Modeling causal structures:
Volterra's struggle and Darwin's success

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July 9, 2012

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Abstract

The Lotka-Volterra predator-prey-model is a widely known example of model-based science. Here we reexamine Vito Volterra's and Umberto D'Ancona's original publications on the model, and in particular their methodological reflections. On this basis we develop several ideas pertaining to the philosophical debate on the scientific practice of modeling. First, we show that Volterra and D'Ancona chose modeling because the problem in hand could not be approached by more direct methods such as causal inference. This suggests a philosophically insightful motivation for choosing the strategy of modeling. Second, we show that the development of the model follows a trajectory from a "how possibly" to a "how actually" model. We discuss how and to what extent Volterra and D'Ancona were able to advance their model along that trajectory. It turns out they were unable to establish that their model was fully applicable to any system. Third, we consider another instance of model-based science: Darwin's model of the origin and distribution of coral atolls in the Pacific Ocean. Darwin argued more successfully that his model faithfully represents the causal structure of the target system, and hence that it is a "how actually" model.

1 Introduction

An ancient Greek fragment says that "the fox knows many things, but the hedgehog knows one big thing". When it comes to confirmation theory, philosophers of science have been persistently hedgehoggish. The goal has been to render all scientific methodology as variations on a single, deep methodological theme. Many candidates for such a unitary account exist: Among the more prominent are Hypothetico-deductivism, Falsificationism and, more recently, Bayesianism and Inference to the Best Explanation. But after decades of debate, there is no consensus view. Perhaps the problem is not that the one true and fully general theory of confirmation has yet to be formulated, but that the hedgehog's approach is ill-suited to the task.

Michael Weisberg (2007) recently suggested a more fox-like stance. It takes its cues from scientific practice, beginning with the analysis of historical case studies. The goal of this naturalistic, bottom-up approach is to split scientific methodology into several distinct practices, in the hope that something philosophically insightful can be said about each of them separately.[1]

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[1] Is it epistemologically significant whether our methodological studies proceed top-down or bottom-up? Perhaps not in principle, and certainly not if it turns out that all cases can be accommodated to a unitary account of confirmation. We would welcome such a result. However, if the

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Weisberg begins the project by identifying two modes of scientific theorizing: "abstract direct representation" (ADR) and modeling. The key distinction between them, as Weisberg sees it, is that ADR is a "direct" investigation of a phenomenon, while modeling is an "indirect" investigation. In ADR the scientist approaches a real-world phenomenon directly by focusing on only a few properties or relations of the phenomenon while ignoring others. Modeling, by contrast, begins with the construction of a model as a representation of aspects of the phenomenon. Much of the investigation is then concerned with the analysis of the model itself instead of the real-world phenomenon.

We agree with Weisberg that disciplined pluralism in reconstructing scientific methodology is a promising approach. However, we wish to improve on his chosen delineation between methods. By re-examining Weisberg's historical case studies, we will carve out a delineation between methods which improves on Weisberg's on two counts: historical adequacy (actual science should reflect the proposed delineation) and philosophical insight (it should become clear why a method is chosen in a given context and why we would expect the method to be truth-tropic).

We follow Weisberg in focusing on one particular aspect of the modeling debate: modeling as a distinctive scientific *practice*. We will not discuss the question of whether all scientific theories should be reconstructed (by philosophers) in terms of models, as proponents of the semantic view of theories would argue. We will also not enter into debates about the metaphysics of models, or other foundational questions concerning the nature of models. Moreover, much of our discussion will focus on models of *causal structures*, again guided by Weisberg's case studies. This excludes such prominent examples of models as the Watson-Crick-model of DNA, which represents the molecule's steric structure and not causal relationships. A unified account of model-based science may well identify many commonalities between these different types of models, but for now, in the interest of tractability, we keep them separate.

We will start by taking a closer look at the historical sources relating to one of Weisberg's main examples of model-based science, Vito Volterra's and Umberto D'Ancona's work on the fluctuations of adriatic fish populations. A close reading of the historical sources, especially of Volterra's and D'Ancona's own remarks on methodology, will suggest a delineation between two types of inquiry: Those in which causal inference is possible, and those in which it is not possible because a

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foxes prove to be right, then a top-down approach may impede progress by obscuring natural categories.

system offers insufficient epistemic access. We will argue that the latter situation makes intelligible a *motivation* for modeling causal structures.

The proposed distinction also provides us with a *goal* for this type of modeling. A model that somehow generates the required phenomenon satisfies only a necessary condition for successful modeling: The further goal is to determine whether the model faithfully represents the target system's actual causal structure (as it would be determined if direct causal investigation of the system were possible). We suggest that there is a vector in model development from models that merely produce the right output ("how possibly" models) to models that actually attain the goal of mirroring the causal structure of a target system ("how actually" models). The Volterra and D'Ancona case study illustrates this vector from "how possibly" to "how actually". It will turn out that Volterra and D'Ancona never fully succeeded in showing that theirs is a "how actually" model of any system.

Finally, we will present the case of Darwin on coral atolls as an example of a successful transition from a "how possibly" to a "how actually" model. Darwin faced a similar epistemic situation as Volterra and d'Ancona in that he was unable to investigate his system fully by causal inference. To overcome this limitation, he constructed a model based on known causal processes and argued for its adequacy by examining, among other things, the model's intermediate stages and its input-output-profile.

2   The predator-prey model

Weisberg's main example of modeling is Volterra's and D'Ancona's work on the dynamics of predator and prey fish species in the adriatic. An account of the story is given in his paper and in the historical literature.[2] Here we briefly review key facts, and in particular the relevant science.

Umberto D'Ancona was a marine biologist and Vito Volterra's son-in-law. As they tell the story, D'Ancona was surprised by fishery statistics from the first world war, which showed an increase in the proportion of predator species in the adriatic sea. For help in working out an explanation of the phenomenon, D'Ancona turned to Volterra, who held the Chair of Mathematical Physics at the University of Rome. The result of this joint research project was a system of coupled, nonlinear differ-

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[2]See Sharon Kingsland (1995) on the history of population ecology, and Judith R. Goodstein (2007) for a book-length biography of Volterra.

ential equations which we now know as the Lotka-Volterra-equations[3]:

$$\frac{dN_1}{dt} = (\epsilon_1 - \gamma_1 N_2)N_1 \tag{1}$$

$$\frac{dN_2}{dt} = (-\epsilon_2 + \gamma_2 N_1)N_2 \tag{2}$$

The system describes the evolution of two main variables over time: the size of a prey population (N_1) and the size of a predator population (N_2). Equation (1) states that the prey population has an intrinsic growth rate determined by a coefficient (ϵ_1), and that the prey are diminished in proportion to the number and voracity of predators in the area ($-\gamma_1 N_2$). Equation (2) states that predators have an intrinsic death rate ($-\epsilon_2$), and that the predator population grows depending on the number and defence capacities of prey ($\gamma_2 N_1$).

From this quantitative description of a predator-prey-system, Volterra was able to derive several results, which he presented in the form of three laws.[4] The first law states that the fluctuations of a predator-prey-system are periodic, with the periods depending on the values assigned to the coefficients. This represents one class of solutions to equations (1) and (2), an example of which is plotted in figure 1. The second law states that the average population sizes remain constant so long as the coefficients do not change. The third law states that the "protection" of both populations (i.e. decreased fishing) favors the predators. The third law explains D'Ancona's initial finding that prompted the investigation: an increase in the proportion of predators in the wartime fishery statistics.

In the following, we are concerned with the method that Volterra and D'Ancona adopted in their research. In the most complete presentation of their results, they devote a full (albeit brief) chapter to methodological reflections: Why is their approach appropriate, and what distinguishes it from other possible approaches? These reflections give us considerable insight into Volterra's and D'Ancona's reasons for choosing the modeling approach.

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[3]Alfred J. Lotka had worked on related problems and obtained similar results independently. We here use Volterra's formulation of the equations as given in Volterra (1928) and Volterra and D'Ancona (1935).

[4]The laws were initially put forward in *Nature* (Volterra, 1926, p. 558) and reappear in later publications (Volterra, 1928; Volterra and D'Ancona, 1935).
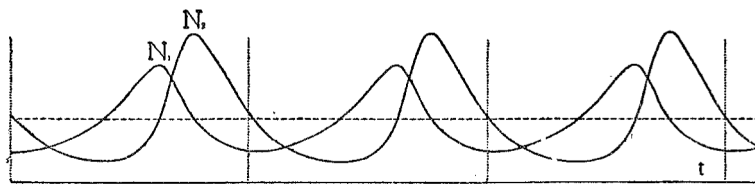
Fɪɢ. 7. — Fluctuations de deux espèces dont l'une dévore l'autre.

Figure 1. A figure from Volterra's and D'Ancona's *Les associations biologiques au point de vue mathematique* (1935, p. 28). The graph shows the oscillating population sizes of a predator-prey-system. This is one possible solution for the coupled, non-linear differential equations (1) and (2) if appropriate values are assigned to the coefficients (see page 5).

3 A motivation for modeling: Volterra and D'Ancona on method

In the first chapter of their joint *Les associations biologiques au point de vue math-ématique* (1935), Volterra and D'Ancona discuss which methods are suitable for quantitative studies in ecology. They consider several methods one by one, explaining why they are desirable, but not suitable for their purposes; then they give reasons for preferring their own (modeling) approach. We will now review this discussion in some detail.

The first case on which the authors focus is that of the physiologist, who performs experiments on individual animals under laboratory conditions. The advantage of this approach, which the authors call "the experimental method" (p. 6), is that it allows the scientist to perform controlled experiments: The role of putative causes can be established by varying them while keeping alternative causes under control. In the authors' words, one must isolate biological phenomena "from external causes which tend to act on their course and to disturb the results"[5]. Thus, the laboratory physiologist's approach may be characterized as causal inference by controlled experiments. However, Volterra and D'Ancona deem this approach unsuitable for studies in ecology, since ecologists, unlike physiologists, study interactions of entire populations and not of individual organisms.[6]

Second, one may transfer the method of causal inference to ecology by per-

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[5]"Mais dans le domaine de l'oecologie ces méthodes [the experimental methods] n'ont été jusqu'à présent que fort peu appliquées et cela s'explique, si l'on songe que les phénomènes biologiques ne sauraient devenir l'objet d'une étude quantitative qu'après avoir été isolés des causes extrinsèques susceptibles d'agir sur leur cours et d'en troubler les résultats" (Volterra and D'Ancona, 1935, p. 6).

[6]We are not denying the possibility of experimental ecology, which today is a rich discipline. We do, however, believe that Volterra and D'Ancona are pointing out real difficulties.

forming controlled breeding experiments on whole populations. Volterra and D'Ancona find breeding experiments problematic as well, however, mainly for two reasons:

1. Spatial and temporal extendedness: The experiment would have to be carried out in a space that is very large relative to the size of animals, and over a long time period relative to breeding cycles.

2. Environmental conditions such as temperature, humidity, and so on, would have to be controlled.

Consequently, only relatively small animals with short breeding cycles are viable for breeding experiments. This limits the scope of the method.

Third, if neither laboratory nor breeding studies are possible, Volterra and D'Ancona suggest the observation of populations in the wild with the aid of statistical methods. However, they believe that this approach, too, is ultimately unsuitable: In the short run, statistical data are unreliable because we have little control over interfering causes. Data collection over many generations would thus be required to cancel out these perturbing factors in the statistical mean. But this is unfeasible in practice, since few organisms would, in Volterra's and D'Ancona's judgment, warrant such intensive effort and use of resources.[7] Volterra and D'Ancona conclude that "the quantitative study of biological associations by means of observation and experience is a difficult matter".[8]

Having reached their verdict about the three methods considered so far, Volterra and D'Ancona suggest that a further option exists – a "deductive" approach. It is explicitly likened to the methods used in classical mechanics and corresponds largely to what we would call modeling. Volterra and D'Ancona write:

> Since it appears too difficult to carry through quantitative studies by experiments and thus to obtain the laws that regulate interspecific relationships, one could try to discover these same laws by means of deduction, and to see afterwards whether they entail results that are applicable to the cases presented by observation or experiment.[9]

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[7]The argument only says that it is too difficult to establish population dynamics in the wild by statistical methods. It does not speak against the use of descriptive statistics, such as the fishery statistics with which D'Ancona tests the applicability of the predator-prey-model.

[8]"[L]'étude quantitative, par voie d'observation et d'expérience, des associations biologiques est chose ardue" (Volterra and D'Ancona, 1935, p. 8).

[9]"D'ailleurs s'il apparait trop difficile d'effectuer l'étude quantitative par voie d'expérience et d'obtenir ainsi les lois qui règlent les rapports interspécifiques dans les associations biologiques, on

This is something less than an explicit user's manual for modeling. But the way Volterra and D'Ancona present their science in the rest of the book fills in at least some of the gaps. On this approach, we do not try to extract ecological laws directly form experimental data or observation (as in the causal inference approach). Instead, we proceed on a constructive path: We begin with hypotheses about basic causal relationships and integrate them into a system of interactions. Then we check whether the constructed system, the model, is applicable to the target system.

To summarize, Volterra and D'Ancona offer an explicit argument for choosing a model-based approach. Their first choice would be to investigate the various factors that determine population fluctuations by causal inference. However, as we have seen, the animals they wish to study are either too large, or their breeding cycles are too slow, or their spatial distribution is too broad, and so on, for the experimental method to be practicable. We suggest that all of these problems can be summarized under the heading of insufficient *epistemic access* to the target system. Thus, Volterra's and D'Ancona's motivation for modeling causal structures is insufficient epistemic access to the target system, which prevents them from approaching the problem straightforwardly through causal inference.

Before we proceed with a discussion of the criteria by which models of causal structures are judged, there are two points to address. First, one might object that the distinction we have outlined strays far from Weisberg's original project of identifying different *modes of theorizing*. No doubt causal inference and modeling are different *practices*, but are they both *theoretical*? We think they are. On the account we are developing, theoretical knowledge frequently takes the form of knowledge about causal structures. Any method by which we gain causal knowledge is in this sense theoretical, be it a method of experimental causal inference, a modeling approach, or something else. In general, we think it is a secondary matter whether the method in question is experimental or not.

Second, to say we have *limited* epistemic access is not to say that we have *no* epistemic access to a target system: Of course, we must be able to observe aspects of a system in order to model it successfully. For instance, we may be able to investigate some of the causal processes underlying the phenomenon, even if we cannot fully assess their interaction without modeling. We will have more to say about how this works in the case of Darwin's explanation of the origin of coral

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pourra tenter de découvrir ces mêmes lois par voie déductive et de voir ensuite si elles comportent des résultat applicables aux cas que présente l'observation ou l'expérience" (Volterra and D'Ancona, 1935, p. 8).

atolls in section 5.

4 The trajectory of a "how possibly" model: Volterra and D'Ancona on population dynamics

Having established a motivation for modeling, what is its goal? The method-ological discussion suggests an answer to this question as well. If Volterra and D'Ancona had more epistemic access to the system, they would establish the sys-tem's causal structure by causal inference. Since this path is closed to them, they employ what they call a "deductive method", or what we would call modeling. They begin with a small number of causal relationships and integrate them into a system of interactions. If successful, they then proceed on this constructive path by expanding their model by additional interactions. The endpoint of the process is a structure of causal interactions that determines population sizes over time. Ideally, this is *the same structure* that the experimental method *would* have generated if it *were* applicable. A faithful representation of the causal structure of the target system is thus a natural goal for this type of modeling.

In the present section, we will discuss three points related to achieving that goal. First, we will discuss generally the criteria for a causal model's adequacy: A model may merely save the target system's phenomena, or it may mirror its actual causal structure. Second, we will take a look at how successful Volterra's and D'Ancona's were in showing that their model is applicable to real-world systems. Third, we will discuss briefly how the applicability of the predator-prey model is assessed today.

Weisberg introduces a useful distinction between a model's "dynamical fi-delity" and its "representational fidelity".[10] When we judge a model's dynami-cal fidelity, we ask whether the model generates the right kind of output. Thus, the question is solely whether the model makes the correct predictions or retrodictions. By contrast, when we judge a model's representational fidelity, we ask whether the model faithfully mirrors the actual causal structure of the target system. The ques-tion is whether the correct output is generated for the right reasons.

In the context of our present discussion, we speak of a "how possibly" model if we are dealing with a model of adequate dynamical fidelity but unknown or low representational fidelity. In other words, a model offers us a possible explanation

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[10]Weisberg (2007), p. 221.

of a phenomenon if it generates the right kind of output. We may be ignorant as to whether or not the right output is generated because the model mirrors the target system's causal structure. In some cases, we may even *know* that a model has low representational fidelity: This would not, however, diminish its status as a "how possibly" model, given adequate dynamical fidelity.[11] By contrast, we speak of a "how actually" model if we are dealing with a model of adequate dynamical fidelity *and* adequate representational fidelity – that is, when we are dealing with a model that generates the right kind of output *because* it mirrors the target system's causal structure. We will have more to say about how we can assess a model's representational fidelity later in this section and especially in section 5.[12]

The trajectory from a "how possibly" model to a "how actually" model seems to be a natural progression for model-building science, which the case of Volterra and D'Ancona illustrates in several ways. In their *Associations biologiques*, Volterra and D'Ancona begin with a chapter on the dynamics of a single species; to this, they then add a second species, so as to show that this is enough to obtain oscillations in population size. At this stage, their model has a strong "how possibly" character: How can oscillations in population size occur without an external cause, such as the passing of the seasons, to drive them?

One way in which Volterra and D'Ancona tried to improve representational fidelity was by adding complexity, or removing known idealizations. From two species they advance to three. Then they consider the possibility that coefficients of their equations, such as growth rate, depend on population density. Next, they introduce what they call "hereditary" effects, by which they mean time-delayed influences of the system at t_1 on the system at t_2. Finally, they introduce age-structure into their model. At the end point of this development, the model would tell us "how actually" population sizes are determined. (Of course, adding complexity does not in itself guarantee representational fidelity – this must be assessed separately.)

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[11]We will argue below that Volterra's model could not be successfully shown to be "actual", but that it retained value on a "how possibly" basis. Some might argue that Volterra's model was not even dynamically adequate. However, it did have many attractive properties such as the "third law" (also known as the Volterra principle) and endogenous oscillations in population sizes. These properties certainly justified that the model was assumed to be a candidate for dynamical adequacy.

[12]The terms "how possibly" and "how actually" have been part of the philosophical discussion for some time in the context of explanations. The distinction has been used in the philosophy of evolutionary biology since at least Brandon (1990), and more recently an analogous distinction was proposed in the philosophy of mechanisms by Machamer et al. (2000). Here we speak of "how possibly" and "how actually" *models*. We think that models are used to give explanations, so the two notions are closely related but distinct.

The shift from a focus on dynamical fidelity and "how possibly" considerations to representational fidelity and "how actually" considerations is also evident when we consider Volterra's earliest publications of his work, as well as its reception.

In his early paper in *Nature*, Volterra claims that the only way to assess his model was through its dynamical fidelity. His third law (see section 2) states that a protection of both populations, for example in the form of decreased fishing, will lead to a relative increase in the proportion of predators. Volterra believes this to be the most interesting of the laws "because it affords the best actual verification so far found of the theory". He continues:

> For Dr. U. d'Ancona, comparing fishery statistics in the Adriatic Sea before the War, during the War (when fishing almost ceased), and after fishing was resumed at the end of the War, has ascertained that the voracious species (selachians), which feed on other fishes, had increased during the War as compared with the preceding and following periods, while the contrary had been the case for the number of individuals of the eaten species.[13]

Initially, this finding is all that Volterra has to offer by way of empirical support for the model. However, at least one of Volterra's critics did not accept that such a dynamical success is sufficient to establish the model's value. In a critical note in *Biometrika*, E. S. Pearson discusses Volterra's early publications of his model. Much of Pearson's critique concerns the adequacy of D'Ancona's fishery statistics. But he also notes that it is doubtful whether the type of statistics provided by D'Ancona could serve as much of a confirmation of the model – even if much more detailed fishery statistics were available. He suspects that a number of alternative causal pathways might account for D'Ancona's findings: for example, changes in fishing methods, perhaps occasioned by the war, or simply the migration of the fish. Pearson ends on a cautious note:

> For the moment the theoretical results can hardly be advanced further without some check from the observational side which will test the reality of the simplifications and assumptions involved.[14]

We interpret "the reality of the [...] assumptions involved" to be a reference to the representational fidelity of the model. And as Pearson rightly notes, the question

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[13]Volterra (1926), p. 559.
[14]Pearson (1927), p. 222.

of representational fidelity could not be settled by the type of successful prediction which Volterra and D'Ancona initially offered as the best evidence in favor of their model.

In their 1935 publication, Volterra and D'Ancona do seem to care more about representational fidelity than before. One indication of this is again their methodological discussion, in which they caution against using the "deductive method" without taking care to stay close to empirical facts:

> Doubtless [the deductive method] has to be carried out with extreme caution because, from a mathematical point of view, we can only construct a series of theorems that, while perfect in their deduction, could be based on speculative presuppositions too far removed from reality. To prevent this danger, one has to choose as a starting point premises based on experience as much as possible; and furthermore it is necessary that in the course of developing the theory, the results, once obtained, be confronted with experience in order to verify their truth, or at least their verisimilitude.[15]

We have here a methodological prescription to ensure representational fidelity: The modeler is to start with premises "based on experience as much as possible" and to remain true to this ideal as the model is expanded.

It may be that Volterra and D'Ancona did not previously comment on methodology because space was limited; but considering that one of Volterra's first publications is over 80 pages in length (Volterra, 1928), we rather doubt this. More likely, Volterra and D'Ancona did not see a need to expand on methodology until they were confronted with criticisms such as Pearson's.

Volterra and D'Ancona tried to find systems whose causal structure corresponds to their model. Perhaps because of this, they also shifted their focus away from Volterra's "third law" and toward oscillations in population sizes as the main explanandum of their theory, for which more empirical support could be obtained.

The twelfth chapter of Volterra's and D'Ancona's *Associations biologiques* is devoted to empirical tests of the theory. Much of the discussion is again taken up

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[15]"Sans doute faut-il procéder dans cette voie avec une extrême prudence car, du point de vue mathématique, on ne peut que construire une série de théorèmes qui, tout en étant parfaits dans leur déduction, pourraient être fondés sur des présuppositions hypothétiques qui s'éloignent trop de la réalité. Pour éviter ce danger il faut prendre pour point de départ des prémisses appuyées le plus possible sur l'expérience; et il faut encore qu'au cours de développement de la théorie, les résultats, chaque fois obtenus, soient confrontés avec les indications de l'expérience pour vérifier leur conformité ou du moins leur vraisemblance" (Volterra and D'Ancona, 1935, p. 8).

by a defense against critics, especially concerning the value of D'Ancona's fishery statistics. Soon, however, the authors turn their attention to experimental work relevant to their theory. They especially rely on experiments by G. F. Gause, whose early work was in part an attempt to put Volterra's mathematics to experimental test.

Gause (1910–1986) was a Russian biologist who worked especially in quantitative and experimental ecology and microbiology. By choosing appropriate microorganisms, he was able to investigate specific scenarios envisioned by Volterra and D'Ancona, such as competition between two species for a shared resource and dynamics between predators and prey.

In effect, Gause was able to overcome the epistemic limitations that motivated Volterra and D'Ancona's modeling work: His microbiological setup allowed him to study interspecific relations in the laboratory, with organisms whose generation time was short. In discussing these experiments last, Volterra and D'Ancona go full-circle: They return to the kind of evidence which, in their methodological discussion, they considered to be the most desirable. Gause's system permitted the study of the components of the model separately: Both the growth rate of the prey in isolation and the destruction of prey by predators could be investigated quantitatively. Moreover, it could be investigated whether the *interaction* of those processes leads to the kinds of oscillations described by the theory. In a system amenable to direct causal investigation, both the dynamical and the representational fidelity of Volterra's and D'Ancona's model could be assessed. So the microbiological system had the potential to be a target system for which the predator-prey model could be shown to be representationally faithful.

Unfortunately, Gause did not succeed in creating a system to which Volterra's and D'Ancona's model is clearly applicable.[16] For the most part, oscillations of the sort envisaged by the model only occurred under narrow experimental conditions. In some cases, oscillations were produced, but were the result of rather different causal processes than those of the model. For example, if the prey could hide from the predators, this allowed them to repopulate the culture after they had been mostly destroyed by the predators.[17]

Ultimately, Pearson's skepticism proved to be well-placed: Today, Volterra's

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[16]Even if Gause had been successful in showing that the microbial system is adequately represented by the Volterra model, the generalization to adriatic fish populations or any other system does not follow. It would still have been necessary to argue separately for each system that it instantiates the Volterra model (see the next section on Darwin's work on coral atolls).

[17]See especially p. 85–89 in Volterra and D'Ancona (1935).

and D'Ancona's model is judged to fall short of providing a "how actually" explanation for any system. For example, J. D. Murray, in his textbook of mathematical biology, discusses Volterra's model at length, noting as a particular mathematical weakness its structural instability: If the system is disturbed even slightly, it will not return to its previous trajectory and may exhibit very large oscillations indefinitely (this is also called "neutral stability").[18]

One of the major objections to the model concerns empirical data. Murray, like Pearson before, notes that dynamical fidelity is not enough, and that representational fidelity must be assessed separately:

> The moral of the story is that it is not enough simply to produce a model which exhibits oscillations but rather to provide a proper explanation of the phenomenon which can stand up to ecological and biological scrutiny.[19]

This does not mean, however, that the model is worthless merely because it is not a true representation of the target system. The Lotka-Volterra-model has heuristic value in that it can guide future research; but more than that, it has value as a "how possibly" explanation:

> The Lotka-Volterra model, unrealistic though it is, does show that simple predator-prey interactions can result in oscillatory behaviour of the populations.[20]

So the Lotka-Volterra-model may not be applicable to any actual populations. But a "how possibly" model still gives us factual insight: In this case, we learn that oscillations in population sizes can, in principle, emerge from nothing but the interaction between two species.

In the next section, we will take a close look at a second case study: Darwin's model of the origin of coral atolls. Again we will argue that this is best understood as an instance of modeling; but Darwin, unlike Volterra and D'Ancona, was successful in showing that the processes described by his model are not only possible, but actual.

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[18]Murray (1989), p. 65.
[19]Murray (1989), p. 68.
[20]Murray (1989), p. 70.

5 From "how possibly" to "how actually": Darwin on coral atolls

One of Weisberg's main examples of "abstract direct representation" (that is, of non-modeling science) is Charles Darwin's explanation of the origin and distribution of coral reefs and atolls in the pacific ocean. We now turn to a reconsideration of this case, for two reasons. First, we believe that Weisberg is mistaken in reconstructing the episode as something other than modeling. Second, we believe that Darwin's model, unlike that of Volterra and D'Ancona, can be successfully applied to its intended target system and so qualifies as a "how actually" model.

Darwin's first significant scientific contribution was an explanation of how coral reefs, barrier reefs and coral atolls are formed. The basics of his explanation are accepted to this day and are presented in textbooks of geology. Darwin's explanation assumes that the land masses in the pacific ocean subside gradually (today, this is explained by processes of plate tectonics). It further assumes that corals grow on solid ground and only at certain, relatively shallow depths of water. Thus, around a volcanic island, where the water is just the right depth, a fringe of corals grows. This explains how so-called "fringing reefs" come about ("that kind," writes Darwin, "which alone offers no difficulty in the explanation of its origin").[21] Darwin then goes on to explain more complex forms of coral atolls in terms of the gradual cumulation of small changes over long periods of time. Thus, as the island subsides, the fringing corals are submerged and die; but new corals grow on top of them. As more and more of the island is submerged, the distance between the fringe of corals and the remaining island increases. This then explains the existence of so-called "barrier reefs", free-standing corals at a certain distance from a land mass. This process goes on until all of the island is submerged, at which point only the latest growth of corals remains visible above sea level. These formations are coral atolls.

Weisberg argues that Darwin's investigation is not a case of model building because "at all times, Darwin was talking about the actual atolls in the Pacific" and there "was no analysis of a constructed model".[22] We think that this assessment is mistaken. The confusion may be due to the fact that Darwin's model has limited scope: It was only meant to be applied to coral atolls, and so, unsurprisingly, the theory only ever refers to coral atolls. Moreover, Darwin's model is qualitative in-

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[21] Darwin (1842), p. 99.
[22] Weisberg (2007), p. 228.

stead of mathematical. Nevertheless, Darwin's investigation has all the hallmarks of model-based science. One way to see this is to consider Darwin's epistemic situation. If Volterra and D'Ancona had applied their methodological considerations to Darwin's case, they would have concluded that modeling is indicated because we have limited epistemic access to the target system: The subsidence of islands and the growth of corals occur over hundreds of thousands of years, distributed over the entire pacific ocean, and so we can have no hope of directly investigating the process. Moreover, Darwin's arguments for the theory are of the sort we would expect if the goal is to move from a "how possibly" to a "how actually" model.

Consider the various claims that constitute Darwin's theory. The growth of corals can be approached directly by observation and experiment, but the subsidence of land is a fact that can only be indirectly ascertained (in Darwin's time, in any case). Even if we take these two core processes as given and accept that their interaction is a *possible* model of the origin of coral formations in the pacific, it must still be shown that the processes included in the model are *actually* responsible for the phenomena. This is the goal that eluded Volterra and D'Ancona.

We think Darwin's argument has three components. As in the case of Volterra and D'Ancona, the first component of Darwin's argument is to establish his theory as a viable "how possibly" model. He asks his readers to mentally simulate the process of coral atoll growth:

> Let us in imagination place within one of the subsiding areas, and island surrounded by a 'fringing reef,'–that kind, which alone offers no difficulty in the explanation of its origin.[23]

He then works through the process from fringing reefs to barrier reefs:

> Now, as the island sinks down, either a few feet at a time or quite insensibly, we may safely infer from what we know of the conditions favourable to the growth of corals, that the living masses bathed by the surf on the margin of the reef, will soon regain the surface. The water, however, will encroach, little by little, on the shore, the island becoming lower and smaller and the space between the edge of the reef and the beach proportionally broader.[24]

Step by step, Darwin's theory can render all the known forms of coral islands, arriving finally at atolls:

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[23]Darwin (1842), p. 99.
[24]Darwin (1842), p. 99.

Let the island continue subsiding, and the coral-reef will continue growing up on its own foundation, whilst the water gains inch by inch on the land, until the last and highest pinnacle is covered, and there remains a perfect atoll.[25]

The second part of Darwin's argument establishes that the causal processes he suggests – subsidence and coral growth – exist and operate as proposed. Thus, he devotes much of chapter four of his book to observations concerning the water depths and conditions favorable to coral growth, and he devotes many pages to evidence showing that the ongoing and gradual subsidence of land is likely.[26]

Finally, the third part of Darwin's argument shows that his model is not only viable on a "how possibly" basis because it is founded on known causal processes and saves the phenomena, but that it is an actual model of coral island formation in the pacific. This is where Darwin is more successful than Volterra and D'Ancona.

Darwin's task can be reformulated as follows. He already knows that his model has dynamical fidelity: It produces the right kind of output, which is to say, free-standing coral atolls in the middle of an ocean. What he needs to show is that the model also has representational fidelity: Are the proposed causal processes the *actual* processes responsible for coral atoll formation?

Darwin's approach to the problem is twofold. First, although he cannot observe the relevant causal process in action, he can get a kind of "sideways glance" at the process by looking at intermediate stages. It is relevant evidence for Darwin's proposed model that it is able to render, as intermediate stages, all the forms of coral islands that are found in the pacific: from fringing reefs to barrier reefs to atolls.

Notice how the analysis of the model *itself* plays a role in this procedure. The alignment of existing coral island formations with intermediate stages in Darwin's proposed model is not self-evident: The pacific coral islands do not conveniently present themselves in temporal order. The alignment only becomes meaningful in the context of the analysis of the proposed model "in imagination", as Darwin puts it.

Another argument along similar lines concerns breaches in coral reefs. Darwin argues that breaches in fringing reefs usually exist where fresh water rivers flow into the sea, since corals do not grow in fresh or turbulent water. He goes on to reason – and again, this is to some extent an investigation of the model itself – that

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[25]Darwin (1842), p. 101.
[26]Darwin (1842), p. 131–137.

we would expect the breaches to remain where they are, even after considerable further subsidence of the island, since in that area no basis of corals (on which further corals could grow) would ever have formed. He notes that in barrier-reefs "the broaches kept open by draining the tidal waters of the lagoon-channel, will generally [. . .] still face the mouths of the larger streams, although removed beyond the influence of their sediment and fresh-water;–and this, it has been shown, is commonly the case".[27] Again, the intermediate steps of the causal process described by the model can be coordinated with actual intermediates. Notice that Darwin distinguishes between a model-based prediction ("the broaches kept open [. . .] will generally still face") and its coordination with empirical facts ("and this [. . .] is commonly the case").

Darwin's second approach to the problem concerns the proposed model's input-output-profile. When we ask whether a "black boxed" process operates in a certain way, it is useful to give it varying inputs and to observe how those inputs are transformed. If we are not free to experiment, we can at least look for telling observations. This is precisely what Darwin does.

As a first example, Darwin argues that there is a striking correlation between areas of elevation, as identified by volcanic activity and other geological findings, and the absence of barrier reefs and atolls. In an area that is rising, Darwin's model predicts only fringing reefs; in areas that are sinking, Darwin's model also predicts barrier reefs, atolls and intermediate forms. So given one input – areas of elevation – we get a specified output A; given another input – areas of subsidence – we get a different specified output B.

The following is a second and even better example of this type of reasoning. Darwin notes that coral atolls would be expected to be like rough outlines of the islands, now submerged, on which they originally formed:

> [W]e might expect that these rings of coral-rock, like so many rude outline charts, would still retain some traces of the general form, or at least general range, of the land, round which they were first modeled.[28]

He goes on to note that known groups of atolls do in fact look like groups of islands, in at least two respects. First, groups of atolls generally share a geographical orientation among each other (for instance, a north-south orientation), much like groups of islands. Second, groups of atolls in a given geographic region tend to have the same overall orientation as groups of islands in the same region.

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[27]Darwin (1842), p. 100.
[28]Darwin (1842), p. 126.

In summary, we see Darwin's argument as based on three pillars: First, he argues for the adequacy of his proposed process on a "how possibly" basis. Second, he demonstrates that the causal processes his model presupposes operate in nature. Third, he advances evidence in support of the claim that the model faithfully represents the *actual* causal processes responsible for the growth of coral atolls. The evidence relevant to the third stage concerns the model's intermediate stages and its input-output-profile.[29]

We do not present Darwin's strategies as a generally applicable schema: It may well be that in other cases, the progress from a "how possibly" to a "how actually" model works differently. There may be many other criteria by which the adequacy of causal models is judged. Moreover, we do not claim that evidence such as Darwin presented is conclusive in the same way that causal inferences by controlled experiments can be conclusive. There is no epistemic magic in play. The Darwin example is supposed to illustrate some of the techniques that are available precisely when it is not possible to take the system apart, as it were, and investigate its causal workings experimentally.

We think that Darwin's approach illustrates at least the *need* for step three: Even if a model is robust in principle and relies only on known causal processes, one still needs to show that the model is *applicable* to the target system. Otherwise, it might well be that all the processes that Darwin's model assumes do in fact operate, but that for some reason they do not have much of a cumulative effect. This is essentially the same problem that Volterra and D'Ancona faced: There is no question that prey species have a growth rate and are eaten by predators; but it is a separate question whether these factors can possibly and do actually account for the determination of population sizes and oscillations.

6 Conclusions

We believe there is great promise in an approach to scientific epistemology which tries to split methodology into philosophically manageable subcategories. In the present paper, we have contributed to this project by considering one of the most widely known examples of model-based science, the Lotka-Volterra predator-prey

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[29]Our model-based reconstruction has many parallels to Darwin's own Herschelian philosophy of science (Hull, 2003, p. 175; Waters, 2003, p. 120). Herschel's view was that *verae causae* are demonstrated in three stages: A cause has to be shown to *exist*, to be adequate or *competent* to produce the effects it is supposed to explain, and to be *responsible* for particular instances of the effect. We think it is a virtue of our account that it accommodates the Herschelian strategy.

model. We have shown that Volterra and his collaborator D'Ancona distinguish between at least two approaches: causal inference by controlled experiment and what we call model-based science. Whether the one or the other approach is chosen largely depends on whether we have sufficient epistemic access to the system to investigate it by causal inference. This offers at least a preliminary answer to the outstanding question – which Weisberg (2007) raised in the conclusion to his paper – of when modeling is an advisable strategy.

We have further shown that the predator-prey model in Volterra's work follows a trajectory from "how possibly" (dynamical fidelity without representational fidelity) to "how actually" (dynamical *and* representational fidelity). However, Volterra and D'Ancona never managed to show that their model faithfully represents any system. We have therefore illustrated a more successful progression from "how possibly" to "how actually" with Darwin's model of the origin and distribution of coral atolls in the Pacific Ocean. Darwin was in a similar epistemic situation as Volterra and D'Ancona in that he could not directly investigate the interaction of the causal processes underlying the various forms of coral islands. But he was nevertheless able to support his causal model by considering its intermediate stages and its input-output profile.

Causal inference and modeling are two natural methodological categories in the sciences with potentially wide applicability. For instance, much (but not all) of molecular biology would probably fall into the category of causal inference, while much (but not all) of population ecology is probably best characterized as modeling. There is the open and intriguing question of how these approaches interact with each other. Moreover, we do not believe that we have offered a comprehensive taxonomy of scientific methodologies. Causal inference and model-based science are presumably just two rough subtypes, with others remaining to be delineated – and all of them remain imperfectly understood.

Acknowledgements

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