Chapter 10
Mathematical Explanation in Biology

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Abstract Biology has proved to be a rich source of examples in which mathematics plays a role in explaining some physical phenomena. In this paper, two examples from evolutionary biology, one involving periodical cicadas and one involving bee honeycomb, are examined in detail. I discuss the use of such examples to defend platonism about mathematical objects, and then go on to distinguish several different varieties of mathematical explanation in biology. I also connect these discussions to issues concerning generality in biological explanation, and to the question of how to pick out which mathematical properties are explanatorily relevant.

Keywords Mathematical explanation • Biology • Indispensability • Optimization

1 Introduction

As is the case for most areas of contemporary science, biology is permeated with mathematics. This situation has potentially interesting implications both for biology and for mathematics. My focus in this paper is on explanation, and in particular on the explanatory role that mathematics sometimes plays in the context of biological theorizing. Philosophers interested in scientific explanation have started to look in more detail at biology as a potential source of test cases for more general theories of scientific explanation. And recent philosophical debates over the nature and role of scientific models have engaged with the issue of the explanatory role of models, in biology and elsewhere.

Philosophical investigation of the role of mathematics in empirical science has the potential to cast light not only on scientific methodology but also on epistemological and metaphysical issues concerning mathematics itself. Interest among philosophers in the topic of applied mathematics has been steadily increasing over the past several decades, spurred on initially by Quine and Putnam's so-called

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"Indispensability Argument" for platonism about mathematics.[1] In its contemporary guise, platonism is the view that abstract mathematical objects exist in some objective sense, and that the goal of mathematics is to give a true description of the realm of mathematical abstracta. According to the Indispensability Argument (IA), we ought rationally to believe in the existence of mathematical objects if we are scientific realists, because quantification over such objects is indispensable to our best scientific theories. Put another way, our grounds for believing in numbers are analogous to our grounds for believing in electrons. Each kind of object plays an indispensable role in science.

Early reaction to IA focused on the further reaches of theoretical physics, because it is here that the most complex and sophisticated mathematical apparatus tends to be employed. Philosophers unsympathetic to platonism (often referred to as nominalists, or – more recently – as fictionalists) tried to show how quantification over mathematical objects might be avoided. Perhaps the most well-known example of this kind of project is that undertaken by Hartry Field in his book, *Science Without Numbers*, where he showed – among other things – how Newtonian gravitational theory might be formulated in a manner that was free of ontological commitment to mathematics.[2] Defenders of IA pointed out that physics has become much more entangled in mathematics since Newton's time. What about the curved geometries of general relativity, or the infinite-dimensional Hilbert spaces of quantum mechanics?

Rather than meet this challenge head on, a second wave of nominalists took a different tack, arguing that more attention needs to be paid to what role mathematics is actually playing in science. Returning to the earlier analogy between numbers and electrons, electrons are not merely indispensable but they also play an *explanatory* role in science. For example, we can explain the track in the cloud chamber by positing that an electron was emitted by the source material. Quine's holism led him to largely ignore the details of which role was played by which theoretical posits in science. For the second-wave nominalists, this was a crucial mistake: we can legitimately resist commitment to abstract mathematical objects unless they play an indispensable *explanatory* role in science. According to such nominalists, there are no genuine mathematical explanations in science. Hence nominalism can be upheld without any need to reformulate our scientific theories.[3]

With this new twist on IA, attention switched away from theoretical physics to other areas of science, and to biology in particular. I shall return in Sect. 4 to consider the question of why biology is such a fertile ground for putative mathematical explanations. For the moment, however, I simply note that the most widely discussed examples of mathematical explanation in science have biological subject matter, as

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[1] Colyvan (2003) gives a good overview of the Indispensability Argument.

[2] Field (1980).

[3] Melia (2000, 2002).

we shall see shortly.[4] As a consequence, the nature of biological explanation has become a topic of considerable interest to many philosophers of mathematics.

The plan for this paper is as follows. In Sects. 2 and 3, I present and briefly discuss two cases of mathematical explanation in biology that have been prominent in the recent philosophical literature. The first concerns the life-cycles of periodical cicadas, and the second concerns the honeycomb-building behaviour of bees. In Sect. 4, I discuss the role of generality in explanation, and say a bit more about the different types of mathematical explanation within biology. In Sect. 5, I take up the question of why biology is so rich in mathematical explanations. In Sect. 6, I look at how to determine which mathematical features of a given biological phenomenon are genuine targets of explanation. I conclude, in Sect. 7, with some remarks about future directions for philosophical investigation into the role of mathematics in biological explanation.

2 Periodical Cicadas

The first case study, featuring a genuinely mathematical explanation of a biological phenomenon, is drawn from evolutionary biology. Its subject is the life-cycle of the North American ‘periodical’ cicada. Three species of cicada of the genus *Magicicada* share the same unusual life-cycle. In each species the nymphal stage remains in the soil for a lengthy period, then the adult cicada emerges after either 13 or 17 years depending on the geographical area. Even more strikingly, this emergence is synchronized among all members of a cicada species in any given area. The adults all emerge within the same few days, they mate, die a few weeks later and then the cycle repeats itself.

Biologists have long found features of the life-cycle of periodical cicadas mysterious, and this is reflected both in the substantial literature devoted to this topic and in biologists’ specific remarks.[5] There are at least five distinct features of this life-cycle for which explanations have been sought by biologists;

(i) The great duration of the cicada life-cycle.
(ii) The presence of two separate life-cycle durations (within each cicada species) in different regions.
(iii) The periodic emergence of adult cicadas.
(iv) The synchronized emergence of adult cicadas.
(v) The prime-numbered-year cicada life-cycle lengths.

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[4] See for instance Breidenmoser and Wolkenhauer (2015, this volume) who stress the importance of theorems such as the “robustness theorem” in biology, and Issad and Malaterre (2015, this volume) who emphasize the explanatory force of mathematical derivation in dynamic mechanistic explanations.

[5] For example, that “periodical cicadas are among the most unusual insects in the world” (Yoshimura 1997, p. 112).

Features (i) and (ii) concern the temporal range of the life-cycle. Biologists have argued that the long life-cycle of *Magicicada* is due both to the poor availability of nutrients for nymphs, and to the low soil temperatures for much of the year. Together these environmental stresses force nymphs to spend several years maturing into adults. Thus both (i) and (ii) seem explicable in terms of specific ecological constraints.

Features (iii) and (iv) concern coordination of the life-cycles of different individuals. Given that cicada nymphs require several years to develop into adults, and that the adult stage is very brief, having a fixed periodic emergence is advantageous in terms of maximizing mating opportunities. It ensures that the offspring of a particular mating generation will all appear at the same time, several years down the line. Synchronization makes sense for the same reason. Especially in areas which can support only a sparse population of cicadas, staggering different subpopulations to emerge at different times may produce so few adults at any one time that it is difficult to find mates. These explanations of (iii) and (iv) rely on (evolutionary) biological 'laws' which potentially apply to any organism with a long life-cycle and brief adult stage.

This leaves feature (v) to be explained, and with it one key question to be answered: why are the life-cycle periods *prime*? In other words, given a synchronized, periodic life-cycle, is there some evolutionary advantage to having a period that is prime? In seeking to answer this question, biologists have come up with two basic alternative theories.

An explanation of the advantage of prime cycle periods has been offered by Goles, Schulz and Markus (henceforth, GSM) based on avoiding predators. GSM hypothesize a period in the evolutionary past of *Magicicada* when it was attacked by predators that were themselves periodic, with lower cycle periods. Clearly it is advantageous – other things being equal – for the cicada species to intersect as rarely as possible with such predators. GSM's claim is that the frequency of intersection is minimized when the cicada's period is prime;

> For example, a prey with a 12-year cycle will meet – every time it appears – properly synchronized predators appearing every 1, 2, 3, 4, 6 or 12 years, whereas a mutant with a 13-year period has the advantage of being subject to fewer predators.[6]

A second explanation, proposed by Cox and Carlton and by Yoshimura, concerns the avoidance not of predators but of hybridization with similar subspecies.[7] A crucial factor for periodical insects is to have sufficient mating opportunities during their brief adult stage. Almost as important, however, is to avoid mating with subspecies that have different cycle periods to their own. For example, if some of a (hypothetical) population of synchronized 10-year cicadas were to mate with some 15-year cicadas then their offspring would likely have a period of around 12 or

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[6] Goles et al. (2001, p. 33).

[7] Cox and Carlton (1988, 1998), Yoshimura (1997).

13 years.[8] These hybrid offspring would emerge well after the next cycle of the 10-year cicadas and hence their mating opportunities would be severely curtailed.

The mathematical underpinnings of both the predation and the hybridization explanations lie in number theory. The mathematical link between primeness and minimizing the intersection of periods involves the notion of *lowest common multiple* (lcm). The lcm of two natural numbers, m and n, is the smallest number into which both m and n divide exactly; for example, the lcm of 4 and 10 is 20. Taking the predation explanation first, let us assume that m is the life-cycle period (in years) of a given cicada species, C_m, and n is the period of a periodical predator, P_n. If C_m and P_n intersect in a particular year, then the year of their next intersection is given by the lcm of m and n. In other words, the lcm is the number of years between successive intersections.

In fact the fundamental property in this context is not primeness but *coprimeness*; two numbers, m and n, are coprime if they have no common factors other than 1 (i.e., neither number is divisible by the other). All that is needed to underpin the above explanations are the following two number-theoretic results;

Lemma 1 *The lowest common multiple of* m *and* n *is maximal if and only if* m *and* n *are coprime.*[9]

Lemma 1 implies that the intersection frequency of two periods of length m and n is maximized when m and n are coprime. We get from coprimeness to primeness *simpliciter* with a second result;

Lemma 2 *A number,* m, *is coprime with each number* $n < 2\,\mathrm{m}$, $\mathrm{n}\ ^{1}\ \mathrm{m}$ *if and only if* m *is prime.*

The mathematics for the predation explanation is already contained in the above two Lemmas. Predators are assumed to have relatively low cycle periods.[10] It therefore suffices to show that prime numbers maximize their lcm relative to all lower numbers. More formally, we need to show that for a given prime, p, and for any pair of numbers, m and n, both less than p, the lcm of p and m is greater than the lcm of n and m. But this follows directly from Lemmas 1 and 2. From Lemma 2, p is coprime with m, since $m < p$. So, from Lemma 1, the lcm of m and p is $m.p$. The highest the lcm of m and n can be is $m.n$, but $n < p$, by assumption, so $m.n < m.p$. Furthermore, only prime numbers maximize their lcm's in this way, so in this respect primes are uniquely optimal.

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[8] Presuming that period length is a heritable trait, which is a presupposition of both candidate explanations.

[9] For proofs of these lemmas, see Landau (1958).

[10] Note that we are, by assumption, restricting attention to *periodical* predators, i.e., predators that have life-cycles that are greater than 1 year. Prime periods remain optimal even if annual predators are included. However, they are no better (or worse) than non-prime periods with respect to annual predators, since the lcm is n in both cases.

The hybridization explanation proceeds along very similar lines. The main difference is that, instead of a cicada species and a periodical predator, we assume that *m* and *n* are the life-cycle periods (in years) of two subspecies of cicada, C_m and C_n. A second difference, which does not affect the number-theoretic framework but may effect the way in which period lengths coevolve, is that there is a mutual benefit in the hybridization case for the two subspecies to have periods that are coprime. This makes it more likely that coprime periods may evolve which are not both prime. For example, if there are just two cicada subspecies in a given area, and they evolve to periods of 9 and 10 years respectively, then this is a local optimum. Nonetheless, primes remain the most robust solution, hence the optimization explanation still goes through.

The basic structure common to the predation and hybridization explanations is as follows:

1. Having a life-cycle period which minimizes intersection with other (nearby/lower) periods is evolutionary advantageous. [**biological 'law'**]
2. Prime periods minimize intersection (compared to non-prime periods). [**number theoretic theorem**]
3. Hence organisms with periodic life-cycles are likely to evolve periods that are prime. [**'mixed' biological/mathematical law**]
   When the law expressed in (3) is combined with
4. Cicadas in ecosystem-type, E, are limited by biological constraints to periods from 14 to 18 years.[11] [**ecological constraint**]
   it yields the specific prediction
5. Hence cicadas in ecosystem-type, E, are likely to evolve 17-year periods.

This explanation makes use of specific ecological facts, general biological laws, and number theoretic results. My claim is that the mathematical component, (2), is both essential to the overall explanation and genuinely explanatory in its own right. In particular, it explains *why* prime periods are evolutionarily advantageous in this case.

Following its initial presentation in Baker (2005), there have been several responses from philosophers with nominalist sympathies attacking various aspects of this example. Some have tried to show that the mathematical component is in fact dispensable.[12] Others have argued that there is a problematic circularity involved, since the fact to be explained – namely the primeness of the periods – itself involves mathematics.[13] Others have accepted the indispensability of the mathematics for the overall explanation, but claimed that the mathematical component is not itself

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[11] Clearly a parallel constraint may be formulated for 13-year cicadas, in which the ecosystem limits potential periods to the range from 12 to 15 years.

[12] Saatsi (2007), Daly and Langford (2009), Rizza (2011).

[13] Bangu (2008). I examine this objection in more detail in Sect. 6, below.

explanatory.[14] Responses to these various objections can be found in Baker (2009), and the debate here is ongoing.

An important point to keep in mind is the way in which the above explanation works at two different levels of abstraction. The same mathematical framework can be used to explain both the general fact that periodic organisms are likely to evolve periods that are prime, and the specific fact that a given cicada subspecies has a 17-year period. One way of conceptualizing this is in terms of the interaction between 'top-down' mathematical constraints and 'bottom-up' physical and biological constraints. General mathematical considerations are enough to derive the conclusion that the cicada periods are prime. When combined with the biological constraints specific to cicada physiology and their environment, which gives a range of viable period lengths between 12 and 18, this entails that the only periods that are both mathematically optimal and biologically possible are 13 and 17. The potential of mathematics to allow different levels of abstraction – and thereby generalization – is a characteristic feature of mathematical explanation in biology, and of mathematical explanation in science more generally. There are of course other, non-mathematical means of obtaining abstract explanations in biology, whether based on functional descriptions of phenomena, or on general principles such as the principle of transcription. However, none of these alternative routes to abstraction has the complete topic-neutrality of mathematics, and hence cannot achieve the level of generality of a mathematical explanation. The mathematics of the cicada explanation applies, in principle, to *any* interacting periodical phenomena, both biological and non-biological.

3 Bees and Honeycombs

For the second example of mathematical explanation in biology, we move from number theory to geometry. Why do honeybees build the cells of their honeycombs in the shape of hexagons? Biologists have long hypothesized that the answer has to do with economizing on the amount of wax per unit area. Wax is energetically costly to produce, so it makes sense for bees to use as little as possible when building their combs. As it turns out, it can be proved that the hexagonal tiling of the plane into unit areas is optimal in terms of minimizing the perimeter of the individual cells. This explains why honeybees build hexagonal cells.[15] I set out one possible regimentation of the explanation below:

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[14] Melia (2002), Yablo (2012).

[15] The first discussion of this example in the philosophical literature, as far as I am aware, is in Lyon and Colyvan (2008), although their remarks on it are relatively brief.

6. Building cells which minimize perimeter per unit area is evolutionarily advantageous (under constraints b_i)[16]
7. Regular hexagons minimize perimeter per unit area (among all tilings of the plane) [geometrical theorem]
8. Hence cell-building organisms are likely to evolve building techniques which produce hexagonal cells
9. Honeybees are limited by biological constraints b_i
10. Hence honeybees are likely to produce hexagonal cells

Biologists generally take this to be the best explanation of why honeybees build their cells in the shape of hexagons, and it clearly makes nontrivial use of mathematics.

One issue that has been the subject of recent debate among philosophers of applied mathematics concerns the link – if any – between mathematical explanation in science (including biology) and the 'internal' explanatoriness or otherwise of mathematical proofs. Mathematicians do seem to make distinctions between the relative explanatoriness of proofs, including between different proofs of the same result. The implication is that there may be proofs which are rigorous and which demonstrate *that* a result holds but which do not, in some important sense, show *why* it holds. However, there is little consensus, either among mathematicians or philosophers, concerning criteria for what makes a proof explanatory. Among the putative features cited are simplicity, non-redundancy, purity, and non-disjunctiveness. In an old paper, Mark Steiner asserts that a genuine mathematical explanation in science (MES) must feature an explanatory proof of whatever mathematical theorem lies at its core.[17] I think that Steiner is wrong about this, and that the honeycomb case study provides a particularly clear counterexample.

The issue turns on whether the core mathematical result has an explanatory proof. In the honeycomb example, we have the following theorem:

(Honeycomb Theorem) Any partition of the plane into regions of equal area has perimeter at least that of the regular hexagonal honeycomb tiling.

Despite the fact that the general conjecture dates back to antiquity, the above theorem was only proved in full generality by Thomas Hales in 2001. I shall begin by sketching some of the key ideas involved in Hales's proof.[18] As already mentioned, the basic problem is one of optimization, namely to minimize perimeter for a collection of cells of unit area. One of the major challenges in proving the Honeycomb Theorem is that it is not true locally. In other words, if the challenge is to enclose a single unit of area with the minimum perimeter then the optimal shape

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[16] The constraints here might include conditions such as it being energetically costly to produce the material to build the walls of the cells, that the cells be contiguous, and that the cells be of uniform area.

[17] Steiner (1978).

[18] Hales (2001). The full proof runs to 18 pages, so this will be of necessity no more than a brief overview.

is not a hexagon but a circle.[19] Once we shift to consider multiple cells, however, it becomes clear that using circles is disadvantageous because they cannot be fitted together without leaving gaps between the cells. When we are dealing with regular polygons, therefore, local performance (with respect to area to perimeter ratio) can be improved by increasing the number of sides, so that the polygon more closely approximates a circle. However, if we want the polygons to fit together without gaps, then it is a direct consequence of Euler's formula ($v–e + f = 2$) that the average number of sides cannot be more than 6.[20] Hence any polygon with more than six sides must be counterbalanced by some other polygon in the tiling that has fewer than six sides. Hales's approach is to encapsulate the above insight by introducing into the key optimization equation a penalty term that quantifies the global 'cost' of a polygon having more than six sides.

A second way of locally enlarging the area enclosed is by using shapes with curved sides rather than straight sides. Thus, for a given polygon, replacing a given straight side with a convex curved side (i.e., one that bulges out) increases its area to perimeter ratio. However this means that one of its neighbouring polygons must have a corresponding side that is concave, thus reducing its own area to perimeter ratio. Hales therefore adds a second penalty term into the governing equation that represents the global cost of a polygon having curved sides. The proof then proceeds by verifying that the penalty terms in the optimization equation correctly characterize the effects of changing the shapes of the constituent polygons in various ways, and then by deriving that the regular hexagon is optimal with respect to these penalty terms.

What I want to argue is that Hales's proof does not provide an *explanation* of the truth of the theorem. There are at least four reasons for thinking that Hales's proof, ingenious though it is, does not explain *why* the hexagonal tiling of the plane is optimal. I shall present and discuss these reasons in increasing order of philosophical abstraction.

The first reason (purely circumstantial, but important nonetheless) is that mathematicians working in this area appear not to find Hales's proof especially explanatory. This is manifested both in comments made about the proof, and also in attempts to 'improve' various aspects of it. Some of these improvements have been in minor technical details (for example Frank Morgan has recently shown that one of the lower bounds in Hales's Chordal Isoperimetric Inequality can be raised from π/8 to π/4). But there have also been attempts, unsuccessful thus far, to find "a simpler, more geometric version of [Hales's] proof."[21]

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[19] This in known in the mathematics literature as the *isoperimetric problem*.

[20] Since every vertex in a finite graph corresponds to at least three half edges, $e \geq (3/2)\, v$, so (by substitution into Euler's formula), $(2/3)\, e–e + f = 2$. Hence $f = (1/3)\, e + 2$, from which it follows that $e < 3f$. Since an edge borders two faces, the average number of edges per face cannot be greater than 6.

[21] Carroll et al. (2006, p. 1). Note the implication that both simplicity and purity will tend to enhance the explanatoriness of a proof.

Secondly, while there seem to be good motivating reasons for including penalty terms of the sort described in the previous section, these reasons do not show why these penalty terms take the particular values that they do. Consider the full statement of Hales's crucial *Hexagonal Isoperimetric Inequality*:

> Consider a curvilinear planar polygon of N edges, area A, and perimeter P. Let P^* denote the perimeter of a regular hexagon of area 1. For each edge, i, let a_i denote how much more area is enclosed than by a straight line. Then
>
> $$P/P* \geq \min\{A,\ 1\} - .5\sum a_i - .0505/24\sqrt{12}\,(N-6),$$
>
> with equality only for the regular hexagon of unit area (Morgan 2000, pp. 161–2)

Even ignoring the technicalities of the background definitions, it is possible to pick out from the above equation the penalty terms for a polygon having curved sides (as a function of a_i) and for having extra edges (as a function of N). Focusing on the second of these, the specific value of the penalty term is $.0505/24\sqrt{12}\,(N-6)$. The presence of the (N – 6) term can be explained by reference to the earlier remarks concerning Euler's formula: we know from this that the average number of sides of polygons tiling the plane cannot be greater than 6, hence it is only at this point that the overall penalty term becomes positive. But what about the coefficient $.0505/24\sqrt{12}$ on the front of the penalty term? Nothing in the general argument motivating Hales's approach gives any guidance about the specific value of this coefficient.[22]

A third reason for questioning the explanatoriness of Hales's proof is foreshadowed in the remark quoted earlier about searching for a 'simpler, more geometric version' of the proof. The fact is that the bulk of Hales's proof of the Honeycomb Theorem involves not geometry but other quite distinct areas of mathematics such as measure theory and numerical analysis. Implicit in the quoted remark is the assumption that a more geometric proof would also be more explanatory. The point behind this is presumably not that there is anything explanatorily distinctive about geometry per se, but rather that the theorem in question is geometrical and hence it makes sense to favour geometrical reasoning in its proof. The presumption is that 'purity' of this sort will, other things being equal, make for a more explanatory proof.

While I am hesitant to emphasize impurity as a reason in its own right for questioning the explanatoriness of Hales's proof, the above discussion does pave the way to a fourth and final reason which has considerably more force. In a nutshell, the problem with Hales's proof lies not with its impurity but rather with the specific non-geometrical apparatus that it utilizes. Recall that one of the two approaches mentioned as featuring in the proof is numerical analysis. The overall goal of this subfield of mathematics is the design and evaluation of techniques to give

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[22] To be clear, Hales's proof is fully rigorous. In other words, the 'mysterious' coefficient works to establish the theorem that regular hexagons are optimal. What is not clear is *why* this coefficient works.

approximate but accurate solutions to ‘hard’ problems in continuous mathematics, in other words problems for which no closed-form solution is available.[23] In his proof of the Honeycomb Theorem, Hales uses numerical analysis to verify – through brute computation – some of the approximations he makes concerning upper and lower bounds. Indeed the central part of the proof involves various subdivisions into arbitrary-looking special cases. As Carroll puts it, Hales’s proof “becomes a long, arduous case analysis using five separate intermediate lower bounds.”[24] The two key features here are disjunctiveness and the role of computations. These are both features that philosophers have argued tend to weaken the explanatory power of mathematical proofs.[25] It also seems to fit with our intuitions. Typically, if a conjecture is broken down into a large number of separate subcases, each of which is then verified by a distinct computation, this in itself does not give a sense of *why* the conjecture is true. Instead it has more of the feeling of a ‘brute force’ verification, as when we check the truth of some claim about a finite domain by going through each case one by one.

I conclude that the Hale’s proof does not explain why the Honeycomb Theorem holds, although it certainly establishes that it holds. It is also clear that the Honeycomb Theorem is an essential part of our best explanation of why bees build hexagonal cells. This is enough to show that Steiner’s thesis is mistaken. *Contra* Steiner, it is not necessary for a mathematical result to have an explanatory proof in order for it to feature in a mathematical explanation of some biological (or other physical) phenomenon.

4 Aspects of Generality

As has already been mentioned, a key function of mathematics in the context of explanation is to facilitate generalization, by piggybacking on the inherent capacity of mathematics for abstraction. Thus the number-theoretic apparatus in the cicada example can potentially be applied to any periodical organism, and is not restricted to cicadas, or even just to insects. Similarly, the results in numerical analysis that underpin the honeycomb example can also be applied to any physical situation that involves perimeter minimization.

Philosophical discussions of scientific explanation often emphasize the connection between explanatoriness and generality, and this holds equally for philosophical discussions of explanation in mathematics. The basic idea – which gets cashed out differently in different analyses – is that an important way of explaining a given

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[23] A distinctive feature of numerical analysis is the use of algorithms, and other methods of numerical approximation. This is in contrast to the symbol manipulation characteristic of purely analytic approaches. Hence there is a greater likelihood of numerical analysis producing methods and results that ‘work’, in some specified domain, but are such that it is not clear *why* they work.

[24] *ibid.*, p. 7.

[25] See e.g., Baker (2008).

phenomenon is to show how it is deducible from, or caused by, or is a special case of some more general phenomenon, law, or pattern. If there is something to this idea, then it would seem to suggest that the generality that contributes to the explanatoriness of a mathematical result in a MES is something that should also make the proof of the result more explanatory in purely mathematical terms.

To see why the above argument is too quick, we need to consider how generality plays out in some actual examples. So let us return to our two favourite case studies from biology. In the cicada case, the explanation is general in the sense of showing why any periodical organism with periodical predators is likely to evolve a life-cycle period that is prime. In the honeycomb case, the explanatory argument generalizes to cover any situation in which it is evolutionarily advantageous to enclose large numbers of equal areas using a minimum of materials. So these explanations are indeed general, in virtue of potentially applying to a wide range of organisms under a wide range of ecological conditions. However, the generality in question is restricted in various ways – to organisms acted upon by natural selection, given the actual laws of chemistry and physics – and thus, I shall argue, falls short of the kind of generality that is explanatorily relevant in mathematics.

Consider once again the honeycomb case. Faced with the core result of the Honeycomb Theorem, mathematicians are interested in whether – and, if so, how – Hales's proof generalizes to scenarios in which various key assumptions are altered or eliminated altogether. For example, are hexagons optimal for tiling other kinds of surface such as the sphere, or the torus, or the Möbius strip? What if we allow a mixture of two different sizes of cells? What if we assume that the walls of the cells have non-negligible width? And so on. None of these various questions are directly answered by Hales's proof, nor by any simple transformation of it, which is another important reason why mathematicians consider it to be relatively unexplanatory.

Notice, however, that there is no contradiction – nor even any real tension – in the honeycomb example featuring a biologically general result with a mathematically non-general proof. The point is that mathematicians are typically interested in a level of generality that is significantly greater than what is relevant to scientific applications. Hence lacking this degree of generality is no handicap to a given MES being a good scientific explanation, even though it may rule it out as being straightforwardly transformable into a good pure mathematical explanation.[26]

The distinction between mathematical and biological generality can also be couched in modal terms. A familiar distinction is between different strengths of possibility (or necessity). A weak form of possibility is logical possibility: any consistent state of affairs is logically possible. Whether mathematical possibility is a distinct kind of possibility is open to debate. In any case, a stronger form of possibility is physical possibility: roughly, a state of affairs is physically possible if it is consistent with the (actual) physical laws. Can sense be made of other more

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[26] Note that nothing I have said here denies the importance of mathematical explanatoriness to scientific explanatoriness. I am simply arguing that the latter is not a sufficient condition for the former.

specific forms of possibility such as chemical possibility, biological possibility, and so on? Intuitively it does seem as if certain physically possible outcomes are not 'biologically possible'. For example, it seems physically possible for there to be a fish that dissolves when placed in water. Yet it is hard to see how such a creature could have actually evolved.

Reflection on the modal aspects of explanation may also be helpful in classifying different kinds of mathematical explanation in science. To date, philosophical discussion of MES has focused on specific case studies, and little attempt has been made to construct any broader classification scheme. As an initial step towards this goal, I suggest that the examples of MES that appear in the literature can be usefully grouped under three general headings: Constraint MES, Equilibrium MES, and Optimization MES.

A *Constraint MES* explains why some physical outcome is impossible by showing that (in some sense) it is mathematically impossible. A classic example of Constraint MES can be found in the Bridges of Königsberg problem, which Euler answered in the early eighteenth century. The question was why no-one could cross the seven bridges of Königsberg without crossing some bridge more than once. Euler's answer was couched in terms of graph theory, and showed that the corresponding pure mathematical graph could not be traversed by traveling along each edge exactly once. The modal link in such cases is very clear: mathematical impossibility entails physical impossibility.[27] There are also further entailments from physical impossibility to other forms of impossibility that are especially relevant to biological phenomena: for example, chemical impossibility, physiological impossibility, and (perhaps) evolutionary impossibility.

An *Equilibrium MES* explains why some physical outcome occurs by showing that it is mathematically inevitable (or almost inevitable) across a wide range of starting conditions. For example, the eventual resting point of a marble that is rolled around the inside of a bowl is insensitive to the initial position, angle, and velocity when it is released. A more sophisticated example of an Equilibrium MES is discussed by Colyvan, and concerns the presence of gaps in the asteroid belt between Mars and Jupiter.[28] Such explanations are often statistical in nature, hence the modal link between mathematical model and physical situation is less straightforward. A well-known example of an Equilibrium MES in biology is Fisher's principle concerning sex ratios. The mathematical argument shows that a 1:1 ratio of males to females is an evolutionarily stable strategy, and that – under a wide range of conditions – any deviation from this ratio will provide an incentive for parents to produce more of the minority sex and thus push the ratio back to 1:1.[29]

An *Optimization MES* explains why some physical outcome occurs by showing that it is mathematically optimal, in some relevant sense. Both the cicada and honeycomb cases lie within this category of MES. The modal element of Optimiza-

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[27] For further discussion and references, see Pincock (2012, 51–54).

[28] Colyvan (2010).

[29] See Gould (2002, pp. 648–9).

tion MES's is easy enough to see. If a certain outcome is mathematically optimal then it is (mathematically) impossible for some distinct, better outcome to occur. However, the mathematically optimal solution may not be physically possible, or biologically feasible, or it may simply not have been 'found' (evolutionarily speaking). Although the cicada case involves a mathematically optimal solution, since the life-cycle periods are prime, and perfect hexagons are mathematically optimal in the honeycomb case, there is a second, related problem related to honeycombs where such mathematical optimality is not present. For there is also a three-dimensional version of the honeycomb problem, in which the cells are thought of as hexagonal 'tubes' and we consider how they should be fitted back-to-back so as to maximize volume to surface area ratio. In 1964, László Tóth discovered that the trihedral pyramidal shape used by bees, which is composed of three rhombi, is not mathematically optimal.[30] A cell end made up of two hexagons and two smaller rhombi would in fact be .035 % more efficient. Presumably the extra complexity of this second solution makes it inferior from an evolutionary point of view. This shows that sometimes the most general mathematical solution to an optimization problem may be undermined by considerations that were inadvertently excluded in the assumptions and constraints used to define the mathematical problem.

In the next section I shall take up the question of why so many of the prominent examples of MES are to be found in biology. One crucial part of the answer turns on the way in which Optimization MES's find a natural home within the biological sciences.

5 Why Biology?

As has already been noted, the history of the debate over the merits of indispensability-style arguments for mathematical platonism has seen a sharp switch of focus away from the higher reaches of theoretical physics and towards other areas of science such as biology and meteorology. Why has this switch taken place? I think that several interrelated reasons can be identified.

Firstly, the fact that explanation is a key component of recent versions of the Indispensability Argument introduces a countervailing pressure on the complexity of examples of applied mathematics. If all that matters is indispensability, then it makes sense to choose examples in which the mathematics (and often the science, also) is as sophisticated as possible. Hence the early predominance of examples from theoretical physics, with complex geometries and esoteric algebraic structures in abundance. But if what we care about is not indispensability per se, but rather indispensability for explanation, then it is better to choose examples in which our intuitions concerning explanatoriness are relatively clear. Such examples tend to be less complex from a mathematical point of view. In general, the special sciences

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[30] Tóth (1964).

are a good place to look for examples of indispensable mathematics playing an explanatory role. Typically, the mathematical component is complex enough not to be trivially dispensable, but not so complex as to muddy the issue concerning explanatoriness. In this respect, the special sciences have a ‘Goldilocks’ aspect: the mathematical apparatus that is employed is neither too complex nor too simple.

A second reason that philosophers have moved away from the most technical examples of applied mathematics in physics is that, because of their highly theoretical nature, the divide between the mathematical and physical components of such examples is often unclear. This is an important drawback in the context of debates over IA, since the ultimate target of IA is to defend platonism, which asserts the existence of abstract objects. If the distinction between abstract and concrete is controversial, or open to interpretation, as is arguably the case in contemporary quantum mechanics, then the force of the examples is thereby undermined. Note that this second reason has nothing directly to do with explanation. It is also worth noting that the issue of where mathematics stops and the physical sciences start can also be an issue in some of the putative examples of MES in the special sciences. Thus in the honeycomb example, the mathematical explanation concerns geometrical objects such as perfect hexagons. But are these geometrical objects abstract or concrete?

The two reasons given so far help explain the shift of attention, in debates concerning IA, towards examples from the special sciences. But there is a further question of why biology in particular is so well-represented in discussions of MES. Here I think the crucial feature is the role of optimization explanations in biology. Optimization MES is one of the three main categories of MES, and there is no doubt that this style of explanation is a distinctive feature of theorizing in biology, especially in evolutionary biology. The use of such explanations is not without controversy, and there is a growing philosophical literature looking both at the pros and cons of optimization explanations and on more fully analysing what, if anything, makes such explanations distinctive.[31] Since my emphasis here is on the import of such examples on debates in the philosophy of mathematics, I will not spend more time here on this particular question. It is worth noting, however, that optimization explanations are not the exclusive preserve of evolutionary biology. Engineering, for example, often addresses itself to problems that involve optimization. In some cases such problems are analogous to ones that are found in evolutionary biology. The honeycomb example, at its core, concerns the problem of achieving a goal using the minimum amount of material, and as such is an optimization problem of the sort that is routinely faced in various human-devised manufacturing processes.[32]

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[31] See e.g., Potochnik (2007). There are also important references in the philosophy of biology literature, for example Orzack and Sober (2001).

[32] More controversially, some physicists have argued for optimization explanations in cosmology, in which the values of the basic physical constants are ‘explained’ in terms of producing universes that are more conducive to the formation of black holes, which in turn (according to certain theories) spawn further universes as ‘offspring.’ For more on such explanations, see Smolin (1999).

6 Salient Mathematical Properties

The final question I shall address in connection with mathematical explanation in biology concerns the choice of mathematical properties that feature in such explanations. Especially if MES is supposed to carry ontological burdens, as is the case in recent versions of the Indispensability Argument, it is important that the mathematical properties involved are legitimate targets of scientific explanation. Otherwise we run the risk of taking on ontological commitments to mathematical entities that may in fact be avoidable. The problem arises because there are a proliferation of mathematical properties that may happen to apply in a given physical situation. Cicadas have periods of 13 or 17 years. These numbers are prime, but they also share other mathematical properties, such as being odd, and being the sum of two perfect squares ($13 = 4 + 9; 17 = 1 + 16$). Does this mean that it is legitimate to ask *why* cicadas have periods that are the sum of two perfect squares?

A more general version of this worry has been articulated by Sorin Bangu as an objection to explanatory versions of IA.[33] Take the cicada example. Bangu points out that the question, "Why is the duration (in years) of the life-cycle of periodical cicadas a prime number?", itself makes reference to mathematical objects. He argues that the indispensability of mathematics (and in particular, number theory) to explaining this fact does nothing to establish the platonist position because it begs the question against the nominalist. The nominalist can simply reject the explanandum, arguing that it is not true that the duration of cicada life cycles is a prime number, because numbers do not exist! I have argued elsewhere that there are various moves that the platonist can make in response to Bangu here, and hence that the circularity objection per se is not fatal to the explanatory Indispensability Argument.

The more specific worry I want to examine here concerns how to distinguish genuine questions concerning mathematical properties of biological phenomena from spurious questions. For example, "Why do cicadas have prime periods?", seems like a genuine question., whereas "Why do human beings have a prime number of legs?" does not. A simple way to draw the distinction would be just to appeal to scientific practice. A question is a genuine scientific question if it is taken seriously by a significant number of experts in the relevant scientific field. If enough biologists take the question of the primeness of cicada periods seriously, then *ipso facto* it is a genuine scientific question.[34]

But can more be said about the distinction, beyond appeal to scientific practice? I think that it can, and I shall sketch an account that aims to draw the distinction in a principled way. The question I am concerned with is the following: what makes

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[33] Bangu (2008).

[34] This approach is explored further in Baker (2012), where the concept of *science-driven mathematical explanation* is introduced.

a mathematical property, *M*, that applies to a physical phenomenon, *P*, a legitimate target of scientific explanation? For ease of exposition, I shall introduce the term *salience*, and say that a mathematical property is salient (in a given physical context) if it is a legitimate target of scientific explanation in that context. My claim is as follows:

> Salience Thesis A mathematical property, *M*, is not salient with respect to a physical phenomenon, *P*, if there is some other mathematical property, *M**, such that the best explanation of why *M* applies to P also explains why *M** applies to *P*, but not vice-versa.

The above Thesis is easier to grasp in the context of an actual example. As mentioned above, the durations of cicada life-cycles have various mathematical properties in addition to primeness. Let *M* be the property of being the sum of two perfect squares. According to the Salience Thesis (ST), this is not a salient property in the cicada example. Why not? Because there is another mathematical property, primeness, that also applies. Moreover, the best explanation of why cicada periods are prime (as presented in Sect. 2), shows why the periods are prime and why they lie in the range $11 < n < 19$. These two facts jointly entail that the periods must be the sum of two perfect squares (since the only primes in this range are 13 and 17) and hence explain it. Conversely, there seems to be no explanation of this latter fact that does not go via the property of primeness. Perhaps there is some such explanation to be found. But it is hard to conceive of how being the sum of two squares could make a difference to the evolutionary fitness of a given period length.

A similar argument applies to the question of why human beings have a prime number of legs. Intuitively, the only reason we have a prime number of legs is that we have 2 legs, and 2 is prime. The salient property here is 2-ness. The property of primeness is not doing any independent explanatory work in this particular context. Or, for a slightly more biologically sophisticated example, consider the fact that *C. Elegans*, a favourite ‘model organism’ in biology, has 1,031 cells, and that 1,031 is a prime number. Why does *C. Elegans* have a prime number of cells? As with the human legs example, if there is an explanation of this fact that it will presumably proceed via an explanation of why *C. Elegans* has 1,031 cells in particular.

It should also be noted that the salience or non-salience of a given mathematical property in a given biological context may itself be an open scientific question, and a question that may end up being answered one way or the other either by further empirical research or by the development of a convincing explanation. Arguably this was initially the case in the cicada example. Until the predation and hybridization explanations were formulated, there were many biologists who assumed that primeness in this context was not a salient property, but merely a coincidental by-product of the fact that the life-cycles had periods 13 and 17. Being the target of scientific explanation is thus neither necessary nor sufficient for salience. In this sense, salience has a normative dimension and does not simply reduce to being coextensive with the web of mathematical properties that feature in actual scientific practice.

7 Conclusion

There are various interesting potential directions for further philosophical work on mathematical explanation in biology. Firstly, there are other areas of mathematics that may play an explanatory role in biology, such as statistics and topology, but which have not yet been discussed in any detail in the context of debates concerning indispensability. Secondly, there are interesting questions concerning the role of laws in biology – whether mathematical or otherwise – and how this impacts on different models of explanation, in particular Hempel's deductive-nomological account of explanation. Thirdly, some recent and scientifically controversial examples of explanation in biology have crucial mathematical components. One example is the formulation of scaling laws, such as laws relating the total length of an organism's vascular system to its body mass, and attempts to explain such laws by appeal to results from fractal geometry.[35] Finally, there is definitely further work to be done in the classification of different types of MES within biology, both to augment the tripartite scheme suggested in Sect. 4, and to get clearer about the philosophically important differences between the different types. There is little doubt, therefore, that biology will continue to be centre stage in debates concerning the explanatory role of mathematics in science.

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[35] West and Brown (2004).

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