

# *Equation or Algorithm: Differences and Choosing Between Them*

## **Acta Biotheoretica**

An international journal on the mathematical and philosophical foundations of biological and biomedical science

ISSN 0001-5342

Volume 59

Number 1

Acta Biotheor (2010) 59:67-79

DOI 10.1007/

s10441-010-9119-4



**Your article is protected by copyright and all rights are held exclusively by Springer Science+Business Media B.V.. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your work, please use the accepted author's version for posting to your own website or your institution's repository. You may further deposit the accepted author's version on a funder's repository at a funder's request, provided it is not made publicly available until 12 months after publication.**

## Equation or Algorithm: Differences and Choosing Between Them

C. Gaucherel · S. Bérard · F. Munoz

Received: 29 July 2009 / Accepted: 22 August 2010 / Published online: 5 September 2010  
© Springer Science+Business Media B.V. 2010

**Abstract** The issue of whether formal reasoning or a computing-intensive approach is the most efficient manner to address scientific questions is the subject of some considerable debate and pertains not only to the nature of the phenomena and processes investigated by scientists, but also the nature of the equation and algorithm objects they use. Although algorithms and equations both rely on a common background of mathematical language and logic, they nevertheless possess some critical differences. They do not refer to the same level of symbolization, as equations are based on integrated concepts in a denotational manner, while algorithms specifically break down a complex problem into more elementary operations, in an operational manner. They may therefore be considered as suited to the representation of different phenomena. Specifically, algorithms are by nature sufficient to represent weak emergent phenomena, but not strong emergent patterns, while equations can do both. Finally, the choice between equations and algorithms are by nature sufficient to represent weak emergent phenomena, but not strong emergent patterns, while equations behave conversely. We propose a simplified classification of scientific issues for which both equation- and/or algorithm-based approaches can be envisaged, and discuss their respective pros and cons. We further discuss the complementary and sometimes conflicting uses of equations and algorithms in a context of ecological theory of metapopulation dynamics. We finally propose both conceptual and practical guidelines for choosing between the alternative approaches.

---

C. Gaucherel (✉)  
INRA—EFPA, UMR AMAP, TA-A.51/PS2, 34398,  
Montpellier, Cedex 5, France  
e-mail: gaucherel@cirad.fr

S. Bérard · F. Munoz  
Université Montpellier 2, UMR AMAP, TA-A.51/PS2, 34000 Montpellier, France

**Keywords** Emergence · Ecology · Metapopulation · Modeling · Semantics · Spatial dynamics · Theory

## 1 Introduction

Powerful computers have changed the way we address mathematical issues, and to some extent tool-centred approaches have come to compete with formal mathematics. Wolfram (2002) has claimed that an approach based on algorithms and intensive computing is more efficient for scientific demonstration, while other mathematicians emphasize the “unreasonable effectiveness” of a formal mathematical representation (e.g. Wigner 1982). Our basic purpose here is to investigate whether, in practice, equations and algorithms are redundant or complementary tools, and in what situations one approach might outperform the other. Whether one or the other is able to characterize a “true” reality or instead a derived, subjective perception, is outside the scope of the present study, and for the purposes of the present we assume that equations and algorithms do not differ in terms of realism.

Although algorithms appeared well before computers, the recent advent of computer-based approaches has led to the nature of algorithms being confused with computer functioning (Cormen et al. 2001). However, designing and executing algorithms does not necessarily require a computer, and the differences between algorithms and equations go further than opposition between qualitative and quantitative models. An algorithm can be qualitative when formally describing, for instance, how to obtain an output from a given input, but may also be quantitative, for instance, when working with numeric values. Likewise, equations can be qualitative—when giving an overall expression of the relationships between variables—as well as quantitative, when dealing with numeric values. Differences between continuous and discrete representations are likewise not relevant as both equations and algorithms may address continuous as well as discrete case studies. Finally, algorithms used to solve equations (Buchberger 1976) are outside the scope of our comparison as we consider the differences between the two approaches when addressing the same scientific problem, not when combining them for the sake of computation.

Although previous studies in the philosophy of mathematics (Shapiro 1997) and of computer science (Turner and Eden 2007; Humphreys 2004) have explored the formal and logical nature of these mathematical objects, there is still a striking need to discuss the practical differences between using equations and/or algorithms, especially in biology and ecology (Berec 2002; Bolker and Pacala 1997; Law et al. 2003; Faugeras and Maury 2007). On the one hand, we have investigated the nature of the two approaches in the light of formal semantics (Plotkin 2004; Schmidt 1986) while, on the other, we have discussed the nature of the phenomena they may represent in the light of theories about emergence (Bedau 2008; Huneman 2008). Based on this framework, we propose here a typology of scientific questions that equation- and/or algorithm-based approaches can address. More specifically, we investigate in detail how the two approaches have been used to address metapopulation dynamics in ecology. And finally, we provide an overview and some practical recommendations.

## 2 Theoretical Context and Practical Issues

### 2.1 Definitions

Creating a formal representation of a real system is the basis of any scientific approach, and means using a set of symbols and descriptors, mathematical or otherwise, of the “real” properties and processes. These properties are modelled using mathematical tools such as equations and algorithms. Let us consider a set of objects that are comparable, e.g. numerical quantities, topological or algebraic objects. An equation is a logical, binary relation between such objects and is not restricted to equalities (Aubin 1997, and references therein) as it can also represent inequalities, inclusions, exclusions etc., in the context of ordered sets (Burris and Sankappanavar 1981). On the other hand, an algorithm differs from specifically deriving an output ( $O$ ) from an input ( $I$ ) using a composition function  $F$  of elementary operations (Cormen et al. 2001).

Algorithmic theories address computational issues for which they are abstract machines such as Turing machine, recursive functions or Lambda calculus. According to the pioneering work conducted by A. Turing and A. Church, all realistic models of computation are equivalent, i.e. they are included in a general framework of computable functions (Church 1941; Turing 1936). Algorithms are said to be recursive when composed of elementary operations applied iteratively up to a conditional stop. Defining an algorithm requires first proving its existence, then formalizing its structure and, finally, writing a corresponding program to compute it. But programming is not always possible, even when the algorithm can be formalized, and to this extent this shows that algorithms are not reducible to computer programs.

On the other hand, both equations and algorithms relate quantities through logical operations or instructions and thus refer to some common mathematical background. They make use of the same relational operators and ordering operations (e.g. parentheses, to be computed first) or directional instructions (e.g.  $a = b$ , where parameter  $a$  is set to the value of  $b$ , not the opposite). To this extent, the design of algorithms and equations relates to a common conceptual background, by first translating the question of interest into abstract concepts, building the model that relates these concepts, optionally demonstrating that it has been correctly handled, and finally solving it in different situations.

### 2.2 Fundamental Differences

Comparing algorithm- and equation-based approaches echoes a central issue of semantics regarding the mathematical nature of computational approaches (Hoare 1999). Denotational semantics describe real objects using integrated mathematical objects that in the main closely represent these objects and their properties (Schmidt 1986), while operational semantics refers to the manner in which objects are characterized through more elementary operations and specifications, as handled by an abstract machine (Plotkin 2004). Algorithms and equations thereby differ in their operational versus denotational nature, respectively, as algorithms rely on abstract machines and a composition of elementary operations, while equations summarize

the properties of the studied system using logical relations that do not fall into more elementary elements. In practice, and especially in applied fields of mathematical biology and ecology, equations and algorithms do not refer to the same level of integration.

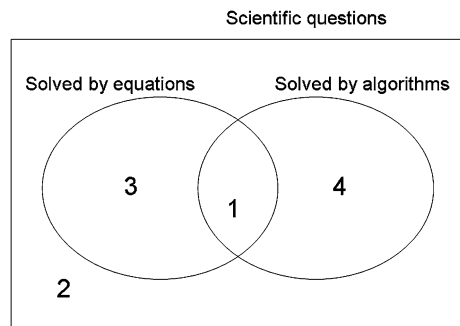
In addition, algorithms and equations can be used to investigate objects of different natures. The notion of emergence describes how patterns arise from a multiplicity of interactions in complex systems and in such a manner that it may be difficult if not impossible to obtain a result from the elementary events. “Weak emergence” occurs when it is impossible to represent a pattern otherwise than by applying the elementary operations in an iterative manner (Huneman 2008) as, for instance, by analyzing interacting and synergetic effects at lower levels of organization. Weak emergence, by its nature, can be addressed using reductionist approaches and operational approaches such as algorithms. Furthermore, no equation is able to express the algorithm’s end state from the input, in weak emergent patterns (incompressibility criterion—Huneman and Humphreys 2008). Weak emergence should show physical monism, systemic (or collective) properties and synchronic determination (Boogerd et al. 2005; Broad 1925; Stephan 1999). “Strong emergence”, on the other hand, represents properties that are irreducible to the interplay of constitutive parts and events (Bedau 2008). This is a less clearly defined and more debated concept which can include synchronic and irreducible, or diachronic and unpredictable, patterns (Boogerd et al. 2005; Broad 1919; Stephan 1999). Because of its irreducible nature, strong emergence cannot be correctly addressed using algorithms, while the use of equations in a denotational approach can be envisaged. An example here is the equation-based treatment of macroscopic properties in physics, for instance in thermodynamics.

### 3 Typology of Scientific Questions

Based on this fundamental difference, we propose that scientific topics can be placed into four categories according to whether equation- or algorithm-based approaches are more appropriate (Fig. 1).

1. *Both equations and algorithms are appropriate: algorithm compressibility* (Fig. 1, Case 1). Fibonacci (in 1202) modelled the reproduction rate of rabbits,

**Fig. 1** Relationships between scientific questions and solving formalisms divide questions into four classes, called cases 1, 2, 3 and 4



without predators, and defined the well-known Fibonacci series where each new element is the sum of the two previous elements (e.g.  $f_{1-13...} = (1,1,2,3,5,8,13,21,34,55,89,144...)$ ). Obtaining the  $n$ th value in the Fibonacci series is straightforward using the following algorithm, with initial values  $a = 1; b = 1; i = 1$ , and the recursion rule while  $(i < n)$ , do{ $c = a + b; a = b; b = c; i = i + 1$ }; and finally *return*  $c$ . The  $n$ th value in the Fibonacci series ( $f_n$ ) may also be obtained using mathematical reasoning, i.e. by calculating the roots  $\varphi_1 = \frac{1+\sqrt{5}}{2} = 1.61803$  and  $\varphi_2 = \frac{1-\sqrt{5}}{2}$  of the polynomial expression  $x^2 - x - 1$  to provide the  $n$ th value  $f_n = \frac{(\varphi_1^n - \varphi_2^n)}{\sqrt{5}}$ . In this case, the algorithm is said to be compressible (Huneman and Humphreys 2008), as an equation is able to provide a shortcut to the result.

2. *Neither equations nor algorithms can be used* (Fig. 1, Case 2). Gödel's incompleteness theorem, on which Turing's computation theory relies, states that some scientific questions, even though embedded in a consistent mathematical framework, cannot be addressed using either equations or algorithms (Case 2). Gödel (1931) showed that any given branch of mathematics contains proposals whose validity cannot be proven using the rules and axioms of that particular mathematical branch. This implies that logical systems of any complexity are, by definition, incomplete and include more true statements than can possibly be proven based on the related set of rules.

3. *No algorithm can solve a problem for which an equation is efficient: irreducibility* (Fig. 1, Case 3). Because an algorithm relies on a finite set of elementary operations, this precludes any problem requiring an infinite number of operations. For instance, calculating the value of limit  $L$  in any geometrical series defined by:  $f_n = \sum_{k=1}^n a^{k-1}$  requires an infinite number of operations to reach the limit value. Hence, algorithms can only provide an approximated value while equations may provide the exact limit, insofar that the series converges (i.e. if  $|a| < 1$ ). A demonstration of this involves identifying the relation  $f_n = \frac{1-a^n}{1-a}$  since  $f_{n+1} = f_n + a^n = \frac{1-a^n}{1-a} + a^n = \frac{1-a^{n+1}}{1-a}$ . The solution to the problem is then given by the limit equation when natural integer  $n$  increases to infinity  $\lim_{n \rightarrow \infty} (f_n) = \frac{1}{1-a}$ . We expect the descriptions of most strong emergent patterns to fall into this case as the irreducibility of strong emergence (Bedau 2008) precludes the use of any operational approach based on algorithms.

4. *No equation can solve a problem for which an algorithm is efficient: algorithm incompressibility* (Fig. 1, Case 4). This is illustrated by the recent proof of Kepler's conjecture (four colour theorem), using a computing approach, while equation-based attempts failed for four centuries. In 1611, Kepler hypothesized that close packing (i.e. cubic or hexagonal packing in a closed volume, both of which have maximum densities of  $\frac{\pi}{3\sqrt{2}} \approx 74.048\%$ ) is the densest possible manner of packing spheres. This assertion is known as Kepler's conjecture. In 1997, Hales showed how Kepler's conjecture might be proved using computer calculations. Hales (2001) subsequently provided the full proof using the theory



of global optimization, linear programming and interval arithmetic. Hales' proof has still been difficult to validate (Szpiro 2003). Therefore, proving Kepler's conjecture illustrates how algorithms may be more helpful than equations (Fig. 1, Case 4). In the case of weak emergent phenomena, algorithms are expected to be able to describe the pattern while equations cannot (Huneman and Humphreys incompressibility criterion, 2008).

If a question is still unanswered, or if a new equation or algorithm is found to address the problem, shifts are possible from one case to another. Conceptions about operational and denotational limits may therefore evolve with scientific progress. For example, although Hales' work is a typical example of algorithm-based computation, an equation-based proof could assign it to Case 1.

## 4 Application in Ecology

The choice between an algorithm- or equation-based approach is often based on practical considerations. In the particular field of ecology, the issue has raised conflicting views, but little philosophical investigation can be conducted into the dichotomy of the two approaches, in contrast with physics and social sciences (Epstein 1999). In addition, an ecological application is of particular interest as an example of how viewpoints may evolve in a relatively young scientific field.

Metapopulation theory investigates the dynamics of populations in a network of scattered, suitable sites, as based on colonization and extinction events. The premise is that every local population is doomed to extinction, even though as a body it is well adapted to local physical and competition constraints, because of random variations in the number of individuals. Many sources of random variation may be cited: fertility, climate, predator density, etc. Population extinction is an absorbing state, i.e. a population with zero individuals cannot regain individuals without being rescued by some external input. And if colonizers arrive from nearby populations, colonizing events can counteract local extinction events.

Therefore, a network of populations, also called a metapopulation, may persist far longer than any single isolated population, and that is why metapopulation theory is of considerable interest in ecology (Hanski 1998; Hanski and Gilpin 1997). The theory considers two main related issues. First, what amount of available suitable space, or habitat, is a species able to occupy at a given time? Second, what connectivity between suitable patches is necessary to allow a species to survive as a metapopulation? This concerns the ability of a species to spread and persist in the context of spatially fragmented suitable habitats like, for instance, in remnant tropical forests.

### 4.1 Population Density at Equilibrium: a Case 1 Issue

Simple equations were initially developed in an attempt to grasp the main features of a metapopulation. The most famous mean-field equation, developed by Levins (1969), accounts for the equilibrium density of populations in a suitable habitat, without any spatial structuring, and may be written as:



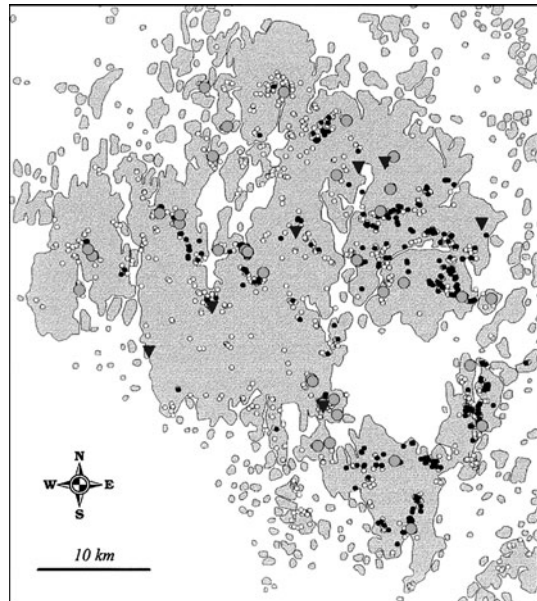
$\frac{dp}{dt} = cp(1-p) - ep$ , where  $p$  is the proportion of populations in the available network of suitable sites,  $c$  is the migration (colonization) rate, and  $e$  is the rate at which local populations become extinct. This is also the master equation for the dynamics of the average local probability of occupancy. As a Markov process, the state of the system at a given time depends on the state of the system a short time before. The equation then represents the balance between colonization and extinction events over a very short time period. The related equilibrium equation  $cp * (1 - p*) - ep* = 0$  gives the deterministic equilibrium density:  $p* = 1 - \frac{e}{c}$ , and the metapopulation can persist if and only if  $\frac{e}{c} < 1$ . This equation-based approach is useful for understanding the overall behavior of a metapopulation and for characterizing its critical behavior as it will switch from stable persistence when  $\frac{e}{c} < 1$  to extinction when  $\frac{e}{c} > 1$ . This is comparable to a phase transition in physics.

An alternative approach is to simulate the random colonization and extinction events at local sites over space and time using the so-called cellular automata algorithm (Bascompte and Sole 1996). Input  $I$  is the state of population occupancy in a matrix of suitable cells at time 0, and output  $O$  is the state of population occupancy during the stationary state. The recursive specification of the algorithm,  $F$ , includes stochastic treatment of extinction and colonisation events at each time step, using random draws. By contrast, the equation-based approach, described above, bypasses the representation of elementary time steps by assuming that colonization and extinction events are overall in balance, and by focusing on a deterministic prediction of the quasi-stationary population density. If simulated over sufficient time and in a sufficiently large area, the algorithm-based approach will also, in terms of statistical expectation, show that population density is stable (Keeling 2002). Therefore, as the algorithm used to predict population density is compressible to the prediction of the mean-field equation, this is a Case 1 situation.

#### 4.2 Spatial and Temporal Structuring: a Case 4 Issue

Later models investigated the effect of habitat scarcity by including a constant density parameter,  $h$  (Lande 1987), such that the equilibrium density becomes,  $p* = h - \frac{e}{c}$  again as a Case 1 issue. This is also a phase-transition model, related here to the density of available habitat, and the transition threshold becomes  $h = \frac{e}{c}$ . Specifically, a small change in habitat structure can cause large-scale extinction of the metapopulation, a phenomenon of considerable concern to ecologists (Bascompte 2003; Ovaskainen et al. 2002; With and King 1999). But more recent investigations highlighted that the topology of suitable patches is also critical for metapopulation persistence, as isolated parts of the habitat may be barely or not at all colonized, and the distribution of the populations is then very heterogeneous in space and time (Fig. 2). This property also pertains to the non-linear nature of the dynamics, and gives rise to self-organized patterns (Vuorinen et al. 2004). When the system is close to the phase-transition threshold, this spatial and temporal structuring becomes very large-scale, and the metapopulation must be followed over a very long period and/or over a very large area if the true stationary features are to be grasped.

**Fig. 2** Famous example of the metapopulation system involving the Glanville fritillary butterfly in the Åland Islands (Finland). Small *open circles* indicate suitable but unoccupied meadows (habitat), while *black circles* and *large symbols* indicate meadows in which Glanville fritillary larvae were present in autumn 1995. Of the 42 local populations sampled, 35 survived to autumn 1996 (*large circles*) and seven became extinct (*triangles*). From Saccheri et al. (1998)



Classical equation-based approach, using either the above-mentioned Levins model or local equations describing colonization-extinction equilibria (Hanski 1997; Gosselin 1999), does not allow such phenomenon to be taken into account and hence is not well suited to predicting the fate of real-world metapopulations in spatially-structured habitats (Solé et al. 1999). This is basically because metapopulation dynamics over networks of suitable sites show a scale-free behaviour (Vuorinen et al. 2004), and scale-dependent equilibrium equations may be dramatically violated in such a context. Therefore, neither discrete nor any continuous treatment of spatial and temporal dynamics can be summarized as formal equalities and relationships, as required for the development of equations (see above). Conversely, a simulation algorithm is able to feature metapopulation dynamics in space and time without any constraints for the nature of equilibrium and colonization-extinction behaviours, such that it can show transient and scale-free correlation properties. This can therefore be used, with appropriate parameterization, to simulate many rounds of metapopulation dynamics in varying habitat landscapes, with varying colonization and extinction dynamics, and to analyze overall behaviour using, for instance, spatial statistics (Munoz et al. 2007).

Such an experimental system (Peck 2004) provides insights of general interest into spatial and temporal structures (Bascompte and Sole 1996). In this regard, metapopulation structure is weakly emergent for it can be predicted by an algorithm but not by an equation (incompressibility). This is a typical Case 4 situation. Furthermore, this algorithm-based analysis can be used to generate empirical laws which can help improve equation-based approaches (Bascompte 2001). More generally, the emergent patterns that stem from observations, when correctly measured, can become general rules. Mixed usage of equations and algorithms can then support theoretical ideas and help reach as general as possible conclusions in a

context of strong emergence or unsolved weak emergence. The role of these empirical laws must be related to the difference between computational templates arising from theory and from the observation of very rough regularities, such as the simulations of traffic congestion (Humphreys 2004).

## 5 Discussion

Equation- and algorithm-based approaches rely on a common mathematical framework, but algorithms specifically relate an output object  $O$  to some input elements  $I$  through a composition of instructions, while equations are based on a single relationship between two mathematical objects. Basically, algorithms are embedded in abstract machine formalism that deals with an overall relationship between output and input through a sequence of oriented operations (operational semantics, Plotkin 2004). On the other hand, equations are used to represent concepts and laws that rely on an integrated level of symbolization (denotational semantics, Schmidt 1986). The denotation-operation duality here represents two different ways of handling the same problem, i.e. either by relating basic processes to higher-level processes, or by directly translating these higher-level properties and concepts into equations.

Based on this conceptual background, an algorithm- or an equation-based approach may be preferred depending on the nature of the phenomena investigated. We have put forward a 4-case categorization of situations where one or both approaches may be used. We have related this categorization to the *compressibility* and the *irreducibility* of the patterns and processes under study. If both an algorithm and an equation can be used, the algorithm is said to be compressible (Case 1). If only an equation can be used, the property represented is irreducible (Case 3). Equations may be the only means, if any, to deal with strongly emergent patterns (Bedau 2008). Yet strongly emergent patterns concern behaviour that follows an equation but cannot be generated from its basic properties through a simulation process. If an algorithm can be used, but no equivalent equation is available, the algorithm is said to be incompressible (Case 4). This includes weak emergent patterns (Stephan 1999). It has also been suggested that strong and weak emergences are synchronic and diachronic processes, respectively (Humphreys 2008). The diachronic representation may hold using the operational approach through a time series of elementary operations and, therefore, algorithm-based approaches can be used to handle weak emergent properties.

Furthermore, the difference between algorithm- and equation-based approaches goes far beyond the dualism of computer-based and formal methods. Despite the fact that algorithm-based approaches are often associated with digital computers and binary logic, computing machines based on analogical signals (electrical, mechanical, pneumatic or hydraulic modules) were commonly used half a century ago, before digital computing (Dewdney 1985), and could outperform digital systems by implementing operations and symbolization in a more integrated fashion (Levi 2009). Also, building and executing algorithms may remain a purely abstract

process, and the operational nature of algorithms is of more general value than any subsequent computational aspects.

### 5.1 Ecology

Our application to metapopulation theory fell into Case 1 and Case 4 situations depending on which property of the same system was investigated. Predicting population density in a network of suitable sites in equilibrium was a Case 1 issue, but their spatial and temporal structures were weakly emergent and therefore required simulation algorithms (Case 4). Founded on the idea that chance extinction is less likely in a network of populations than in any single isolated population, the equation-based approach considers a large-scale balance in colonization and extinction events to provide the expected equilibrium population density (Hanski and Gilpin 1997; Levins 1969). This proved to be very useful and intuitive (Hanski 1997, 1998), but failed to grasp the local and transitory features pertaining to the non-linear nature of colonization dynamics. That is why metapopulation theory developed into Case 4 situations, and related works have employed algorithm-based approaches.

The mean-field equation of metapopulation dynamics (Levins 1969) assumed that colonization is unlimited in space (equal probability of colonization everywhere), and that extinction probability is constant everywhere. The mean-field assumption is common to other scientific fields, such as physics, but is clearly unrealistic as a direct measure of colonization events whenever local contagion effects are predominant (diffusive processes, such as in reaction–diffusion models). But the mean-field assumption is not a direct measure of colonization, but rather integrates a large number of colonization events averaged over time and space into a more general concept of mean-field colonization incidence. Levins' equation works at large scales by using fairly integrated objects, but it is not well-suited to addressing the multiscale nature of metapopulation dynamics.

On the other hand, the local effects of population dynamics and related emergent patterns are better represented by simulation experiments for a finer representation of colonization is required. Intensively-used simulation algorithms can thereby provide appropriate theoretical experiments to investigate population dynamics (Peck 2004), yield empirical laws and describe patterns (Bascompte 2001; Munoz et al. 2007). Such algorithmic treatments may then give rise to new equations and integrated concepts as a translation from a Case 4 to a Case 1 situation. Here, a theoretical experiment will provide computational templates based on a theory, while real experiments provide computational templates based on observations (Humphreys 2004). This ecological application therefore illustrates how equations, like some more integrated objects, can be more accurate representations of the particular conceptions and preconceptions at the heart of a theory, i.e. in our example the global balance between colonization and extinction events. By using less integrated concepts, algorithms generate integrated objects that are not predicted directly by the theory, and therefore are part of an experimental approach. Finally, the oscillation between Case 1 and Case 4 situations illustrates the necessary transfer from the denotational to the operational approach, and vice versa.

It would therefore be misleading to recommend a defined/fixed approach. Thanks to increasingly powerful computing facilities, the algorithm-based manner of denotation, through theoretical experiments, will probably modify the operational philosophy of algorithms.

## 5.2 Recommendations

Some practical guidelines may be useful in grasping the relevance of using one, the other, or both formalisms when both can be used (Case 1 in Fig. 1):

1. Algorithms are straightforward to use in the sense that less integrated parameters are easier to handle than their more integrated counterparts in equations. In the case of the metapopulation example, the mean-field equation is fairly synthetic and useful, but the mean-field concept of colonization is fairly difficult to handle and properly discuss. The simulation-based counterpart can be used to understand how the local rules of colonization dynamics may affect overall patterns. In the same perspective, turbulent fluids can sometimes be modelled with a few different local fluxes instead of a complicated energy balance equation.
2. Extended computation time, in particular if real-time treatments are needed, may preclude the use of intensive algorithmic treatments or too hard-to-solve equations. This may also have crucial implications on the accuracy and ability to obtain solutions. Some trade-off in terms of realism and generality may be required depending on the accuracy and robustness of the approaches employed (Levins 1966).
3. The nature of random processes cannot be considered in the same manner at different scales and levels of integration in stochastic models. Stochastic equations refer to the deterministic features of probability distributions (i.e. mean, standard deviations, etc.) in a denotational manner, while the operational nature of algorithms allows them to mimic sequences of realizations in random processes, within the limits of our ability to generate random numbers. The resulting features we grasp may critically differ from one approach to the other.
4. The researcher's personal conceptions clearly influence his/her choices, and this depends greatly on cultural and scientific background (Latour 1987; Morin 1982). Specifically, the political, religious and economic context may have a marked impact on the way we solve scientific questions. For instance, the rise of Darwin's model of natural selection in the 19th century may be related to the social and economic upheavals of the industrial revolution.

Algorithms and equations are complementary tools, though they are far from being interchangeable. The philosophical differences between denotational and operational approaches go far beyond using a tool for a specific need, but rather question the emergence and development of scientific theories. The need for generality competes with the need for accuracy, and the need for realism—using less integrated concepts—competes with the need for universality on the basis of more abstract and more integrated concepts (Levins 1966).

We have shown that the balance between algorithm- and equation-based approaches, and the sometimes heated debates that surround them, clearly highlights this intrinsic dualism in scientific research. By providing a straightforward categorization and the discussion of a specific situation in ecology, our investigation bridges the gap between philosophical discussion and practical priorities in a way that may help the reader make a choice based on fresh insight.

Finally, differences between equation- and algorithm-based approaches echo the debate between strong and weak emergences. While weak emergence needs elementary operations to yield emergent properties, strong emergence (if a relevant concept, a point still under debate) seems to be closer to the synchronic and integrated representation of equation-based approaches. This questions the link between operational semantics and weak emergence on the one hand, and between denotational semantics and strong emergence on the other, which is an issue of widespread interest in scientific research.

**Acknowledgments** We are grateful to the organizers of the European Conference on Computing And Philosophy (ECAP 2008). We warmly thank P. Huneman for advices on an earlier version of this paper.

## References

- Aubin D (1997) The withering immortality of Nicolas Bourbaki: a cultural connector at the confluence of mathematics. *Sci Context* 10:297–342
- Bascompte J (2001) Aggregate statistical measures and metapopulation dynamics. *J Theor Biol* 209:373–379
- Bascompte J (2003) Extinction threshold: insights from simple models. *Ann Zool Fennici* 40:99–114
- Bascompte J, Sole RV (1996) Habitat fragmentation and extinction thresholds in spatially explicit models. *J Anim Ecol* 65(4):465–473
- Bedau MA (2008) Is weak emergence just in the mind? *Mind Mach* 18(4):443–459
- Berec L (2002) Techniques of spatially explicit individual-based models: construction, simulation, and mean-field analysis. *Ecol Model* 150(1–2):55–81
- Bolker B, Pacala SW (1997) Using moment equations to understand stochastically driven spatial pattern formation in ecological systems. *Theor Popul Biol* 52:179–197
- Boogerd FC, Bruggeman FJ, Richardson RC, Stephan A, Westerhoff HV (2005) Emergence and its place in nature: a case study of biochemical networks. *Synthese* 145:131–164
- Broad CD (1919) Mechanical explanation and its alternatives. *Proc Aristotelian Soc* 19:86–124
- Broad CD (1925) In: Kegan Paul T (ed) *The mind and its place in nature*. Trubner & Co, London
- Buchberger B (1976) Theoretical basis for the reduction of polynomials to canonical forms. *ACM SIGSAM Bull* 10(3):19–29
- Burris SN, Sankappanavar HP (1981) *A course in universal algebra*. Springer Verlag, Berlin
- Church A (1941) *The calculi of lambda-conversion*. Princeton University Press, Princeton
- Cormen TH, Leiserson CE, Rivest RL, Stein C (2001) (eds) *Introduction to algorithms*, 2nd edn. The Massachusetts Institute of Technology, USA
- Dewdney AK (1985) Analog gadgets that solve a diversity of problems and raise an array of questions. *Sci Am* 252(5):18–24
- Epstein J (1999) Agent-based computational models and generative social science. *Complexity* 4(5):41–60
- Faugeras B, Maury O (2007) Modeling fish population movements: from an individual-based representation to an advection-diffusion equation. *J Theor Biol* 247(4):837–848
- Gödel K (1931) Über formal unentscheidbare Sätze der principia mathematica und verwandter systeme. I. *Monatshefte für Mathematik und Physik* 38:173–198
- Gosselin F (1999) Test of mathematical assumptions behind the ‘incidence function’ estimation process of metapopulations’ dynamic parameters. *Math Biosci* 159(1):21–32

- Hales TC (2001) The honeycomb conjecture. *Discrete Comput Geom* 25(1):1–22
- Hanski I (1997) Predictive and practical metapopulation models: the incidence function approach. In: Tilman D, Kareiva P (eds) *Spatial ecology—the role of space in population dynamics and interspecific interactions*. Princeton University Press, Princeton, pp 21–45
- Hanski I (1998) Metapopulation dynamics. *Nature* 396:41–49
- Hanski IA, Gilpin ME (eds) (1997) *Metapopulation biology*, vol 1. Academic Press, San Diego
- Hoare CAR (1999) A theory of programming: denotational, algebraic and operational semantics, in, [http://www.research.microsoft.com/users/thoare/A\\_theory\\_of\\_programming.pdf](http://www.research.microsoft.com/users/thoare/A_theory_of_programming.pdf)
- Humphreys P (2004) *Extending ourselves: computational science, empiricism, and scientific method*. Oxford University Press, Oxford
- Humphreys P (2008) Synchronic and diachronic emergence. *Mind Mach* 18(4):431–442
- Huneman P (2008) Emergence made ontological? computational versus combinatorial approaches. *Philos Sci* 75(5):595–607
- Huneman P, Humphreys P (2008) Dynamical emergence and computation: an introduction. *Mind Mach* 18(4):425–430
- Keeling MJ (2002) Using individual-based simulations to test the Levins metapopulation paradigm. *J Anim Ecol* 71(2):270–279
- Lande R (1987) Extinction thresholds in demographic models of territorial populations. *Am Nat* 130:624–635
- Latour B (1987) *Science in action, how to follow scientists and engineers through society*. Harvard University Press, Cambridge Mass
- Law R, Murrell DJ, Dieckmann U (2003) Population growth in space and time: spatial logistic equations. *Ecology* 84(1):252–262
- Levi M (2009) *The mathematical mechanic: using physical reasoning to solve problems*. Princeton University Press, Princeton
- Levins R (1966) Strategy of model building in population biology. *Am Sci* 54(4):421
- Levins R (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull Entomol Soc Am* 15:237–240
- Morin E (1982) *Science avec conscience*. Vol. (new edition). Collection Points, Fayard
- Munoz F, Cheptou P-O, Kjellberg F (2007) Spectral analysis of simulated species distribution maps provides insights into metapopulation dynamics. *Ecol Model* 105:314–322
- Ovaskainen O, Sato K, Bascompte J, Hanski I (2002) Metapopulation models for extinction threshold in spatially correlated landscapes. *J Theor Biol* 215:95–108
- Peck SL (2004) Simulation as experiment: a philosophical reassessment for biological modeling. *Trends Ecol Evol* 19(10):530–534
- Plotkin GD (2004) A structural approach to operational semantics. *J Log Algebraic Program* 60–61:17–139
- Saccheri I, Kuussaari M, Kankare M, Vikman P, Fortelius W, Hanski I (1998) Inbreeding and extinction in a butterfly metapopulation. *Nature* 392
- Schmidt DA (1986) *Denotational semantics. A methodology for language development*. Allyn and Bacon, Inc., Boston
- Shapiro S (1997) *Philosophy of mathematics: structure and ontology*. Oxford University Press, Oxford
- Solé RV, Manrubia SC, Benton M, Kauffman S, Bak P (1999) Criticality and scaling in evolutionary ecology. *Trends Ecol Evol* 14(4):156–160
- Stephan A (1999) Varieties of emergentism. *Evol Cogn* 5(1):49–59
- Szpiro G (2003) Mathematics: does the proof stack up? *Nature* 424(6944):12–13
- Turing AM (1936) On computable numbers, with an application to the entscheidungsproblem. *Proc Lond Math Soc* 2(42):230–265
- Turner R, Eden AH (2007) The philosophy of computer science: introduction to the special issue. *Mind Mach* 17(2):129–133
- Vuorinen V, Peltomäki M, Rost M, Alava MJ (2004) Networks in metapopulation dynamics. *Euro Phys J B* 38(2):261–268
- Wigner E (1982) On science and its evolution. *J Phys* 43(NC-8):435–438
- With KA, King AW (1999) Extinction thresholds for species in fractal landscapes. *Conserv Biol* 13(2):314–326
- Wolfram S (2002) *A new kind of science*. Wolfram media, Champaign