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Evolutionary Game Theory and Interdisciplinary Integration

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Interdisciplinary research is becoming more and more popular. Many funding bodies encourage interdisciplinarity, as a criterion that promises scientific progress. Traditionally this has been linked to the idea of integrating or unifying disciplines. Using evolutionary game theory as a case study, Till Grüne-Yanoff (2016) argued that there is no such necessary link between interdisciplinary success and integration. Contrary to this, this paper argues that evolutionary game theory is a genuine case of successful integration between economics and biology, shedding lights on the many dimensions along which integration can take place.

Keywords: Interdisciplinarity; integration; evolutionary game theory; biology; economics.

1. *Introduction*

For much of the 20th century, reductionism was the dominant approach in philosophy of science (see Nagel 1935, 1949, 1979). However, with the demise of logical empiricism, reductionism as a regulative ideal of science has become more and more criticized by historians and philosophers of science (see Feyerabend 1962; Kuhn 1962; Schaffner 1967). Many subfields within philosophy of science such as biology, have even developed an anti-reductionist consensus (see Kitcher 1984, 1990; Rosenberg 1985, 1994; Dupré 1993). Similar debates currently unfold

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in the philosophy of economics (see Sugden 2001; Fumagalli 2013). In fact, reductionism has become almost a dirty word, with only a minority willing to embrace the term as a badge of honour (see Rosenberg 2006).

Over time, reductionism has been replaced by a new ideal, i.e. unification or integration (see Kitcher 1999). According to Till Grüne-Yanoff (2016) the increasing popularity of interdisciplinary research, as a scientific virtue, is due to interdisciplinary success being linked to integration between fields or disciplines. In fact, Holbrook argues that the "notion of 'integration' is so widespread in the [interdisciplinarity] literature that to question whether [interdisciplinarity] involves integration is almost heretical" (2013: 13). However, Grüne-Yanoff (2016) argues that there is no such necessary link between interdisciplinary success and integration, contrary to what others have argued before him (Lattuca 2001; Klein 2010; Holbrook 2013).

Grüne-Yanoff illustrates his case with two separate case-studies for interdisciplinary model exchange. First, evolutionary game theory as an example of interdisciplinary exchange between economics and biology, and secondly hyperbolic discounting as an example of interdisciplinary exchange between economics and psychology. Considering the wide recognition of both examples as interdisciplinary successes, Grüne-Yanoff (2016) was wise to choose them in order to ward off objections that his case-studies do not warrant the judgement that despite interdisciplinary success there was no "integration of disciplines, concepts or methods" (2016: 344).

However, this naturally leaves him open for the opposite criticism that I spell out in this paper. Highly abstract and simplified models are, of course, used across scientific disciplines (Veit 2019a). Both economists and philosophers wary of the common criticism directed against economic models being unrealistic or unreliable have drawn on modelling practice in biology to justify and improve 'unrealistic' economic models (see Sugden 2001, 2009, 2011; Rosenberg 2009; Odenbaugh and Alexandrova 2011). In one very fascinating case, however, economists went so far as to import a model framework from biology in its entirety, i.e. evolutionary game theory, a model framework that has previously been adopted by biologists applying game-theoretic tools from economics to biology. In this paper, I argue that evolutionary game theory, contrary to Grüne-Yanoff (2016) is in fact, a case of both interdisciplinary success and integration. Nevertheless, I agree with Grüne-Yanoff's (2016) general sentiment that there is no necessary link between interdisciplinary success and integration, though their relation is stronger than he suggests.

This paper is structured as follows: Section 2 discusses how Grüne-Yanoff defines the conditions for interdisciplinary success and integration. Section 3 sketches the history of evolutionary game theory and explains the two most fundamental concepts used within it. Section 4 provides an argument that EGT has led to a methodological integration between biology and economics. Section 5 provides an argument that there has also been conceptual integration. Section 6, finally concludes the discussion.

2. *Interdisciplinary Success without Integration*

In order to understand whether EGT is a case of interdisciplinary success and integration between biology and economics, we will first require to clear up the meaning of both terms. In doing so, I closely follow Grüne-Yanoff's (2016) definitions as my disagreement merely lies in his mischaracterization of EGT. As Grüne-Yanoff (2016) points out, the first relevant question to ask is what interdisciplinary success entails and why it is valued, with a further distinction opening up by asking whether interdisciplinarity is valued as a goal in itself or only instrumentally. Grüne-Yanoff (2016: 345) cites the Economic and Social Research Council (ESRC) that justifies its funding of interdisciplinary projects by highlighting the instrumental goals that can be achieved in such a way:

> many of the most pressing research challenges are interdisciplinary in nature, both within the social sciences and between the social sciences and other areas of research. (ESRC 2013)

On the other side, Grüne-Yanoff (2016: 345) cites the director of the National Health Institute (NIH), Elias A. Zerhouni, who explains the aims of its funding projects with the goal:

> to encourage and enable change in academic research culture to make interdisciplinary research easier to conduct for scientists who wish to collaborate in unconventional ways. (NIH News 2007)

Grüne-Yanoff suggests that this is a case of interdisciplinarity valued for its own sake. However, this conclusion is far from obvious. The growing support for interdisciplinary may simply rest on the belief that *unconventional research* has historically shown to have the best prospects for achieving scientific progress, such as "detailed explanations, more accurate predictions or more effective control", examples Grüne-Yanoff lists himself (2016: 345). Evidence for this can easily be found. Some famous examples are Gregor Mendel's study of peas and Galileo's experiments that were at least at the time unusual. If so, interdisciplinarity would only be valued because it is unconventional and perhaps requires financial support to bridge the gaps between disciplines. Hence, there need not be a necessary link between interdisciplinarity and the goal of unification, a conclusion Grüne-Yanoff would certainly embrace, but it is not so clear that the view he is attacking is actually in the majority.

Nevertheless, Grüne-Yanoff (2016) provides a useful and succinct philosophical analysis of the literature on interdisciplinarity with two criteria emerging on which interdisciplinarity can be understood. First: "the disciplines involved in interdisciplinary interaction change their identity in some relevant way" (346). Second: "the change that disciplines undergo in successful interdisciplinary exchanges leads them to integrate in a relevant way" (346). Though Grüne-Yanoff agrees with the former, he argues against the latter. As already alluded to, I agree with this general sentiment of his argument. However, the connections between integration and interdisciplinarity are deeper than he himself suggests. The first criterion provides a straight-forward case for measuring interdisciplinary exchange (though not necessarily interdisciplinary success). In the case of evolutionary game theory, it is already widely agreed that the application of game theory to biology and the use of EGT in economics has been quite successful. Whether the disciplines changed in a relevant way is less obviously clear, and stands in an direct relationship with the degree of integration taking place.

The case Grüne-Yanoff (2016) makes is a perhaps unintuitive, but possible: disciplines can change by *de-integrating*, i.e. moving further apart. This may seem unappealing, but as Grüne-Yanoff successfully argues it is a real possibility and could nevertheless qualify as scientific progress. Grüne-Yanoff is aware of this connection and points to the unificationist ideas that underlie the arguments from "defenders of the interdisciplinary-as-integration" (2016: 348) view, such as Klein: "the roots of the concepts lie in a number of ideas that resonate through modern discourse—the ideas of a unified science, general knowledge, synthesis and the integration of knowledge" (Klein 1990: 19). As alluded to in the introduction, reductionism has become less and less popular among philosophers of science. The unity of science thesis by Carnap was untenable given its strong formulation: "science is a unity, [such] that all empirical statements can be expressed in a single language, all states of affairs are of one kind and are known by the same method" (Carnap 1934: 32). However, the disunity of science was and is a position, many philosophers of science would like to avoid, hence leading to a variety of less strict conditions for the unification of science (see Kitcher 1999; Brigandt 2010). One such alternative is integration. The key then is to understand what integration entails.

Grüne-Yanoff (2016) summarizes the literature on integration and comes to several conclusions. Firstly, integration goes beyond mere theory: it "affects the concepts they use, both in their explanations, as well as in their ontological content" and it "affects their practices, specifically their terminology, their methods and their data" (2016: 347). Secondly, integration can be measured by the increase in overlap in at least one of these categories (see O'Malley 2013; Grüne-Yanoff 2016). A strong view on the necessary link between interdisciplinary success and integration emerges that Grüne-Yanoff characterizes as follows:

The Strong View (SV):

> "[I]nterdisciplinary research is successful if it integrates disciplines, creates *new academic programs and ultimately new disciplines*." [italics added] (Grüne-Yanoff 2016: 348)

As successful *de-integration* of disciplines is a real possibility, the SV is literally too strong. In fact, some authors such as van der Steen (1993) have explicitly argued for the de-integration of scientific fields, such as biology, due to the danger of overgeneralization. One example within biology is the use of different notions of functions (see Garson 2017) and genes (see Rosenberg 2006) within different sub-fields. Historically, much confusion has been created by authors who interpreted terms differently, for example during the group selection debate (see Okasha 2006, Veit 2019b). So even though biology might seem like a field, where integration seems to be an inherently valuable goal, it could come at a severe cost if unification is merely searched for the sake of unification. Furthermore, as Grüne-Yanoff points out: the failure of an attempt to integrate may simply be explained by the fact that the two disciplines cannot be unified (see O'Malley 2013). Hence, contrary to Klein (2008), failing in an attempt to integrate two disciplines need not imply failure.

Nevertheless, the SV highlights a possibility Grüne-Yanoff has disregarded, i.e. *the emergence of new academic programs and disciplines*. In the following, I am going to argue that despite differences in microstructure between biology and economics, EGT has developed a sophisticated set of models to deal with a macro-phenomena common to both. Unrecognized by Grüne-Yanoff, this has led to the creation of a new field, i.e. the field of *evolutionary dynamics*. In the following section, I characterize the history of EGT and point out some differences to Grüne-Yanoff's analysis offered across multiple papers (2011a, 2011b, 2013, 2016).

3. *The history of evolutionary game theory*

Now widely used in biology and the social sciences, though primarily economics, EGT has had an interesting history of success. In the following, I provide a short history and explain the development of the most important tools of EGT: The equilibrium concept of an *evolutionary stable strategy* (ESS), introduced by Maynard Smith and Price (1973) and the formal equation of the *replicator dynamics* introduced by Taylor and Jonker (1978). Though these tools are used in both biology and the social sciences and share the same formal framework and equations, they often have to be interpreted differently depending on the discipline.

EGT is most often associated with John Maynard Smith, who together with George Price (1973) introduced the concept of an ESS to analyse conflicts between animals. More broadly they introduced EGT to explore questions regarding how well a phenotype does, depending on the phenotypes present in a population, i.e. frequency-dependent fitness. The first traces of such a methodology, however, can be traced back as far as 1930, when R. A. Fisher (1930), worked on a mathematical solution to explain the equal sex ratio in animals. As a vast number of field studies shows, the majority of males in many species do not reproduce suggesting the benefit of a female-biased sex ratio. Fisher argued that the equal sex ratio can be explained by treating this situation as a game of strategic interaction. If the population consists of a majority of females, male offspring will have a higher expected fitness value than female offspring until their share in the population evens out, despite the fact that the actual fitness of many males will be zero. As this example shows, strategies are a central component in evolution and it was only natural that game theory could be successfully applied to biology (Veit 2021a).

According to Maynard Smith previous models of evolution have been insufficient to analyse three common characteristics: “group selection, kin selection and frequency-dependent selection” (1974: 210). What EGT provides, is a formalism in which all of these explanatory strategies can be captured in the terms of individuals, their strategies and associated fitness. Surprisingly, Maynard Smith himself initially took this formalism to be almost so simplistic that it could only be trivial.

Nowadays, however, EGT has illuminated many problems such as the evolution of cooperation, trust and language (Veit 2019c). Given its origin, the structure of EGT, naturally, bears great resemblance to the individualism espoused in game theoretic explanations of social behaviour, with individuals, their strategies and preferences over outcomes, i.e. utility. Game theory was invented thirty years prior by von Neumann and Morgenstern in the *Theory of Games and Economic Behavior* (1944) and has become one of the most influential works in the social sciences. During a stay at the University of Chicago, Maynard Smith was so enamoured with the simplicity and generality of game theoretic tools that he was led to adopt the formal structure of game theory for problems in biology. However, seemingly supporting Grüne-Yanoff’s argument, Maynard Smith did not think of his work as an integration between biology and economics, something that is emphasized by the following quote from Maynard Smith’s influential book *Evolution and the Theory of Games*:

> Sensibly enough, a central assumption of classical game theory is that the players will behave rationally, and according to some criterion of self-interest. Such an assumption would clearly be out of place in an evolutionary context. Instead, the criterion of rationality is replaced by that of population dynamics and stability, and the criterion of self-interest by Darwinian fitness. (Maynard Smith 1982: 2)

Since then, models and simulations have become an integral part of the biologist’s toolkit. Back when Maynard Smith introduced EGT, however, many biologists where openly hostile to the mathematization of the discipline. In fact, the *Journal of Theoretical Biology*, in which Maynard published a more extensive treatment of his idea to import game theory into biology (1974) was only founded in 1961. Maynard Smith, who served as an engineer for civil planes during the second world war, was familiar with the use of highly idealized models, in fact, he knew that one could put faith in them even when human lives where at stake. "I also acquired the ability, rare among biologists, to perform massive numerical operations [...] and without making mistakes; a mistake could mean that someone got killed" (1985: 349). His trust in the power of mathematical models would later lead him to study under J. B. S. Haldane and apply his acquired modelling skills to biological problems.

In game theory, institutions and social phenomena are fully accounted for in terms of individual choices. This underlying individualism is also the methodology of EGT. Instead of a kind of biological holism accounting for its complexity, EGT espouses a mechanistic form of empirical research. Maynard Smith, rather than advocating the use of dubious concepts such the *good of the species*[1] aimed to explain apparently unfit behaviour, such as altruistic warning calls that alert the group of a predator, but putting the individuals own fitness at risk, purely in terms of kin-selection. As we shall see EGT models are often directed against impossibility[2] claims according to which selection on the level of the individual could not be responsible for the evolution of cooperation and altruism. In EGT, underlying mechanisms such as kin-selection or frequency-dependent selection are to be analysed isolated from interfering forces. Naturally, this takes away much of the realism from the model world that is created with only loose resemblance to the real world. However, Maynard Smith (1974) argues that it is necessary to start from very simple assumptions to learn about the mechanism itself. Whether the hypothesized mechanism operates in the real world is a distinct, albeit important question. Cognitively limited agents such as us could otherwise not understand complex phenomena in economics and biology. This abstraction is, as I shall argue in the next section, the key towards understanding how EGT integrated biology and economics.

However, let us first take a look at the process of building an EGT model. Unlike game theory, EGT models do not maximize utility but fitness, i.e. reproductive success. While it might be impossible to unify human desires into a single utility scale, the concept of fitness allows for a comparatively straightforward way of assigning values to outcomes. For players to rank their preferences and make coherent choices, game theory assumes players to be rational. EGT, on the other hand, does not even require the 'players' to be conscious. Strategies are hard-wired behaviour, or more broadly, alternative phenotypes. Unlike rational agents, individuals in EGT can truly *just be* animals unaware of the game they are playing. Not even the ability to 'play' a different strategy is a necessary requirement, as long as strategies are passed on to one's offspring. While there are many refinements of the Nash equilibrium

[1] A thesis endorsed by influential biologists such as Wynne-Edwards (1962) and Konrad Lorenz (1966).

[2] Or at least near impossibility.

in game theory, each liable to criticism, EGT employs multiple stability solution concepts: the most famous one being the evolutionary stable strategy (ESS) provided in John Maynard Smith and Price (1973). If a strategy i is evolutionary stable, there cannot be another invading strategy j with a higher fitness, i.e. $u(i) > u(j)$. Hence, the payoff u of a member of the population playing i against another member playing i must be higher than a mutant playing j against a member of the population playing i, or if their payoff is the same, the incumbent strategy must do better against a mutant than the mutant would do playing against another mutant. The interaction payoffs can be represented formally as follows:

(1.1) $$u(i,i) > u(j,i)$$

Or

(1.2) $$u(i,i) = u(j,i) \quad and \quad u(i,j) > u(j,j)$$

The ESS captures a Nash equilibrium (NE), i.e. condition 1.1, in which, the equilibrium cannot be invaded by a low share of mutants playing an alternative strategy. Hence, every ESS is a NE but not every NE is a ESS. However, just like the possibility of multiple NE, this refinement of the NE allows for multiple ESS. In which state a population ends up depends upon the initial conditions. Let us take a look at Maynard Smith's original and most famous EGT model, the highly idealized *Hawk-Dove Game*[3]:

Table 1 *The payoff matrix for the* Hawk-Dove Game

	Hawk	Dove
Hawk	$\frac{1}{2}$ (V – C)	V
Dove	0	V/2

In their simplest form, EGT models represent two-player games within populations that are infinite, with interactions happening at random and consisting of indistinguishable individuals.[4] In the *Hawk-Dove Game*, there are only two pure strategies in response to a resource contest: Hawk refers to the aggressive strategy leading either to the withdrawal of the opponent or an escalated conflict, i.e. battle with the cost of a potential injury C. Dove refers to the passive strategy of displaying and retreating when the opponent escalates. If a Hawk meets a Dove it will always win and receive a resource associated with a value V. Both V and C are expressed in terms of change in fitness. Hence, if V > C, i.e.

[3] Based on an updated treatment in Maynard Smith (1982) *Evolution and the Theory of Games*.

[4] All of these assumptions can made more realistic leading to agent based models, e.g. finite populations or the introduction of population structure via cellular automata.

the value of the resource for reproduction is higher than the negative effect of an injury on fitness, Hawk would be the dominant strategy. Doves would be driven to extinction, even when there is only a single Hawk mutant in a Dove population. However, when C > V the result will be a mixed strategy. Even though Hawks always win against Doves, they risk injury when meeting other Hawks. Doves encountering other Doves, on the other hand, share the resource. Whereas mixed strategies in game theory are randomizations, in EGT mixed, ESS are either stable polymorphic populations playing pure strategies or randomized but encoded strategies in individuals. The mixed strategy can be calculated by solving the following equation:

$$u(H,I) = u(D,I) \quad (1.3)$$

The result of solving equation (1.3) is P = V/C with P representing the share of Hawks or the probability of individuals playing Hawk.[5] If the fitness value of the resource is 1 and the cost of fighting 2, or generally twice as large as the value of the resource the population will be in a mixed equilibrium with either 50% playing Hawk and 50% playing Dove or a mixed strategy randomizing between Hawk and Dove. By putting these arbitrary values into the payoff-matrix, this result can be easily illustrated:

Table 2 *The payoff matrix for the* Hawk-Dove Game*

	Hawk	Dove
Hawk	–0.5	1
Dove	0	0.5

Only when the population plays Hawk and Dove with equal probability of 50% are the payoffs for both strategies equal, i.e. an expected fitness value of 0.25. Here numbers do not refer to any real properties of the real world but rather the logical possibilities of symmetric contests within a *model population*. Such conceptual exploration of a model is familiar from economic modelling practice. In order to increase the realism of the model, this game has been extended in various ways, most importantly through the addition of asymmetric cues.

However, several authors (see Huttegger and Zollman 2012, 2013) argue that the generality and simplicity of a fundamentally static concept such as the ESS faces severe limits in understanding the dynamics of evolutionary processes. For the purposes of this paper, I can only reiterate their call for a pluralistic methodology (see also Veit 2021b), employing both static and dynamic game theoretic tools, some of which

[5] A mathematical proof for this result is provided in the very same book by Maynard Smith (1982).

originate in economics. The most famous dynamical approach in EGT goes back to Taylor and Jonker (1978), who developed the *replicator dynamics* with the explicit goal to fill the dynamical gap the ESS left. As already alluded to, EGT allows for both biological and cultural interpretations explaining the interdisciplinary interest in EGT. While the biological form of these models treats replication as inheritance, replication has to be interpreted as learning or imitation in the cultural setting. Replicator dynamics (RD) are an attempt to model the relative changes of strategies in a population. These can be either instantiated biologically or culturally. Strategies with higher fitness than the population average prosper and increase their share in the population, while those with lower fitness are driven to extinction. RD in the biological setting are thus an attempt to model the dynamics of reproduction and natural selection. The following is the continuous replicator dynamics equation:

(1.4) $$\frac{dx_i}{dt} = [u(i,x) - u(x,x)] * x_i$$ (Weibull 1995: 72)

In each round individual strategies, *i* increase their share within a population linear to their success compared to the average fitness in the population. Just as the ESS, RD assume infinite population size or at least infinite divisibility and random interaction. These idealisations serve the purpose to analyse the frequency-dependent success of different strategies, whether they are biologically or culturally transmitted.

Robert Axelrod (1980) is the perhaps most famous author for applying EGT in the social sciences. Himself a political scientist, he sought to explain the emergence of cooperation. While the traditional prisoner's dilemma (PD) game from game theory seemed to suggest that defection is always the rational move, things change when games are repeated. Axelrod coined the term *tit-for-tat* as a strategy that is forgiving, starts fair and only retaliates once the opponent cheats. When the other player returns to cooperation and the tit-for-tat player notices this, he returns himself back to cooperation in the next round. When two tit-for-tat players meet, they always cooperate. Such a cooperative strategy was later observed in sticklefish (see Milinski 1987) and also given a biological interpretation by Axelrod. As Sugden (2001) and Grüne-Yanoff (2011a) point out, early economists were dissatisfied with the rationality requirements of classical game theory. Let me now turn to my criticism of Grüne-Yanoff's characterization of EGT and argue that biology and economics have indeed become more integrated. Following Grantham's (2004) distinction between theoretical and practical integration, I argue for this thesis along two lines. First, I argue that biology and economics have become integrated on a practical dimension increasing the overlap between model-building in the two disciplines. Secondly, I argue that biology and economics have become theoretically integrated, bridging the strong divide between the study of rational agents and organisms.

4. *Methodological Integration*

Compared to biology, modelers in economics rarely attempt to bridge the gap between conclusions in the model world to conclusions about the real world, even when they are using the very same formal structure for their models (see Grüne-Yannoff 2011a, 2011b). Contrary to Grüne-Yanoff (2016) I argue that despite this difference the history of EGT shows that economic and biological modelling practice, in fact, moved closer together. Perhaps due to a sort of physics envy, beginning with Robbins (1932), economists have been reluctant to use inductive methods that are widespread in biology and could have helped them to provide better explanations. Rosenberg (1992) has argued that economics rather than being a genuine scientific discipline has just been a form of applied mathematics, studying diminishing returns and optimization without any significant improvement in predictive power since Adam Smith. A significant change, however, took place when EGT was introduced into economics, something Robert Sugden calls the *evolutionary turn*:

> Evolutionary game theory is still in its infancy. A genuinely evolutionary approach to economic explanation has an enormous amount to offer; biology really is a much better role model for economics than is physics. I just hope that economists will come to see the need to emulate the empirical research methods of biology and not just its mathematical techniques. (Sugden 2001: 128)

Eight years after Sugden's article on the evolutionary turn in game theory, Rosenberg (2009) recognized the transition economics underwent in the past three decades to a discipline much closer biology, for at least three reasons: First and here agreeing with Sugden (2001), EGT provides a foundation for the results of game theory that are far less ontologically demanding. than the strong rationality requirements of classic rational choice theory. In fact, Ken Binmore in the foreword to Jörgen Weibull's book *Evolutionary Game Theory* (1995) points out that Maynard Smith led economists to reconsider their rationality assumptions that seemed to put a clear dividing line between biology and economics.

> Maynard Smith's book Evolution and the Theory of Games directed game theorists' attention away from their increasingly elaborate definitions of rationality. After all, insects can hardly be said to think at all, and so rationality cannot be so crucial if game theory somehow manages to predict their behavior under appropriate conditions. (Ken Binmore, foreword in Weibull 1995: x)

Unlike Maynard Smith criticism of economic modelling suggests, economists were positively thrilled about applying EGT to economics. Second, a revolution in experimental economics took place, importing models and data from psychology and neuroscience, familiar from the testing of EGT models in biology. Third, the weakening of assumptions concerning perfect information. Much work since then has been done on information and signaling games in both biology and the social sciences, often employing various EGT models (see Skyrms 2010; Grafen 1990). Recognizing that economic explanations like biological ones are "path-dependent, subject to historical contingencies, and in many respects, inherently unpredictable" (Sugden 2001: 113) should highlight how economic modelling practice moved closer to biological modelling. The practices integrated.

Hutteger and Zollman (2013) draw a new dividing line: one between biological game theory and game theory used in the social sciences. This may be a more useful distinction, as EGT has led to a new discipline applicable to both economics and biology, i.e. the field of evolutionary dynamics.

5. *Conceptual Integration*

Unlike the import of game theory from economics to biology, the import of EGT from biology to economics involved, at least in the beginning, only minor adjustments. Instead, Grüne-Yanoff argues, that "particularly in the early years" economists "explored the consequences of introducing existing formal concepts into the body of economic modelling" (2011a: 395). As alluded to in Section 4, economists and philosophers alike hoped that the methodological integration of economics and biology could lead to ontological integration. However, Grüne-Yanoff importantly points out that the biological interpretation of EGT is often incompatible with the social phenomena economist aim to explain. Grüne-Yanoff even goes so far to suggest that "[b]ecause economists lacked resources to provide a more fitting re-interpretation, they often engaged in analogy construction, as for example illustrated by the meme concept" (2011a, 395). However, the meme (see Dawkins 1976, Dennett 1995, Schlaile et al. Forthcoming) as a cultural analogy to the gene in biology, is not necessarily as problematic as Grüne-Yanoff suggests. After all, if there is a straightforward analogy to be found here, it seems hard to deny that at least some integration actually took place. Furthermore, it is unclear how the concept of memes is any more problematic than the concept of utility-maximization of rational agents. Nevertheless, evolutionary game theorists working on cultural evolution have made it clear that no entity such as memes need be postulated for EGT to work in a cultural setting (see Alexander 2009). However, the same may be said for the gene, left omitted in the biological interpretation of EGT models. Even in a contrafactual world where the genetic code was not yet discovered, these models would have considerable explanatory and predictive power.

While evolutionary game theory has undergone significant changes from the original game theory, Grüne-Yanoff (2011a, 2011b) rightly criticized economists for a myopic use and import of EGT models into their own discipline disregarding the different microstructure in biology. Concepts such as biological replication need to be replaces by learning or imitation mechanisms. However, going further Grüne-Yanoff (2013) quotes Mayntz (2004) to argue that there is, in fact, no common causal core between the biological and social mechanisms the RD represents. As I argue against this claim it is useful to take a look at the quote ourselves:

> Processes identified in the causal reconstruction of a particular case or a class of macrophenomena can be formulated as statements of mechanisms if their basic causal structure (e.g., a specific category of positive feedback) can also be found in other (classes of) cases. The mobilization process observed in a fund-raising campaign for a specific project can, for instance, be generalized to cover other outcomes such as collective protest or a patriotic movement inducing young men massively to enlist in a war. A particular case of technological innovation like the QWERTY keyboard may similarly be recognized as a case in which an innovation that has initially gained a small competitive advantage crowds out technological alternatives in the long run. This is already a mechanism of a certain generality, but it may be generalized further to the mechanism of "increasing returns," which does not only apply to technological innovations but has also been used in the analysis of institutional stability and change . . . "Increasing returns," of course, is a subcategory of positive feedback, an even more general mechanism that also operates in the bankruptcy of a firm caused by the erosion of trust or in the escalation of violence in clashes between police and demonstrators. (Mayntz 2004: 254, quoted in Grüne-Yanoff 2013: 86)

Grüne-Yanoff argues that the different interpretations of the replicator dynamics in biology and economics constitute an *isolation gap* and hence do not "share a common abstract causal structure" (2013: 83). However, though there is a gap in EGT often leaving out how strategies are replicated, I argue that Grüne-Yanoff's argument does not provide sufficient reason not to treat both cultural and biological evolution as more abstract Darwinian processes following the same causal mechanism. This question relates to the program of a generalized theory of evolution covering not only biological but also cultural evolution. As Godfrey-Smith (2009) argued, how strategies are replicated is not essential for the theory of natural selection. In fact, before the modern synthesis, Darwin's theory had no substantive, nor accurate theory of how phenotypes could be inherited. The gene-concept similarly was treated as *whatever is responsible for replication*. With progress in genetics and molecular genetics, we have gained much understanding of how this mechanism works. But natural selection was a well-established theory with considerable explanatory power well before that. What is established is no less than a mathematical truth, a theorem that predicts evolutionary change if certain conditions are met. This had made Karl Popper worried about the unfalsifiability of evolution (1976), only later changing his mind when such a position seemed to be a good *prima facie* reason to reject falsificationism itself (1978). Popper certainly would not have anticipated the now widespread use of his criterion among creationists. Because evolution is a substrate-neutral algorithm (see Dennett, 1995) and applies at every level of organization, we can have confidence that an abstract

Darwinian process operates within not only the biological but also the social realm. This is a big advantage evolutionary models share: the confidence that at their most fundamental level they are modelled with a well-established mechanism that does not rely on the demanding rationality assumptions of classical game theory. EGT models are able to explain the emergence and stability of local equilibria. Criticizing the highly abstract EGT models for particular mechanisms such as learning, imitating and reproduction are instantiated differently misses the point, whether or not a theoretical entity such as *memes* are postulated. These models share a common Darwinian core that is explored in the field of evolutionary dynamics.

6. *Conclusion*

In this paper, I argued that EGT is in fact, a paradigm case of integration between two disciplines. Contrary to Grüne-Yanoff (2016) I argued, that the history of EGT a case of both interdisciplinary success and integration. Though I agreed with the general message of Grüne-Yanoff's (2016) argument, that there is no necessary link between interdisciplinary success and integration, I argued against his claim that the history of EGT is one of de-integration between biology and economics.

Having provided a short history of how biologists adopted game theory and developed new concepts such as the ESS and the RD, I have argued that these events were a clear case of integration in methodology. During the last century, biology went from a discipline in which mathematical models were viewed as hostile, to a discipline in which mathematical models play a key role and at least fundamental mathematical skills have become a necessity to work in the field of theoretical biology and EGT played a not minor role in this shift.

Perhaps due to Darwin (1859), who himself regretted the lack of mathematical skills and provided his account of natural selection purely with verbal arguments led generations of biologists to hold the view that there is no need for mathematics in biology. Furthermore, economists started to be more concerned with the realism of their models seeking to conduct experiments, simulations and gather empirical data. But there has not only been methodological integration between the disciplines. The concept of strategic interaction plays a crucial role in modern biology, and the strong rationality assumptions of classical game theory have been weakened. Hence, the concepts in both fields have moved closer together. Perhaps most interestingly, a new field has emerged, i.e. the field of evolutionary dynamics, studying both cultural and biological evolution as instantiations of a more abstract causal process. While the integration between economics and biology might be considered relatively minimal, that is a very different conclusion than the denial that integration took place. But it is precisely these gradual and perhaps hard to see changes that historians and philosophers of science should pay attention to.

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