The Productive Tension:

Mechanisms vs. Templates in Modeling the Phenomena

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We argue that there is a tension present in the modeling practice between the aim of capturing the specific mechanisms underlying the phenomena and the use of general cross-disciplinary computational templates to study them. To illuminate this tension we examine the Lotka-Volterra model, which has provided a powerful template for population biology and other areas of research. We will compare the respective approaches of Alfred Lotka and Vito Volterra. What makes this comparison especially interesting is that although they ended up presenting models that from the formal point of view looked identical – and were subsequently treated like that – they nevertheless followed different kinds of modeling strategies.

> [T]he ability to support a tension that can occasionally
> become almost unbearable is one of the prime requisites
> for the best sort of scientific research.

Thomas Kuhn 1977, 226

1. Introduction

One characteristic feature of scientific modeling is the way modelers recycle equations, algorithms and other formalisms around different domains, in which process the formalisms obtain different interpretations depending on the domains they are applied to. Often these domains are situated far away from each other, with seemingly nothing in common between them. Although this feature of modeling has been frequently noticed by the philosophers of science, as yet it has not really been targeted by philosophical analysis. There may be several reasons for this neglect: It seems partly to be due to the representational approach to models which focuses on the relationship of a single model and its real world target system. Such a narrow unit of analysis looses the sight of the cross-disciplinary nature of modeling: theoretical and methodological dissemination between different disciplines happens frequently through modeling. On the other hand, although philosophers of science have discussed the importance of analogies, metaphors and off-the-shelf models in theoretical transfer, these topics have remained somewhat disparate in the absence of a common concept that would draw them together. What is needed, then, is a new unit of analysis that would simultaneously extend the traditional perspective and offer a concrete key to the interdisciplinary exchange of concepts and representational means characteristic of modeling.

It seems to us that the concept of computational template introduced by Paul Humphreys (2002, 2004) meets the bill. Computational templates are genuinely cross-disciplinary computational devices, such as functions, sets of equations, and computational methods, which can be applied to different problems in various domains. Examples of computational templates are for instance the Poisson distribution, the Ising model (Hughes 1999), and the Lotka-Volterra model and different agent-based models. As purely syntactic objects computational templates are interestingly double-faced. On the one hand, Humphreys claims that "syntax matters" meaning that the specific form of a mathematical representation is crucial for application (2004, 97, see also Vorms this volume). On the other hand he stresses that computational templates are results of complex processes of construction, which endow them with intended interpretation and initial justification that are not readable solely from the syntactic form.

Computational templates may have their origin in formal disciplines like the Poisson distribution in the probability theory or they may have been intended as theoretical models of a certain system and subsequently applied to different domains (like the Ising model and the Lotka-Volterra model). In this latter case, a theoretical template underlying a theoretical model becomes a genuine computational template first when it is separated from the original theoretical context and used to model other often different types of phenomena.[1] The main motivation for this transfer lies in the former successes and the tractability of the template: The distinguishing mark of computational templates is their tractability, theoretical templates need not be tractable. "The inability to draw out computational templates from theoretical templates", argues Humphreys, "underlies the enormous importance of a relatively small number of computational templates" (2004,

[1] A computational template that has its origin in a model of a certain system can eventually become a technique. Neural networks provide an example of subject matter independent computational templates that are used as techniques of data-analysis.

64; 68). Apart from tractability considerations Humphreys explains the versatility of computational templates by their generality, which he attributes to the fact that: "[…] templates [use] components that are highly general, such as conservation laws and mathematical approximations, and it would be a mistake to identify many of these components with a specific theory or subject matter" (2004, 90).

Computational templates usually occur embedded in *computational models*. Often theoretical or computational templates form a basis for a family of models taking into account different characteristics of the phenomenon of interest. A computational model, according to Humphreys, is a constellation on different components. Apart from the computational template, it consists of the construction assumptions that were used in arriving at the computational template, an initial justification of the template, a correction set, an interpretation and an output representation. The construction assumptions of the computational template consist of an ontology, idealizations, abstractions, constraints and approximations. An ontology specifies the kinds of objects referred to by a model. The correction set in turn is linked to the construction assumptions in that it relaxes some of the idealizations, abstractions, constraints and approximations made and thus determines, which parts of the model are intended to be interpreted realistically. Complemented with all these components, a computational template converts into a fully-fledged model.

Humphreys's emphasis on the role cross-disciplinary computational templates play in contemporary modeling practice resonates interestingly with the historian of science Giorgio Israel's (1993) views on mathematical modeling. He claims that in the twentieth century a new kind of idea on the relationship of mathematics to the reality was born. Whereas the classical reductionist approach relied on the "fundamental uniqueness of the mathematical representation" (472) the modeling approach makes use of the "*multiplicity* of representation" (473). The quest for general and unifying principles gave way to applying same abstract mathematical representations to multitude of domains. This modeling activity revolves around "formal structures capable of representing a large number of isomorphic phenomena" and used by way of mathematical analogy (478). Israel's formal structures, it seems to us, come close to Humphrey's templates.

The overall usability of computational templates is thus based on their tractability and generality that make them suitable for modeling different and heterogeneous phenomena showing some similarities under certain descriptions. But the question then arises whether the perceived similarities between different phenomena are really produced by the same kinds of mechanisms. We take it that a great deal of scientific modeling aims to study the mechanisms that produce natural and social phenomena. The goal is to learn about the "behavior of a system in terms of the functions performed by its parts and the interactions between these parts" as it has been put by Bechtel and Richardson (1993, 16). In the recent discussion on mechanisms several notions of mechanisms have been suggested, all of them geared towards capturing the characteristics of certain kinds of mechanisms (e.g. Machamer, Darden and Craver 2000, Glennan 2005, Bechtel and Abrahamsen 2005). What is common to these accounts is their focus on the causal productivity of mechanisms that is due to the component parts, their various operations, and their interaction. Mechanisms are seen as real entities, and any model trying to depict them should thus aim for specifying their key components, operations, and organization. But how apt are general computational templates in accomplishing this task?

Computational templates are usually applied to modeling certain phenomena if they succeed to exhibit some overall features of it. Yet the success of a computational template in this task does not guarantee that it has captured the specific mechanisms underlying the phenomenon. Quite the contrary, it is doubtful that the processes of (re)interpreting and correcting a general computational template can deliver a mathematical description of a specific mechanism decomposed into its components and operations. Consequently, there seems to be a tension inherent in the modeling practice that is due to scientists' aim to depict the basic mechanisms underlying some specific phenomena in a certain domain and the general cross-disciplinary templates used in this task. This tension, we suggest, is a central driving force of modeling practice, being productive in different ways. On the one hand modelers borrow from other disciplines computational templates, which often do not easily lend themselves to the description of the phenomenon of interest and may thus require adjustments on the theoretical level in form of, for example, conceptual changes. In this process the templates themselves are also molded to better suit the domain of interest, which gives often rise to a family of models often aiming at depicting their targets more realistically in detail. On the other hand, the interest in a certain phenomenon may lead to the construction of a new template as the available mathematical means turn out unsuitable or lacking. The Lotka-Volterra model is a case in point.

In the following we will illuminate the tension inherent in capturing the specific mechanisms by means of general cross-disciplinary templates through examining the Lotka-Volterra model both from the historical and philosophical perspective.[2] The Lotka-Volterra model, we suggest, displays this tension present in the modeling practice in two different levels. Firstly, the tension is reflected by the different modeling strategies of Lotka and Volterra. Secondly, it is also felt internally in their respective modeling endeavors, especially in the work of Volterra, who eventually accomplished something else than what he set out to do. While he aimed to isolate a mechanism, he created a template. We will also highlight how the tension arises partly from the conflict between the limited mathematical means available and the complexity of the real systems to be modeled. Finally, our analysis sheds new light on the notion of computational template by showing that its tractability may come in degrees and can be historically evolving, and on how complicated the process of transferring mathematical formalisms actually is. It typically includes the attempt to apply a certain *method of modeling* that has proven successful elsewhere with its characteristic *mathematical tools*, *problem solutions* and *associated concepts*. They are introduced by drawing analogies between the two domains, a procedure that Volterra utilized repeatedly in his theorizing. Lotka's template-oriented approach, on the other hand, pointed towards the emerging systems theory with its study of complex forms of interaction.

[2] Michael Weisberg has recently used the Lotka-Volterra model as an example of modeling (Weisberg 2007), that for the reasons of space we cannot deal with here. Weisberg suggests that models are indirect representations in the sense of describing hypothetical entities. While there is much to Weisberg's suggestion, it seems to us that his presentation of Volterra is somewhat too stylized in that he aimed to isolate a real mechanism, but had to resort to the method of hypothesis (see below).

2. Two different approaches to the design of the Lotka-Volterra model

The Lotka-Volterra model of predator-prey dynamics is a central model in population biology but it is also used outside of population biology in such areas as chemistry and social sciences (Epstein 1997). The model was independently introduced in the 1920's by Alfred Lotka and Vito Volterra. Few scientists at that time were aware of the different origins of the model because they mostly read Volterra's paper. Lotka's work was regarded as eclectic. Later on the model sparked a lot of discussion about the use of mathematical models in biology and had an impact on the development of alternative modeling approaches in population biology (see Levins 1966, Kingsland 1985). What makes the comparison of Volterra and Lotka especially interesting is that although they ended up in presenting a model that from the formal point of view looks the same – and was subsequently treated like that – they nevertheless followed different kinds of modeling strategies. Whereas Volterra attempted to isolate the essential or "sufficient" components of the predator-prey system and their interaction in "sea fisheries", Lotka started from a very general perspective and applied his model template both to the analysis of biological and chemical systems.

2.1. Volterra and the idea of an analytical biology

Vito Volterra (1860-1940) was a world-renowned and very influential Italian mathematician and theoretical physicist. One of his main interests was to bring mathematics into the field of biology and social sciences. He aimed to transform these fields into analytical sciences that make use of quantitative methods. An insight into this program is provided by his Inaugural Address delivered at the opening of the academic year at the University of Rome in 1901. The address was entitled *On the Attempts to Apply Mathematics to the Biological and Social Sciences* (Volterra 1901) but it shows that Volterra's program went beyond using mathematics merely as a tool in these fields. He wanted to "translate natural phenomena into arithmetical or geometrical language" and by doing so "open a new avenue for mathematics" and to transfer social sciences and biology into analytical sciences. This goal was:

> [...] to study the laws of the variation of measurable entities, to idealize these entities, to strip them of particular properties or attribute some property to them, to establish one or more elementary hypotheses that regulate their simultaneous and complex variation – all this marks the moment when we lay the foundation on which we can erect the entire analytical edifice (Volterra 1901, 250).

Thus measurable entities and empirical data provided the basis on which analytical biology and social sciences should be built. A further important ingredient in this transformation process was mechanics: biology and social sciences should be modeled on mechanics. For Volterra mechanics constituted "together with geometry, if not the most brilliant then surely the most dependable and secure body of knowledge" (ibid). What Volterra especially appreciated in mechanics was the practice of idealization and abstraction, which meant for him the identification of the essential components and interactions contributing to the observed phenomena and separating them from mere perturbations.

However, there seemed to be also something anachronistic about Volterra's endeavor as physics at the beginning of the 20th century was marked by debates concerning the failure of the mechanistic worldview. As regards this crisis Volterra wrote:

> [...] we have abandoned many illusions about giving a mechanical explanation of the universe. If we are no longer confident of explaining all physical phenomena by laws like that of universal gravitation, or by a single mechanism, we substitute mechanical models for those collapsed hopes-models that may not satisfy those who look for a new system of natural philosophy but do suffice for those who, more modestly, are satisfied by analogy, and especially mathematical analogy, that somewhat dissipates the darkness enshrouding so many phenomena of nature. (Volterra 1901, 255)

What was thus to be saved from the mechanistic view was the use of mechanical models applied to other domains by way of mathematical analogies. Consequently, and in relevance to our central theme concerning the centrality of computational templates in modeling, along the mechanical models also "a large part of the mathematical physics would still be saved from destruction" (Volterra 1906, 3) and with it the central use of differential equations.

Summing up, Volterra's view on how biology and social sciences should be modeled on mechanics included transforming qualitative elements in quantitative measurable elements, measuring the variations, idealizing and abstracting the systems and processes under investigation – and using the mathematical tools of mechanics by way of analogies.

If, for example, the phenomenon consisted of oscillations of one of the variables of the system of interest, like oscillations in the number of predators, analogies could be drawn to oscillatory systems in mechanics enabling the use of the respective mathematical tools. Moreover, according to Volterra only those components and interactions should be taken into account that were assumed to underlie the observed phenomena. This is a realistic approach in some areas of physics where comprehensive and well-confirmed background theories exist giving the resources with which to estimate the effect of distortions introduced by specific idealizations, and providing guidance on how to attain particular levels of accuracy and precision. But the situation is different in such fields as biology, or social sciences, because of missing background theories and the complexity of the phenomena in question. Thus mechanical approach cannot be transferred offhand into population biology, which is shown by Volterra's subsequent attempt to apply it in modeling the predator-prey system.

2.2. The construction of the Lotka-Volterra model by Vito Volterra

In 1925 Volterra's son-in-law Umberto D'Ancona presented him a problem concerning the fluctuations in the number of predatory fish in the Upper Adriatic. D'Ancona had collected some statistical data on the percentages of predator fish in the total catch of fish during World War I. The data showed an unusual increase in predators during the final period of the war and immediately after, when fishing was hindered by the war. Volterra, being a theoretical physicist, embarked on finding a mechanism underlying the predator-prey dynamics which would explain the observed fluctuations in the predator population.

Thus Volterra aspired to identify those component parts, components operations, and their working together, that caused the fluctuations. In this endeavor he faced two interrelated problems: First, the degree of the complexity of the system was far beyond most of the systems studied in mechanics, and second, he did not possess the appropriate mathematical tools for the description and analysis of the mechanism. The mathematical methods and techniques developed in mechanics could not be applied directly to the study of the predator-prey dynamics. Even if the variations observed in populations living in the same environment showed some well known characteristics observed in many mechanical systems, such as oscillatory behavior, it was unclear which of the components of the system did interact, and in what ways. On the one hand, the complexity of the system had to be rendered manageable enough to be modeled by mathematical tools. But on the other hand, the available mathematical tools exhibited a serious constraint on the kinds of complex structures and processes that could be studied. These two points created an essential part of the tension Volterra faced as he tried to apply the available computational templates to depict the underlying mechanism of the predator-prey dynamics.

Volterra was very much aware of this tension, as the following passage shows:

> [T] he question presents itself in a very complex way. Certainly there exist periodic circumstances relating to environment, as would be those, for example, which depend upon the changing of the seasons, which produce forced oscillations of an external character in the number of individuals of the various species.

> But are there others of internal character, having periods of their own which add their action to these external causes and would exist even if these were withdrawn? […] But on the first appearance it would seem as though on account of its extreme complexity the question might not lend itself to a mathematical treatment, and that on the contrary mathematical methods, being too delicate, might emphasize some peculiarities and obscure some essentials of the question. To guard against this danger we must start from the hypotheses, even though they be rough and simple, and give some scheme for the phenomenon. (Volterra 1901, 255)

Voterra's statement: "[…] the question may not lend itself to a mathematical treatment" expresses nicely the described tension between the complexity of the phenomenon and the nature of the available mathematical methods. As a consequence, Volterra attempted to reduce the complexity of the problem by trying to set apart those components of the complex system that could be neglected and thereby rendering the problem describable by well known mathematical tools (or using Humphreys's notion, computational templates). The goal was to "isolate" those components which supposedly contributed to the variations in the number of individuals in the respective species[3]:

> Biological associations (biocoenosis) are established by many species, which live in the same environment. Ordinarily the various individuals of such an association contest for the same food, or else some species live at the expense of others on which they feed. [...] The quantitative character of this phenomenon is manifested in the variations of the number of individuals, which constitute the various species. (Volterra 1928, 4)

[3] On isolation as a strategy of modeling, see Knuuttila 2009.

However, in complex environments, such as the sea, there are a lot of different factors, which have an impact on the observed variations such as changes in climate and weather, as well as seasons. This raises the question of how to identify the fundamental factors contributing to the dynamics of the predator and prey populations. What kind of assumptions had to be made and how could they be justified?

Volterra started out by distinguishing between “external” and “internal” causes. External causes are “periodic circumstances relating to the environment, as would be those, for example, which depend upon the changing of the seasons, which produce oscillations of an external character in the number of the individuals of the various species.” (Volterra 1928, 5) Volterra wanted to focus on internal causes and leave aside external causes: “[...] but are there others of internal character, having periods of their own which add their action to these external causes and would exist even if these were withdrawn” (ibid.). Yet one cannot take for granted that it is possible to separate the external and internal causes, since they could be – and in fact they often are – interrelated in complex ways. Consequently, interacting species in a changing environment constituted a problem of a much higher degree of complexity than the systems studied in classical mechanics – which made it far from clear whether the modeling approach taken from mechanics could be imported to population biology.

Thus Volterra had to “start from the hypotheses” as he put it himself (see the quotation above). Since he could not isolate internal causes from the external causes due to the complexity of the interactions between the components of the system of interest, he constructed a hypothetical system with the help of some assumptions concerning them. The central assumptions made in the construction process of the model were:

- The species increase or decrease in a continuous way, which makes them describable by using differential equations.
- Birth takes place continuously and is not restricted to seasons. The birthrate is proportional to the number of living individuals of the species. The same assumption is made for the death rate.
- Homogeneity of the individuals of each species, which neglects the variations of age and size.

Accordingly, Volterra concentrated exclusively on the dynamics between predators and preys leaving aside any interactions with other species or external factors. This strategy of formulating a simplified hypothetical system allowed Volterra to start out from well known mathematical tools and computational templates, and to explore their applicability which offered at the same time some protection against the above mentioned difficulty that the "mathematical methods, being to delicate, might emphasize some peculiarities and obscure some essentials of the question." It is important here to appreciate the difference between idealizing or abstracting away many aspects of a real system and starting out from few fundamental assumptions, which approaches Volterra himself clearly distinguished from each other.[4] Abstraction is often approached as an operation

[4] This is in accord with Weisberg's (2007) claim that Volterra did not arrive at his model by abstracting away properties of real fish but rather constructed it by stipulating certain of their properties (p. 210).

in which theorist mentally strips away all that seems irrelevant as regards the problem at hand, in order to focus on some single property or set of properties (see Cartwright 1983, 187). Apart from the fact that it is often difficult to decompose the system of interest theoretically, let alone to decide which of the components and their interactions are irrelevant, posing the problem of abstraction in this way tends to by-pass the difficulties of mathematical representation. It is as if the components and the interactions of the supposed real mechanism laid bare for the theorist to choose from, to be then described by suitable mathematical means.

In deriving the equations of the development of the two species, one of which feeds upon the other, Volterra started out from the situation in which each of the species is alone. In this situation, he assumed, the prey would grow exponentially and the predator in turn would decrease exponentially, because of missing food resources. Translated into the language of mathematics, the respective situations of prey and predator populations is described by the following two differential equations describing the change in time of the prey and predator populations.

$dN_1/dt = \varepsilon_1 N_1$, $dN_2/dt = -\varepsilon_2 N_2$, (Equation 1a,b)

Integration of the two differential equations leads to an exponential increase of the prey and an exponential decrease of the predator population, with N_0 referring to the numbers of individuals at t=0

However, as we have shown, this was not what Volterra originally aimed at. Yet in practice he had to resort to hypotheses.

$N_1=N_0 \exp(\varepsilon_1 t)$, $N_2=N_0 \exp(-\varepsilon_2 t)$, (Equation 2a,b)

Exponential growth or decrease is the most basic way of describing the development of a population in time. This first mathematical formulation of the problem does not take into account any environmental changes interacting with the population or the obvious fact that there is an upper limit in the resources provided by the environment. Rabbits do not multiply unlimited. Moreover, these quantitative descriptions of the predator and prey populations do not take into account any interaction between the two populations.

In the next step Volterra introduced the interaction between prey and predator populations by introducing a coupling term. The interacting predator and prey system is described by the following set of differential equations:

$dN_1/dt =(\varepsilon_1 - \gamma_1 N_2)N_1$, (Equation 3a)

$dN_2/dt =(-\varepsilon_2 + \gamma_2 N_1)N_2$, (Equation 3b)

The proportionality constant γ_1 links the prey mortality to the number of prey and predators and γ_2 links the increase in predators to the number of prey and predators. The set of differential equations is non-linear and coupled. Given that there does not exist analytical solutions to non-linear coupled differential equations, Volterra faced serious challenges in analyzing the dynamic behavior of his novel kind of model. Non-linear differential equations lie outside the classical study of oscillations, which are usually described by linear equations. Examples of such ordinary oscillations are harmonic and damped oscillators described by the following differential equations:

$m\, d^2x/dt^2 + kx = 0$ and $m\, d^2x/dt^2 + b\, dx/dt + kx = 0$, (Equation 4a,b)

An example of a harmonic oscillator is a spring, where $m\, d^2x/dt^2$ is the restoring force which is proportional to the displacement x, and k is a constant. Damping is introduced by friction proportional to the velocity and is described by the damping term b dx/dt. The differential equations of the harmonic and damped oscillators have the advantage of being linear. This feature allows the calculation of analytical solutions. But the differential equations for harmonic and damped oscillators could not be applied to the case of interacting predator and prey systems because it does not account for the interaction between them. This interaction is described by the product N_1N_2 in the Lotka-Volterra equations, which turned a set of coupled differential equations into a set of coupled non-linear differential equations. Thus the tension between the complexity of the system under study and the available mathematical tools led to the development of a novel model describing the dynamics of a predator-prey system by the coupled non-linear differential equations. This mathematical model of a predator-prey system became itself a computational template but interestingly only after it became mathematically tractable, a point to which we will return below.

A further critical point in the construction of the differential equations is related to the assumptions that the coefficients of increase $-\varepsilon_2$ and decrease ε_1 in equation (3a,b) are linear in relation to N_2 and N_1. To justify this assumption Volterra drew an analogy to mechanics by using the method of encounters according to which the number of collisions between the particles of two gases is proportional to the product of their densities. Thus Volterra assumed that the rate of predation upon the prey is proportional to the product of the numbers of the two species. The consequent mathematical analysis of the resulting equations gave Volterra some important results, including a solution to D'Ancona's problem concerning the relative abundancy of predatory fish during the war years when fishing was thwarted. Volterra summarized his results in what he called the "three fundamental laws of the fluctuations of the two species living together." (Volterra 1928, 20) The third law states that if an attempt were made to destroy the individuals of the predator and prey species uniformly, the average number of the prey would increase and the average number of the predator would decrease. This case corresponds to heavy fishing. Next, Volterra explored small fluctuations in the two species, which corresponds to light fishing. In this case the opposite scenario would occur: The average number of the prey would decrease and the average number of the predator to increase. This result supported the empirical findings of D'Ancona.

2.3. The construction of the Lotka-Volterra model by Alfred Lotka

Alfred Lotka was born in Lemberg, Austria (today Ukraine) in 1880 and he died in 1949 in the US. In contrast to Volterra, Lotka struggled to get recognition from the scientific community for his entire life. Herbert Simon has characterized Lotka as a "*forerunner* whose imagination creates plans of exploration that he can only partly execute, but who exerts great influence on the work of his successors – posing for them the crucial questions they must answer, and disclosing more or less clearly the direction in which the answer lies" (Simon 1959, 493). It was only later in the context of general systems theory that scientists like Ludwig von Bertalanffy, Norbert Wiener, and Herbert Simon took up Lotka's work, especially his book *Elements of Physical Biology* (Lotka 1925) to which we will return below.

In 1920 Alfred Lotka published two papers. The first appeared in May in the Proceedings of the National Academy of Science entitled "Analytical note on certain rhythmic relations in organic systems" (Lotka 1920a) and the second paper "Undamped oscillations derived from the law of mass actions" appeared in June in the Journal of the American Chemical Society (Lotka1920b). In both articles one finds a pair of equations that have the same form as the model Volterra independently arrived at some years later. In the first paper the equations are applied to the analysis of a biological system and in the second paper to a chemical system.[5] In the case of the biological system Lotka began from very general considerations:

> Starting out first from a broad basis, we may consider a system in the process of evolution, such a system comprising a variety of species of matter $S_1, S_2, \ldots, S_n$ of mass $X_1, X_2, \ldots, X_n$. The species of matter S may be defined in any suitable way. Some of them may, for example, be biological species of organisms, others may be components of the "inorganic environment".

[5] Lotka dealt with the rhythmic effects of chemical reactions already in his earlier writings, see e.g. Lotka 1910.

> Or the species of matter S may be several components of an inorganic system in the course of chemical transformation.
>
> We may think of the state of the system at an instant of time as being defined by statement of the values of $X_1,X_2,\ldots,X_n$; of certain parameters Q defining the character of each species (in general, variable with time); and of certain other parameters P. The parameter P will, in general, define the geometrical constraints of the system, both at the boundaries (volume, area, extension in space), and also in its interior (structure, topography, geography); they will further define such factors as temperature and climate conditions. (Lotka 1920a, 411)

On the basis of these considerations he described the evolution of organic as well as inorganic systems by the following systems of differential equations:

$$dX_i/dt = F_i(X_1,X_2,\ldots,X_n;P,Q) \quad \text{(Equation 5)}$$

describing evolution as a process of redistribution of matter among the several components X_i of the system. The function F describes the mode of physical interdependence of several species and their environment. In this general equation the components as well as the interactions between them are not further specified. This has to be done separately for each specific system studied by using Lotka's systems approach. Defining systems in such a general way Lotka freed his approach from any specific scientific disciplines and theories – as Bertalanffy (1968) did later with his general systems theory. In his attempt of using methods, techniques and concepts from statistical mechanics to describe and analyze biological systems Lotka had realized the problems attached to the transfer of methods, techniques, and concepts from physics into biology.

Frequently, the methods and techniques are not directly applicable to biology as the concepts from physics are not often apt to describe biological phenomena. Yet Lotka did not deny that the processes observed in biological systems are based on the principles of statistical mechanics and thermodynamics. He described this problem in the following passage of his book *Elements of physical biology* published in 1925:

> So long as we deal with volumes, pressures, temperatures, etc., our thermodynamics serve us well. But the variables in terms of which we find it convenient to define the state of biological (life bearing) systems are others than these. We may have little doubt that the principles of thermodynamics or of statistical mechanics do actually control the processes occurring in systems in the course of organic evolution. But if we seek to make concrete applications we find that the systems under consideration are far too complicated to yield fruitfully to thermodynamic reasoning; and such phases of statistical mechanics as related to aggregation of atoms or molecules, seem no better adapted for the task. To attempt application of these methods to the prime problems of organic evolution is much like attempting to study the habits of an elephant by means of a microscope. It is not that the substance of the elephant is inherently unfitted to be viewed with a microscope; the instrument is ill adapted to the scale of the object and the investigation. (Lotka 1925, 53)

Lotka’s fundamental equation (Equation 5) is an attempt to formulate a suitable, general enough instrument. The approach of Lotka is thus markedly different from that of Volterra. While Volterra is trying to specify the predator-prey dynamics in sea-fisheries by making analogies to mechanics, Lotka is making use of general templates: his analysis is not limited to biological systems but also includes “components of the inorganic environment" like chemical components. Starting out from this general outlook Lotka deduces under assumption that P and Q are constant the equations describing a system consisting of the individuals of two hypothetical species S_1 and S_2. In this system S_2 is a herbivorous animal species which lives on the plant species S_1. The equations are of the form:

$dS_1/dt = (A_1 – B_1S_2)S_1$, (Equation 6a)

$dS_2/dt = (-B_2 + A_2S_1)S_2$, (Equation 6b)

They are of the same form as those presented by Volterra.

Having derived these equations Lotka analyzes the stable states of the system and shows that the system under given conditions performs undamped oscillations. He concludes his paper remarking that the system of equations is identical in form with a system describing certain chemical reactions. The chemical system in question is analyzed in the paper, which was published one month later in June 1920 (Lotka 1920b). In this paper Lotka also uses the model, which he has deduced from his general considerations of how to describe the evolution of organic and inorganic systems. Consequently, he makes use of his model in the sense of a computational template: he applies the general template by adjusting it to different subject matters.

The model applying both to a biological and a chemical system can thus be regarded as a computational template. But does Lotka's set of general coupled differential equations by itself form also a computational template? Due to its generality and unspecificity it does not lend itself directly to the modeling of specific phenomena like the Ising model or the Poisson distribution. It has to be manipulated by specifying the mechanism by identifying components and their interactions for the specific systems under study. Lotka's set of general differential equations could maybe best characterized as a very general form of a computational template linked to the general systems approach of for example Ludwig von Bertalanffy. von Bertalanffy characterized systems consisting out of interacting components but without any further specification of the kind of components or their interactions (von Bertalanffy 1968).[6]

3. Mechanisms vs. templates

The different approaches of Lotka and Volterra intersected at the analysis of the predator-prey interaction resulting at similar formalisms. This is in line with Paul Humphreys's claim that the process of model construction cannot be read from the formalism alone: "identical templates can derived on the basis of completely different and sometimes incompatible assumptions" (2004, 72). The tension inherent in modeling practice

[6] The complex systems studied by systems theory are sometimes called mechanisms, perhaps because they describe any group of objects interacting together to produce some result. Thus for instance Kuorikoski (2009) argues that there are two concepts of mechanism, the other referring to "componential causal system" and the other to "abstract form of interaction". In our sense these abstract forms of interaction are better seen as templates that are used to model mechanisms and the use of them is characteristic of model-based representation. Real mechanisms can be studied also in other ways, for instance by schematic pictures or diagrams. They are often more suitable for the tasks of decomposition and localization that are important for such disciplines as medicine and neuroscience, for example (see Bechtel and Abrahamsen 2005). As mere computational templates the "abstract forms of interaction" comprise the object of study of formal disciplines, such as complexity theory.

between capturing the components and interactions of the supposed real causal mechanisms operative in the world and using general templates as a means in this task can be clearly seen in the opposed strategies of Lotka and Volterra. Volterra's goal was to "mathematically explain" D'Ancona's data on "temporal variations in the composition of species" (Volterra 1927b, 68). He aimed at depicting a mechanism consisting of "*the intrinsic phenomena* due to the voracity and fertility of the co-existing species" (ibid. italics of the original) and had thus clearly a certain target phenomenon in view. By contrast Lotka started his physical biology program from the general description of the interaction between species expressed as a set of simultaneous differential equations. Predator-prey dynamics, which he treated analogously to host-parasite dynamics, was just one concrete case to which his general approach could be applied. Different models of interaction could be created by choosing components and their interactions in different ways. Not all of these would necessarily correspond to real situations but Lotka was eagerly looking for real world situations allowing for the application of his modeling approach. Thus whereas Volterra approached modeling from the perspective of the causal explanation of real mechanisms, Lotka approached it from the perspective of applying a general template to specific cases.

The tension is clearly present also inside the work of both Lotka and Volterra. Not surprisingly, Volterra's endeavor was more marked by it as he had a certain target system in mind at the outset. Although he aimed at "isolating those factors one wishes to examine, assuming they act alone, and by neglecting others" (Volterra 1927b, 67), in formulating his basic model he made intensive use of formalisms and problem solutions adapted from physics by way of analogies. And when he in his subsequent studies expanded his model to cover any number of species and to take into account different new features he went on in this task in drawing further analogies to physics (see e.g. Kingsland 1985, Israel 1993). Consequently, in his attempt to create more *realistic* variants of the basic model, Volterra continued borrowing from mechanics some concepts and associated formalisms, which attests to the kind of tension inherent to modeling practice that we are arguing for. Volterra's excuse for making such extensive use of the principles of mechanics was that eventually his work was to be regarded as pure mathematics (see Kingsland 1985, 113). Scudo and Ziegler note that most of his original research papers "were technical and dry, especially for biologists" (1978, 58). However, being faithful to his earlier methodological pronouncements Volterra was also interested in testing his theories on empirical data, but he typically kept the mathematical, technical treatments and the empirical accounts separate from each other.

Lotka, in turn, perceived as problematic both the use of other disciplines such as mechanics, or statistical mechanics, as a model for biology, as well as the associated transfer of methods, techniques, and templates. Accordingly, Lotka attempted to ground his theoretical endeavor in a basic formal approach that could be used to deal with various systems, whether biological, chemical or social. Kingsland (1985) notes his careful use of analogies and his skepticism of taking metaphorical entities for real ones, contrasting his approach with that of Volterra: "[h]e did not adopt Volterra's course. He was aware that the equations which he and Volterra had developed independently were formal statements which need not have any deeper significance" (Kingsland 1985, 125).

It should be noted, however, that Lotka had also a model science in mind that guided his approach to biology. In his *Elements of physical biology* he applied to biological systems the methods used in the mathematical description of the dynamics of chemical reactions. This was in line with his grand vision of evolution interpreted as mass and energy relationships cutting across species boundaries. Where chemical components exchanged matter between the components of the system, biological entities exchanged energy. Thus the tension between capturing real mechanisms and using general formal templates was present also in Lotka's work albeit in a rather programmatic level. Although he ambitiously sought for general principles guiding no less than the behavior of all organic and inorganic systems, what he eventually accomplished was a system of general templates capable of being applied to various kinds of systems thus paving way to general systems theory.

The Lotka-Volterra case shows also how along with the formalisms also some characteristic methods, problem solutions and concepts are transferred from one discipline to the other. It reveals an interesting linkage between Humphreys's account of computational templates and the philosophical literature on the role of analogies and metaphors in modeling (e.g. Black 1962, Hesse 1966, Bailer-Jones 2000). More often than not analogies and metaphors have been relegated to the domain of heuristics due to their supposedly vague nature. This vagueness is also affirmed by Israel (1993), who claims that the "modeling approach" employs formalisms offered by the mathematical theory on the basis of vague feelings concerning the similarities between various phenomena. We have shown that in the case of Lotka and Volterra this was certainly not the case. They did not take the mathematical means they used from some supposed stock of mathematical forms, instead they applied the modeling methods, as well as some techniques and concepts of some (for them) paradigmatic disciplines. All these were transferred along with the mathematical representations from one domain to another.

Consequently, we suggest that the concept of computational template gives some rigor to the discussion on modeling heuristics. The point is that the discovery and the justification of models cannot be separated clearly from each other, relegating analogies and metaphors to the side of heuristics. Analogies and metaphors can rather be treated as devices that also contribute to the justification of a model in allowing the introduction of successful computational templates and modeling methods to a new field. Through these methods and techniques the model gets some initial built-in justification (Boumans 1999), and as a result of the subsequent construction process it gains additional credibility as the borrowed modeling methods and techniques are adapted to the new domain. This in turn suggests that the notion of computational template provides a convenient unit of analysis for the study of interdisciplinary exchange that is typical of modeling. As concrete "pieces of syntax" computational templates are relatively easy to follow and in drawing together the methods, theoretical concepts, and analogies made use of in modeling they provide a unitary perspective from which to approach the theoretical and methodological transfer between disciplines.

Moreover, our analysis of the history of Lotka-Volterra model shows that since mathematical forms such as computational templates are typically already rooted in the already established ways of modeling certain domains, their uses and interpretations in the original domain provide a clue for how to model the new domain of interest. This highlights the importance of the paradigmatic cases of how formalisms are applied at some problems. Mere templates do not carry the ways they can be used up their sleeves.

Another issue in which our account complements Humphreys's insight on computational templates concerns the question of tractability. Namely, it shows that tractability is a relative matter and in this sense historical. The mathematical model of a predator-prey system became itself a computational template, but only after it was rendered mathematically tractable. Systems exhibiting non-linear dynamics are very challenging from the mathematical point of view. Usually it is not possible to find analytical solutions for non-linear differential equations. Computer simulations are an essential tool in studying the complex dynamics represented by non-linear differential equations. The advancements of computer technologies in the 1970's sparked a new interest in the Lotka-Volterra model and its dynamic behavior. Robert May (1974) argued that especially such "simple" models as the Lotka-Volterra model offer a valuable resource for studying the basic complex behavior of non-linear systems. Turned into a computational template the Lotka-Volterra model became a formal object of study in itself.

While Lotka and Volterra could not employ modern computational tools, both of them introduced mathematical methods allowing for the study of the stable states of the model system. One of the big successes of the Lotka-Volterra model was that it provided tools for the study of non-linear dynamics. For instance, Lotka examined his fundamental equation (Equation 5) by showing that without knowing the precise form of the function F_i the properties related to the stable states of the system can still be discussed. In his discussion of the stable states associated with the fundamental equation Lotka started out by making the assumption that both the environment and the genetic constitutions are constant. By the means of a Taylor series expansion Lotka calculated the possible stable states of the system. This mathematical procedure was taken up by many scientists dealing with non-linear differential equations and it was especially praised by Herbert Simon (1959, 495). Consequently, we suggest, that a model *in combination with the mathematical tools enabling the study of it* can turn into a computational template: Computational templates are made productive by the methods and solutions that accompany them.

The notion of a template solves also an interesting priority puzzle as regards the Lotka-Volterra model. Namely, Lotka claimed the priority for the model on the basis of his *Elements of Physical Biology* published in 1925, although he had presented what looked like the same model already in his 1920 articles as discussed above. Israel (1993) takes this to show that neither Volterra nor Lotka was a follower of the modeling approach but that they rather approached the use of mathematics in a classical reductionist way (see above). From the mathematical modeling conception, argues Israel, "a chemical model and a biological model described by the same equation are fundamentally the same thing, and Lotka's and Volterra's models are just two concrete examples of the same nonlinear oscillator" (1993, 500). Making a distinction between a template and a model shows that this is not the case: a chemical model and a biological model are quite different things, although the templates were the same. Lotka, the self-conscious user of templates, claimed priority not on the basis of a hypothetical possibility derived from his basic template, but on what could be considered a model of a real system. Namely, in Lotka 1920a he draws the Lotka-Volterra equations from his system of equations inspired by chemical dynamics without any discussion of *empirical* biological systems. In 1925 he lays down the equations as descriptions of a host-parasite system citing also W.R. Thomson (1922) and L.O. Howard (1987) on this topic. Moreover, later on in the same book Lotka discusses “the interspecies equilibrium” in “aquatic life”, though this time the discussion draws on other sources being unconnected to the discussion on Lotka-Volterra equations. The ensuing priority discussion shows well the differences between Lotka and Volterra as regards the tension between mechanisms and templates in modeling. Volterra acknowledges Lotka’s priority, but stresses that what he had formulated were principles concerning “sea-fisheries” (Volterra 1927a) and writes to Lotka “It is the analogy between the biological case and the chemical case that has guided you” (Draft of a letter, Volterra archive, quoted in Israel 1993, 499).

4. The productive tension

We have argued that the tension between capturing the specific real mechanisms underlying the observed phenomena and using general computational templates to study them lies at the heart of contemporary modeling practice. In the case of the Lotka-Volterra model this tension is displayed by the different modeling styles of Volterra and

Lotka, of whom Volterra seek to isolate the real mechanism whereas Lotka aimed at developing a genuine multidisciplinary template. The tension was also felt internally in their theoretical endeavors, although it was more conspicuous in Volterra's case because of the template-orientation of Lotka's work. As we have discussed above, Lotka developed what we would call today a systems approach: mathematical techniques to model systems composed of interacting components developing in time.

The tension we have discussed is strongly present in the interdisciplinary theoretical and methodological transfer, in which computational methods and templates are applied to new domains. As such research program making use of the tools and methods of another domain stabilizes, the tension might go unnoticed but tends still to cause conceptual problems due to the uneasy fit between the representational tools and the nature of the domain they are applied to. That this tension is highly productive can be seen from the subsequent development of the Lotka-Volterra model. For Volterra the application of the tools of mechanics to inter-species dynamics provided for a more than decade long research program (see Volterra 1931) and since then the Lotka-Volterra model has been extended from the study of the interaction between species to the exploration of basic biological mechanisms. An example of this line of research is the investigation of the temporal organization in biological systems such as circadian rhythms, which produce oscillatory day and night rhythm in organisms (Goodwin 1963, see also Loettgers 2007). Today Lotka-Volterra model is mostly used as a basic template for further modeling. For population biologists it serves as the "simplest imaginable model of predator-prey system" (Roughgarden 1979, 432). For scientists and mathematicians in the field of systems theory the Lotka-Volterra model has formed an ideal case for studying non-linear dynamics.

As for the notion of computational template, the case of Lotka-Volterra sheds light on it in several ways. First of all, it shows that the distinction between a theoretical and a computational template is relative, since the tractability of a theoretical template may evolve due to new tools. Because of the nonlinearity of the Lotka-Volterra equations they are not analytically solvable, but both Lotka and Volterra used methods, which allowed them to calculate the properties of the stable states of the model system, such as the oscillatory behavior. Later on the tractability of the model was greatly enhanced due to advanced computers. Secondly, computational templates are important as stabilized representational tools, whose paradigmatic uses have significant impact on what can be represented and how, guiding thus theoretical development and template transfer across the disciplines. Thirdly, we have shown how part of the tension between mechanisms and templates is due to the uneasy fit of the available representational tools to some specific subject matter, which sometimes gives a rise to a new template as in the case of the Lotka-Volterra model. This might make it seem that the tension is largely due to the limitations of cross-disciplinary templates as means of representation. But this is just one part of the story: Computational templates provide also a powerful way to generalize. Paying attention to this property of computational templates shows how the tension between specific mechanisms and general templates permeates already the aims of modeling. It is apparent, for instance, in the recent discussions in systems and synthetic biology, where identifying the mechanisms underlying specific biological functions is joined by the study of the basic design principles of the spatial and temporal organization of biological systems.

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