some have complained its lack of explanatory power and called for a revival of a type or natural-kind based concept of biological species (Boyd 1999).

To this debate between individualists and typologists, this paper introduces yet another thesis according to which species taxa are models of scientific theory. Model is a notoriously equivocal concept, but in this paper it is understood as a set-theoretic entity that makes sentences of a given theory true or false. This implies that biological species are mathematical, rather than biological or even tangible, entities. To work out this claim I begin Section 2 with a reconstruction of various (e.g., phenetic, cladistic, biological etc.) species concepts in terms of formal models that licence characteristic sets of inferences. The model-theoretic rendering illustrates logical connections among different species concepts and provides a platform to evaluate them as a problem of *model selection*. Section 3 then expounds on philosophical implications of the model-theoretic interpretation. Identifying species with models entails that the organism-species relationship is not instantial or mereological, but rather representational; i.e., species as models *represent* individual organisms. This opens the possibility of applying general philosophical discussions on scientific representation and realism to vexed questions concerning the epistemic and ontological status of biological species. Through these arguments this paper puts the species problem under broader contexts of model selection, scientific representation, and scientific realism, depicting it as a special case of the generic question as to how science investigates the world.

## 2 Species as models

This section fleshes out the main claim of this paper by reconstructing various species concepts as set-theoretic models. The central idea is that species concepts specify theories that underpin biological inferences and descriptions, and species are models that satisfy such theories.

### 2.1 Typological species concepts

The traditional typological view defines species by its essence, or necessary and sufficient conditions or traits. This finds a straightforward expression as a biconditional form  $\forall x(Sx \leftrightarrow T_1x \wedge T_2x \wedge \dots)$ . The extension of species  $S$  that satisfies this formula then is the intersection  $\bigcap_i \mathbf{T}_i$  (see Figure 1(a)).

Though crude as it is, the biconditional formulation allows certain inferences from traits to species and vice versa. It is this kind of logical reasoning that has enabled, for example, the famous French zoologist George Cuvier to reconstruct the anatomy of a whole organism from just a single piece of bone. As is well known, however, such inferences have very restricted validity, because in most cases it is impossible to find a definite set of phenotypic or genetic characteristics that exclusively defines a given species. Evolution implies species boundaries to be necessarily “fuzzy,” which undermines simple biconditional forms. The typological species concept has thus been criticized for its lack of expression ability: a simple algebra of trait-sets cannot capture the nuanced reality of biological species.

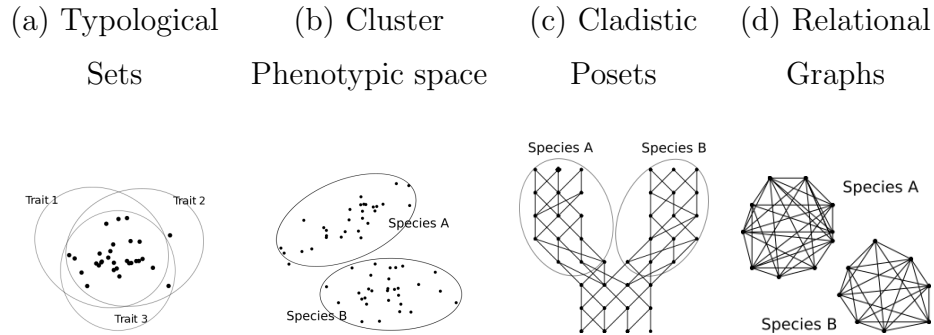


Figure 1: Illustrations of models of various species concepts, with corresponding formal setups. In each model dots/nodes represent individuals. See text for explanation.

## 2.2 Cluster species concepts

The cluster species concepts avoid this difficulty by defining a species as a group or cluster of similar organisms that do not necessarily share a common set of traits. The question then is how to define similarity. Its earliest variant, the phenetic species concept, represents organisms in a multi-dimensional space each axis of which defines a recorded trait (Sokal and Sneath 1963). Phenotypic similarity is then measured by the euclidean distance between two points/organisms, and a chunk or cluster of organisms in this euclidean space is identified as a species (Figure 1(b)). The choice of euclidean distance is not obligatory. One could, for example, measure similarity by the cosine between two points in the normalized phenotypic space, in which case the similarity amounts to correlation, with a species being identified as a correlated cluster or more generally a *probability distribution* over the phenotypic space (Boyd 1999).

The phenotypic space with a certain metric or probability distribution is certainly a much richer machinery than overlapping sets and allows for more nuanced expressions and inferences. The sophisticated theoretical background (euclidean geometry or

probability theory) enables one to measure the similarity among organisms and to make a trait-species inference in the absence of necessarily or sufficient criteria. To what extent such clustering and inference reflect objective species boundaries, however, was disputed, for the similarity calculation depends much on which phenotypic characters are taken into account. It should also be noted that, like the typological concept, the cluster concepts are purely static and lack a means to express the evolutionary past, the point often criticized by more historical approaches to species.

### 2.3 Cladistic species concepts

The cladistic species concepts focus on evolutionary history and define species solely in terms of phylogenetic relationships, as a “branch” (monophyletic group) in the evolutionary tree (Hennig 1966). Since ancestral relationship is antisymmetric and transitive, phylogeny forms a (strict) *partially ordered set* or *poset*  $(\Omega, \prec)$ , with  $\Omega$  corresponding to a set of organism and  $\prec$  meaning “is an ancestor of.” A cladistic species is then defined as descendants from some founder organism(s)  $\omega_f$ :

$$\{\omega \in \Omega : \omega_f \prec \omega\}. \tag{1}$$

An obvious advantage of the cladistic concepts is that it is faithful to the fact of evolution, and for this reason it has been most well received by biologists and philosophers alike. It is not, however, without flaws. For one, although the requirement of monophyly specifies a necessary condition, it is silent as to how big a branch must be to qualify as a species (for even a small family can satisfy (1)), and so far no satisfactory sufficient condition was given (Velasco 2008). The monophyly requirement has also been

criticized to be too strong, for it would count birds as reptiles because the smallest monophyletic group including lizards, snakes, and crocodiles also includes birds. That is, the cladistic species concepts make paraphyletic groups like reptilia *meaningless* (*Sensu* Narens 2007), which strikes some to be too high a price to pay.

## 2.4 Relational species concepts

Another popular approach is to define a species as a group of individuals in a certain relationship to each other. The biological species concept, for instance, defines species as “groups of interbreeding populations that are reproductively isolated from other such groups (Mayr 1942)” so that the required relationship here is mutual crossability. Other variants focus on reproductive competition (Ghiselin 1974) or organisms’ capacity to recognize each other as a possible mate (Paterson 1985). All these proposals try to reduce species into mutual relationships (interbreeding, competition, recognition, etc.) between a pair of organisms. If we represent such relationships by an edge between nodes/organisms, a relational species can be defined as an isolated complete subgraph or *clique* in an undirected graph, that is, a group of nodes in which every two distinct nodes are connected but none is connected to outside (Figure 1(d)). Relational species thus find their model in graph theory, where edges represent the relation in question.

A common criticism of relational species concepts is that the focal relationship such as crossability sometimes fails to induce isolated cliques because some organisms at a species boundary can often mate with organisms that are thought to belong another species (e.g. ring species). Moreover, the biological species concept has been criticized to imply every asexually reproducing organism forms a distinct species (for any singleton

node is complete). These criticisms suggest that the real biological network is so “messy” that just a single relationship cannot divide it into distinct cliques in a non-trivial way.

## 2.5 “Combo” solutions

The model-theoretic rendering makes explicit what each species concept can and cannot meaningfully say about the biological world. Given that most of the criticisms we have seen concern the “cannot say” part, one way to deal with these difficulties is to combine different theories to obtain more complex definitions of species.

For instance, one may combine the cluster and cladistic species concepts and define a species as a *lineage that shares the same or similar phenotypic distribution*:

$$\{\omega \in \Omega : \omega_f \prec \omega \wedge \theta(\omega_f) = \theta(\omega)\} \quad (2)$$

where  $\theta : \Omega \rightarrow \mathbb{R}^n$  assigns distribution parameters to each organism  $\omega \in \Omega$ .<sup>1</sup> On this definition one may meaningfully define paraphyletic species and distinguish birds from other reptiles on the basis of the difference in their phenotypic or genetic profiles. It can also account for anagenesis (speciation without branching) and continuity of species between a cladogenesis (splitting event).

If one replaces  $\theta$  in (2) with a different function  $\nu : \Omega \rightarrow N$  that maps organisms  $\omega \in \Omega$  to their *niche*  $\nu(\omega) \in N$ , it becomes the *ecological species concept* which defines a species as “a lineage ... which occupies an adaptive zone minimally different from that of

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<sup>1</sup>For non-parametric cases, we can set  $\theta : \Omega \rightarrow \mathbb{R}^\infty$  and modify the definition as  $\{\omega \in \Omega : \omega_f \prec \omega \wedge D(\theta(\omega_f), \theta(\omega)) < k\}$  where  $D(\bullet)$  is a divergence measure (such as the Kullback-Leibler divergence) and  $k$  is a constant.

any other lineage in its range (Van Valen 1976, 233).”

Yet another combination is that of the cladistic and biological species concepts, which would define a species as a maximum monophyletic lineage that can mutually interbreed, so that

$$\{\omega_x, \omega_y \in \Omega : \omega_f \prec \omega_x \wedge \omega_f \prec \omega_y \wedge \omega_x \sim \omega_y\} \quad (3)$$

where  $\sim$  stands for crossability.<sup>2</sup> This will make up for the lack of a sufficient condition in the cladistic species concept, and accord well with the so-called *evolutionary species concept* which emphasizes the unique “evolutionary tendencies and historical fate” of each species (Wiley 1978, 17). It should be noted that this could also avoid the problem of ring species because two crossable organisms may not necessarily share the same ancestor.

## 2.6 The scientific species problem as a problem of theory choice

The above discussion shows that (i) major species concepts can be defined as models of formal theories, and that (ii) more complex concepts can be obtained by combining basic ones. The model-theoretic approach characterizes each species concept with the formal apparatus it assumes, which in turn determines its expressive power or what can meaningfully be stated about organisms and/or their history (Narens 2007). In general, a richer theoretical apparatus allows for more nuanced expressions, which makes it less liable to counterexamples. This is illustrated in the progression from the typological to

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<sup>2</sup>As in the case of the biological species concept, the crossability here must take into account the existence of two sexes.



cluster and then to cluster-cladistic concepts, where in each step the species concept acquires the ability to deal with fuzzy boundaries and evolutionary history, respectively.

It does not necessarily follow, however, that a richer concept is always desirable, because it tends to have a greater degree of freedom and requires more data in actual application. While only phylogenetic information suffices to demarcate cladistic species, the cluster-cladistic concept also requires phenotypic or ecological information, which in many cases may not be available. A stronger semantic power thus comes with a higher epistemic cost, as is often emphasized by pheneticists or cladists in their respective advocacy of the phenotypic cluster and cladistic species concepts.

This suggests that the competition among various species concepts should be understood as a problem of model selection, where different models are evaluated on the basis of their explanatory or descriptive power versus parsimony or operationality (Sober 2008). Indeed, most disputes among advocates of different species concepts arise from their differential emphasis on what aspects of the biological world a desirable species concept needs and needs not take into account (Ereshefsky 2001), but the difficulty is that these emphases are often implicit and incommensurable. Although the model-theoretic approach does not arbitrate these debates, it provides a common formal framework that makes explicit the explanatory power and operationality of species concepts and facilitates evaluation of their respective advantage.

## 3 Philosophical implications

### 3.1 Species are models

Upon the model-theoretic reconstruction of various species concepts, we now turn to the philosophical thesis that species taxa should be construed as models proposed above, i.e., as set-theoretic entities. To proceed, let me first begin with an analogy from classical mechanics. Classical mechanics is a theory about Newtonian particles, which are customary defined as volumeless points or vectors in a three-dimensional Euclidean space. Newton’s celebrated laws like  $\mathbf{F} = m\mathbf{a}$  describe temporal evolution of a system composed of such “particles.” This system is to be distinguished from any actual physical systems, say the solar system, for one thing, no concrete bodies are volumeless, nor do they indefinitely continue rectilinear motion as prescribed by Newton’s first law. Newton’s theory, or any other physical theories for that matter, is a description of idealized and abstracted models and not of actual phenomena (Cartwright 1983). That is, models of classical mechanics — which make its laws and statements true — are not concrete, physical entities, but rather abstract mathematical objects that can be constructed within set theory (McKinsey et al. 1953).

The role of models in science has been emphasized by the so-called semantic or model-based view of scientific theories (e.g. van Fraassen 1980; Suppe 1989).<sup>3</sup> In the traditional, logical-positivist view, a scientific theory was supposed to directly describe

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<sup>3</sup>This label (“the semantic view”) has been used to describe different, and logically independent, theses. In particular, while some philosophers (e.g. Suppes 2002) take a scientific theory as a *description* of models, others *identify* it with a set of models (van Fraassen 1980). In this paper I adopt the former thesis without committing to the latter.

observed data. This has set for positivists the difficult task of reducing theoretical concepts that seemingly lack direct empirical contents to observation vocabulary by way of *bridge laws* or *partial interpretations*. To avoid this difficulty, proponents of the model-based view take a model, rather than observation, as the primary descriptive target of a scientific theory. In this view, a theory specifies an abstract model that idealizes and extracts just salient factors, and only indirectly relates to actual phenomena via such an model.

I submit that the species problem is a variant of the positivist conundrum. Species is a highly theoretical concept, and various proposal of “species concepts” in the past can be understood as attempts to build bridge laws for reducing it to a set of observational or operational criteria. To date more than a dozen of different concepts have been proposed<sup>4</sup>, with no general consensus — each has its own strength, but also weakness and exceptions when applied to the rich and heterogeneous biological world. The assumption has been that a species concept must be a faithful description of *actual* biological features or phenomena. But what if this assumption is untenable, or at least unreasonable? The model-based view has been quite popular among philosophers of biology (e.g. Beatty 1981; Lloyd 1988). If we adopt this view and construe evolutionary theory as describing models, then species too must be defined accordingly, i.e., as (a part of) abstract models that satisfy descriptions and/or inferences of the corresponding theory.

What, then, are theories about species? Without claiming to be exhaustive, this paper adopts Suppes’s (2002) thesis that a scientific theory must be defined as a set-theoretical predicate. The foremost advantage of this approach is that it enables one

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<sup>4</sup>Mayden (1997), for example, counts at least 22 concepts of species.

to easily harness a theory with mathematical apparatus necessary for sophisticated reasoning. As discussed above, contemporary studies on species rely heavily on quantitative methods to calculate similarity or reconstruct a phylogenetic tree from phenotypic or genetic data. Given that such mathematical reasoning requires matching formal models of calculus or probability theory, the straightforward way to define a species is to build it upon these mathematical backgrounds as an extension of these formal models. Section 2 is a preliminary sketch of applying this Suppesian program to various species concepts. If this attempt turns out to be successful, biological species are to be understood as parts of set-theoretic structures, just like Newtonian particles. That is, they are mathematical and abstract constructs, rather than physical or biological entities.<sup>5</sup>

The purpose of the set-theoretic exposition is not just to accommodate quantitative reasoning. Even with less quantitative cases like the biological species concept, it makes implicit assumptions explicit and suggests a way to deal with counterexamples. The problem of ring species, for example, arises from a conflict between the presumption that each biological species must be isolated and the fact that crossability is not necessarily transitive and thus fails to induce equivalence classes. One possible response to this charge then would be to weaken the former assumption and redefine a species just as a (not necessarily isolated) clique in the reproductive network. Clarification of theoretical assumptions helps us to assess other species concepts as well. For example, the phenetic species concept is often claimed to be “theory-free” in that it does not depend on any evolutionary hypothesis. But as we have seen in Sec. 2.2, the calculation of phenotypic

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<sup>5</sup>Hence the present thesis should not be confused with the view that species are sets or collections of *organisms* (Kitcher 1984), which, after all, are concrete biological entities.

similarity presupposes a phenotypic space equipped with a particular (e.g., euclidean) metric, which is a fairly strong theoretical assumption. Also, cladists often stress the simplicity and purity of their monophyletic species definition that only considers phylogenetic relationships. But in order to make use of likelihood methods to infer such relationships, as is common in practice, a simple poset is not enough: one also needs to assume some genetic or phenotypic distribution, and then there is no in-principle reason to exclude non-monophyletic taxa from the definition of species (as (2) in Sec. 2.5).

The final but not least merit of the set-theoretic approach is its flexibility: it allows for a construction of a new species concept by combining existing ones (Sec. 2.5) or adding new theoretical assumptions. For instance, it is common in experimental biology to characterize a species by shared developmental or causal mechanisms: developmental biologists often talk about “the development of the chicken” and medical doctors rely on causal extrapolation when they prescribe a clinically-tested drug for their patient. Such a “causal species” may be defined by isomorphic *causal models*, which combine a probabilistic distribution and a causal graph over variables. Hence the discussion in Section 2 covers just a few samples that can be constructed within this general framework. This does not of course mean that every possible species concept can and must be formalized, but does suggest the potential of the set-theoretic approach to accommodate the use of existing species concepts and to develop novel ones.

## 3.2 Philosophical implications

Identifying species with theoretical models sheds new light on some vexed philosophical issues, one amongst which concerns how individual organisms are related to species taxa.

Philosophers have long debated whether the organism-species relationship is instantial (organisms are particular *instances* of a species *qua* class), membership (they are *members* of a species *qua* set; Kitcher 1984), or mereological (they are *parts* of a species *qua* genealogical entity; Ghiselin 1997). The model-theoretic approach suggests an alternative account, according to which a species *represents* (a group of) individual organisms. Just as the Rutherford-Bohr model represents the microscopic structure of atoms, models proposed in Section 2 represent biological populations: for example, nodes and edges consisting of the biological species model in Figure 1(d) respectively represent organisms and crossability. Representation captures our intuitive notion that a model and its target phenomenon share salient static or dynamic features up to a certain precision. Given that said, it must be admitted that the criteria and nature of scientific representation are diversified and still open questions (Frigg and Nguyen 2016). Hence calling the species-organism relationship representational does not necessarily demystify it, but at least implies that the problem is not endemic to evolutionary theory: it is rather a version of a broader philosophical issue as to how the use of scientific models help us understanding the world. This means that the arsenal of this rich philosophical literature can and should be consulted to elucidate the nature of the species-organism relationship. Another, more immediate implication is that the membership and mereological accounts must be both abandoned, for whatever the relationship between a model and phenomena turns out to be, the latter must certainly not be a member or part of the former.

Neither is representation identity or instantiation. Ideal gas is not identical to any actual gas, but only approximates thermodynamic characteristics of some. Hence strictly speaking it has no instantiation, but this does not detract its epistemic validity. Likewise

species concepts, as specifications of ideal models, need not directly apply to actual populations. No wild population big enough to qualify as a species would strictly satisfy the requirement of the biological species concept, because actual mating chance is often hindered by physiological, geographical, and other contingencies. In the same vein, a phenetic or genetic cluster is expected to have outliers when applied to a real population. However, the presence of such exceptions should not immediately invalidate the corresponding species concepts, because the value of a species concept consists less in its universal validity than its epistemic serviceability for inferences and explanations of evolutionary or biological phenomena. These two criteria often conflict: Cartwright (1983) even argues that explanatory theories necessarily distort the reality by idealizing the situation and extracting only relevant features, so that properly speaking they are “lies” by design. Cartwright’s examples are physics and economics, but her idea also applies to the present context. The primary function of a species concept is to explain biological phenomena rather than to save them, so that a few discrepancies should not be taken as a falsification.

The conflict between exceptionlessness versus explanatory power also underlies the realism-nominalism debate over species. The proponents of the nominalistic thesis who claim a species to be nothing but a totality of individual organisms have motivated their view by criticizing the realist interpretation of species-as-class for its commitment to the typological thinking and failure to deal with the evident heterogeneity of biological phenomena (e.g. Ghiselin 1997). On the other hand, those who attach weight on the role of species concept in induction and explanation have upheld a realist position and treated species as natural kinds (Boyd 1999). The present thesis offers a third alternative, recognizing the explanatory role of species concept without committing to

the ontologically heavy assumption of natural kinds. As we have seen in Section 2, species as models licence particular sets of inferences. The cluster and typological species/models underpin an expectation that physiological or genetic features found in, say, laboratory animals would also be shared by other individuals of the same species, while the evolutionary species concept explains the reason of such intra-specific similarities. These explanations are effectuated by the same model representing numerically distinct individuals or phenomena to be explained. Note that this procedure no more presupposes the existence of the model as an independent, real entity, than do explanations based on, say, ideal gas. Indeed, explanations may be based on fictional models, as is the case with the Ising model in statistical mechanics.

This does not of course mean that models *must be* fictions, or that species do not exist. Recent advocates of scientific realism argue that successful scientific models capture some, especially structural, aspect of reality (Ladyman 2016). Given its affinity to the model-based view of scientific theories, species realists may well apply this line of reasoning to the present context, taking the set-theoretic structures as discussed in Section 2 as representing the reality or “essential feature” of biological species. Whether and to what extent such an argument carry over, however, remain to be examined by a further study.

## 4 Conclusion

The past debates over biological species have been based on the assumption that species concepts must describe actual biological phenomena, the strict adherence to which tends to rule out all but cladistic species as typological or inexact. The present paper



challenged this assumption and argued that the primary referent of a species concept is a (set-theoretic) model that licences a certain set of inferences specified by the concept. The model-theoretic rendering articulates explanatory power and theoretical assumptions of each species concept and illuminates logical relationships among them. Once species are specified as models, the long-standing competition among different species concepts reduces to a common problem of model selection. This suggests that evaluation of relative merits and demerits of species concepts must be based more on their explanatory power than on exceptionlessness.

On the philosophical side, the shift in the ontological status of species means that the organism-species relationship is not that of instantiation, membership, or mereology, but rather representation. The vexed issue that has troubled philosophers for decades, therefore, boils down to the broader problem as to how and why scientific models can be used to represent and explain the world. This suggests the possibility to apply the rich literature on scientific representation and realism to elucidate the epistemological and ontological nature of biological species.

In sum, the take home message of the present paper is that the species problem is not endemic to biology or evolutionary theory, but rather is a variant of general scientific and philosophical issues of model selection, scientific representation, and realism. The purpose of this paper was just to establish such a parallelism: determining its philosophical implications on specific debates such as realism or pluralism concerning biological species will be a task for future studies.

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