Measuring as a new mode of inquiry that bridges evolutionary game theory and cancer biology

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Abstract

We show that as game theory was transferred from mathematical oncology to experimental cancer biology, a new mode of inquiry was created. Modelling was replaced by measuring. The game measured by a game assay can serve as a bridge that allows knowledge to flow backwards from target (cancer research) to source (game theory). Our finding suggests that the conformist and creative (Houkes & Zwart, 2019) types of transfer need to be augmented. We conclude by introducing the expansive and transformative types to get a four-tier typology of knowledge transfer.

1 Introduction

Cancer is being increasingly recognized as an evolutionary disease. A malady due in part to the evolutionary dynamics of somatic cells within our bodies. Thus, understanding and treating cancer has required scientists to adopt ideas and develop new methods from evolutionary theory.[1]

Mathematical oncology is a field in cancer research that focuses on using mathematical and computational modeling to study cancer. Evolutionary game-theoretic (EGT) modeling is a prominent strain of modeling in mathematical oncology. It developed through knowledge transfer from theoretical evolutionary biology and economics.

In mathematical oncology, as we discuss in Section 2, a typical EGT modeling paper begins by imagining – in the style of Weisberg's (2013; Ch. 4) folk ontology – a scenario of two or more cells competing. The theorist views the interacting cancer cells as having different behaviors, analyzes potential outcomes of the interaction, and summarizes them in terms of Darwinian fitness in a "payoff matrix." The mathematical oncologist then feeds this payoff matrix as a parameter to differential equations or computer simulations for further analyses (for a philosophical introduction to evolutionary game-theoretic analyses, see O'Connor (2020)).

Starting with the imagining of interactions limits the EGT modeler to indirect representations (in the sense of Weisberg (2007)). To address this limitation of EGT modeling, Kaznatcheev et al. (2019) developed a "game assay" as we discuss in Section 3. This game assay uses a specifically designed experimental measurements to produce a formal fitness function and game payoff matrix from empirical cancer systems in the lab. To the cancer biologists, the game assay offers a new method of studying cancer.

[1]For a recent philosophical discussion of cancer, see Plutynski (2018).

To the philosophers, the game assay offers an opportunity to deepen our understanding of templates in knowledge transfer. Theoretical templates are 'general representational devices occuring within a theory' (Humphreys, 2019, p. 114) that 'can be successfully used to represent a variety of different phenomena within the domain of that theory.' Certain computational templates allow scientists to both represent a target system and also facilitate quantitative manipulation (Houkes & Zwart, 2019). Of the knowledge that is transferred between disciplines, templates are some of the most studied in the recent knowledge transfer literature (Herfeld & Lisciandra, 2019).

By using Weisberg's (2007) definition of modeling, we can see that much of the recent literature is focused on the use of templates in the theoretical modeling mode of inquiry. This is unsurprising, given the origin of the concept of templates in Humphreys's (2002) analysis of computational models. Does this mean that templates cannot transform from theoretical to experimental modes? We give a resounding no. In Section 4, we detail how the game assay created measurement as a non-modeling mode of inquiry for game templates during their transfer from mathematical oncology to experimental cancer biology. We use this to show that templates do not have to respect the theoretical-vs-experimental boundary implicit in Humphreys (2019).

As philosophers, we need to elaborate the mapping from a formal template to a target domain, if we want to understand how the game assay transformed its mode of inquiry. In Section 5, we show how to decompose any template-to-target mapping into two parts: conceptual and concrete. In our case study of the transfer of games as templates from mathematical oncology to experimental cancer biology, it is the conceptual part of the map that was transformed. This allowed the change in mode of inquiry. The malleability of the conceptual part of the mapping challenges Houkes and Zwart's (2019) claim of the inseparability of a template from its intensional interpretation.

A fundamental consequence of this new measuring mode of inquiry is that it allows for a reversal in the flow of knowledge from target to source. This allows us to explore the template-as-bridge metaphor in Section 6.

We conclude in Section 7 with a typology of knowledge transfer that augments Houkes and Zwart's (2019) conformist-vs-creative forms of transfer with our new dimension of change in the mode of inquiry. We hope that this new four-tier typology will allow philosophers of science to better study the application of mathematical constructs beyond theoretical modeling.

2 Reductive games: EGT modeling in mathematical oncology

Evolutionary game theory (EGT) in mathematical oncology is used in much the same way as EGT in more traditional theoretical biology. The game structure is interpreted from the perspective of individuals, except the charismatic macroscopic animals of zoology are replaced by the cancer cells of oncology (Hummert et al., 2014; Wölfl et al., 2021).

As an example of a typical use of EGT modeling in mathematical oncology, consider the Go vs Grow game introduced by Basanta et al. (2008). One of the key steps in going from a benign tumor to a malignant cancer is metastasis or the ability of a cancer to spread from one organ to another non-adjacent organ. According to Basanta et al. (2008), to achieve this, a cancer cell has to transition from a simple proliferative cell to a motile one. However, motility usually involves a cost to the cell. Basanta et al. (2008) represent this cost by the payoff matrix:

$$G^{\text{Go vs Grow}} = \begin{pmatrix} \frac{b}{2} + \frac{1}{2}(b-c) & b-c \\ b & \frac{b}{2} \end{pmatrix} \tag{1}$$

Where the first row corresponds to the payoffs for a Motile (or Go) cell and the second row corresponds to the payoffs for a Proliferative (or Grow) cell. As in traditional macroscopic EGT,

the description of this game features two cells, with the strategy of the first cell determining the row of the matrix and the strategy of the second cell determining the column – the matrix element thus specified is then the fitness effect on the first cell.

The particular kind of payoff matrix in equation (1) is meant to represent the intuition of how two cells interact as follows. When meeting at random in a resource spot, if both cells are motile, then one of them gets to stay in the resource spot and consume all the resources, and the other has to pay a cost c to move and find a new empty site with resources b. Which case happens to a particular cell is by chance, so they are weighted by $1/2$. On the other hand, if a motile cell meets a proliferate cell, then the motile cell will have to move for sure $(b-c)$ but the proliferate can stay and eat all the resources (b). Finally, if two proliferate cells are in the same resource spot then they simply share the resources with $b/2$ for each.

Given that the kind of explanation above tends to reduce the game to the interactions of (or a few) individuals, Kaznatcheev (2017, 2018) calls this sort of game a *reductive* game. Theorists in this tradition tend to explain population-scale phenomenon by citing interactions between individual units that make up that population. This interpretation takes players as individuals, strategies as behaviors-of-individuals, and payoff as token fitness.

A salient feature of reductive games are their imaginary origins in a folk ontology (Weisberg, 2013, Ch. 4). Like in the Go-vs-Grow, where we imagine two hypothetical cells that might meet and might move or not. Mathematical oncologists, or biologists in general, may give the imagined scenario more realism by, for instance, substituting in the language of specific motility transitions for the strategies (e.g., the epithelial-mesenchymal transition and its reversal process). Indeed, gradually complexifying a model with biological details has been a standard approach in biology more broadly, with the conviction that as simple models get more complex, 'they come to resemble the world more' (Dawkins, 1976, p. 79). However, no amount of refining the terms used to describe the interaction changes the imaginary nature in how a reductive game is conceived.

3 Effective games: Game assay in experimental cancer biology

To avoid this first step of imagining a reductive game, Kaznatcheev et al. (2019) develop an experimental procedure called the game assay to determine a game's payoff matrix in an empirical non-small cell lung cancer (NSCLC) system in a glass plate (in vitro).

Kaznatcheev et al. (2019) start by identifying the strategies. In the clinic, NSCLC initially responds to a drug Alectinib but eventually becomes resistant to this therapy. Thus, Kaznatcheev et al. (2019) grew a patient-derived drug sensitive cell line (henceforth "parental") and – through a drug-escalation protocol – created a drug resistant cell line (henceforth "resistant"). Cells of "parental" and "resistant" types were genetically modified to express a green and red fluorescent protein, respectively, so that they could be distinguished under the microscope. The resultant green and red fluorescent "parental" and "resistant" cells were taken by Kaznatcheev et al. (2019) as the two strategies to be studied.

With the strategies identified, Kaznatcheev et al. (2019) considered four different environments in which to study the evolution of these two cell types. The cells were grown on glass plates (in vitro) with or without the presence of Alectinib and with or without the presence of cancer-associated fibroblasts (CAFs; another cell tell that is known to be important to NSCLC, but that are not themselves cancer cells) resulting in four conditions: DMSO (no drug, no CAFs), DMSO + CAF, Alectinib, and Alectinib + CAF. These four global environmental conditions stand in for different situations that a NSCLC patient encounters prior to and during treatment.

The actual experiments then consisted of seeding the glass plates with different initial pro-

portions of resistant vs parental cells and growing them for 5 days while filming the change in green vs red fluorescence under the microscope. The change in the number of red and green under the microscope over the 5 day period provides an estimate of the growth rate of the two types. Plotting this growth rate against the initial seeding proportion (p) of the two types produces a discrete approximation of a fitness function. By taking the line of best fit to these discrete points, Kaznatcheev et al. (2019) get a fitness function. The $p = 0$ and $p = 1$ interscepts of this fitness function then serve as the entries for the payoff matrix. Thus, Kaznatcheev et al. (2019) arrive at a measurement of the four payoff matrices corresponding to the four conditions:

$$\begin{aligned} G^{\text{DMSO}} &= \begin{pmatrix} 2.5 & 2.4 \\ 4.0 & 2.7 \end{pmatrix} \\ G^{\text{DMSO + CAF}} &= \begin{pmatrix} 2.6 & 3.5 \\ 3.1 & 3.0 \end{pmatrix} \\ G^{\text{Alectinib}} &= \begin{pmatrix} -1.0 & -1.3 \\ 4.3 & 2.3 \end{pmatrix} \\ G^{\text{Alectinib + CAF}} &= \begin{pmatrix} 0.5 & -0.4 \\ 3.8 & 2.4 \end{pmatrix} \end{aligned} \tag{2}$$

Note that here, unlike the reductive games, the entries of the payoff matrix are in terms of type fitness. They do not represent an imagined interaction between two individual cells, but instead are just measurement of the magnitude of a type-type coupling. Kaznatcheev (2017, 2018) calls this sort of game an *effective* game. Here, the population-scale phenomenon is explained by citing interactions between the types that constitute the population where the types are operationalized in terms of an experimental procedure (fluorescent area of green vs red). This interpretation takes the player as a type-structured-population, strategies as types, and payoff as type fitness.

4 Measurement as a new mode of inquiry

To understand the mode of inquiry, we follow Weisberg (2007) by considering both the procedures and way in which the scientist represents their phenomena of interest. Weisberg contends that in dealing with complex phenomena, scientists have to choose among a number of options, with one of them being modeling. Weisberg (2007) argues that when modeling, the modeler first imagines an abstract structure, she then describes it using equations, pictures, graphs, etc. for further analysis or refinement. Finally, if appropriate, "she assesses the relationship between the model and the world" (Weisberg, 2007, p. 209).

Weisberg calls these representations model descriptions. When the modeler intends to explain a real-world phenomenon citing what she learns from analyzing the model description, her effort is said to be an indirect theoretical investigation of the real-world phenomenon. The indirectness in modeling is due to the fact that a model description is a representation of the imagined structure, which in turn is a representation of a real-world situation.

As we saw in Section 2, traditional EGT modelers follow this three step process. Basanta et al. (2008) first imagine a scenario of competition between cells and summarize it as a game payoff matrix. Second, they study the behavior of this game structure by feeding a payoff matrix as a parameter into the replicator equation (or – more generally – some other evolutionary dynamic). In this sense, the equation and the payoff matrix determine the behavior of a game. Finally, they make a heuristic or qualitative comparison of the results of their analysis to their knowledge of cancer.

The game assay does not follow the process. In fact, Kaznatcheev et al. (2019) largely invert the above process. In the game assay, the replicator equation is used to extract, not determine, the game structure from the behavior of the experimental system. The games extracted are an abstract summary of an experimental dynamic that was actually unfolding between the red ("parental") and green ("resistant") cell lines in the microscopic systems in the lab. These games are thus a direct representation of what is happening in the glass plate.[2]

Traditional EGT modeling is a theoretical inquiry whereas the game assay is a formal-experimental hybrid mode of inquiry. Given that the game assay takes a concrete object of an experiment as 'input' and produces an theoretical object of a game as 'output' – we call this the measurement mode of inquiry. Thus, although the game template is still representational in both EGT modeling and the game assay, the mode of inquiry to arrive at the representation has changed during the knowledge transfer from mathematical oncology to experimental cancer biology. Although both approaches can produce representations with empirical content, they do so by different modes of inquiry.

In regards to these modes of inquiry, Humphreys (2019, p. 118) notes in his conclusion that 'experimental knowledge, in the sense of knowing how to effectively carry out experiments or observations, does not seem to be a domain-transferable skill in the modern era.' With this statement, Humphreys creates a boundary between the theoretical mode of formal mathematical templates – where transfer between domains is rampant – and the experimental mode. Our case study of the game assay, however, shows that formal templates do not actually respect this boundary between the theoretical vs experimental modes. Through the complex act of knowledge transfer, a formal template can switch from the theoretical modeling mode to an experimental measurement mode.

5 Expanding the template-to-target mapping

Humphreys (2019) defines a formal template as having no empirical content and all empirical content is gained from the mapping from the formal template to a target system (what we will call the template-to-target mapping). In our case study, the formal template is the game and its associated game-theoretic terms (player, strategy, payoff, etc); the target system in cancer. Humphreys (2019, p. 116) notes that "these mappings can be very complex and often consist of multiple embedded mappings" but does not elaborate on the details or subdivide the mapping into different parts. We think it is instructive to study the template-to-target mapping further by carefully subdividing it. In particular, the mapping between a formal template and the target domain can always be broken down into the parts: conceptual and concrete.

First, there is a conceptual mapping between the formal template and theoretical concepts in the target domain. For example, reductive games map the template's player to the domain-concept of 'individual' while an effective game instead maps player to the domain-concept of 'type-structured population'. At this point, the template with conceptual mapping still has no empirical content and cannot be false, but it can be wrong. The template terms and domain-concept terms must respect a shared 'grammatical' structure. For example, in the formal template of games, players are 'containers' of strategies and so for reductive games in the target domain individuals are 'containers' of behaviors and for effective games type-structured populations are 'containers' of types. If one instead mapped players to behaviors and strategies to individuals then one would be wrong because

[2]The 'happening in the glass plate' is essential for the representation to be considered direct. If the system of interest is cancer in the human body rather than in glass plate, then the game assay has something in common with the indirect-representation of modeling. Here, the indirectness comes not from the theorists imagination (i.e., folk ontology) but from the experimentalist's design. But the game assay shares this kind of indirectness with all in vitro studies: the cancer cell in vitro is not the same as cancer in the patient (in vivo).

behaviors do not 'contain' individuals. But this wrongess is akin to a grammatical mistake rather than a falsehood.

It is only in the second part of the mapping – the concrete mapping from concepts to objects in the target domain – that empirical content can enter the template. Since this part of the mapping is fully within the target domain, it's validity and truth-value can be determined by the standards of that domain. It is only at this point that a template can be false, if – for example – the template specifies that two variables should have a specific numerical relationship but in the target domain, the objects those variables map to actually a different numerical relationship.

This two part mapping lets us make sense of how templates are interpreted. Humphreys (2002, p. 10) notes 'the inseparability of the template and its interpretation.' Houkes and Zwart (2019) restrict this inseparability to just their notion of intensional interpretation (roughly equivalent to our conceptual mapping) and not their notion of an analytic interpretation (similar to our concrete mapping). For Houkes and Zwart (2019), the inseparability of the intensional interpretation and the formal template is essential for templates to be more than 'mere formalisms'.

We find that this inseparability is true in the sense that a template cannot be used without an interpretation – the conceptual mapping is a part of any mapping between a formal template and the target domain. But our case study shows that this inseparability is false in another sense. During the transfer from EGT in mathematical oncology to EGT in experimental cancer biology, a game was separated from its reductive interpretation which was then replaced by the effective interpretation. Thus, we show that a template (i.e., a game) can be separated from its typical interpretation (i.e., player as individual; strategy as behaviour, etc.). Knowing when and how to separate template from its typical interpretation and which alternative interpretation to use can be central to successful knowledge transfer. Contrary to Houkes and Zwart's (2019) claim, wisely separating a template from intensional interpretation does not reduce the template to mere formalism but instead allows the template to transform in remarkable ways.

6 Templates as knowledge bridges

What we find to be the most remarkable transformation of the game-theoretic template in moving from mathematical oncology to experimental cancer biology is that it transforms from being a transferred object to a bridging object.

In everyday use, 'transfer' is usually read as the movement of a fixed object from some source to some target. It does not imply modification of the transferred object, nor a modification of the source or target beyond the target now containing an object that it did not previously contain. But knowledge objects are not this static.

Some of these departures from the everyday use of 'transfer' with static objects has already been noted by philosophers of science. For example, we already know that the transferred object might be modified through translation (Herfeld & Doehne, 2019) or sanctioning (Bradley & Thébault, 2019) and that the target domain might be modified through the creation of a lanzing zone (Price, 2019). These insights perturb the 'transfer' metaphor but they do not force us to replace it with something else.

The case of the game assay, however, suggests that templates can act as bridges. First, the bridge metaphor can better represent how scientists employ a newly transferred template in their reasoning. Second, the transferred template can act as a way for knowledge to move 'back' from target to source. This transfer is done not by passing another template, but 'through' or 'over' the representation set up by the template.

To see this, let us return to the four games in equation (2) measured by Kaznatcheev et al.

(2019). All four of these payoff matrices are quantitatively different, but more important for Kaznatcheev et al. (2019) the matrices are of two qualitatively different kinds. The DMSO + CAF matrix is of a 'LEADER' game kind (located in the upper right quadrant of game space in Figure 4b of Kaznatcheev et al. (2019)), while the other three are of a 'DEADLOCK' game kind (all located in the bottom right quadrant of game space in Figure 4b of Kaznatcheev et al. (2019)). Two matrices are of qualitatively different kinds and correspond to different kinds of games if the relationship of inequalities between the payoff elements changes. So DMSO, Alectnib, and Alectinib + CAF all have $G_{2,1} > G_{2,2} > G_{1,1} > G_{1,2}$, but DMSO + CAF has $G_{1,2} > G_{2,1} > G_{2,2} > G_{1,1}$. This leads to qualitatively different dynamics, with the former tending toward an end point with a single type (the resistance cancer cells) in the population, while the latter tends toward an end point of the two types (parental and resistant) co-existing in the population.

None of these game structures had been previously imagined in the theoretical literature of EGT modeling in mathematical oncology. But the occurrence of the LEADER game in the DMSO + CAF case, that Kaznatcheev et al. (2019) argue as corresponding most closely to an untreated patient, is used as a potential explanation of why therapy resistance can emerge so easily (and why there is no 'cost-of-resistance'). Let us look at the structure of this explanation, it follows three steps:

1. all games in the upper right quadrant of game space (see Figure 4b of Kaznatcheev et al. (2019)) have a mixed strategy equilibrium, and

2. mixed strategy equilibria correspond to the co-existence of the two types in the population, and

3. co-existence of the sensitive and resistant type make it easier for therapy resistance to emerge.

Where step (1) is a statement in the source domain, step (2) is a translation statement on the bridge, and step (3) is in the target domain. In this way, the template – or more specifically the conceptual template-to-target mapping – acts as a way for the scientists to combine their knowledge of both the source and target domain and arrive at a new conclusion.

Note that contrary to the claim of Humphreys (2019) – and in support of the arguments by Bradley and Thébault (2019) and Lin (2021) – knowledge of both the target and source domain seems to be necessary for the above explanation. In fact, without knowledge of the source domain, there is simply no reason to measure a game. One could simply describe the dynamics of the system without noting the connection to named games like LEADER or DEADLOCK. The reason that terminology from the source domain is used is so that knowledge from the source domain can have direct bearing on the target.

It also allows knowledge from the target domain to affect the source. The game assay helps scientists focus on which of the possible game structures to study. Whereas the EGT modelers chose games based on theoretical interest, the game assay can tell us which games tend to occur in empirical systems. This gives us knowledge of which games are interesting.

Finally, the shared representation between reductive and effective games allows scientists to jump between the measuring and modeling mode. For example, Farrokhian et al. (2021) use the game assay to measure the payoff matrix for parental vs resistant types interacting under different doses of the cancer drug gefitinib. But they then use those measured games as starting points for traditional EGT modeling by taking the payoff matrices as parameters for subsequent replicator dynamics and even Lotka-Volterra models. The shared representation of the template forms a bridge not just between mathematical oncology and experimental cancer biology but also between modeling and measuring.

		Interpretation of the game structure	
		In Sync	*Diverged*
Mode of Inquiry	*Matched*	Conformist	Creative
	Mismatched	Expansive	Transformative

Table 1: Four-tier typology for the transfer of knowledge objects

7 Conclusion

Throughout this article, we showed that transformations in the mode of inquiry are one of the ways that templates can change during knowledge transfer. This suggests a two-dimensional, four-tier typology for transformative transfer that we summarize in Table 1.

The first dimension in our typology roughly follows Houkes and Zwart's (2019) distinction between the conformist and the creative transfers. Crucial to Houkes and Zwart's differentiation is whether a modeler follows the typical structure of interpretation of the mathematical object being transferred, which in our case are the game structures. In terms of the way game structures are interpreted, any two episodes of EGT work may either be "in sync" or "diverge" from one another. The second dimension in the typology is concerned with the mode in which scientists use EGT to study their chosen subject. The modes can be matched – as in prior discussions of template transfer where both uses shared a common modeling mode of inquiry – or mismatched. Jointly, these two dimensions give us a typology of four types of transfers: conformist, creative, expansive and transformative.

Applying these distinctions in the typology, we find that EGT modeling in mathematical oncology can be matched and in sync with the standard EGT in evolutionary biology, but the work involving the game assay is mismatched and diverged from the two. Since Houkes and Zwart's (2019) gave examples of conformist and creative transfers, and the game assay serves as an example of a transformative transfer, it would be interesting for future work to look at the final type of expansive transfer.

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