## The Undeniable Effectiveness of Mathematics in the Special Sciences

Mark  $Colyvan^*$ 

#### Abstract

In many of the special sciences, mathematical models are used to provide information about specified target systems. For instance, population models are used in ecology to make predictions about the abundance of real populations of particular organisms. The status of mathematical models, though, is unclear and their use is hotly contested by some practitioners. A common objection levelled against the use of these models is that they ignore all the known, causally-relevant details of the often complex target systems. Indeed, the objection continues, mathematical models, by their very nature, abstract away from what matters and thus cannot be relied upon to provide any useful information about the systems they are supposed to represent. In this paper, I will examine the role of some typical mathematical models in population ecology and elsewhere. I argue that while, in a sense, these models do ignore the causal details, this move can not only be justified, it is necessary. I will argue that idealising away from complicating causal details often gives a clearer view of what really matters. And often what really matters is not the push and shove of base-level causal processes, but higher-level predictions and (non-causal) explanations.

# 1 The Philosophical Problems of Applied Mathematics

The applications of mathematics to empirical science raise a number of interesting philosophical issues. Perhaps the most well known of

<sup>\*</sup>Department of Philosophy, University of Sydney, Sydney, NSW, 2006, Australia and Stellenbosch Institute for Advanced Study (STIAS), Wallenberg Research Centre at Stellenbosch University, Stellenbosch, South Africa. *Email:* mark.colyvan@sydney.edu.au

these issues is the so-called unreasonable effectiveness of mathematics. The issue here is to account for the success of mathematics in helping empirical science achieve its goals. It is hard to say precisely what the crux of the issue is supposed to be, let alone what an adequate explanation would look like. The problem is usually attributed to Eugene Wigner [34] in his well known essay on the topic,<sup>1</sup> where he suggests that

"[t]he miracle of the appropriateness of the language of mathematics for the formulation of the laws of physics is a wonderful gift which we neither understand nor deserve." [34, p. 14]

I take it that the problem, in its most general form, is to account for the applicability of mathematics in empirical science. Put this way, though, there are a number, of interrelated problems. There's the unreasonable effectiveness of arithmetic, of calculus, of differential geometry, of algebraic topology, and so on.<sup>2</sup> There's the way different philosophies of mathematics draw different conclusions to help explain the applications of mathematics.<sup>3</sup> There's the issue of the different roles mathematics can play in science—the different ways mathematics might be thought to be unreasonably effective. And, of course, physics is not the only scientific consumer of mathematics. Mathematics might also be thought to be unreasonably effectiveness in economics, in biology, in chemistry, in psychology, and elsewhere. Finally, there's the problem of understanding the nature of the modelling process itself and why mathematical modelling is so often an effective way of advancing our knowledge.<sup>4</sup>

Many of these issues are interrelated but, still, a great deal of confusion has resulted from running some of the issues together and failing to state exactly what is supposed to be unreasonable about the effectiveness in question. Having been guilty myself of such carelessness in the past [8, p. 15], my aim here is a modest one. I intend to look at the use of mathematical models in the special sciences. As my primary example I'll consider the use of mathematics in population ecology. The issue here is that the mathematical models in question seem to leave out the relevant causal detail, yet still manage to both predict and (arguably) explain population-level phenomena. The task, then,

<sup>&</sup>lt;sup>1</sup>There has been a great deal of subsequent discussion on the issue, for example [1, 10, 20, 22, 33, 35] and this discussion has helped clarify the problem and its solution.

<sup>&</sup>lt;sup>2</sup>Not to mention the much less appreciated problem of the unreasonable effectiveness of inconsistent mathematics [12].

 $<sup>^{3}</sup>$ See, for example, [9, 17, 33].

<sup>&</sup>lt;sup>4</sup>See, for example, [4, 6].

is to give an account of how mathematical models can succeed in such tasks.

### 2 Case Study: Population Ecology

Population ecology is the study of population abundance and how this changes over time. For present purposes, a population can be thought of as a collection of individuals of the same species, inhabiting the same region. Population ecology is a high-level special science, but relies heavily on mathematical models. (It is thus a soft science in one sense—in the sense of being high level and quite removed from physics—but in another sense it is a hard science—in the sense that it is mathematically sophisticated.) There are a number of issues associated with applying mathematics to population ecology, but my focus here will be on an issue that is of significance for working ecologists and has a direct bearing on the way they go about their business.<sup>5</sup>. The issue I will address arises from the fact that mathematical models apparently ignore the relevant biology and would thus seem ill-equipped to offer explanations of ecological phenomena. Mathematical models in population ecology would thus seem to be (at best) predictive models. In what follows I will argue that this is not right. I will argue that while, in a sense, mathematical models ignore the relevant biology, this does not mean that these models cannot be explanatory. I will also provide a sketch of how mathematics can succeed in delivering explanations, despite turning away from much of the biological causal detail.

Before I begin the main task, however, it will be useful to present a couple of typical mathematical models, of the kind we are interested in here. First consider *the logistic equation* [19, chap. 2]. This is a model of a single population's abundance, N—exponential at first and then flattening out as it approaches carrying capacity, K:

$$\frac{dN}{dt} = rN(1 - \frac{N}{K})$$

where r, is the population growth rate and t is time.

Another key example is the Lotka-Volterra equations [5, chap. 9] These equations model the population of the predator and the prey via two coupled first-order differential equations:

$$\frac{dV}{dt} = rV - \alpha VP$$

<sup>&</sup>lt;sup>5</sup>See for example [26, 28] for some discussion on this and related issues by prominent ecologists.

$$\frac{dP}{dt} = \beta VP - qP$$

Here V is the population of the prey, P is the population of the predator, r is the intrinsic rate of increase in prey population, q is the per capita death rate of the predator population, and  $\alpha$  and  $\beta$  are parameters: the capture efficiency and the conversion efficiency, respectively. These equations can give rise to complex dynamics, but the dual outof-phases, population oscillations of predator and prey are the best known.

Of course both these mathematical models are overly simple and are rarely used beyond introductory texts in population ecology. For example, the logistic equation treats the carrying capacity as constant, and the Lotka-Volterra equations treats the predators as specialists, incapable of eating anything other than the prev in question. Both these assumptions are typically false. These models do, however, serve as the basis for many of the more realistic models used in population ecology. The more serious models add complications such as age structure, variable growth rates and the like. These complications do not matter for my purposes in this paper, though. Even in these more complicated models, biological detail is deliberately omitted and yet the models are adequate for the purposes at hand. The issues I am interested to explore can be raised with the more complicated models, but it's easier to see the issues in the simpler models. We will not be losing any generality by focussing our attention on the simpler text-book population models.

We are now in a position to state the philosophical problem posed by mathematics in population ecology. Population abundance is completely determined by biological facts at the organism level—births, deaths, immigration and emigration—but the (standard) mathematical models leave out all the biological detail of which individuals are dying (and why), which are immigrating (and why), and so on. That is, the mathematical models ignore the only things that matter, namely, the biological facts. The mathematical models here—the relevant differential equations—seem to ignore the biology, and yet it is the biology that fully determines population abundances. How can ignoring that which is most important ever be a good strategy?

We might put the point in terms of explanation: the mathematical models are not explanatory because they ignore the causal detail. The model may tell us that the abundance of some population at time t is N, but without knowing anything about the organism-level biology, we will not know why the population at time t is N and will have little confidence in such predictions. A full account of the relevant biology, on the other hand, would include all the causal detail and would provide the required explanations. Let's focus on this explanatory version of the puzzle because I think it is what underwrites the less-specific worries expressed in the previous paragraph.

Before I go any further, it will be useful to say a few words about explanation and philosophical theories of explanation. First, I take it that we simply cannot deny that there are population-level explanations in ecology. To deny this would, in effect, amount to giving up on explanation in the special sciences. Unlike physics, in the special sciences we do not have the option of reserving all genuine explanation for the fundamental level (or the fundamental laws). So the issue we are meant to be addressing is not that there can be no explanation in the special sciences. Rather, we take it for granted that there are explanations in the special sciences but that the mathematical models used in special sciences such as population ecology can not deliver explanations.

Next we might reasonably ask for a philosophical account of explanation, so that we are all on the same page. But that turns out to be difficult for a number of reasons, not least of which is that there is no generally-accepted philosophical account of scientific explanation. So, for present purposes, I shall be rather liberal about what counts as an explanation. I suggest that an intuitive understanding of an explanation as an answer to a "why questions" will do.<sup>6</sup> It is important to keep in mind that explanation should not be confused with a more limited class of explanation known as *causal explanation*. There is no denying that causal explanation—tracing the relevant causal history of an event of interest—is one kind of explanation. I deny, however, that this is the only kind of explanation.<sup>7</sup> Explanations must be enlightening, and that's about all we really need to assume here.

### 3 The Role of Mathematics

Now I turn to the task of investigating what makes these mathematical models in ecology tick. I will argue that there is no reason to suggest that mathematical models in ecology are not explanatory. I will suggest three different ways in which the models in question can

<sup>&</sup>lt;sup>6</sup>I also take an explanation to be that which is accepted as such in the relevant scientific community. This, of course, is not a philosophical account of explanation; it's just a constraint that I take very seriously. I think philosophical accounts of explanation need to (largely) agree with scientific uses of the notion of explanation. A philosophical account of explanation that does violence to scientific practice is of little interest to we naturalistic philosophers.

<sup>&</sup>lt;sup>7</sup>It would take us too far afield to argue for this here, but see, [9, chap. 3], [30], [31], and [32].

explain. First, the mathematical models do not ignore the biological detail—at least sometimes the models in question are offering biological explanations, albeit explanations couched in mathematical terms. Second, understanding a system often does involve ignoring, or rather, abstracting away from, causal detail in order to get the right perspective on it. Finally, I'll suggest that mathematics can offer explanation for empirical phenomena.

Recall that we started out with the charge that mathematical models leave out all the relevant biological detail. But this is not quite right. Often the mathematical model is just representing the biology in a mathematical form. For example, in the logistic equation, all the information about births, deaths, immigration and emigration is packed into r and all the information about the resources is packed into the constant K. The information about the predators' impact on the per capita growth rate of the prev is summarised in the Lotka-Volterra equation in  $\alpha$ —the capture efficiency parameter—and the information about the predators' ability to turn prev into per capita growth of the predator population is summarised by  $\beta$ —the conversion efficiency parameter. You might have misgivings about the representation of this information<sup>8</sup>, but this is a different objection. It's now a concern about the simplicity of the model. As I mentioned before, we can provide more complex models that relinquish some of the more unrealistic idealisations. These more complex models also have their idealisations, though. Indeed, it is part of the very enterprise of modelling that some details are ignored. So the basic concern about biological detail not being represented in the mathematical models under consideration is misplaced. Of course not all the biological detail is present in the model, but the fact remains that many of the key terms of the mathematical models have natural biological interpretations, or at least are representing or summarising the biological information in mathematical form. The mathematical models have a lot more biology represented in them than is typically appreciated.

In cases where the biology is represented in mathematical form, the model is indeed capable of offering perfectly legitimate biological explanations. For instance, think of the standard story of how population cycles arise as a result of predator–prey interactions. The cycles in question are solutions to the coupled differential equations in question [5, chap. 9] but there is also a very natural biological explanation that can be extracted from the mathematical model: when the predator population is high the predators catch many of the prey so that the latter's population falls, but then there is less food for

 $<sup>^8 \</sup>mathrm{You}$  might, for example, object that r and K are represented in the logistic model as constants.

the predators, so after a time the predator population also falls; but now there is less pressure on the prey population, so it recovers and this, in turn, supports an increase in the predator population (after a similar time lag). This cyclic behaviour falls out of the mathematics, but the explanation, once suitably interpreted, is in fact a perfectly respectable ecological explanation.

Next, notice that ignoring some detail can lead to insights via analogy.<sup>9</sup> Sometimes similarities between systems will not be apparent until certain details are ignored. Mathematics is a particularly useful tool for drawing out such similarities because mathematics allows one-indeed forces one-to abstract away from the causal detail and notice abstract similarities. For example, Newton's law of cooling/heating is just the logistic equation with abundance replaced with temperature of the body in question, and carrying capacity replaced with ambient room temperature.<sup>10</sup> Why are such connections between systems important? One reason is that it saves work: one can import results already at hand from work done elsewhere. Once the connection between the logistic equation and the cooling/heating equation are recognised, results from either area can be used by the other area (suitably interpreted, of course). Moreover, these rather abstract connections—often only apparent via the mathematics—can lead to new developments and, as we'll see shortly, even help with explanations.

We have already seen that mathematics can be the vehicle for delivering biological explanations, but often the mathematics can facilitate more transparent explanations. Mathematical models can sometimes do more than just represent the biology in mathematical form and then deliver essentially biological explanations of biological facts (albeit in mathematical guise). Sometimes the mathematics delivers explanations that would not be apparent otherwise. For example, the explanation of the different kinds of complex behaviour a population can exhibit as it approaches its carrying capacity—damped oscillations, asymptotic approach, overshooting and crashes—may be best seen via the mathematics of the logistic equation.

Finally, and most controversially, I'll argue that there can be genuinely mathematical explanations of empirical facts. Alan Baker [2, 3], Aidan Lyon [27] and I [9, 11, 13] have argued that mathematical models can provide genuinely mathematical explanations of biological facts. A couple of much-discussed examples from the literature

<sup>&</sup>lt;sup>9</sup>See [15] for more on analogical reasoning in ecology.

<sup>&</sup>lt;sup>10</sup>And, as Ginzburg and I have argued elsewhere, the inertial view of population growth is mathematical similar to celestial mechanics (they both employ the same second-order differential equations) [14, 18].

on this topic will help. Consider the question of why hive-bee honeycomb has a hexagonal structure. The answer, it turns out, is because of the honeycomb theorem [21]: a hexagonal grid represents the most efficient way to divide a surface into regions of equal area with the least total perimeter of cells [27]. There are some biological and pragmatic assumptions required for this explanation to succeed. These include the assumption that bees have a limited supply of wax and need to conserve it while maximising honey storage space. They also need to do this while still being able gain access to the hive from the outside.<sup>11</sup> But with these assumptions in place, the important part of the explanation seems to be purely mathematical and is provided by the honeycomb theorem. Any purely biological explanation will be too specific—it will tell the story of how one particular group of bees built one particular hive with a hexagonal structure—and will miss the general point that all hives built under such constraints *must* have a hexagonal structure. The hexagonal structure is a solution to an evolutionary optimisation problem and as such is not a mere accident of any particular hive construction.

Alan Baker [2] offers an ecological example of a mathematical explanation. Baker considers why a particular species of North American cicadas have life cycles which are prime numbers: 13 and 17 years. The explanation of this surprising ecological fact is provided by number theory: having a prime number life cycle is a good strategy for avoiding predators. With a sufficiently large prime cycle any predators with similar life cycles will very rarely coincide with the most vulnerable stage of the cicada life cycle. It is also interesting to note that the two known cases of this phenomenon yield consecutive prime numbers—13 and 17—as the life cycles in question. This suggests that larger primes such as 19, 23, and so on, are impractical for biological reasons. And the smaller primes of 5, 7, and 11 leave the cicadas open to predators with life cycles of 10 years (as well as to predators with life cycles of 15 and 20 years), 14 years, and 22 years respectively. Again it looks like the mathematics—in this case elementary number theory—is carrying the bulk of the explanatory load here.

One final example of a mathematical explanation in ecology. Here I will also illustrate how analogical reasoning can play an important role in delivering the mathematical explanation. As I noted earlier, populations cycles are one of the more well-known solutions of the Lotka-Volterra equations, but there are other, more general models of population cycles. The more general models invoke a second-order differential equation (instead of the coupled first-order equations in the Lotka-Volterra model) and allow for single-species population cycles

<sup>&</sup>lt;sup>11</sup>Hence the problem is a tiling problem and not a sphere-packing problem.

[18]. This more general approach to population cycles is mathematically very similar to two-body problems in celestial mechanics, with its periodic solutions to two-body problems.<sup>12</sup> This interdisciplinary connection is interesting in its own right but it is much more than a mere curiosity. This analogy has the potential to drive a number of developments in population ecology. First, the similar mathematical treatment suggests that there ought to be an ecological counterpart of inertia in physics, and this has lead to investigations into "ecological inertia" (essentially cross-generational time lags in population responses to changes in environment) [23].

A second development arising from the analogy in question is that there should be stable and unstable orbits, as is the case with satellite orbits. In the rings of Saturn, for instance, there are well-defined gaps marking out the unstable orbits of this system. Similarly, in the asteroid belt between Mars and Jupiter there are gaps—the Kirkwood gaps—and these represent unstable orbits as a result of resonance effects with other massive bodies (most notably Jupiter). One might well expect to see similar gaps in population cycles [18, pp. 52–57] and these gaps, if they exist, would be explained mathematically, by appeal to very general structural features of the systems in question (essentially by an eigen-analysis). Not only would such explanations be mathematical, they would have been discovered by way of an analogy, facilitated by the mathematics in question.

If Baker, Lyon and I are right about such cases being cases of mathematics carrying the bulk of the explanatory load, there is still an interesting question concerning how mathematics can do this. There are several possibilities here:

- (i) Mathematics can demonstrate how something surprising is possible (e.g. stable two-species population cycles).
- (ii) Mathematics can show that under a broad range of conditions, something initially surprising must occur (e.g. hexagonal structure in honeycomb).
- (iii) Mathematics can demonstrate structural constraints on the system, thus delivering impossibility results (e.g. certain population abundance cycles are impossible).
- (iv) Mathematics can demonstrate structural similarities between systems (e.g. missing population periods and the gaps in the rings of Saturn).

<sup>&</sup>lt;sup>12</sup>Hence the phrase "ecological orbits", and the analogy of population cycles in ecology with planetary orbits [18].

If all this is right, it is simply a mistake to assume that because mathematical models ignore some of the biological detail they are not capable of delivering explanations. Indeed, to deliver the explanation in at least some of these cases might *require* that some biological detail be ignored.<sup>13</sup> Given the modal character of the three kinds of explanation just mentioned (involving possibility, necessity, and impossibility), it is hard to see how any causal explanation can deliver such explanations.

#### 4 A Cure for Physics Envy

Let me finish with a word of caution, lest I be accused of "physics envy". Physics envy is the intellectual crime of being over impressed with the technical, theoretical accomplishments of physics and trying to shoehorn ecology into more sophisticated mathematical treatments than are warranted by ecological data and theory [7, 16]. The mistake in question is not a mistake of using mathematics at all in ecology; it's the mistake of using inappropriate—and, in particular, overlycomplicated, inappropriate, and physics-inspired mathematics-in ecology.<sup>14</sup> Rather than being guilty of physics envy, I have been attempting to offer a cure for it—or at least offer something to ease some of the associated discomfort it brings on. I have argued that in at least some cases importing mathematical models from physics and liberating mathematical models in ecology of some of the biological detail can genuinely advance ecology. I am not advocating mathematics for mathematics sake (at least not here). Great skill is required to use mathematics in ecology in such a way to enlighten and not obscure<sup>15</sup> All I have argued is that when used effectively, mathematics can play a number of important roles in ecological theory. Moreover, the full range of these roles has not been fully appreciated in at least the philosophical literature on the applications of mathematics. Once the roles of mathematics in the special sciences are better appreciated and understood—especially the explanatory roles—the effectiveness of

 $<sup>^{13}</sup>$ See [4] for more on the role of abstraction in such explanations.

<sup>&</sup>lt;sup>14</sup>It is interesting to note that the pioneering work on population ecology, conducted independently by Lotka and Volterra, demonstrated quite different attitudes towards mathematization. Lotka was more inclined to import mathematics from physics and to invoke analogies to motivate such importation [25, 24]. While it would be unfair to charge Volterra with physics envy, still he seemed to have had no hesitation in adopting the mathematical methods of physics when developing ecological theories. In this sense, the debate over physics envy might well be traced back to differences in the methods of the two founding fathers of population ecology.

 $<sup>^{15}</sup>$ See [28] for more on this.

mathematics seems less unreasonable.

I have argued that mathematics can play a number of useful roles in ecological theory. Mathematics can represent biological facts and it is often able to do this is such a way as to make certain biological explanations more accessible. Mathematics is well suited to drawing attention to similarities between apparently different systems (and often provide the appropriate level of abstract representation for investigating the similarities). This, allows each of these areas to learn from one another, and reduces duplication of research. Finally, I argued that there are explanations in ecology where the mathematics carries the bulk of the explanatory burden, and these explanations are appropriately seen as mathematical explanations of biological phenomena.

Although I have focussed on ecology as my primary case study, I suspect that much of what I have said will carry over fairly straight-forwardly to at least some other special sciences. In particular, similar debates about the role of mathematical models, physics envy, and the like can be found in economics [29]. Not surprisingly, very similar models are employed in both economics (especially macroeconomics) and ecology (since both have exponential growth and decline as a fundamental assumption in their respective dynamics) so the generalisation to economics is not much of a stretch at all. Casting my net wider to other special sciences is not so straightforward, although I do expect similar stories, albeit with quite different mathematical models in the applications of mathematics in one special science, namely population ecology.<sup>16</sup>

### References

- [1] Azzouni, J. 2000. 'Applying mathematics: an attempt to design a philosophical problem', *Monist*, 83(2): 209–227.
- [2] Baker, A. 2005. 'Are there genuine mathematical explanations of physical phenomena?', *Mind*, 114(454): 223–238.

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- [3] Baker, A. 2009. 'Mathematical explanation in science, British Journal for the Philosophy of Science, 60: 611–633.
- [4] Batterman, R.W. 2010. 'On the explanatory role of mathematics in empirical science', The British Journal of Philosophy of Science, 61(1): 1–25.
- [5] Boyce, W.E. and DiPrima, R.C. 1986. Elementary Differential Equations and Boundary Value Problems, fourth edition, New York: John Wiley.
- [6] Bueno, O. and Colyvan, M. 2011. 'An inferential conception of the application of mathematics', Noûs, 45(2): 345–374
- [7] Cohen, J.E. 1971. 'Mathematics as metaphor', Science 172(14 May): 674–675.
- [8] Colyvan, M. 1999. 'Confirmation theory and indispensability', *Philosophical Studies*, 19(1): 1–19.
- [9] Colyvan, M. 2001. The Indispensability of Mathematics, New York: Oxford University Press.
- [10] Colyvan, M. 2001. 'The miracle of applied mathematics', Synthese, 127(3): 265–278.
- [11] Colyvan, M. 2002. 'Mathematics and aesthetic considerations in science', *Mind*, 111(441): 69–74.
- [12] Colyvan, M. 2009. 'Applying inconsistent mathematics', in O. Bueno and Ø. Linnebo (eds.), New Waves in Philosophy of Mathematics, Basingstoke UK: Palgrave MacMillan, pp. 160–172. Reprinted in M. Pitici (ed.), 2011. The Best Writing on Mathematics 2010, Princeton: Princeton University Press, pp. 346–357.
- [13] Colyvan, M. 2010. 'There is no easy road to nominalism', Mind, 119(474): 285–306.
- [14] Colyvan, M. and Ginzburg, L.R. 2003. 'The Galilean turn in ecology', *Biology and Philosophy*, 18(3): 401–414.
- [15] Colyvan, M. and Ginzburg, L.R. 2010. 'Analogical thinking in ecology', Quarterly Review of Biology, 85(2): 171–182.
- [16] Egler, F.E. 1986. 'Physics envy in ecology', Bulletin of the Ecological Society of America 67(3): 233–235.
- [17] Frege, G. (edited by P. Geach and M. Black) Translations from the Philosophical Writings of Gottlob Frege. Blackwell, Cambridge, 1970.
- [18] Ginzburg, L. and Colyvan, M. 2004. Ecological Orbits: How Planets Move and Populations Grow, Oxford: Oxford University Press.

- [19] Gotelli, N.J. 2001. A Primer of Ecology, third edition, Sunderland MA: Sinauer Associates.
- [20] Grattan-Guinness, I. 2008. 'Solving Wigner's mystery: the reasonable (though perhaps limited) effectiveness of mathematics in the natural sciences', *The Mathematical Intelligencer*, 30(3): 7–17.
- [21] Hales, T.C. 2001. 'The Honeycomb Conjecture', Discrete Computational Geometry 25: 1–22.
- [22] Hamming, R.W. 1980. 'The unreasonable effectiveness of mathematics,' American Mathematics Monthly, 87, 81–90.
- [23] Inchausti, P. and Ginzburg L.R. 2009. 'Maternal effects mechanism of population cycling: a formidable competitor to the traditional predator-prey view', *Philosophical Transactions of the Royal Society B*, 364: 1117–1124.
- [24] Israel, G. 1988. 'On the contribution of Volterra and Lotka to the development of modern biomathematics', *History and Philosophy* of the Life Sciences, 10, 37–49.
- [25] Kingsland, S.E. 1985. Modelling Nature: Episodes in the History of Population Ecology, Chicago: University of Chicago Press.
- [26] Levins, R. 1966. 'The strategy of model building in population biology', American Scientist, 54: 421–431.
- [27] Lyon, A. and Colyvan, M. 2008. 'The explanatory power of phase spaces', *Philosophia Mathematica (3)*, 16(3): 227–243.
- [28] May, R.M. 2004. 'Uses and abuses of mathematics in biology', Science, 303(6 February): 790–793.
- [29] Mirowski, P. 1989. More Heat than Light: Economics as Social Physics, Physics as Nature's Economics, Cambridge: Cambridge University Press.
- [30] Ruben, D.H. 1990. Explaining Explanation, London: Routledge.
- [31] Smart, J.J.C. 1990. 'Explanation—opening address', in D. Knowles (ed.), *Explanation and Its Limits*, Cambridge: Cambridge University Press.
- [32] Sober, E. 1983, 'Equilibrium explanation', *Philosophical Studies*, 43: 201–210.
- [33] Steiner, M. 1998. The Applicability of Mathematics as a Philosophical Problem, Cambridge, MA: Harvard University Press.
- [34] Wigner, E.P. 1960. 'The unreasonable effectiveness of mathematics in the natural sciences,' Communications on Pure and Applied Mathematics, 13: 1–14.

[35] Wilson, M. 2000. 'The unreasonable uncooperativeness of mathematics in the natural sciences', *Monist*, 83(2): 296–394.